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Phylogenetic position of Oncomelania lorelindoensis and taxonomic reassessment of former Oncomelania minima and selected snails (Pomatiopsidae)

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Article

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Abstract

The genus *Oncomelania* comprises important intermediate hosts of *Schistosoma japonicum* across East, Southeast Asia, and Africa. However, evolutionary relationships and taxonomic boundaries among several lineages remain unresolved. This study investigated mitochondrial sequence similarities and phylogenetic relationships involving COI and complete mitochondrial genomes. NCBI BLAST was used to compare sequence identities and generate relationship trees, while PhyML provided complementary maximum-likelihood analyses. The results support *Oncomelania lorelindoensis* as a basal lineage within the genus and indicate that *O. minima* represent a distinct evolutionary lineage outside *Oncomelania*. The distinct evolutionary position of *O. minima* supports that it represents a separate family, called here as Mewengkangiidae. Sequence identity analyses also support reassignment of *O. hupensis chiui* as *O. nosophora*, based on approximately 95% identity with *O. nosophora*. Similarly, *O. hupensis*, including *O. hupensis hupensis*, is reassigned as *O. nosophora nelwanii*, based on approximately 94% sequence identity. These eliminate the *O. hupensis* complex as a taxonomic grouping within the revised classification. Overall, the findings provide a revised interpretation of *Oncomelania* evolution and highlight the importance of comparative mitochondrial sequence analyses for taxonomic investigations.

Introduction

Schistosoma japonicum is an important public-health problem because it causes schistosomiasis japonica in humans and other vertebrate hosts (Zhao et al., 2010; Nelwan, 2024a; Xu et al., 2026). Its transmission depends on suitable intermediate-host snails, the genus *Oncomelania* (Nelwan, 2024b; Zou et al., 2026). The parasite occurs in China, Indonesia, and the Philippines (Nelwwan, 2024c; Ahmed & Alharbi, 2025; Utami et al., 2025; Tatem-Dokter & Gobert, 2026), with a reported occurence in Ethiopia, Africa (Abatneh et al., 2025). In Sulawesi, Indonesia, *Oncomelania lorelindoensis* serves as the intermediate host.(Nelwan, 2022, 2024a, 2024b). Previous studies documented infections in humans and animals and the occurence of the parasite in Central Sulawesi (Kurniasih et al., 2002; Budiono et al., 2019; Gordon et al., 2019; Nelwan, 2024c). Historical records also documented infections in Palu and the Lindu Valley (Sudomo, 1983; Nelwan, 2024c). The snail occurs in the Bada, Lindu, and Napu valleys (Garjito et al., 2008, 2014; Nurwidatati et al., 2019; Sutrisnawati et al., 2022; Koraag et al., 2024; Nelwan, 2024b), with potential addtional distributions along rivers in Central, South, and West Sulawesi (Nelwan, 2024b).

The genus *Oncomelania* has traditionally included *O. hupensis, O. lorelindoensis, O. minima, O. robertsoni*, and *O. quadrasi* (Attwood et al., 2025; Nelwan, 2022; Nelwan 2024a). The *O. hupensis* group has been classified into subspecies, including *O. hupensis hupensis, O. hupensis chiui, O. hupensis formosana*, and *O. hupensis nosophora* (Attwood et al., 2015; Nelwan, 2022). *O. lorelindoensis* and *O. robertsoni* occur in highland regions of Central Sulawesi and southwestern China, respectively (Attwood et al., 2015; Koraag et al., 2024; Nelwan, 2024b). Morphological and ecological differences also distinguish these snails. *O. lorelindoensis* is amphibious and is a small amphibious snail with a conical, yellowish-brown shell, whereas *O. minima* is aquatic (Kameda & Kato, 2011; Nelwan, 2024b). Environmental conditions may

further influence the distribution of *O. lorelindoensis*, including temperature and habitat suitability (Niu et al., 2019; Nelwan, 2024b).

The evolutionary relationships and taxonomic positions of these snails remain important questions. Previous studies have discussed the basal position of *O. minima* within *Oncomelania* (Okamoto et al et al., 2003; Liut et al., 2014). However, mitochondrial sequence comparisons approximately 85% identity between former *O. minima*, *Neotricula aperta*, and *O. robertsoni* raising questions about its placement within the genus. Earlier analyses also proposed recognizing *O. lorelindoensis, O. robertsoni*, and *O. quadrasi* as species distinct from the *O. hupensis* group (Nelwan, 2022, 2024a). These findings warrant further examination of the relationships among *Oncomelania* and related taxa. The aquatic ecology and sequence relationships of former *Oncomelania* also raise the possibility that it represents a lineage outside *Oncomelania*, potentially requiring a separate taxonomic placement.

This study therefore evaluates mitochondrial sequence similarities and phylogenetic relationships among selected *Oncomelania* taxa and related snails using NCBI BLAST and maximum-likelihood analysis with PhyML. It examines the evidence relevant to the evolutionary position of former *O. minima* and reassesses relationships within the previously recognized *O. hupensis* group, including *O. nosophora*. The basal position of *O. lorelindoensis* is evaluated separately using previously published evidence, particularly Okamoto et al. (2003) and Nelwan (2022, 2024a), because its sequence was unavailable in GenBank for the present analyses. The results provide a basis for reconsidering the taxonomy of these snails and evaluating the proposed placement of former *O. minima* in Mewengkangiidae.

Matherial and methods

Sequence retrieval and taxon selection

Representative nucleotide sequences were obtained from GenBank to provide geographic representation across China, Japan, and the Philippines. The selected data included *T. hortensis*, former *O. minima, O. robertsoni*, and *O. quadrasi*. *T. hortensis* was included as a comparative taxon in analyses examining relationships between *Tricula* and *Oncomelania* (Table 1). The complete mitochondrial genome of *T. hortensis* was selected as the Query Sequence and one as Subject Sequence, whereas sequences from other intermediate hosts were used as Subject sequences. These included cytochrome c oxidase subunit I (COI) gene sequences form former *O. minima, O. robertsoni*, and *O. quadrasi*. COI sequences were also included to assess the evolutionary relationships of *O. nosophora* relative to taxa previously assigned to the *O. hupensis* complex.

Table 1
Data for Tricula hortensis, genus Oncomelania, and their accession numbers and locations

Species	accession	location
T. hortensis	NC_013833.1	Sichuan, China
T. hortensis	EU440735.1	Sichuan, China
O. minima	AB611791.1	Ishikawa, Japan
O. minima	AB611795.1	Niigata, Japan
O. quadrasi	DQ112287.1	Leyte, Philippines
O. quadrasi	LC276227.1	Philippines
O. robertsoni	KR002675.1	Sichuan, China
O. robertsoni	AF253074.1	China
O. hupensis	GU367391.1	Nanning, China
O. h. hupensis	KR002674.1	Jiangxi, China
O. nosophora	DQ112286.1	Honshu, Japan
O. nosophora	DQ112284.1	Honshu, Japan
O. nosophora	KR002673.1	Honshu, Japan
O.: Oncomelania, T.: Tricula		

BLAST sequence similarity and cladogram analysis

NCBI BLAST was used to obtain sequence percentage identities, E-values, and slanted and rectangle cladograms illustrating sequence relationships. BLASTn was performed when the initial megablast search did not yield significant results. The E-value threshold was set at 0.05. Other parameters included match/mismatch scores of 1/-2, a gap-opening penalty of 1, filtering low-complexity regions, and masking applied to the lookup table only. BLAST was selected because it enables direct, reproducible comparisons of nucleotide sequences deposited in GenBank and provides pairwise sequence similarities alongside tree-view representations (Nelwan, 2025).

The BLAST results were used to investigate relationships among *Tricula* and *Oncomelania* taxa across East and Southeast Asia. The analyses examined the proposed basal position of *O. lorelindoensis* within *Oncomelania* and the possible taxonomic separation of former *O. minima*. These findings were also considered in evaluating the proposed placement of former *O. minima* within the proposed family

Mewengkangiidae, distinct from the genus *Oncomelania*. Moreover, the results were used to evaluate the relationships of *O. nosophora* to taxa previously classified within the *O. hupensis* complex.

Taxonomic interpretations followed the sequence-identity criteria described by Nelwan (2025). Percentage identities of 95–100% were interpreted as supporting conspecific status, whereas identities of ≥ 90% but < 95% were interpreted as supporting subspecies-level differentiation. These criteria were applied to mitochondrial sequence comparisons among the examined *Oncomelania* taxa. E-values between 0.0 and 0.01 were considered when interpreting the BLAST results.

Maximum-likelihood phylogenetic analysis

Maximum-likelihood phylogenetic analysis was conducted using PhyML. ETE3 was used to examine the resulting phylogenetic relationships and bootstrap support. The inferred phylogenetic relationships were compared with those represented in the NCBI BLAST slanted and rectangular cladograms. This comparison was used to assess the consistency of the inferred relationships and support interpretation of the evolutionary positions of the examined taxa.

Results

Mitochondrial sequence similarity

The BLAST analyses revealed differences in mitochondrial sequence identity among *T. hortensis*, former *O. minima*, and the examined *Oncomelania* taxa. Using the complete mitochondrial genome of *T. hortensis* as the query, sequence identity was 100% with the other *T. hortensis*, approximately 86% with *O. robertsoni* and 85% with former *O. minima*. Identity with other examined *Oncomelania* taxa was approximately 83% (Table 2).

Table 2
Sequence analyses of Tricula hortensis, former Oncomelania minima

and *Oncomelania* species			
Species			***T. hortensis***
	Accession	E-value	**NC_013833.1**
T. hortensis	EU440735.1	0.0	100%
O. minima	AB611791.1	0.0	85.50%
O. minima	AB611795.1	0.0	84.90%
O. robertsoni	AF253074.1	0.0	86.52%
O. robertsoni	KR002675.1	0.0	85.95%
O. quadrasi	LC276227.1	0.0	83.91%
O. quadrasi	DQ112287.1	0.0	82.76%
O. hupensis	GU367391.1	0.0	82.92%
O. h. hupensis	KR002674.1	7e-176	82.61%
O. nosophora	DQ112284.1	0.0	83.39%
O. nosophora	DQ112286.1	0.0	83.39%
Species			**O. minima**
	Accession	**E-value**	**AB611791.1**
O. minima	AB611795.1	0.0	96.27%
O. nosophora	KR002673.1	1e-171	82.36%
O. nosophora	DQ112284.1	0.0	82.29%
O. nosophora	DQ112286.1	0.0	82.29%
O. h. hupensis	KR002674.1	0.0	82.19%
O. hupensis	GU367391.1	0.0	81.97%
Species			*O. nosophora*
	Accession	E-value	KR002673.1
O. nosophora	DQ112284.1	0.0	95.15%
O. nosophora	DQ112286.1	0.0	95.15%
O. hupensis	GU367391.1	0.0	94.81%

and *Oncomelania* species			
Species			***T. hortensis***
O. h. hupensis	KR002674.1	0.0	93.97%
h.: hupensis; O.: Oncomelania; T.: Tricula			

The COI comparisons also revealed differences among *O. nosophora* and taxa previously assigned to the *O. hupensis* complex. The sequence identity between *O. nosophora* and *O. hupensis chiui* was approximately 95%, whereas comparisons with the other examined *O. hupensis* taxa showed identities of approximately 94%. These values distinguished *O. nosophora* from examined taxa and provided the sequence-similarity evidence used to assess their taxonomic relationships (Table 2).

BLAST cladogram relationships

The NCBI BLAST cladograms showed distinct branches for *T. hortensis*, former *O. minima*, and the examined *Oncomelania* taxa (Fig. 1A and 1B). Former *O. minima* occupied a separate branch from the other examined *Oncomelania* taxa. The cladograms also displayed relationships among the included *O. hupensis, O. robertsoni*, and *O. quadrasi* sequences.

In the COI comparisons involving *O. nosophora* and taxa previously assigned to the *O. hupensis* complex, *O. nosophora* occupied a basal position relative to the examined members of that group. This pattern was observed across the BLAST cladograms (Fig. 1A and 1B).

Maximum-likelihood phylogenetic relationships

The PhyML maximum-likelihood tree showed relationships broadly comparable to those displayed in the BLAST cladograms (Fig. 1A and 1B). The tree distinguished former *O. minima* from the examined *Oncomelania* taxa (Fig. 2), consistent with the sequence-similarity results.

The PhyML analysis of *O. nosophora* and taxa previously assigned to the *Oncomelania hupensis* complex also placed *O. nosophora* basally relative to the other examined members of the group (Fig. 2). This topolgy was consistent with the relationships shown in the BLAST cladograms (Fig. 1A and 1B).

Discussion

Oncomelania lorelindoensis as the basal lineage of Oncomelania

The life cycle of *Schistosoma* involves molluscan intermediate hosts and vertebrate definitive hosts (Li et al., 2023; Fourjour & Kwarteng, 2025). In Indonesia, *S. japonicum* transmission is associated with *O. lorelindoensis* and definitive hosts, including humans and cattle (Budiono et al., 2019; Nelwan, 2024c). Schistosomes can adapt to different hosts, highlighting the importance of a One Health approach to

schistosomiasis control (Diaz et al., 2023; Nelwan, 2024b). Birds can serve as definitive hosts for schistosomes (Walker, 2011), although their role in transmitting *S. japonicum* in Sulawesi still needs further investigation. Human and animal movements may also influence parasite distribution and the dispersal of intermediate-host populations (Crellen et al., 2016).

The present study advances the hypothesis that *O. lorelindoensis* represents the basal lineage of the genus *Oncomelania*, replacing former *O. minima* in this interpretation. This proposal is supported by the comparative sequence analyses and the earlier fidings of Nelwan (2022, 2024a), which identified substantial separation between former *O. minima* and the principal *Oncomelania* lineages. The hypothesis also provides an alternative framework for interpreting the origin and subsequent geographical diversification of the genus.

The mitonchondrial 12S rRNA comparisons reported by Okamoto et al. (2003) are relevant to this argument. Their study reported a pairwise-difference of 8.3 between former *O. h. lindoensis* and former *O. minima*, compared with values of 9.1–10.5 in other relevant comparisons. Okamoto et al. also recovered former *O. h. lindoensis* as an independent clade within their sampled taxa. These results establish the distinctive genetic position of the Indonesian lineage and provide comparative evidence consistent with the hypothesis developed by Nelwan (2024a). Although pairwise genetic distances alone cannot establish a basal position, their interpretation alongside phylogenetic topology and other sequence comparisons supports further consideration of *O. lorelindoensis* as the basal lineage of *Oncomelania*.

The current hypothesis also challenges the conventional placement of former *O. minima* at the base of *Oncomelania*. In the analyses discussed by Nelwan (2022, 2024a), former *O. minima* showed approximately 85% identity with *N. aperta* and approximately 84% identity with *O. robertsoni*. These comparisons indicate that former *O. minima* has a distinct sequence relationship to the other taxa examined and warrant reassessment rather than automatic retention within *Oncomelania*. The proposed transfer to the genus *Mewengkangae*, as *Mewengkangae minima*, reflects this interpretation.

The limitation must nevertheless be distinguished from the central hypothesis. The GenBank accesion list presented in Table 1 and Table 2 do not include an *O. lorelindoensis* sequence. Therefore, unless a separate sequence containing this taxon was included in the phylogenetic analyses, the current BLAST and PhyML trees cannot independently establish its position. The basal placement proposed here should consequently be attributed to the combined interpretation of the comparative results, Okamoto et al. (2003), and the earlier analyses of Nelwan (2024a), rather than to a direct placement of *O. lorelindoensis* in a tree from which it was absent. This limitation does not invalidate the hypothesis, but it defines precisely which additional sequence comparisons would provide a direct test.

Habitat differences further distinguish these two snail lineages: *O. minima* is aquatic and inhabits mountain streamlets, whereas *O. lorelindoensis* and other *Oncomelania* species are amphibious (Kameda & Kato, 2011; Nelwan 2022). In Central Sulawesi, *O. lorelindoensis* occurs in wet rice fields, irrigation, grasslands, plantations, and other moist environments around Lorelindu National Park (Kurniasih et al.,

2002; Sutrisnawati et al., 2022; Koraag et al., 2024; Nelwan, 2024b). These ecological differences complement the molecular evidence distinguishing the two taxa, although habitat alone cannot establish their phylogenetic positions.

Oncomelania nosophora and the evolutionary history of the Oncomelania hupensis complex

The phylogenetic relationships recovered in the present study support a reconsideration of the evolutionary history and taxonomic classification of the *O. hupensis* complex. In particular, results support the interpretation that *O. nosophora*, currently classified as *O. hupensis nosophora* (Kameda & Kato, 2011; Nelwan, 2022, 2024a; Nihei et al., 2025), represents an early-diverging lineage associated with the origin of the complex rather than a derivative of an early established *O. hupensis* lineage. This interpretation is consistent with the early BLAST analyses reported by Nelwan (2022), in which the outgroup sequence formerly identified as *O. minima* showed a closer relationship to *O. nosophora* than to several other *O. hupensis* taxa. The slanted cladogram also placed *O. nosophora* on a branch that diverged before the remaining *O. hupansis* group (Nelwan, 2022). This findings of Nelwan (2024a) provide further comparative support reassessing the evolutionary relationships among *Oncomelania* taxa.

The sequence comparisons reported by Nelwan (2022) showed approximately 95% identity with *O. nosophora* and *O. h. chiui*, and approximately 94% identity between *O. nosophora* and other Chinese members of the *O. hupensis* group. These similarities values, considered together with the cladogram topology and the subsequent phylogenetic results, support the interpretation that *O. nosophora* occupies a distinct evolutionary position within this assemblage. The evidence therefore challenges the assumption that *O. nosophora* should necessarily remain classified as a subspecies of *O. hupensis*. Instead, it supports the hypothesis that the lineages currently grouped under the *O.hupensis* complex diversified from an ancestral lineage represented by, or closely related to *O. nosophora*.

Attwood et al. (2015) reported that *O. robertsoni* was nearly monophyletic, whereas former *O. hupensis* and *O. nosophora* formed monophyletic groups. In contrast, *O. hupensis hupensis, O. hupensis tangi*, and *O. hupensis formosana* showed polyphyletic patterns, indicating that these named taxa did not consistently form exclusively evolutionary lineages. A monophyletic group comprises a common ancestor and all its descendants, whereas a polyphyletic group combines lineages without including their most recent common ancestor as a defining member. These findings highlight inconsistencies between traditional taxonomic assignments and inferred evolutionary relationships, supporting further reassessment of the *O. hupensis* complex in light of comparative mitochondrial sequence identities.

The taxonomic revision of the *O. hupensis* complex is based on sequence identity analyses. Based on approximately 95% sequence identity (Table 2), *O. hupensis chiui* from Taiwan is assigned to *O. nosophora*, rather than retained as a separate subspecies. In contrast, *O. hupensis*, with approximately 94% identity to *O. nosophora*, is proposed as the subspecies *O. nosophora nelwanii*. *O. nosophora nelwanii* is proposed to include the taxa formerly identified as *O. hupensis, O. hupensis formosana, O. hupensis tangi*, and *O. hupensis hupensi*. Accordingly, the *O. hupensis* complex is no longer retained as a

taxonomic grouping in this revised classification. The taxonomic reassignment follows the comparative approach by Nelwan (2025), who proposed *Bulinus nasustus wrighti* based on BLAST sequence identity analysis. Similarly, the present analysis supports the reassignment of *O. hupensis hupensis* to subspecies of *O. nosophora*, designated Taiwanese *O. nosophora* and *O. nosophora nelwanii*, respectively.

Okamoto et al. (2003) also demonstrated substantial genetic differentiation within the group. Their mitochondrial 12S rRNA philogeny place *O. minima* as the sister group to the sampled *O. hupensis* subspecies and recovered *O. h. lindoensis* from Indonesia as a distinct clade. Although their tree did not directly establish *O. nosophora* as the ancestral source of the complex, it showed that the traditional subspecific classification did not fully represent the genetic structure of the sampled populations. Their findings therefore provide an important comparative basis for the taxonomic reassessment proposed here. The present interpretation builds on that evidence by incorporating the relationships identified in Nelwan (2022, 2024a) and the last BLAST and PhyML analyses.

Taxonomic implications of former O. minima

The sequence relationships discussed above also raise questions about the systematic position of former *O. minima*. The Pamatiopsidae has traditionally been divided into the subfamilies Pomatiopsinae and Triculinae (Kameda & Kato, 2011; Liu et al., 2014). Pomatiopsinae includes *Oncomelania*, whereas Triculinae includes taxa such as *Neotricula* and *Tricula*. Previous studies have described substantial phylogenetic and geographical diversification among pomatiopsid lineages, including the distribution of Triculinae in southwestern China and Southeast Asia (Liu et al., 2014; Attwood et al., 2015; Wang et al., 2021). Attwood et al. (2019) also documented geographical and population-genetic differentiation of *N. aperta*, illustrating the broader diversity within Pomatiopsidae.

The present sequence comparisons suggest that former *O. minima* does not fit readily within the same sequence group as the sampled *Oncomelania* taxa. Its relationships with *N. aperta, O. robertsoni*, and *T. hortensis*, together with its distinct position in the BLAST-derived cladograms (Fig. 1A and 1B) and the broadly comparable PhyML topology (Fig. 2), support reconsideration of its genetic and subfamilial placement. Nelwan (2022, 2024a) previously proposed that this taxon should be removed from *Oncomelania*. It is beyond *Oncomelania* complex in slanted cladograms. The present interpretation extends that proposal by recognizing *Mewengkangae* as a separate genus and *Mewengkangae minima* as the corresponding species name. Therefore, it is possible to place it as under subfamily Mewengkangiinae and family Mewengkangiidae.

The molecular and ecological differences between amphibious *Oncomelania* and former *Oncomelania* support reconsideration of their taxonomic placement. Pomatiopsinae includes amphibious *Oncomelania*, whereas Pommatiopsidae also includes aquatic Triculinae, represented by *T. hortensis, N. aperta*, and *Robertsiella*. The distinct BLAST relationships observed in this study, together with previously reported phylogenetic and morphological differences (Okamoto et al., 2003; Kameda & Kato, 2011), support consideration of former *O. minima* as a separate lineage within the proposed Mewengkangiidae.

Biogeoraphic implications for Oncomelania

The biogeographic history of *Oncomelania* should be interpretd alongside the evolutionary of Pomatiopsidae and related freshwater gastropods. Previous phylogenetic studies have proposed different scenarios for the origin and dispersal of Pomatiopsidae, including an Australian origin and subsequent radiation across East and Southeast Asia (Liu et al. 2014). The present analysis provides a basis for reassessing these scenarios through comparative mitochondrial sequence identities and phylogenetic relationships.

Under the evolutionary scenario proposed here, Pomatiopsidae arose at c.a. 132-c.a. 112 million years ago (Ma) (Liu et al. (2014). In addition, proto-Mewengkangiidae (former *O. minima* arose at approximately 40 – 20 Ma. Mewengkangiidae formed genus *Mewengkangae* and *Mewengkangae minima* as a subspecies of the genus. Proto-*Oncomelania lorelindoensis* (Pomatiopsinae) arose at 20 – 15 Ma, giving rise to *O. lorelindoensis.* Subsequent dispersal and diversification of proto-*Oncomelania lorelindoensis* are proposed to have contributed to the emergence of *O. quadrasi, O. nosophora*, and *O. robertsoni* at approximately 14.5-5 Ma. This interpretation places *O. lorelindoensis* near the base of the evolutionary history of *Oncomelania* and provides an alternative framework for interpreting the geographic distribution of the genus across East and Southeast Asia.

The evolutionary position of *O. minima* raises a separate taxonomic question. If its distinct phylogenetic placement reflects divergence outside Pomatiopsidae, its classification require reconsideration at the family level. Accordingly, Mewengkangiidae is proposed here as a family containing *M. minima* (former *O. minima*). Mewengkangiinae represents the corresponding subfamily-level name if the lineage is retained within a broader family classification. These alternatives require careful distinction: if Mewengkangiidae is recognized as a separate family, a separate subfamily designation would generally be unnecessary unless additional internal lineages justify it. The proposed classification therefore depends on the phylogenetic interpretation and the taxonomic rank ultimately supported by the evidence.

Triculinae diverged from proto-*Oncomelania lorelindoensis* at c.a. 7 Ma. *N. aperta* arose approximately 2.4 Ma (Liu et al., 2014; Atwwood et al., 2019). Liu et al. (2014) discussed the divergence of *Robertsiella* from Mekong Pachydrobiini in the Pahang River drainage of Malaysia during approximately 2.6–0.8 Ma. Attwood et al. (2019) further examined genetic differentiation within *N. aperta*, reporting geographically structured populations and discussing the timing of evolutionary divergence among lineages. Their findings provide comparative context for interpreting the diversification of freshwater pomatiopsid snails in Southeast Asia

Taken together, these comparisons support renewed evaluation of the evolutionary relationships, taxonomic boundaries, and historical dispersal of *Oncomelania* and related lineages. The proposed placement of *O. lorelindoensis* near the base of *Oncomelania* and the possible recognition of Mewengkangiidae represent testable taxonomic hypothesis that can be evaluated through addtional molecular, morphological, and biogeographic evidence.

Interpretation of BLAST and PhyML results

The broadly comparable relationships recovered by the BLAST-derived cladograms and the PhyML tree are consistent with the use of both approaches as complementary evidence. Nelwan (2025) previously reported a similar comparison between BLAST-based relationships and PhyML results. In the present study, agreement between the outputs supports the reproducibility of the principal relationships within the sampled dataset. The taxonomic interpretations proposed here should nevertheless be assessed in the context of the sequence regions, accessions, taxon sampling, and limitations of the analyses, rather than on the assumption that agreement between two methods independently proves evolutionary conclusion.

Limitations and future directions

The absence of an *O. lorelindoensis* accession from the sequence list used for the present tree analyses limits direct testing of its proposed basal position. Future analyses should include comparable mitochondrial sequences from *O. lorelindoensis, O. nosophora*, and the *O. hupensis* complex.

These limitations define the next steps for testing the hypotheses; they do not remove the significance of the patterns identified in the present and previous analyses. Taken together, the results reported here and the earlier findings of Nelwan (2022, 2024a) support two principal taxonomic propositions: *O. nosophora* warrants reassessment as a distinct lineage associated with the origin of the *O. hupensis* complex, and *O. lorelindoensis* warrants further evaluation as the basal lineage of *Oncomelania*. The sequence relationships of former *Oncomelania* likewise support reconsideration of its placement outside *Oncomelania*, under the proposed name *Mewengkangae minima*. These propositions provide a basis for revising the evolutionary interpretation of the genus and for further evaluating the proposed subfamily Mewengkangiinae and its possible family-level status as Mewengkangiidae.

Conclusion

Comparative mitochondrial sequence analyses support the evolutionary differentiation and phylogenetic relationships of *Oncomelania* lineages across their geographic distributions. The results support *O. lorelindoensis* as a basal lineage within the genus, while *O. nosophora* represents a basal lineage associated with the disversification of Chinese *Oncomelania* forms. Sequence identity analyses support the reassignment of *O. hupensis chiui* as *O. nosophora*. Similarly, *O. hupensis* and *O. hupensis hupensis*, are assigned as *O. nosophora nelwanii*. These proposed reclassifications eliminate the *O. hupensis* complex as a taxonomic grouping and establish a revised framework for interpreting relationships among these lineages. Furthermore, the distinct evolutionary position of *O. minima* supports further consideration of its taxonomic placement relative to Pomatiopsidae. Together, these findings establish a revised taxonomic framework for *Oncomelania*, supporting *O. lorelindoensis* as the basal lineage of the genus, *O. nosophora* as the basal lineage of the former *O. hupensis* complex, and the proposed family Mewengkangiidae to accomodate former *O. minina* as a distinct lineage outside *Oncomelania*.

Declarations

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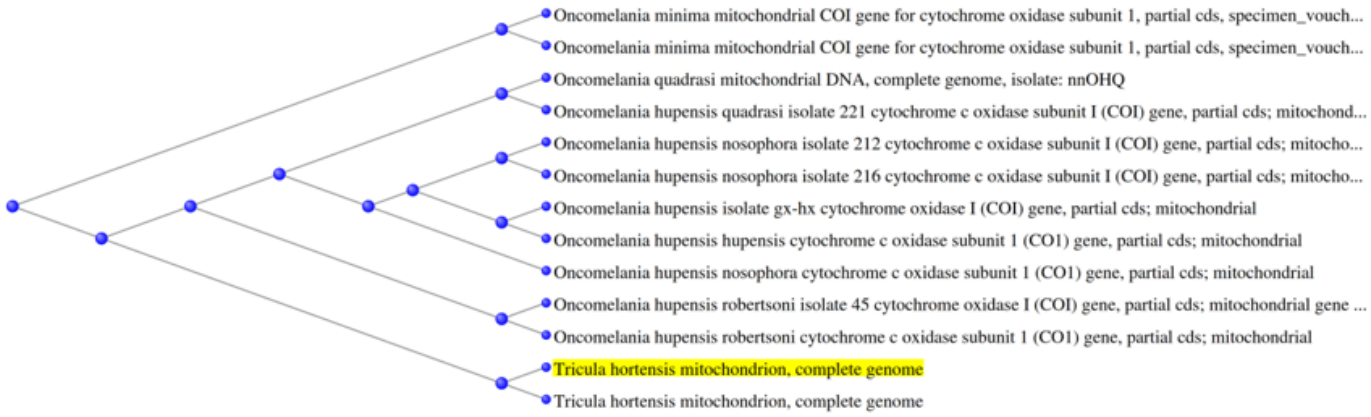
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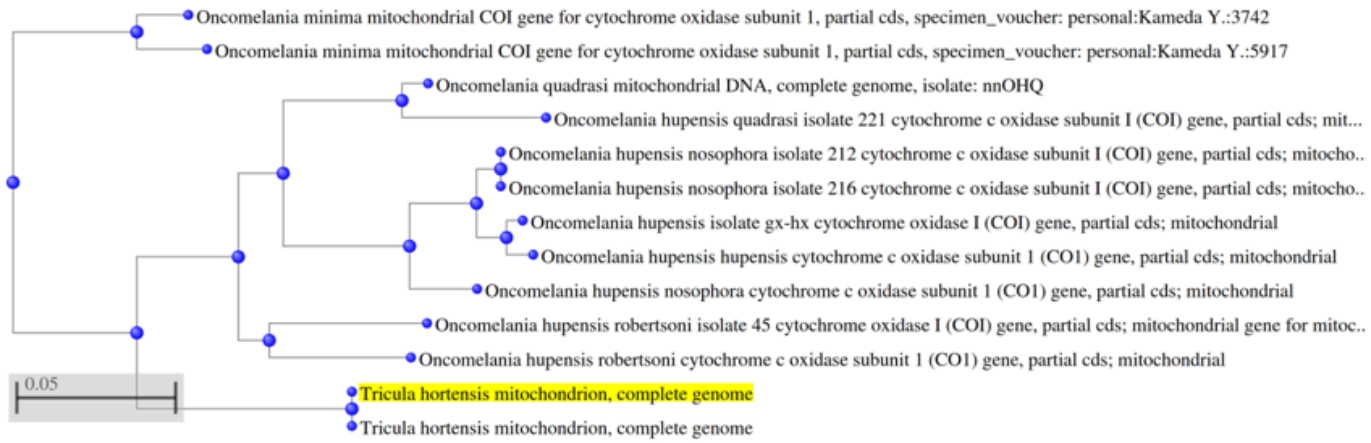
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Figures



A



B

Figure 1

1A. Nodes 25 (0 selected) and view port at (0,0) of 948x336. NCBI output for slanted cladogram illustrating phylogenetic relationships of *T. hortensis,* former *O. minima,* and *Oncomelania* species. The yellow highlighting part in the figure body is Query Sequence and others are Subject Sequence.

1B. NCBI output for the *T. hortensis,* former *O. minima,* and *Oncomelania* species relationships.

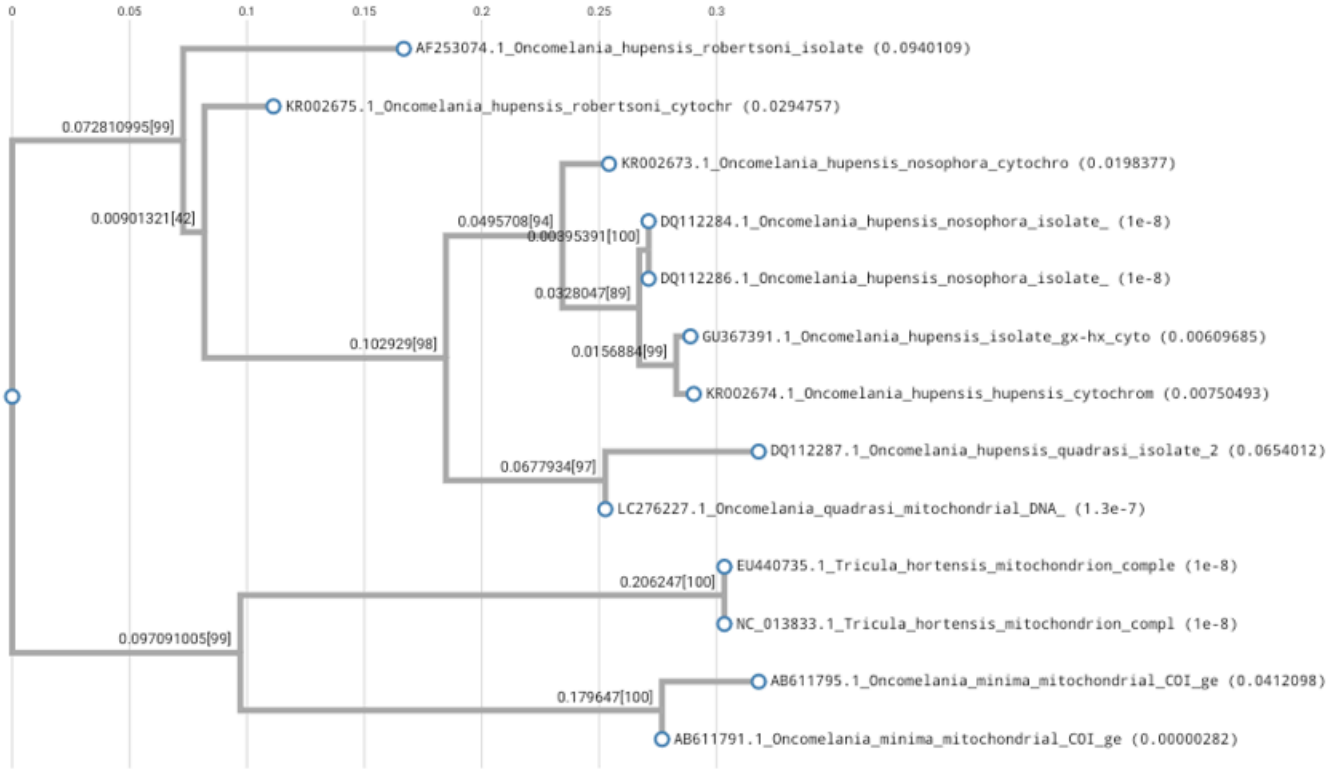


Figure 2

PhyML output for the *T. hortensis,* former *O. minima,* and *Oncomelania* species relationships. Phylogenetic analysis pipeline by ETE3. Workflow mafft_default-none-none-phyml_default_bootstrap. Method includes 1) Alignement and phylogenetic reconstructions were performed using the function “build” of ETE3 3.1.3 (Huerta-Cepas et al., 2026) as implemented on the GenomeNet (https://www.genome.jp/tools/ete); 2) Alignment was performed with MAFFT v6.861b with the default options (Katoh et al., 2005); 3) ML tree was inferred using PhyML v20160115 ran with model and parameters: --pinv e --alpha e --nclasses 4 -o tir –f m --bootstrap 100 (Guindon et al., 2010); and 4) Branch supports are computed of 100 bootstraped trees.