

Research article

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Abstract. A new genus of freshwater mussels (Bivalvia: Unionidae) is described from the Mekong River Basin as *Namkongnaia* gen. nov. The validity of the new genus is supported by its unique conchological characteristics, namely the lack of hinge dentition and elongated shells, together with its evolutionary distinctiveness as estimated by multi-locus phylogenetic analyses (mitochondrial COI and 16S, and nuclear 28S genes). The new genus includes two lineages with deep divergence, shown by 5.10% uncorrected COI p-distance. One lineage is a type species described herein as *Namkongnaia inkhavilayi* gen. et sp. nov. The other is a recognized species under the name ‘*Pilsbryconcha lemeslei* (Morelet, 1875)’. Molecular phylogenetic analysis further shows that the new genus belongs to the tribe Pseudodontini, and evolutionarily is closely related to the genus *Monodontina* Conrad, 1853. However, its conchology is similar to the genus *Pilsbryconcha* Simpson, 1900. Time-calibrated phylogeny suggests that the main radiation events of the tribe Pseudodontini occurred during the Late Cretaceous to the Eocene, with the divergence between the new genus and *Monodontina* placed in the Miocene. The discovery of new freshwater mussel taxa in this study highlights the importance of the Mekong River Basin as one of the world’s biodiversity hotspots for freshwater fauna.

Keywords. Indochina, freshwater mussels, multi-locus phylogeny, new taxa, time-calibrated phylogeny.

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Introduction

The Mekong River is the longest river in Southeast Asia. The river and its tributaries cover a vast range of geographic and climatic zones that support various aquatic habitats, including the river's mainstream, mountainous streams, tributaries, floodplains, lakes, wetlands, and estuaries (Coates *et al.* 2003). As a result, the basin contains one of the most unique and diverse freshwater faunas on Earth (Köhler *et al.* 2012; Kang & Huang 2021). Freshwater mussels (Unionidae) are of special interest for their high species diversity in the Mekong River Basin (Graf & Cummings 2021a); furthermore, it has been hypothesized to be one of the locations of origin for mussel radiation prior to their spread worldwide (Bolotov *et al.* 2017a). The currently known richness of freshwater mussels in the Mekong River Basin comprises 67 species across 21 genera (Graf & Cummings 2021a; Konopleva *et al.* 2021). Several of these genera and a dozen of these species were discovered within the last decade (Kongim *et al.* 2015; Jeratthitikul *et al.* 2019a; Konopleva *et al.* 2019, 2021; Bolotov *et al.* 2020; Pfeiffer *et al.* 2021). Moreover, 59 species are endemic to the basin, and five genera are considered monotypic, highlighting the extraordinary endemism within the tributaries (Brandt 1974; Pfeiffer *et al.* 2018; Bolotov *et al.* 2020; Graf & Cummings 2021a; Konopleva *et al.* 2021). However, freshwater mussels in the Mekong River Basin are at severe risk of population decline and even extinction from the significant threats of pollution, natural habitat modification, urbanization, and overharvesting (Lopes-Lima *et al.* 2018; Ngor *et al.* 2018). Meanwhile, efforts to conserve these fragile animals in the region have made little progress due to the lack of essential data, especially regarding population size and distribution range. Their taxonomic classification also remains uncertain (Lopes-Lima *et al.* 2018; Zieritz *et al.* 2018).

Pseudodontini Frierson, 1927 represents one of the most taxonomically diverse group of freshwater mussels in Southeast Asia. At least 44 valid species are recognized, and half are distributed in the Mekong River Basin (Graf & Cummings 2021a). This family-group name was first proposed as a subfamily by Frierson (1927) based on “large high (pseudocardinal) teeth, one in each valve”, and included the genus *Pseudodon* Gould, 1844. Modell (1942) redefined and relocated this subfamily under Margaritiferidae Henderson, 1929 and included several genera from Asia, Europe, and North America based on the reduced pseudocardinal teeth. Subsequent revisionary works synonymized this subfamily with either Unioninae Rafinesque, 1820 (Haas 1969a, b) or Ambleminae Rafinesque, 1820 (Subba Rao 1989). Later, Brandt (1974) resurrected the subfamily rank and incorporated a second genus, *Pilsbryconcha* Simpson, 1900. He also expanded diagnostic characters as “hinge teeth either completely missing or reduced to a knob-like pseudocardinal in each valve”. However, all of these taxonomic opinions were based mainly on shell morphology. Molecular phylogenetic studies do not accept Brandt's (1974) classification, but instead reassign *Pseudodon* and *Pilsbryconcha* to Gonideinae (Whelan *et al.* 2011; Pfeiffer & Graf 2015). The nominal name was recently recognized as a valid tribe, Pseudodontini, within Gonideinae Ortmann, 1916 by Lopes-Lima *et al.* (2017) with two genera, *Pseudodon* and *Pilsbryconcha*. The authors also suggested that the V-shaped fossette present in the inner shell at the posterior end of the hinge structure is a diagnostic character of the tribe. This classification was followed and supported by several studies using various molecular markers and techniques (Zieritz *et al.* 2018; Pfeiffer *et al.* 2019; Bolotov *et al.* 2020; Zieritz *et al.* 2020; Graf & Cummings 2021a; Konopleva *et al.* 2021). Controversially, the subfamily rank has also been used by some molecular phylogenetic studies (Bolotov *et al.* 2017a, 2017b, 2018; Huang *et al.* 2019).

Initially, Pseudodontini includes two genera, *Pseudodon* and *Pilsbryoconcha* (Lopes-Lima *et al.* 2017). Bolotov *et al.* (2017b) used multi-locus phylogenetic approaches to revise genus-level clades within this group. They revealed a polyphyletic relationship of at least five clades within *Pseudodon* s. lat., and applied two previously available names and erected three new genera. Hence, a total of seven genera are currently included in Pseudodontini (Bolotov *et al.* 2020; Graf & Cummings 2021a). Bolotov *et al.* (2020) further suggested classifying Pseudodontini into a monotypic subtribe Pseudodontina and subtribe Pilsbryoconchina containing the other six genera. These two subtribes are genetically different and can be distinguished by their morphology. Shells of Pseudodontina are relatively thick, and pseudocardinal teeth are tubercle-like, rather solid, and prominent. In contrast, shells of Pilsbryoconchina are thinner, and pseudocardinal teeth are reduced or lacking (Bolotov *et al.* 2017b).

In the present study, we propose another new genus from the Middle Mekong River Basin belonging to Pseudodontini. This new genus has long been recognized under *Pilsbryoconcha* s. lat. (Haas 1920, 1969a; Brandt 1974; Graf & Cummings 2007; Zieritz *et al.* 2018; Ng *et al.* 2020; Graf & Cummings 2021a). We further include two species: the new species described herein, and another previously recognized as '*Pilsbryoconcha lemeslei*'. The validity of these taxa is supported by their unique conchological characteristics and their evolutionary distinctiveness as estimated through multi-locus phylogenetic analyses using sequences from both mitochondrial and nuclear genes. Furthermore, the evolutionary relationship and estimation of divergence times within Pseudodontini are also discussed.

Material and methods

Specimen sampling

Animal use protocol in this study was approved by the Faculty of Science, Mahidol University Animal Care and Use Committee, SCMU-ACUC (MUSC63-026-534).

Specimens were collected by hand and euthanized by a two-step method (AVMA 2020): living specimens were placed in a container filled with fresh water. Then, 95% (v/v) ethanol was gradually added to the container starting from approximately 5% (v/v) concentration until specimens were fully anesthetized. Specimens were moved to 70% (v/v) ethanol to complete the process and for tissue fixation. Shells were separated from the soft body and were then gently cleaned to remove residual tissues. Tissues from the foot and/or mantle were cut and preserved in 95% (v/v) ethanol at -20°C for DNA extraction. The other remaining soft parts were preserved in 70% (v/v) ethanol for anatomical study and kept together with their shells to serve as vouchers.

Shell morphology was compared among specimens, the type series, and photographs from museum collections available on the online database (i.e., MUSSELp Database; Graf & Cummings 2021b). Shell comparisons were done based on shell shape, shell size, umbo position, teeth, and adductor muscle scars. Shell length, height, and width were measured using a digital Vernier calliper (± 0.01 mm). Anatomical characteristics, i.e., excurrent and incurrent aperture, labial palps, and gills, were examined under a stereomicroscope.

Abbreviations used in the text

AICc	=	Akaike Information Criterion
BI	=	Bayesian inference
BS	=	Bootstrap support
BPP	=	Bayesian posterior probability
ESS	=	Effective Sample Sizes
HPD	=	Highest posterior density interval
MCC	=	Maximum clade credibility

MC-MCMC	=	Metropolis-coupled Markov chain Monte Carlo
ML	=	Maximum likelihood
Mya	=	Million of years ago

Acronyms

ANSP	=	Academy of Natural Sciences, Philadelphia, USA
BMNH	=	Natural History Museum, London, UK
CUMZ	=	Chulalongkorn University Museum of Zoology, Bangkok, Thailand
MCZ	=	Museum of Comparative Zoology, Cambridge, USA
MNHN	=	Muséum national d'Histoire naturelle, Paris, France
MUMNH	=	Mahidol University Museum of Natural History, Bangkok, Thailand
SMF	=	Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt a. M., Germany
USNM	=	National Museum of Natural History, Washington, USA

Molecular analysis

Total genomic DNA was extracted from small pieces of foot or mantle tissue using a DNA NucleoSpin® extraction kit for animal tissue (MACHEREY-NAGEL, Germany) following the standard procedure of the manual. Fragments of the mitochondrial cytochrome c oxidase subunit I (COI) and the 16S small ribosomal RNA (16S) genes, and the nuclear 28S ribosomal RNA gene (28S) were amplified by polymerase chain reactions (PCR). Primers used for the COI gene were LCO1490 and HCO2198 (Folmer *et al.* 1994); for 16S gene were 16sar-L-myt and 16Sbr-H-myt (Lydeard *et al.* 1996), and for 28S gene were C1 and D2 (Jovelin & Justine 2001). Thermal cycling was started at 94°C for 3 min; followed by 35 cycles of 94°C for 30 s; annealing at 48°C for COI, 46°C for 16S rRNA, and 58°C for 28S rRNA, for 60 s; extension at 72°C for 90 s; then a final 72°C for 5 min. Amplicons were purified using a MicroSpin purification kit (Qiagen, USA). Each amplicon was bi-directionally sequenced using the same primers used for amplification on the ABI 3730XL DNA Analyzer (BIONEER, Republic of Korea). The derived consensus nucleotide sequences newly obtained in this study were deposited in the GenBank database under accession numbers MZ822395–MZ822416 for COI, MZ822895–MZ822916 for 16S and MZ822917–MZ822938 for 28S (Table 1).

Phylogenetic analyses

Phylogenetic analyses were based on 55 sequences covering all genera from Pseudodontini. Sequences from other tribes were used as outgroups (Table 1). The details of taxon sampling used in phylogenetic analysis are shown in Table 1. Sequence alignments were generated using the MUSCLE option as implemented in MEGA ver. 7.0.26 (Kumar *et al.* 2016). The final concatenated alignment used in phylogenetic tree construction contained 1967 bp: 660 bp of COI, 501 of 16S, and 806 bp of 28S.

The best-fit evolutionary model for each gene and gene partition was calculated by PartitionFinder2 ver. 2.3.4 (Lanfear *et al.* 2016), based on the corrected Akaike Information Criterion (AICc) and using a heuristic search algorithm. The program suggested dividing the concatenated dataset into five partitions, consisting of partitions for 16S and 28S genes and for each of three codon positions of the COI gene. The best-fit model was GTR+I+G for the first codon position of COI, 16S, and 28S; F81+I for the second codon position of COI; and GTR+G for the third codon position of the COI gene. This partition setting was used in subsequent Bayesian inference (BI) analysis. The BI analysis was carried out by running two runs of 10 million generations of Metropolis-coupled Markov chain Monte Carlo (MC-MCMC) in MrBayes ver. 3.2 (Ronquist *et al.* 2012). Each MCMC run consisted of two sets of three heated chains and one cold chain. Each run used a random tree as starting tree and collected a sampling tree every 1000th generations. The first 25% of the obtained sampling trees were discarded as burn-in. Maximum likelihood analysis (ML) was performed through 1000 ML bootstrap replicates using

Table 1 (continued on next two pages). Voucher ID, locality information, and GenBank accession numbers for specimens used in phylogenetic analysis. Those which are marked with * are newly sequenced in this study.

Taxa	VoucherID	Localities	GenBank accession		
			COI	16S	28S
UNIONIDAE Rafinesque, 1820					
GONIDEINAE Ortmann, 1916					
PSEUDODONTINI Frierson, 1927					
Ingroups					
<i>Namkongnaia</i>	MUMNH-UNI2831	Laos: Mekong	MZ822395*	MZ822895*	MZ822917*
<i>inkhavilayi</i> gen. et sp. nov	MUMNH-UNI2832	River Basin, local	MZ822396*	MZ822896*	MZ822918*
	MUMNH-UNI2833	market near Xe	MZ822397*	MZ822897*	MZ822919*
	MUMNH-UNI2834	Bangfai River	MZ822398*	MZ822898*	MZ822920*
<i>Namkongnaia lemeslei</i>	MUMNH-UNI2825	Cambodia: Tonle	MZ822399*	MZ822899*	MZ822921*
(Morelet, 1875 gen. et	MUMNH-UNI2826	Sap Basin, Kam-	MZ822400*	MZ822900*	MZ822922*
comb. nov.)	MUMNH-UNI2827	pong Kdei River	MZ822401*	MZ822901*	MZ822923*
	MUMNH-UNI2828		MZ822402*	MZ822902*	MZ822924*
	MUMNH-UNI2829		MZ822403*	MZ822903*	MZ822925*
	MUMNH-UNI2830		MZ822404*	MZ822904*	MZ822926*
<i>Monodontina vondem-</i>	BIV1822	Malaysia	MK994774	MK994774	n/a
<i>buschiana</i> (Lae, 1840)					
<i>Monodontina mekongi</i>	RMBH biv0122	Thailand: Mekong	KX865861	KX865632	KX865733
Bolotov <i>et al.</i> , 2020		River Basin, Phong			
		River			
<i>Monodontina laosica</i>	UMMZ 304650	Laos: Mekong	KP795029	KP795052	n/a
Bolotov <i>et al.</i> , 2020		River Basin,			
		tributary of the			
		Vang Ngao River			
<i>Monodontina</i>	n/a	Thailand	KX822660	n/a	KX822616
<i>cambodiensis</i> (Petit, 1865)					
<i>Monodontina lenyanensis</i>	RMBH biv0628_2	Myanmar: Lenya	MN275055	MN307246	MN307187
Bolotov <i>et al.</i> , 2020		River Basin,			
		14 Mile Stream			
<i>Bineurus mouhotii</i>	RMBH biv0182_2	Laos: Mekong	KX865876	KX865647	KX865747
(Lea, 1863)		River Basin,			
		Nam Long River			
<i>Bineurus exilis</i>	MUMNH-UNI2660	Cambodia: Tonle	MZ822405*	MZ822905*	MZ822927*
(Morelet, 1866)	MUMNH-UNI2728	Sap Basin, Sangker	MZ822406*	MZ822906*	MZ822928*
	MUMNH-UNI2730	River, Battambang	MZ822407*	MZ822907*	MZ822929*
	RMBH biv0474_1	Thailand: Mekong	MN275052	MN307243	MN307184
		River Basin, Mun			
		River, upstream of			
		upper reservoir			
<i>Thaiconcha callifera</i>	RMBH biv0120_3	Thailand: Mekong	KX865865	KX865636	KX865737
(Martens, 1860)		River Basin, Phong			
		River			
<i>Sundadontina cumingii</i>	X115	Malaysia	KX051295	n/a	n/a
(Lea, 1850)					
<i>Sundadontina tumida</i>	UMMZ 304349	Cambodia: Mekong	KP795027	KF011261	KP795010
(Morelet, 1866)		River Basin			

Table 1 (continued). Voucher ID, locality information, and GenBank accession numbers for specimens used in phylogenetic analysis. Those which are marked with * are newly sequenced in this study.

Taxa	VoucherID	Localities	GenBank accession		
			COI	16S	28S
<i>Sundadontina brandti</i> Bolotov <i>et al.</i> , 2020	RMBH biv0475_2	Thailand: Mekong River Basin, Mun River	MN275058	MN307249	MN307190
<i>Sundadontina taskaevi</i> Bolotov <i>et al.</i> , 2020	RMBH biv0475_1	Thailand: Mekong River Basin, Mun River	MN275061	MN307251	MN307192
<i>Nyeinchanconcha nyeinchani</i> Bolotov <i>et al.</i> , 2020	UMMZ 304648	Laos: Mekong River Basin, Nam Phiat River	KP795025	KP795050	KP795008
<i>Pilsbryoconcha exilis</i> (Lea, 1838)	MUMNH-UNI2481	Indonesia: Java Basin, Bogor Botanical Gardens	MZ822408*	MZ822908*	MZ8229230*
	MUMNH-UNI2482		MZ822409*	MZ822909*	MZ8229231*
	MUMNH-UNI2483		MZ822410*	MZ822910*	MZ8229232*
	MUMNH-UNI0290	Thailand: Chao Phraya River Basin, Pasak River, Phetchabun	MZ822411*	MZ822911*	MZ8229233*
<i>Pilsbryoconcha linguaeformis</i> Morelet, 1875	MUMNH-UNI2779	Thailand: Chao Phraya River Basin, Sakae Krang River, Uthai Thani	MZ822412*	MZ822912*	MZ8229234*
	MUMNH-UNI2625	Cambodia: Tonle Sap Basin, Tonle Sap Lake, Boeng Tonle Chhma	MZ822413*	MZ822913*	MZ8229235*
	MUMNH-UNI2624	Cambodia: Tonle Sap Basin, Tonle Sap Lake, Chhnok Tru	MZ822414*	MZ822914*	MZ8229236*
	MUMNH-UNI2741	Cambodia: Tonle Sap Basin, Tonle Sap Lake open area	MZ822415*	MZ822915*	MZ8229237*
	MUMNH-UNI2698	Thailand: Bang Pakong River Basin, Hanuman River, Prachin Buri	MZ822416*	MZ822916*	MZ8229238*
<i>Pilsbryoconcha 'lemeslei'</i> sensu Bolotov, 2020	n/a	Vietnam	KX822657	n/a	n/a
<i>Pseudodon cf. inoscularis</i> (Gould, 1844)	RMBH biv0110_5	Myanmar: Ayeyarwady River Basin, a tributary of Lake Indawgyi	KX865858	KX865629	KX865730
<i>Pseudodon bogani</i> Bolotov <i>et al.</i> , 2017	RMBH biv0241_4	Myanmar: Sittaung River Basin, Kanni River	MF352216	MF352290	MF352348
<i>Pseudodon manuelei</i> Kono-pleva <i>et al.</i> , 2017	RMBH biv0246_1	Myanmar: Sittaung River Basin, Pyowne River	MF352228	MF352300	MF352358

Table 1 (continued). Voucher ID, locality information, and GenBank accession numbers for specimens used in phylogenetic analysis. Those which are marked with * are newly sequenced in this study.

Taxa	VoucherID	Localities	GenBank accession		
			COI	16S	28S
<i>Pseudodon salweenianus</i> (Gould, 1844)	RMBH biv0639_1	Myanmar: Salween River Basin, unnamed stream	MN275037	MN307237	MN307178
<i>Pseudodon kayinensis</i> Bolotov <i>et al.</i> , 2020	RMBH biv0618_3	Myanmar: Ataran River Basin, Winyaw River	MN275045	MN307240	MN307181
Outgroups					
GONIDEINI Ortmann, 1916					
<i>Sinosolenia carinata</i> (Heude, 1877)	n/a	China	KX822669	NC_023250	KX822626
<i>Gonidea angulata</i> (Lea, 1838)	RMBH biv0294_1	USA: Okanagan Lake	MN402615	MN396726	MN396722
<i>Leguminaia wheatleyi</i> (Lea, 1862)	RMBH biv0177_7	Turkey: Karasu River	MN402614	MN396725	MN396721
LAMPROTULINI Modell, 1942					
<i>Lamprotula leaui</i> (Griffith & Pidgeon, 1833)	RMBH biv0200_1	Vietnam	MN402616	MN396727	MN396723
<i>Potomida littoralis</i> (Cuvier, 1798)	RMBH biv0177_10	Turkey: Karasu River	MN402617	MN396728	MN396724
<i>Pronodularia japonensis</i> (Lea, 1859)	NCSM 27183	Japan	KX822659	AB055625	KX822615
CHAMBERLAINIINI Bogan, Froufe & Lopes-Lima <i>in</i> Lopes-Lima <i>et al.</i> 2017					
<i>Chamberlainia hainesiana</i> (Lea, 1856)	BIV46	Thailand	NC044110	n/a	KX822592
<i>Sinohyriopsis cumingii</i> (Lea, 1852)	16_NCU_XPWU_SU177	China	NC011763	NC011763	MG595614
RECTIDENTINI Modell, 1942					
<i>Hyriopsis bialata</i> Simpson, 1900	BIV1774	Malaysia: Pahang River, Pahang	KX051274	MT993644	MT993697
<i>Ensidens ingallsianus</i> (Lea, 1852)	MUMNH-UNI0074	Thailand: Chao Phraya River Basin, Song River, Phrae	MT993541	MT993687	MT993739
<i>Rectidens sumatrensis</i> (Dunker, 1852)	RMBH biv0211_1	Malaysia: Perak River, Perak	MF352288	n/a	MF352405
CONTRADENTINI Modell, 1942					
<i>Lens contradens</i> (Lea, 1838)	MUMNH-UNI0197	Thailand: Chao Phraya River Basin, Sakae Krang River, Uthai Thani	MG581991	MT993693	MT993745
<i>Physunio superbus</i> (Lea, 1843)	MUMNH-UNI0199	Thailand: Chao Phraya River Basin, Chao Phraya River, Nakhon Sawan	MG582020	MT993689	MT993741
<i>Trapezoideus foliaceus</i> (Gould, 1843)	UF507879 (=ICH-02104)	Thailand: Mae Klong River Basin, Pachee River	MH345984	MH346024	MH346004

RAxML ver. 8.2.10 (Stamatakis 2014) and with the GTRGAMMA model. Both BI and ML analyses were conducted at the San Diego Supercomputer Center through the online CIPRES Science Gateway (Miller *et al.* 2010).

Average genetic distances among taxa were estimated for the COI data set using uncorrected pairwise genetic distances as implemented in MEGA ver. 7.0.26 (Kumar *et al.* 2016).

Estimation of divergence times

Divergence time was estimated by constructing a time-calibrated phylogeny as implemented in BEAST ver. 2.6.1 (Bouckaert *et al.* 2019) through the online CIPRES Science Gateway (Miller *et al.* 2010). The same multi-locus dataset as for phylogenetic analyses was used. The external COI evolutionary rate of $0.265 \pm 0.06\%$ substitutions per site per million years as previously estimated for Unionidae (Fonseca *et al.* 2016) was applied for tree dating. The use of evolutionary rates taken from literature without calibration by fossils or geological events may give inappropriate results and should be interpreted with caution. Nevertheless, a previous study that used this evolutionary rate showed reliable estimation results (Bolotov *et al.* 2020), which were largely congruent with those estimated from mitogenomic data (Fonseca *et al.* 2016) and those using fossil data as calibration points (Bolotov *et al.* 2017a). The evolutionary model for each partition was set separately, following the suggestion of jModelTest ver. 2.1.10 (Darriba *et al.* 2012). The evolutionary rate was implemented only for the COI partition and was set as estimated for other partitions. The analyses were run using a lognormal relaxed clock algorithm (Drummond *et al.* 2006). A random tree generated from the COI dataset with the Yule speciation process was used as a tree prior. Two independent MCMCs were run for 50 million generations, and tree sampling was collected every 1000th generation. The output files were checked for convergence diagnostics and Effective Sample Sizes (ESS) using Tracer ver. 1.7 (Rambaut *et al.* 2018). The effective sample size (ESS) values were greater than 1500 for all parameters. Results from two independent runs were compiled with 25% burn-in using LogCombiner ver. 2.6.2 (Bouckaert *et al.* 2019) and then summarized for the maximum clade credibility (MCC) tree in TreeAnnotator ver. 2.6.2 (Bouckaert *et al.* 2019).

Results

Phylogenetic analysis and divergence time estimation

Both ML and BI analyses returned similar topologies. Therefore, only the tree topology from ML is presented in Fig.1. All of the genera in Pseudodontini are recovered as highly supported clades, with 95–100% bootstrap support (BS) values for ML and Bayesian posterior probability (BPP) of 1 for BI, except *Sundadontina* Bolotov *et al.*, 2020, which shows poor support (BS = 32%, BPP = 0.79). The pairwise distance analysis also reveals a large genetic distance among these genera, with 10.65–13.59% uncorrected COI p-distance (Table 2).

Among available clades, there is one highly supported clade that is distantly separated from other genera, with pairwise uncorrected COI p-distance ranging from 11.02% to 12.42%. This clade shows unique morphological characteristics distinguishable from other genera. Therefore, it is described herein as *Namkongnaia* gen. nov. The new genus further includes two well-defined clades (BS = 99–100%, BPP = 0.99), with a deep divergence of 5.10% uncorrected COI p-distance. Both clades are morphologically distinct from each other. One clade has long been recognized under the name '*Pilsbryconcha lemeslei*' and the other is described herein. Interestingly, a sequence recognized as *Pilsbryconcha lemeslei* sensu Bolotov *et al.* (2020) fails to group with our specimens; instead, it is placed within *Pilsbryconcha* s. str. (BS = 95%, BPP = 0.99).

The phylogenetic relationship among genera within Pseudodontini is uncertain and with poor support. Nevertheless, the phylogenetic tree reveals a monophyletic relationship among six genera

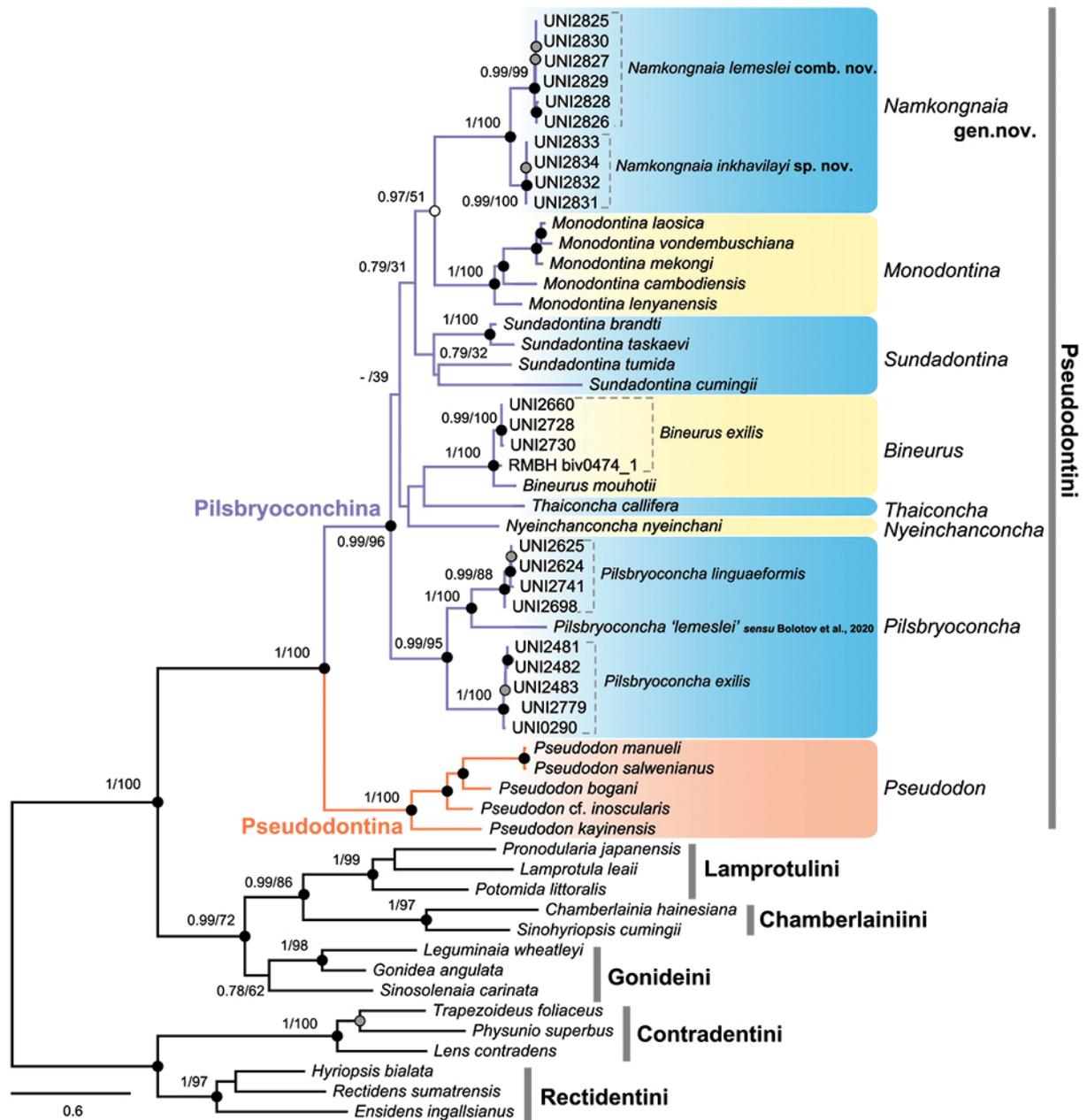


Fig. 1. Maximum likelihood (ML) tree of the subfamily Gonideinae based on the concatenated dataset of COI + 16S + 28S genes. Bootstrap values from ML and posterior probabilities from Bayesian inference analysis (BI) of the major nodes are listed as ML/BI. Nodes with posterior probabilities of BI ≥ 0.95 and ML bootstrap support values ≥ 70 were considered as sufficiently supported nodes (Huelsenbeck & Hillis 1993; Larget & Simon 1999), and are marked with black circles (supported by both BI and ML), white circles (supported only by BI), or grey circles (supported only by ML).

in Pilsbryconchina (BS = 96%, BPP = 0.99) and separates them from Pseudodontina (only the genus *Pseudodon* currently belongs to this subtribe). The average genetic distance between these subtribes is 12.5% uncorrected COI p-distance. In addition, the new genus is suggested as a sister clade with *Monodontina*, although with only 0.97 BPP support from BI.

A reconstructed time-calibrated phylogeny (based on $0.265 \pm 0.06\%$ substitutions per site per million years of COI evolutionary rate) is shown in Fig. 2. Based on this, Pseudodontini diverged in the Late Cretaceous (mean age = 91.9 Mya, 95% HPD = 67.8–116.9 Mya), while Pilsbryconchina appears to have radiated into several genera within the Late Cretaceous to the Eocene (mean age = 70.8–49.3 Mya). The most recent split within Pilsbryconchina was between this new genus and *Monodontina* during the Eocene (mean age = 49.3 Mya, 95% HPD = 35.4–63.7 Mya). The divergence between the two species of the new genus is placed in the Miocene (mean age = 17.2 Mya, 95% HPD = 9.8–24.9 Mya). This timing is consistent with the diversification events in other genera between the Eocene to Miocene (mean age = 39.6–10.9 Mya). Moreover, *Sundadontina* is recovered as polyphyletic in ‘BEAST’ analysis, in which *Sundadontina cumingii* is placed separately from other congeners.

Taxonomy

Given the results of the morphological examination and multiple lines of molecular evidence mentioned above, we thus propose describing the novel discovered clade in Pilsbryconchina as *Namkongnaia* gen. nov., together with a new species from Laos. We also transfer *Anodonta lemeslei* Morelet, 1875 to this new genus.

Family Unionidae Rafinesque, 1820
Subfamily Gonideinae Ortmann, 1916
Tribe Pseudodontini Frierson, 1927
Subtribe Pilsbryconchina Bolotov *et al.*, 2017

Genus *Namkongnaia* gen. nov.

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Type species

Namkongnaia inkhavilayi gen. et sp. nov., by present designation.

Differential diagnosis

The new genus is distinguished from other genera in Pseudodontini by having a narrow, elongated, and less inflated shell. It is also represented as a distinct clade in multi-locus phylogenetic analyses.

Description

Shell Medium-sized, thin, narrow and elongated, rather compressed, very inequilateral; anteriorly round; posteriorly round or somewhat pointed; umbonal area not elevated and usually eroded. Ligament very narrow. Hinge without dentition, posterior end of the hinge structure with V-shaped fossette. Anterior adductor muscle scar shallow, ovate, and fused with pedal retractor muscle scars; posterior adductor muscle scar very shallow. Excurrent aperture smooth, shorter than incurrent; incurrent with 1-2 rows of conical papillae. Gills elongated and slightly ribbed; anterior margin of inner gills slightly longer and wider than outer gills.

Etymology

The generic name “*Namkongnaia*” is from the word “*Namkong*”, a name for the Mekong River used by Thai and Lao peoples, and Greek word “*naiad*” meaning freshwater mussels. The name of this genus thus means “freshwater mussels from Mekong River”.

Distribution

Mekong River and its tributaries in Laos, Cambodia, and Thailand (Fig. 3; Brandt 1974; Ng *et al.* 2020). The distribution range may include the Mae Klong River Basin in Thailand (Brandt 1974), although the taxonomic status of the specimens recorded in Brandt (1974) needs to be confirmed.

Remarks

The new genus is currently composed of two species, which are confirmed by our multi-locus molecular data. Other potential species are probably among those previously recognized under the name ‘*Pilsbryconcha lemeslei*’ by Brandt (1974). This includes the specimens from ‘Bang Pae’, Mae Klong River Basin, Ratchaburi Province (USNM-786217, SMF-BR2663, and ANSP-H19041). These specimens show elongate and narrow shell, which are diagnostic characters of the genus, but differ from other species by having a minute concave ventral margin, and truncated posterior margin with a pointed posterior end. Further examination of fresh materials and DNA investigation would confirm the taxonomic status of these populations.

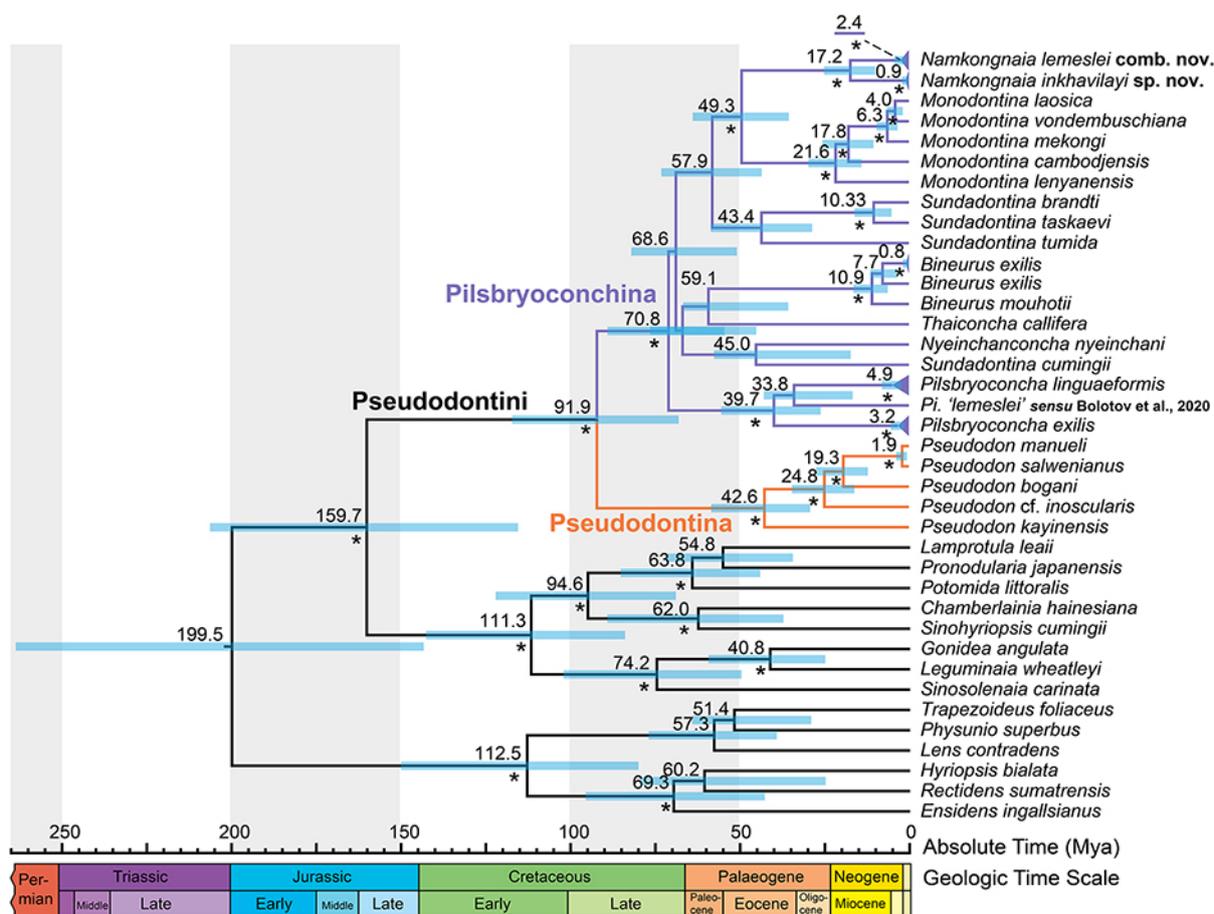


Fig. 2. Time-calibrated tree of the subfamily Gonideinae based on the concatenated alignment dataset of COI + 16S + 28S genes. Nodes present time estimates since the most recent common ancestor (tMRCA) in millions of years ago (Mya). Node bars indicate 95% highest posterior density interval (HPD) of the node ages. Sufficiently supported nodes (BPP > 0.95) are marked with ‘*’. The geologic time scale is according to the Geological Society of America, 2019.

Namkongnaia inkhavilayi gen. et sp. nov.

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Figs. 3, 4A–B; Tables 1, 3

Pilsbryconcha lemeslei – Brandt 1974: 263, pl. 18 fig. 22 (in part, only records from “Nang Rong (Prov. Buriram)”, Thailand) [non *Anodonta lemeslei* Morelet, 1875].

Etymology

This new species is dedicated to our colleague and distinguished malacologist, Dr Khamla Inkhavilay, from the National University of Laos.

Type material

Holotype

LAOS • Kammoune Province, Bunghona Market, 7 km N of Xe Bangfai River; 17.13674°N, 104.98591°E; E. Jeratthitikul, K. Wisittikoson, A. Fanka, N. Wutthituntisil and P. Prasankok leg.; sold by local people; MUMNH-UNI2831.

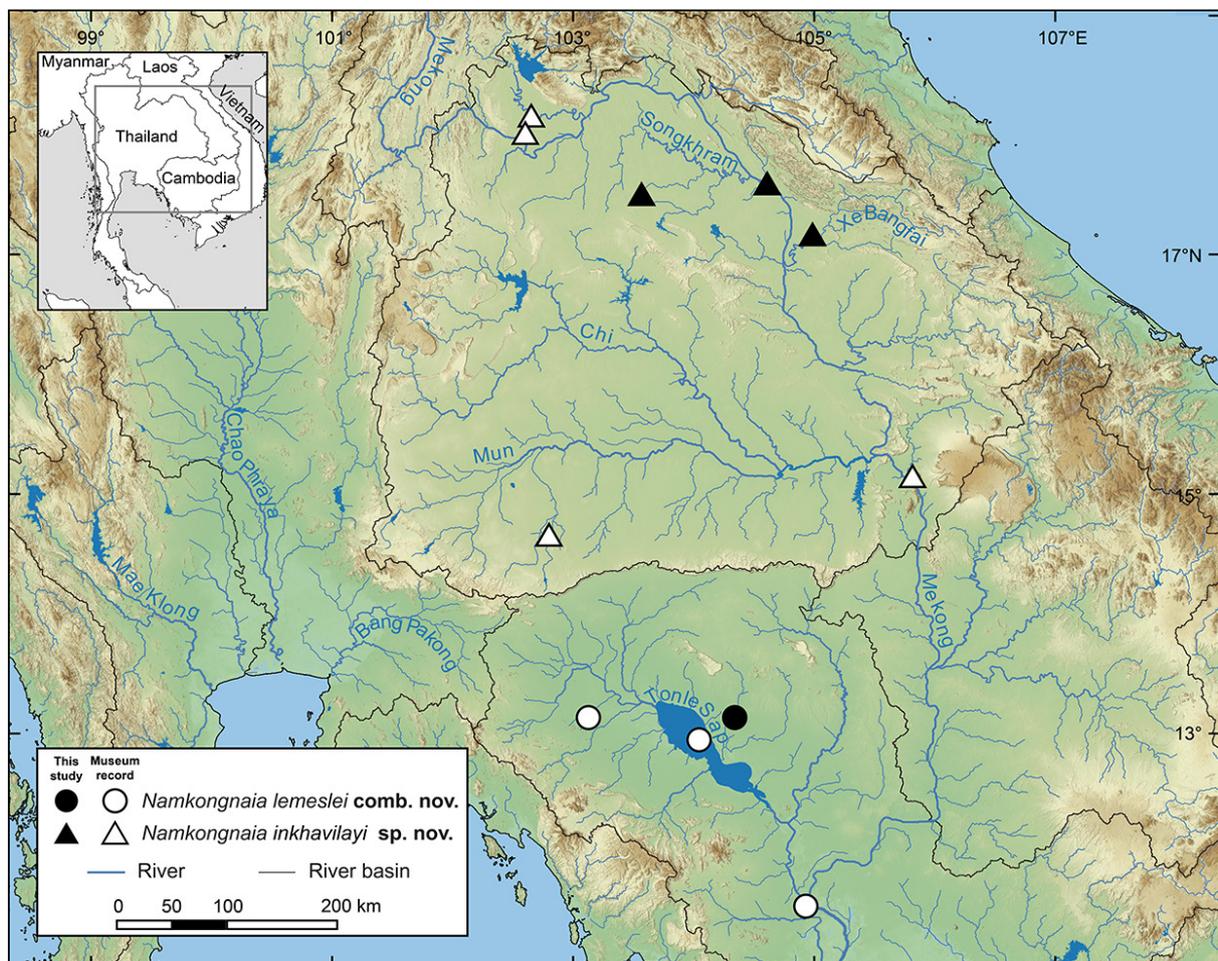


Fig. 3. Map showing distribution localities of *Namkongnaia* gen. nov. Boundaries of river basins follow Abell *et al.* (2008).

Table 2. Average genetic divergence based on uncorrected p-distance of 660-bp COI gene fragment sequences of freshwater mussel genera in the tribe Pseudodontini (% ± S.E.).

Taxa	1.	2.	3.	4.	5.	6.	7.
1. <i>Namkongnaia</i> gen. nov.							
2. <i>Monodontina</i>	11.02 ± 1.00						
3. <i>Sundadontina</i>	12.01 ± 1.05	12.06 ± 0.98					
4. <i>Bineurus</i>	11.60 ± 1.19	11.90 ± 1.09	11.92 ± 1.09				
5. <i>Thaiconcha</i>	11.81 ± 1.23	13.53 ± 1.21	11.97 ± 1.09	11.92 ± 1.29			
6. <i>Nyeinchanconcha</i>	11.70 ± 1.25	12.58 ± 1.20	10.65 ± 1.00	10.75 ± 1.24	12.80 ± 1.37		
7. <i>Pilsbryoconcha</i>	12.41 ± 1.15	11.85 ± 1.01	12.16 ± 1.02	10.93 ± 1.08	12.36 ± 1.22	11.44 ± 0.17	
8. <i>Pseudodon</i>	12.42 ± 1.10	12.78 ± 1.06	13.13 ± 1.02	12.27 ± 1.10	13.35 ± 1.16	12.69 ± 1.17	12.23 ± 01.01

Paratypes

LAOS • 5 shells; same collection data as for holotype; MUMNH-UNI2832 to UNI2835.

Other material

LAOS • 2 shells; Nong Njang, N of Vientiane; R. Brandt leg.; BMNH-MP-D262 • 1 shell; Nong Bua Thong near Vientiane; R. Brandt leg.; ANSP-H19043 • 2 shells; Nong Bua Thong near Vientiane; R. Brandt leg.; MCZ-280932 • 2 shells; Nong Bua Thong near Vientiane; R. Brandt leg.; SMF-258771 • 2 shells; Nong Bua Thong, Vientiane; R. Brandt leg.; SMF-319294 • 1 shell; Bang Jian near Vientiane; R. Brandt leg.; ANSP-H19044 • 6 shells; Nang Njang near Vientiane; MNHN-MP-3154 • 4 shells; Nang Njang near Vientiane; R. Brandt leg.; MNHN-MP-3157 • 3 shells; swamp near Pakse; R. Brandt leg.; SMF-225743.

THAILAND • 1 shell; Nakhon Phanom, Tha Uthen, Tha Uthen, Thuai River; 17.56221° N, 104.60890° E; E. Jeratthitikul, K. Wisittikason and P. Prasankok leg.; MUMNH-UNI2706 • 1 shell; Sakon Nakhon, Sawang Daen Din, Bong Tai, Songkhram River; 17.39570° N, 103.30048° E; E. Jeratthitikul and K. Wisittikason leg.; MUMNH-UNI0318 • 1 shell; Buriram, Nang Rong, Huai Tadjek; R. Brandt leg.; USNM-786219 • 1 shell; Buriram, Nang Rong, Huai Tadjek; R. Brandt leg.; SMF-220822 • 4 shells; Buriram, Nang Rong; SMRL-2662 • 1 shell; Buriram, Huai Ta Djek near Nang Rong; ANSP-H19042.

Description

Shell medium-sized, length 80.9–102.2 mm, height 26.2–37.2 mm, width 13.6–19.1 mm (Table 3). Shell rather thin, narrow and elongated (H/L ratio = 0.32–0.36), very inequilateral, compressed. Dorsal margin straight, anterior at the same level as posterior. Umbonal area eroded, not elevated. Anterior margin round; posterior margin elongated and rounded. Ventral margin almost straight, slightly curved upward posteriorly. Posterior ridges low, wide and obtuse, not prominent. Periostacum thin, greenish to dark brown, the eroded part coppery-brown. Shell surface with fine growth lines. Ligament very narrow. Hinge without dentition, posterior end of the hinge structure with V-shaped fossette. Anterior adductor muscle scar placed relatively far from the dorsal margin, shallow, ovate, fused with pedal retractor muscle scars; posterior adductor muscle scars very shallow, almost invisible. Pallial line very faint. Nacre whitish with cream tint near the umbo. Excurrent aperture smooth, shorter than incurrent. Incurrent with 1–2 rows of conical papillae, varying in length. Small epithelial folds form a fused bridge separating excurrent and incurrent aperture. Gills elongated and slightly ribbed. Anterior margin of inner gills slightly longer and wider than that of inner outer gills. Glochidia unknown.

Distribution

This new species appears to occur in the Lower Mekong watershed. In Laos, it was recorded from several locations near Vientiane, Kammoune, and Champasak Provinces. In Thailand, it is known from the Songkram and Mun river basins in the northeast region (Brandt 1974).

Habitat

Specimens of the new species were bought on a local market near the Xe Bangfai River. However, specimens from the Thuai and Songkhram Rivers in Thailand were found buried in the mud substrate of still water. Brandt (1974) also reported ponds as a general habitat of this species.

Remarks

The specimens recorded by Brandt (1974) from Nang Rong, Buriram, Thailand (SMF-220822) show a shorter but wider shell and a relative rounded ventral margin. In addition, although the hinge area of this species has no dentition, the trace of a rudimentary pseudocardinal tooth is seen as a very tiny tubercle in some individuals.

Namkongnaia lemeslei (Morelet, 1875) gen. et comb. nov.

Figs 3, 5; Table 1

Anodonta lemeslei Morelet, 1875: 328, pl.14 fig. 1.

Pilsbryconcha lemsleyi [sic] Simpson, 1900: 558.

Anodonta lemeslei – Crosse & Fischer 1876: 333. — Morlet 1889: 167.

Pilsbryconcha lemeslei – Simpson 1914: 244. — Haas 1920: 300, pl. 37 fig. 4.; 1969a: 382.

— Brandt 1974: 263 (in part, only records from “Aranyaprathet (Prov. Prachin Buri)”, Thailand).

— Graf & Cummings 2007: 311. — Zieritz *et al.* 2018: 29–44. — Ng *et al.* 2020: 122, fig. 3j.;

— Graf & Cummings 2021a: 22.

Type material

Syntype

CAMBODIA • 2 shells; “Cambodge, Marecages de Battambang”; Le Mesle leg.; MNHN-MP-3150.

Other material

CAMBODIA • 6 shells; Siem Reap, Chi Kraeng, Kampong Kdei, Kampong Kdei River; 13.13279°N, 104.33989°E; E. Jeratthitikul, C. Sutcharit, W. Siriwut, S. Chhuoy and T.H. Ng leg.; MUMNH-UNI2825

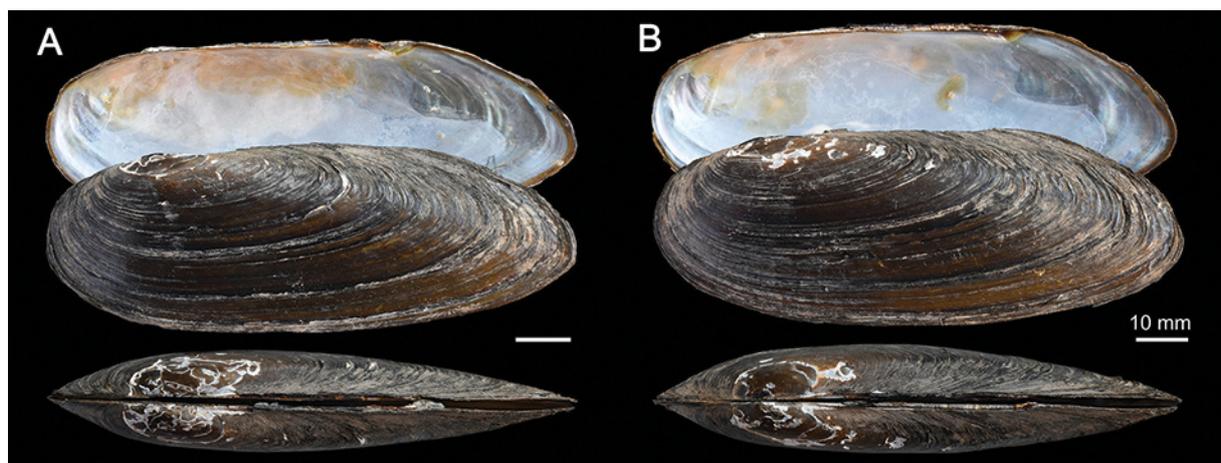


Fig. 4. *Namkongnaia inkhavilayi* gen. et sp. nov. **A.** Holotype MUMNH-UNI2831. **B.** Paratype MUMNH-UNI2836, both from the type locality in Xe Bangfai River, Kammoune Province, Laos. Scale bars: 10 mm.

Table 3. Shell measurements for the type series of *Namkongnaia inkhivilayi* gen. et sp. nov. Measurements in millimetres (mm).

Type status	Specimen voucher	Shell length	Shell height	Shell width
Holotype	MUMNH-UNI2831	102.18	35.82	18.00
Paratype	MUMNH-UNI2832	79.00	26.23	13.62
Paratype	MUMNH-UNI2833	91.31	29.03	16.36
Paratype	MUMNH-UNI2834	80.89	28.41	14.64
Paratype	MUMNH-UNI2835	88.74	31.12	16.31
Paratype	MUMNH-UNI2836	101.76	37.16	19.06

to UNI2829, UNI2669 • 5 shells; Grand Lacs; MNHN-MP-3156 • 2 shells; Phnom Penh; MNHN-MP-3158 • 4 shells; Cambodge; MNHN-MP-3163, MNHN-MP-3171.

Differential diagnosis

This species resembles the type species, but it can be distinguished by the relatively smaller size with a shell length of 67.0–81.0 mm (vs 80.9–102.2 mm), anterior adductor muscle scar placed near the dorsal margin (vs relatively far from the dorsal margin), adductor muscle scar relatively deep for the thin shell (vs shallower, although thicker shell), nacre yellowish (vs whitish), anterior margin rounded and little shouldered (vs wider and not shouldered), and the anterior portion of the dorsal margin somewhat lower than the posterior (vs at the same level in both anterior and posterior portions).

Description

Shell medium-sized, rather thin, narrow and elongated (H/L ratio = 0.39), very inequilateral, compressed. Dorsal margin straight; somewhat lower anteriorly than posteriorly. Umbonal area eroded, not elevated. Anterior margin round, little shouldered; posterior margin elongated, somewhat pointed. Ventral margin almost straight, or minutely concave in the middle in old specimens, posteriorly slightly curved upward. Posterior ridges low, wide and obtuse, not prominent. Periostracum thin, yellowish to dark brown, the eroded part coppery-brown. Shell surface with fine growth lines. Ligament very narrow. Hinge without dentition, posterior end of the hinge structure with V-shaped fossette. Anterior adductor muscle scar placed near the dorsal margin, relatively deep for the thin shell, ovate, fused with pedal retractor muscle scars; posterior adductor muscle scars very shallow, almost invisible. Pallial line very faint. Nacre yellowish with creamy tint near the umbo.

Additional description

Examination of the soft body of newly collected specimens in this study yielded additional description of the animal: excurrent aperture smooth, shorter than incurrent; incurrent with 1–2 rows of conical papillae, similar in length; small epithelial folds form a fused bridge separating excurrent and incurrent aperture; gills elongated and slightly ribbed; anterior margin of inner gills slightly longer and wider than that of outer gills. However, no brooding specimens were available to examine glochidia.

Distribution

This species is restricted to Tonle Sap Lake and its tributaries in Cambodia. Its distribution probably reaches the headwater of Tonle Sap basin in eastern Thailand (Brandt 1974).

Habitat

This species was recorded in mud substrate in still sections of rivers or in lentic habitat, i.e., ponds and lakes (Morelet 1875; Morlet 1889; Brandt 1974).

Remarks

This species has been noted for its rarity (Brandt 1974; Ng *et al.* 2020). Only a few lots are available in museum collections. We obtained additional fresh materials from the Kampong Kdei River, Siem Reap Province. These specimens resemble the syntype MNHN-MP-3150 (Fig. 5D). The only detected variations are less erosion of the umbo area and more yellowish-brown colour of the periostracum. Morelet (1875) described *Anodonta lemeslei* based on specimens collected by M. Le Mesle. The figured specimen is eroded, with a concave ventral margin (Fig. 5B–C), while another

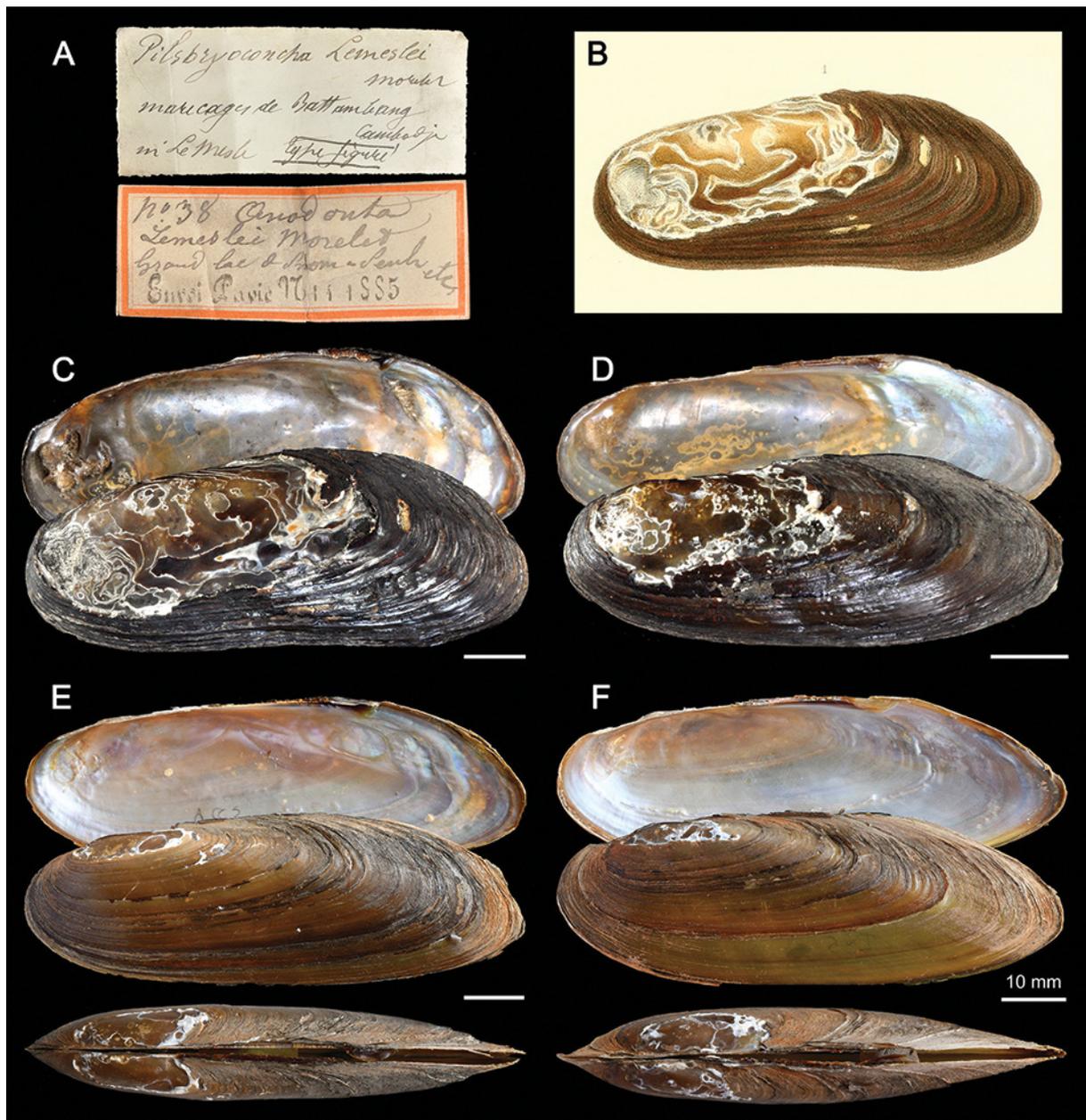


Fig. 5. *Namkongnaia lemeslei* gen. et comb. nov. **A.** Labels associated with the syntype lot. **B.** Original figure (after Morelet 1875: pl. 14 fig. 1). **C–D.** Syntype MNHN MP 3150 (photographs by V. Heros and M. Caballer) from Battambang Province, Cambodia. **E.** Specimen MUMNH-UNI2669. **F.** Specimen MUMNH-UNI2829 from Kampong Kdei River, Siem Reap Province, Cambodia. Scale bars: 10 mm.

shell has a relatively parallel shell and a straight ventral margin (Fig. 5D). Morelet (1875) identified the ventrally concave specimens as fully-grown individuals, while the ventrally straight specimens were considered to be young individuals. The concavity trait is quite unusual for species that live in stagnant water habitats. Nevertheless, some specimens from Tonle Sap Lake (MNHN-MP-3156) also show the characteristic of a concave ventral margin. However, all of our specimens have a straight ventral margin. This raises some suspicions about the existence of both variations. In this study, we retain both variations as the same species until topotype specimens with concave ventral margin are available for DNA analysis.

Apart from a ventral margin, other morphological variations are also observed. The posterior ends of some specimens are more or less rounded than others. Crosse & Fischer (1876) noted that some specimens from Cambodia are narrower and more elongated than the type figure. The posterior dorsal margin in some specimens is also somewhat higher. Morelet (1875) noted that one of his type specimens is undoubtedly similar to *Anodonta schomburgki* Martens, 1860 [= *Pilsbryconcha compressa* (Martens, 1860)]. However, it is more or less narrow, and the high posterior cannot be considered a posterior wing as in *Anodonta schomburgki* Martens, 1860.

Several records and specimens previously identified as *Pilsbryconcha lemeslei* have been examined and listed in this species. However, a specimen from Khanh Hoa, Vietnam, is conchologically different and does not belong to this species (Thach 2007; Do *et al.* 2018); rather, it is probably a species of *Pilsbryconcha*. This specimen shows more or less curved ventral margin and relatively wider shell.

Similarly, the DNA sequence of specimen assigned to *Pilsbryconcha lemeslei* by Bolotov *et al.* (2020) and Konopleva *et al.* (2021) is recovered as monophyletic within the *Pilsbryconcha*, together with specimens of *Pilsbryconcha exilis* from Java, Indonesia (type species) and *Pilsbryconcha linguaeformis*, another sympatric species with *Namkongnaia lemeslei* gen. et comb. nov., from Tonle Sap Lake, in our phylogenetic analyses. However, without examination of the specimen mentioned in Bolotov *et al.* (2020) and Konopleva *et al.* (2021), it can only be classified to the genus *Pilsbryconcha*.

Discussion

Our morphological and molecular analyses strongly suggest that freshwater mussels that have long been recognized as '*Pilsbryconcha lemeslei*' from the Mekong River Basin represent a new genus in Pseudodontini. These mussels are morphologically distinct from all other genera by having narrow, elongated, and less inflated shell. Additionally, the ancient divergence (approximately 49.3 Mya; Fig. 2) and large genetic distances from other genera (11.02–12.42% uncorrected COI p-distance; Table 2) also support it as a distinct genus. The discovery of a new mussel genus from Southeast Asia, and especially from the Mekong River Basin, is not unexpected since several new genera and a dozen new species were discovered during the last decade (Kongim *et al.* 2015; Jeratthitikul *et al.* 2019a; Konopleva *et al.* 2019, 2021; Bolotov *et al.* 2020; Pfeiffer *et al.* 2021).

The new genus shares shell characteristics with other genera in Pseudodontini by having a V-shaped fossette at the posterior end of the hinge structure, and absent or reduced pseudocardinal teeth (Brandt 1974; Lopes-Lima *et al.* 2017). Another distinct morphological character of the tribe is a double-looped or W-shaped sculpture on the umbonal area (Lopes-Lima *et al.* 2017). Unfortunately, the umbonal area of all specimens from either the type species or specimens of *Namkongnaia lemeslei* gen. et comb. nov. is heavily eroded, even in young specimens. Therefore, we are unable to confirm this character for the new genus. In the same way, we were unable to examine the glochidia of the new genus, since no brooding individuals were collected in this study. Nevertheless, the glochidia of the new genus are most likely present as an unhooked and semi-elliptical structure, which is the general shape of glochidia among the Gonideinae (Pfeiffer & Graf 2015; Lopes-Lima *et al.* 2017).

Phylogenetic analyses in this study reveal a close relationship between the new genus and *Monodontina*, although with moderate support by only the BI analysis (BPP = 0.97; Fig. 1). As far as we know, the only shared feature among members of the new genus and *Monodontina* is the presence of a V-shaped fossette at the posterior end of the hinge structure on the inner surface of the shell. *Monodontina* differs from the new genus by its ovate to obovate shell with obtuse pseudocardinal teeth (Conrad 1853). However, some species have relatively weak and flattened pseudocardinal teeth, although never absent (Bolotov *et al.* 2020). Future investigation to confirm the sister relationship between them should include longer sequences and additional gene fragments, or incorporate more informative molecular markers, such as mitogenomic or nuclear genomic data, which have been successfully used in the phylogenetic study of freshwater mussels (Pfeiffer *et al.* 2019; Froufe *et al.* 2020; Zieritz *et al.* 2020).

On the contrary, the new genus is similar in conchology to *Pilsbryconcha*, another widespread genus in rivers of Indochina. Both genera share an elongated and laterally compressed shell and completely absent or very reduced pseudocardinal teeth (Brandt 1974). They also have a rounded anterior end with a straight dorsal margin, while other genera in Pseudodontini have a somewhat concave dorsal margin around the position of pseudocardinal teeth. Because of several shared shell characters, the new genus thus has been hidden in the name “*Pilsbryconcha lemeslei* (Morelet, 1875)” for more than a hundred years (Simpson 1914; Haas 1969a; Brandt 1974; Graf & Cummings 2007, 2021a; Zieritz *et al.* 2018; Ng *et al.* 2020). The present molecular phylogenetic analysis recovers both genera as a distinct clade (Figs 1–2) and with a deep divergence of 12.41% uncorrected COI p-distance (Table 2). Our phylogenetic analysis included the type species, *Pilsbryconcha exilis*, from Java, Indonesia, which is assumed to be the type locality (Graf & Cummings 2021b). In addition, both genera are distinctly separated by several shell characters. The new genus has a narrower shell, with a lower posterior dorsal margin and an almost straight ventral margin. In contrast, *Pilsbryconcha* s. str. is wider, elongate linguiform shaped, with a higher dorsal margin and slightly arched ventral margin (Brandt 1974). Some species of *Pilsbryconcha* exhibit a high dorsal margin, creating a posterior wing, such as *Pilsbryconcha linguaeformis* (Morelet, 1875) from Tonle Sap Lake (Ng *et al.* 2020).

Pseudodontini is divided into two subtribes, Pseudodontina and Pilsbryconchina. These two subtribes exhibit a deep genetic divergence from each other, with an average genetic distance of 12.5% uncorrected COI p-distance and estimated at about 91.9 Mya (95% HPD = 67.8–116.9 Mya) (Fig. 6). In the present-day sense (i.e., Graf & Cummings 2021a), Pseudodontina is a monotypic clade consisting of thirteen valid species from western Indochina rivers, the Yangtze River Basin in China, and northern Vietnam (Graf & Cummings 2021b). In contrast, Pilsbryconchina comprises at least six genera and is distributed mainly in the Mekong River and Chao Phraya River basins, the Malay Peninsula, and southern Sunda islands (Graf & Cummings 2021b). Such a deep divergence is consistent with the division of freshwater biogeography of mainland Southeast Asia into the western Indochina and Sundaland subregions (Bolotov *et al.* 2020). The separation of two subtribes and later a rapid diversification of genera within Pilsbryconchina may be a consequence of the palaeo-drainage rearrangement of the large rivers in East Asia as a result of the Cenozoic uplift of the Tibetan Plateau (Wang *et al.* 2012; Zhang *et al.* 2019), and in concert with favourable climatic and hydrological conditions in the early Palaeogene (Carmichael *et al.* 2017), followed by range fragmentation during the abrupt climate change at the Eocene–Oligocene boundary (Buerki *et al.* 2013). This coincides with the divergence time estimation in this study, which suggests rapid radiation events of the Pilsbryconchina genera approximately during the Late Cretaceous to Eocene times (mean age = 70.8–49.3 Mya). The common ancestor of the palaeo-Mekong Gonideinae may have separated from the palaeo-Yangtze drainage in the Albian–Cenomanian times (Froufe *et al.* 2020), and had subsequent radiations in the palaeo-Mekong River Basin in the Late Cretaceous or Paleocene (Bolotov *et al.* 2017a, 2017b; Zieritz *et al.* 2020).

The new genus consists of two well-defined clades with a deep divergence of 5.10% uncorrected COI p-distance, and are recognized here as two distinct species. These two species are separated by a deep genetic divergence and are distributed in different geographical drainages. *Namkongnaia inkhavilayi* gen. et sp. nov. is distributed in tributaries in the Middle Mekong River Basin in Laos and the Korat Plateau, Thailand, while *N. lemeslei* gen. et comb. nov. is found in Tonle Sap Lake and its tributaries in Cambodia (Fig. 3). The separation of closely related taxa between the Middle Mekong River and Lower Mekong River basins is well documented in other unionid mussels. Almost all the examined genera display this biogeographic pattern (Pfeiffer *et al.* 2018, 2021; Muanta *et al.* 2019), suggesting a shared biogeographic history among these taxa.

This study included museum specimens collected from Huai Tadjek, Nang Rong and, Mun River basins on Korat Plateau, Thailand (SMF-220822) for *N. inkhavilayi* gen. et sp. nov. These specimens agree well with our new species (Brandt 1974: pl. 18 fig. 22). However, they show some variation by having a rather shorter but wider shell and a relatively rounded ventral margin. Unfortunately, we failed to obtain fresh material from this population, and therefore cannot test for its genetic and phylogenetic entity. Nevertheless, freshwater mussels from the Mun River Basin generally show a deep genetic divergence from other parts of the Mekong River Basin (i.e., Songkhram River Basin in the northern Korat Plateau and Tonle Sap Basin in the Lower Mekong River Basin). Usually, they are represented as distinct species (Pfeiffer *et al.* 2018, 2021; Jeratthitikul *et al.* 2019b; Muanta *et al.* 2019). Therefore, there is a possibility that the population from the Mun River Basin is a different species from the currently assigned *N. inkhavilayi* gen. et sp. nov.

Similarly, several specimens in the museum collection were collected from the Chao Phraya River basin and provisionally identified as '*Pilsbryoconcha lemeslei*' (i.e., USNM-786217, SMF-BR2663, and ANSP-H19041). These specimens have an elongated and narrow shell which is the diagnostic characteristic of this new genus, but possess some differentiated characters by having a minute concave ventral margin and truncated posterior margin with a pointed posterior end. These specimens are also waiting further confirmation. Therefore, after DNA examination of the two populations in question, the number of members in the new genus will likely increase.

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Disclosure statement

No potential conflict of interest is reported by the authors.

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