Integrative Taxonomy Reveals a New Species of Freshwater Mussel, *Pseudodon septuaginta* sp. nov. (Unionidae: Pseudodontini), from the Mekong River Basin in Northeastern Thailand

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ABSTRACT.– This study investigated the taxonomy and phylogenetic relationships of the freshwater mussel genus *Pseudodon* Gould, 1844, with a specific focus on Indochinese populations, using a comprehensive molecular dataset and morphometric analyses. Our findings confirm the valid status of seven among the nine currently recognized extant *Pseudodon* species, and include the discovery of a new cryptic species, *P. septuaginta* sp. nov., from the Mekong River Basin in northeastern Thailand. The new species is characterized by a compressed, sub-trigonal shell outline, the presence of a posterior wing, weakly developed pseudocardinal teeth, and obsolete lateral teeth. Phylogenetic analysis revealed this new species as the sister taxon to the adjacent allopatric *P. vagulus*, which is distributed in Mekong River tributaries in the upper Khorat Plateau, exhibiting a 6.71% uncorrected COI p-distance. Despite some morphological overlap, these two species are distinguishable by pseudocardinal tooth structure and overall shell shape. Furthermore, phylogenetic analyses support a potential Bornean origin for *Pseudodon*, followed by dispersal into Myanmar and Indochina, with paleo-drainage isolation driving diversification within the Indochinese lineages.

KEYWORDS: biogeography, evolutionary history, Indochina, new species, Unionidae

INTRODUCTION

The tribe Pseudodontini Frierson, 1927 (Unionidae) represents one of the most species-rich groups of freshwater mussels in Southeast Asia (Bolotov et al., 2023). There are eleven genera and at least 51 species currently recognized (Jeratthitikul et al., 2025). Almost all of these species are distributed in the Indochina and Sundaland drainage systems (e.g., Mekong, Chao Phraya, and Mae Klong rivers, the Thai-Malay Peninsula drainages, and Greater Sunda Islands), and with a few taxa remarkably extending their distribution range into the West Indochina drainages (i.e., Ayeyarwady and Salween rivers in Myanmar; Bolotov et al., 2023; Jeratthitikul et al., 2024, 2025). Among these accepted genera, *Pseudodon* Gould, 1844, has been marked by considerable taxonomic complexity and has undergone several revisions throughout history. This name was initially established as a subgenus to include *Anodon inoscularis* Gould, 1844 (type species) and *Anodon salweniana* Gould, 1844, both from the Salween River Basin in Myanmar, and two other species (Gould, 1844). In the later revisionary works, Simpson (1900, 1914) raised *Pseudodon* to a distinct genus, subdivided it into seven subgenera, and then incorporated at least 32 nominal species with a vast geographical range spanning from East to Southeast Asia into the genus

based on the characteristics of a relatively thick and elongated oval shell, one pseudocardinal tooth on each valve, and obsolete lateral teeth. Then, the genus was subjected to revision by Haas (1920, 1969), who adopted the previous subgeneric classification, together with adding one subgenus, *Indopseudodon* Prashad, 1922; however, members of the genus appeared to comprise only 22 distinct species. Brandt's (1974) monograph 'The non-marine aquatic Mollusca of Thailand', which is considered the foundation of the study of freshwater molluscs in the region, recognized four species and nine subspecies from Thailand. This seemed to reflect the high degree of morphological variation of the so-called '*Pseudodon*'.

This traditional subgeneric classification by Simpson (1900, 1914) and Haas (1920, 1969) continued to be acknowledged and used until the early 21st century (i.e., Graf and Cummings, 2007), although some authors disregarded these subgenera (i.e., Brandt, 1974; Zieritz et al., 2018). However, the systematics of freshwater unionid mussels has been considerably transformed in the past two decades by the advent and application of molecular phylogenetic methods, and *Pseudodon* s.l. has received significant attention. Molecular phylogeny of Southeast Asian unionid mussels using multi-locus data has revealed the polyphyletic relationship within *Pseudodon* s.l. (Bolotov et al.,

2017a). Consequently, the genus has undergone systematic revision, leading to the recognition of at least five distinct genera, including *Pseudodon* s.s., *Bineurus* Simpson, 1900, *Monodontina* Conrad, 1853, *Sundadontina* Bolotov et al., 2020, and *Thaiconcha* Bolotov et al., 2020 (Bolotov et al., 2017b, 2020). Regardless of the molecular data from its respective type species, Bolotov et al. (2020) has provisionally demarcated the taxa restricted to the West Indochina drainages (i.e., river basins in Myanmar) to the *Pseudodon* s.s., which is based on conchological similarity and biogeographic evidence alone. However, when incorporating *P. inoscularis*, the type species, into phylogenetic analysis, it was retrieved as clustered within *Monodontina*, which is mainly distributed in the Indochina drainages. This led to the synonymization of *Monodontina* under *Pseudodon* and to the resurrection of *Indopseudodon* for the remaining taxa from Myanmar (Bolotov et al., 2023). This reclassification has not only shed a greater understanding of evolutionary relationships within the *Pseudodon* s.l. but has also extended reclassifications of genus and tribe groups. Therefore, with these recent phylogenetic classification frameworks, *Pseudodon* s.s. includes seven species distributed in Southeast Asia, plus one species reported from the Nicobar Islands, India (Bolotov et al., 2023; Jeratthitikul et al., 2024).

In this study, all *Pseudodon* species across Thailand were studied using an integrative taxonomic approach, with specific aims (1) to estimate the phylogenetic relationships of *Pseudodon* species and reveal hidden cryptic diversity using mitochondrial COI and 16S rRNA and 28S rRNA nuclear markers; (2) to quantify morphological variation among *Pseudodon* species found in Thailand using Fourier shape morphometric analysis; and (3) to provide a taxonomic account for *Pseudodon* species found in Thailand, including the description of one new species from northeastern Thailand.

MATERIALS AND METHODS

Sample collection and material examined

A total of 217 individuals of freshwater mussels classified in the genus *Pseudodon* were newly collected in this study from 44 sites across Thailand, as well as some locations in Cambodia and Laos (Fig. 1). Specimens were manually gathered and subsequently euthanized at the collection points following a two-stage procedure described by the AVMA (2020). Living specimens were initially placed in a container filled with 5% (v/v) ethanol until they were fully anesthetized, which could be observed by the fully relaxed foot and adductor muscles. Subsequently, the anesthetized specimens were transferred to a separate container containing 70% (v/v) ethanol for tissue fixation. A small amount of foot or mantle tissue was snipped, preserved in 95% (v/v) ethanol, and stored at -20 °C for later DNA isolation. The remaining specimens were separated into soft tissues and shells. The soft tissue components were stored in 70% (v/v) ethanol for anatomical analysis, while the shells were scrubbed inside and out to remove remaining tissue and extraneous material and retained as dry samples. Shells and soft tissue specimens were cataloged and deposited as vouchers. The aforementioned animal use in this study was approved by the Faculty of Science, Mahidol University Animal Care and Use Committee under approval protocol numbers MUSC65-013-606 and MUSC66-016-646.

Species identification was initially based on descriptions in taxonomic literature (i.e., Lea, 1840; Haas, 1969; Brandt, 1974; Bolotov et al., 2020) or by comparison with type series deposited in museum reference collections or digitized photographs available in online databases (i.e., the MUSSELp; Graf and Cummings, 2025). We did not apply the subspecies classifcation of *P. vondembuschianus* in this study, although some studies have suggested the recognition of five subspecies (i.e., Bolotov et al., 2023; Konopleva et al., 2023; Jeratthitikul et al., 2024). Shell morphology was assessed by examining various characteristics, including the outline, size, thickness, surface sculpture, umbo shape and position, hinge dentition, and muscle scars. Shell length, height, and width were measured to the nearest 0.01 mm using a digital Vernier caliper. Soft body anatomy was also investigated under a stereo-microscope.

Dot distribution maps were generated using QGIS v.3.36 based on the information of newly obtained materials in this study and distribution data gathered from previous publications (i.e., Pfeiffer and Graf, 2015; Bolotov et al., 2020, 2023; Konopleva et al., 2023; Zieritz et al., 2024). The map was created using information of freshwater river basins from the Freshwater Ecoregions of the World (Abell et al., 2008), river and lake topology from the HydroSHEDS database (https://www.hydrosheds.org), and map raster data from the NASA EARTHDATA (https://www.earthdata.nasa.gov/).

Sequencing and alignments

Genomic DNA was extracted from foot or mantle tissues using a NucleoSpin Tissue Extraction Kit (Macherey-Nagel, Germany). The extracted DNA was diluted to approximately 10 ng/µl and used as template DNA in polymerase chain reaction (PCR) to amplify
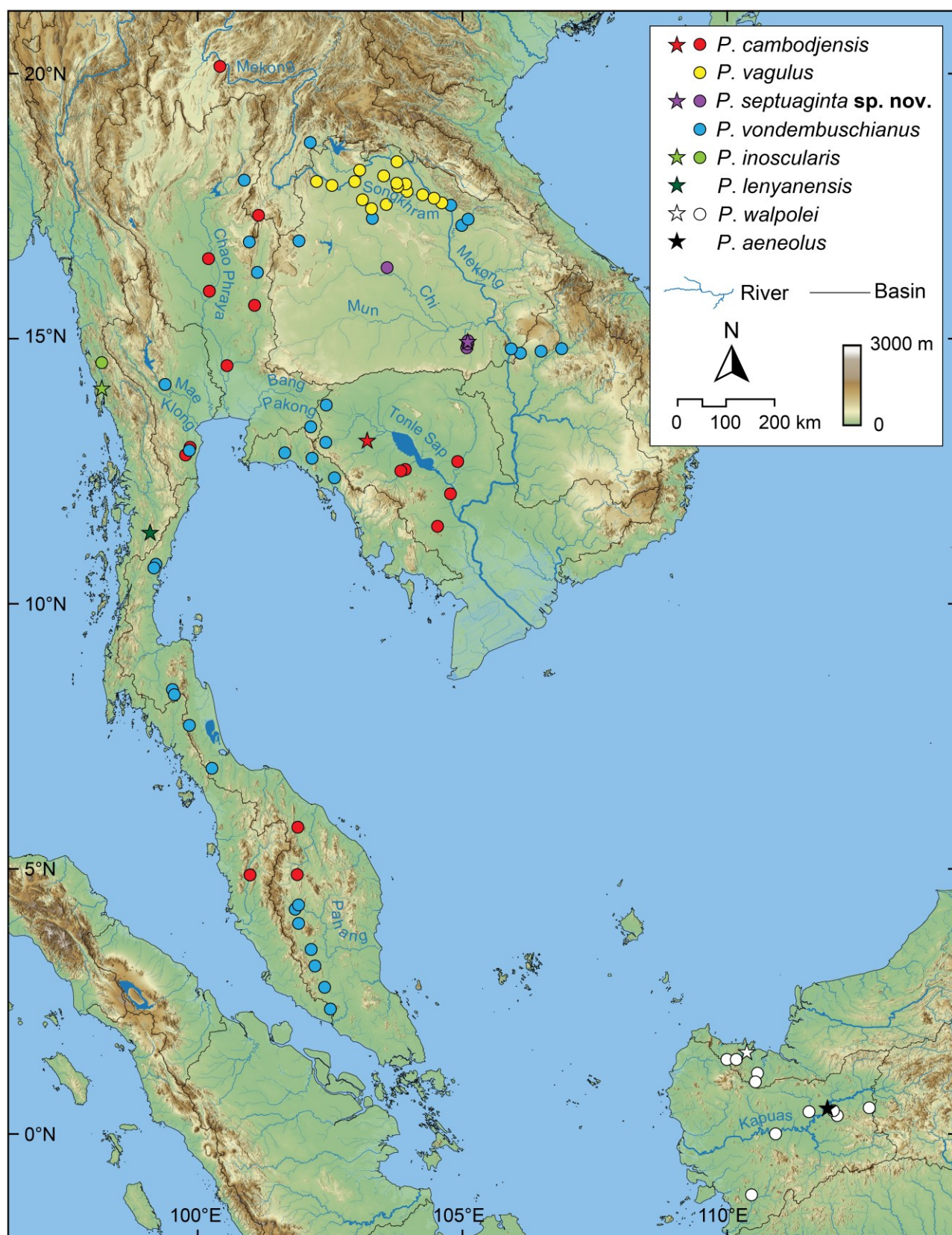
FIGURE 1. Distribution map of *Pseudodon* species showing the type localities (stars) and sampling localities (circles) based on specimens collected in this study and from previous publications (i.e., Pfeiffer and Graf, 2015; Bolotov et al., 2020, 2023; Konopleva et al., 2023; Zieritz et al., 2024).

partial fragments of the mitochondrial cytochrome c oxidase subunit I (COI), mitochondrial large ribosomal subunit rRNA (16S rRNA), and nuclear 28S large ribosomal subunit rRNA (28S rRNA) genes. The PCR primers used included LoboF1 and LoboR1 for COI (Lobo et al., 2013), 16sar-L-myt and 16Sbr-H-myt for 16S rRNA (Lydeard et al., 1996), and C1 and D2 for 28S rRNA (Jovelin and Justine, 2001). PCR was performed using a T100™ thermal cycler (BIO-RAD) with a final reaction volume of 30 μL, consisting of 15 μL EmeraldAmp GT PCR Master Mix, 1.5 μL of each primer, 10 ng template DNA, and distilled water to a total volume of 30 μL. The thermal cycling conditions for PCR followed the recommendations provided in the original literature. The amplified PCR products were purified using the MEGAquick-spin™ plus Fragment DNA Purification Kit and sequenced in both directions using an automated sequencer (ABI PRISM 3730XL). The resulting sequences were assembled and aligned using MEGA11 v.11.0.13 (Tamura et al., 2021), and were confirmed by visual inspection. The sequences obtained in this study have been uploaded in the GenBank Nucleotide sequence database under accesssion numbers PV788093–PV788122 for COI, PV789116–PV789145 for 16S rRNA, and PV789086–PV789115 for 28S rRNA (Table 1). Separate multiple alignments were performed for each gene using the ClustalW algorithm in MEGA11 v11.0.13 (Tamura et al., 2021). These alignments were then combined into a single concatenated dataset for phylogenetic analyses.

Phylogenetic analyses

Phylogenetic trees were reconstructed using maximum likelihood (ML) and Bayesian inference (BI) analyses using the dataset of 50 *Pseudodon* specimens newly obtained in this study, as well as sequences from previous publications as an ingroup (Table 1). Two nominal taxa, *P. aeneolus* from Borneo and *P. nicobaricus* from the Nicobar Islands, were excluded from the phylogenetic analyses due to unavailable DNA sequences. Representative taxa from other genera within Pseudodontina (i.e., *Isannaia* Jeratthitikul et al., 2024; *Sundadontina*; *Namkongnaia* Jeratthitikul et al., 2021; and *Pilsbryoconcha* Simpson, 1900) were selected as the outgroup, following the recent phylogenetic trees presented by Jeratthitikul et al. (2025). The best-fit model of nucleotide substitution for this dataset was selected using Partition Finder2 v2.3.4 (Lanfear et al., 2017) under the corrected Akaike Information Criterion (AICc) with a five-partition scheme (3 codons of COI + 16S rRNA + 28S rRNA). The selected models were as follows: HKY+I for the first codon partition of COI; GTR+G for the second codon partition of COI; and GTR+I+G for the third

codon partition of COI, the 16S rRNA partition, and the 28S rRNA partition. These nucleotide substitution models were subsequently used in the phylogenetic analyses.

Phylogenetic trees were reconstructed using Bayesian inference (BI) analysis as implemented in MrBayes v.3.2.7 (Ronquist et al., 2012) and maximum-likelihood (ML) analysis as implemented in IQ-TREE v2.2.2.7 (Minh et al., 2020). For BI analysis, two simultaneous Markov Chain Monte Carlo (MCMC) runs (three heated chains and one cold chain) were executed for 10,000,000 generations, with trees sampled every 1,000 generations. Markov chains were considered to have reached stationarity when the effective sample sizes (ESS) of all parameters were greater than 200. The first 25% of the sampled trees were discarded as burn-in, and the remaining trees were used to estimate consensus tree topology, node support, and branch lengths. For ML analysis, a phylogenetic tree was reconstructed with 10,000 ultrafast bootstrap replicates to assess nodal support (Hoang et al., 2018). The resulting phylogenetic trees from both BI and ML analyses were visualized and edited using FigTree v.1.4.4 (http://tree.bio.ed.ac.uk/software/figtree/). Clades with bootstrap (BS) support values ≥95% from the ML analysis and Bayesian posterior probabilities (BPP) ≥0.95 from the BI analysis were considered well-supported clades (San Mauro and Agorreta, 2010; Hoang et al., 2018). All phylogenetic analyses were performed using the online CIPRES Science Gateway (Miller et al., 2010). In addition to phylogenetic analyses, raw genetic divergence between the COI sequences was assessed using uncorrected p-distances, as calculated using MEGA11.

Morphometric analysis

Shell shape variation among *Pseudodon* species occurring in Indochina was assessed using Fourier shape morphometric analysis as implemented in SHAPE v.1.3 (Iwata and Ukai, 2002). The left valves were photographed in an anterior-posterior orientation using a Nikon D5300 camera equipped with an AF-S VR Micro-Nikkor 105 mm f/2.8G IF-ED lens. The shell photographs were processed into black-and-white bitmap images using Adobe Photoshop v.25.1.0 (Adobe Systems). The prepared images were then analyzed to obtain a chain code for the object contour. The chain code was subsequently used to calculate normalized Elliptic Fourier Descriptors (EFDs), followed by principal component analysis (PCA) on the resulting EFDs from the first 20 harmonics of the Fourier coefficients. The coefficients of EFDs were also calculated at −2 and +2 standard deviations (SD) for each principal component (PC), and the respective

TABLE 1. List of specimens used in phylogenetic analyses. Specimens marked with "*" indicate type materials. References: 1 = Bolotov et al. (2023); 2 = Bolotov et al. (2020); 3 = Froufe et al. (2020); 4 = Konopleva et al. (2023); 5 = Lopes-Lima et al. (2017); 6 = Zieritz et al. (2016); 7 = Pfeiffer and Graf (2015); 8 = Zieritz et al. (2024); 9 = Jeratthitikul et al. (2024); 10 = Jeratthitikul et al. (2021b); 11 = Jeratthitikul et al. (2022).

Taxa/ Voucher ID	Locality	Genbank accession			Reference
		COI	16S rRNA	28S rRNA	
Ingroup					
Pseudodon inoscularis (Gould, 1844)					
RMBH biv1027/1	Myanmar: Dawei (Tavoy) River Basin, Yae Pone Stream	OQ836329	OQ832401	OQ832365	1
RMBH biv1027/2	near Yae Pone village	OQ836330	OQ832402	OQ832366	1
RMBH biv1027/3		OQ836331	OQ832403	OQ832367	1
Pseudodon lenyanensis Bolotov et al., 2020					
RMBH biv0628/2*	Myanmar: Lenya River Basin, 14 Mile Stream	MN275055	MN307246	MN307187	2
RMBH biv0628/3		MN275056	MN307247	MN307188	2
Pseudodon vondembuschianus (Lea, 1840)					
BIV1822	Malaysia: Negeri Sembilan, Muar, Kampung Jambu Lapan	NC_044112	NC_044112	MZ684028	3
MUMNH-UNI2537	Thailand: Eastern Gulf of Thailand Drainages, Huai Raeng Stream	PV788093	PV789116	PV789086	This study
MUMNH-UNI2915	Thailand: Thale Sap Songkhla Basin, Patthalung, Tha Nae Stream	PV788094	PV789117	PV789087	This study
MUMNH-UNI2872	Thailand: Thale Sap Songkhla Basin, Songkhla, Tum Stream	PV788095	PV789118	PV789088	This study
UMMZ 304650	Laos: Mekong River Basin, tributary of the Vang Ngao River	KP795029	KP795052	n/a	2
MUMNH-UNI1897	Laos: Mekong River Basin, Attapue, Huay Phong Stream	PV788096	PV789119	PV789089	This study
MUMNH-UNI2521	Laos: Mekong River Basin, Local market near Xe Bangfai River	PV788097	PV789120	PV789090	This study
MUMNH-UNI0299	Thailand: Tonle Sap Basin, Sa Kaeo, Phrom Hot Stream	PV788098	PV789121	PV789091	This study
RMBH biv1272/1	Thailand: Tapi River Basin, Nakhon Si Thammarat, Min Stream	OP729818	OP735377	n/a	4
RMBH biv1272/2	Thailand: Tapi River Basin, Nakhon Si Thammarat, Min Stream	OP729819	OP735378	OP735361	4
MUMNH-UNI0831	Thailand: Tapi River Basin, Nakhon Si Thammarat, Min Stream	PV788099	PV789122	PV789092	This study
MUMNH-UNI0835	Thailand: Tapi River Basin, Nakhon Si Thammarat, Min Stream	PV788100	PV789123	PV789093	This study
RMBH biv1321/1	Thailand: Malay Peninsula Eastern Slope Drainages, Thasae Stream	OP729822	OP735379	OP735364	4
MUMNH-UNI2602	Thailand: Eastern Gulf of Thailand Drainages, Rayong, Prasae Rive	PV788101	PV789124	PV789094	This study
MUMNH-UNI2511	Thailand: Mae Klong River Basin, Kanchanaburi, Taphoen Stream	PV788102	PV789125	PV789095	This study
MUMNH-UNI2864	Thailand: Chao Phraya River Basin, Phetchabun, Khek Noi River	PV788103	PV789126	PV789096	This study
RMBH biv0122	Thailand: Mekong River Basin, Khon Kaen, Phong River	KX865861	KX865632	KX865733	2
Pseudodon cambodjensis (Petit de la Saussaye, 1865)					
--	Thailand	KX822660	n/a	KX822616	5
MUMNH-UNI2498	Thailand: Chao Phraya River Basin, Na Khon Sawan, Huai San Stream	PV788104	PV789127	PV789097	This study
MUMNH-UNI2900	Thailand: Phetchaburi River Basin, Phetchaburi, Phetchaburi River	PV788105	PV789128	PV789098	This study
MUMNH-UNI1815	Thailand: Mekong River Basin, Chiang Rai, Ing River	PV788106	PV789129	PV789099	This study
MUMNH-UNI0574	Thailand: Chao Phraya River Basin, Ayutthaya, Lop Buri River	PV788107	PV789130	PV789100	This study
MUMNH-UNI2191	Thailand: Mekong River Basin, Loei, Nam Man River	PV788108	PV789131	PV789101	This study
BIV1658	Malaysia: Perak, Pulau Raya Island, Sungai Siput	KX051298	n/a	n/a	6
X154	Malaysia: Kelantan, Sungai Seting	KX051299	n/a	n/a	6
X198	Malaysia: Kelantan, Sungai Lanas tributary	KX051297	n/a	n/a	6
UMMZ 304350	Cambodia: Tonle Sap Basin, Pursat River	KP795028	KF011262	KP795011	7
MUMNH-UNI2764	Cambodia: Tonle Sap Basin, Kampong Thom, Stung Sen River	PV788109	PV789132	PV789102	This study
MUMNH-UNI2765	Cambodia: Tonle Sap Basin, Pursat, Pursat River	PV788110	PV789133	PV789103	This study
MUMNH-UNI2924	Cambodia: Mekong River Basin, Kampong Speu, Stung Prek Tnaot River	PV788111	PV789134	PV789104	This study
MUMNH-UNI2770	Cambodia: Tonle Sap Basin, Tonle Sap Lake, Kampong Chhnang	PV788112	PV789135	PV789105	This study

TABLE 1. Continued.

Taxa/ Voucher ID	Locality	Genbank accession			Reference
		COI	16S rRNA	28S rRNA	
Pseudodon vagulus (Fischer, 1891)					
RMBH biv0811_1	Laos: Mekong River Basin, Nam Ngum River	OQ836225	OQ832370	OQ832334	1
MUMNH-UNI2205	Thailand: Mekong River Basin, Udon Thani, Huai Luang River	PV788113	PV789136	PV789106	This study
MUMNH-UNI2112	Thailand: Mekong River Basin, Udon Thani, Nam Som	PV788114	PV789137	PV789107	This study
MUMNH-UNI2184	Thailand: Mekong River Basin, Nakhon Phanom, Nam Mao Stream	PV788115	PV789138	PV789108	This study
MUMNH-UNI0902	Thailand: Mekong River Basin, Nakhon Phanom, Songkhram River	PV788116	PV789139	PV789109	This study
MUMNH-UNI2209	Thailand: Mekong River Basin, Nakhon Phanom, Huay Thuai River	PV788117	PV789140	PV789110	This study
Pseudodon septuaginta sp. nov.					
MUMNH-UNI3423*	Thailand: Mekong River Basin, Ubon Ratchathani, Dom Yai River, tributary of Mun River	PV788118	PV789141	PV789111	This study
MUMNH-UNI2557*	Thailand: Mekong River Basin, Ubon Ratchathani, Dom Yai River, tributary of Mun River	PV788119	PV789142	PV789112	This study
MUMNH-UNI2543*	Thailand: Mekong River Basin, Ubon Ratchathani, Dom Yai River, tributary of Mun River	PV788120	PV789143	PV789113	This study
MUMNH-UNI3197	Thailand: Mekong River Basin, Kalasin, Pao River, tributary of Mun River	PV788121	PV789144	PV789114	This study
MUMNH-UNI3172	Thailand: Mekong River Basin, Kalasin, Pao River, tributary of Mun River	PV788122	PV789145	PV789115	This study
Pseudodon walpolei (Hanley, 1871)					
CIIMAR BIV6753/x578	Indonesia: Laur, Laur River catchment, a tributary of the Pawan River basin	PP697622	n/a	PP693718	8
CIIMAR BIV6676/x501	Indonesia: Sebroang River, West Kalimantan	PP697592	PP693689	PP693717	8
Outgroup					
Isannaia fortunata Jeratthitikul et al., 2024					
MUMNH-UNI1950	Thailand: Mekong River Basin, Thuai River	OR987590	OR987516	OR987525	9
Isannaia occultata Jeratthitikul et al., 2024					
MUMNH-UNI2895	Thailand: Mekong River Basin, Yang Stream	OR987594	OR987520	OR987529	9
Namkongnaia inkhavilayi Jeratthitikul et al., 2021					
MUMNH-UNI2831	Laos: Mekong River Basin, Local market near Xe Bangfai River	MZ822395	MZ822895	MZ822917	10
Namkongnaia lemeslei (Morelet, 1875)					
MUMNH-UNI2825	Cambodia: Tole Sap Basin, Kampong Kdei River	MZ822399	MZ822899	MZ822921	10
Sundadontina cumingii (Lea, 1850)					
X115	Malaysia	KX051295	n/a	n/a	6
Sundadontina tumida (Morelet, 1866)					
UMMZ 304349	Cambodia: Mekong River Basin	KP795027	KF011261	KP795010	7; Genbank
Pilsbryoconcha exilis (Lea, 1838)					
MUMNH-UNI2481	Indonesia: Java Basin, Bogor Botanical Gardens	MZ822408	MZ822908	MZ822930	10
Pilsbryoconcha mekongiana Jeratthitikul & Prasankok, 2022					
MUMNH-UNI0843	Thailand: Mekong River Basin	OP589114	OP595945	OP595874	11

contour shapes were reconstructed using an inverse Fourier transformation to visualize the shape variation along each PC. The first ten PC axes were then used as input data for further statistical analysis and graphical interpretation, as implemented in PAST v.5.2.1 (Hammer et al., 2001). A scatter plot of the first two PCs was constructed to visualize the morphological variation within and among the putative species. Individual points on the plot were colored according to the putative species, and 95% confidence ellipses were drawn for each putative species. Multivariate analysis of variance (MANOVA) was performed to test for statistically significant differences in shell shape variation between putative species. Linear discriminant analysis (LDA) was also employed to assess the rate of accurate group assignments based on shell shape variation.

Institutional abbreviations

MUMNH   Mahidol University Museum of Natural History, Department of Biology, Faculty of Science, Mahidol University, Bangkok, Thailand

MNHN Muséum national d'Histoire naturelle, Paris, France

NHMUK   Natural History Museum, London, United Kingdom

SMF Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main, Germany

USNM National Museum of Natural History, Washington, USA

RMBH Russian Museum of Biodiversity Hotspots, N. Laverov Federal Center for Integrated Arctic Research of the Ural Branch of the Russian Academy of Sciences, Arkhangelsk, Russia
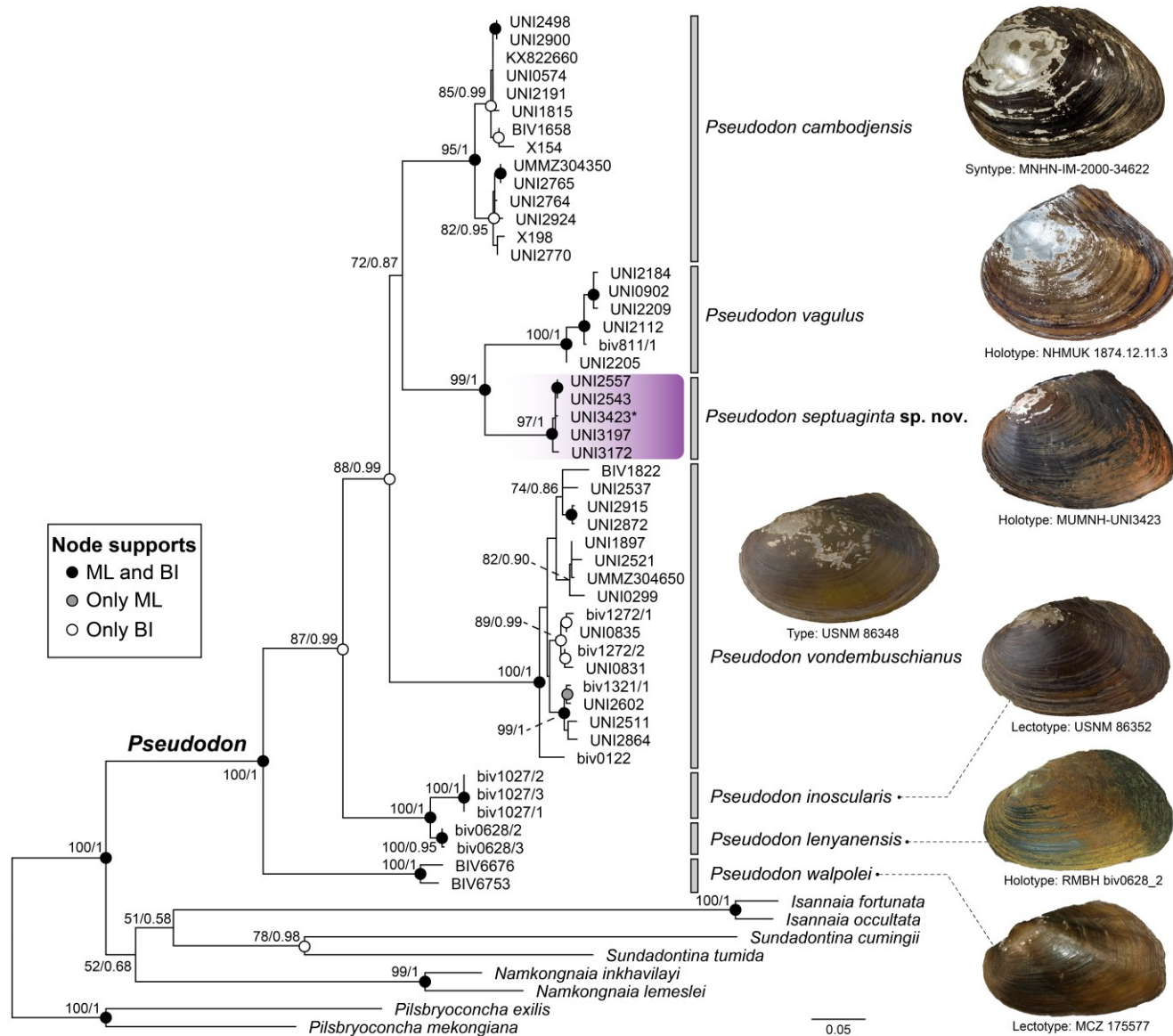
FIGURE 2. Maximum likelihood (ML) phylogenetic reconstruction of *Pseudodon* and outgroup taxa, based on a 1,957-bp concatenated alignment of mitochondrial (COI and 16S rRNA) and nuclear (28S rRNA) loci. A clade of the new species, *Pseudodon septuaginta* sp. nov., is highlighted in purple. Node support is represented as ML bootstrap/posterior probability values from Bayesian inference analysis. The scale bar represents the branch length. Photographs of the left shell from type specimens are presented for each species (shells not to scale). Photo credits: *P. cambodjensis*, M. Caballer (RECOLNAT-ANR-11-INBS-0004 project); *P. vagulus*, Kevin Webb (NHMUK Photographic Unit); *P. vondembuschianus* and *P. inoscularis*, USNM collection database; *P. lenyanensis*, E. S. Konopleva (Bolotov et al., 2020); and *P. walpolei* from the MCZ collection database.

MCZ Museum of Comparative Zoology, Cambridge, USA

RESULTS

Phylogenetic analysis and genetic divergence

The BI and ML phylogenetic trees exhibited nearly identical topologies and similar nodal support values. Therefore, only the ML tree generated by IQ-TREE is presented in Figure 2 and used for the subsequent discussion. The phylogenetic analysis based on a concatenated dataset of mitochondrial (COI and 16S rRNA) and nuclear (28S rRNA) genes revealed a monophyletic clade for the genus *Pseudodon* with high nodal support in both analyses (BS = 100%, BPP = 1). Within *Pseudodon*, all examined species formed a monophyletic clade with high nodal support (BS = 95–100%, BPP = 1). *Pseudodon walpolei* from Borneo was positioned at the basal group of the *Pseudodon* clade. Then, a highly supported monophyletic clade (BS = 100%, BPP = 1) of two southern Myanmar species, *P. lenyanensis* and *P. inoscularis*, subsequently diverged, followed by a monophyletic clade of four species found in Indochina. These deep node

relationships received significant support only from the BI analysis (BS = 87–88%, BPP = 0.99). Three lineages from Indochina corresponded to the previously recognized nominal species: *P. vondembuschianus*, *P. cambodjensis*, and *P. vagulus*. Another distinct lineage included individuals from the Mun and Chi River basins in northeastern Thailand. This lineage is morphologically similar to *P. vagulus*, however it possesses several distinguishable characters sufficient to warrant its recognition as a distinct species. Therefore, it is herein proposed as a new species and described as *Pseudodon septuaginta* sp. nov. This new species was placed as sister to *P. vagulus* with high nodal support (BS = 97%, BPP = 1), and then nested with *P. cambodjensis*, although this relationship lacked significant statistical support (BS = 72%, BPP = 0.87). The nominal *P. vagulus* was assigned to the clade distributed in the upper part of the Khorat Plateau based on conchological characters shared between the type specimen and newly collected specimens in this study (see taxonomic comment below), whereas *P. cambodjensis* was fixed by the topotype specimens to a clade containing populations primarily from the Tonle Sap Basin. Within *P. cambodjensis*, intraspecific structure was further observed as two subclades, although both received support only from the BI analysis. One subclade comprised individuals from river basins in central Thailand and the Malay Peninsula, while the other subclade originated mainly from the Tonle Sap Basin, Cambodia, and included one individual from the Malay Peninsula.

Pairwise genetic distances as expressed by uncorrected COI p-distance among *Pseudodon* species were 8.47% on average (Table 2). These distances ranged from a minimum of 2.52% between *P. inoscularis* and *P. lenyanensis* to a maximum of 11.03% between *P. walpolei* and *P. vondembuschianus*. The new species exhibited the least genetic divergence from *P. vagulus* (6.71%). The genetic divergence between the two subclades of *P. cambodjensis* was 2.08%. The intraspecific distances within each species were low, with an averaging of 0.92%. However, *P. vondembuschianus* showed a comparatively high intraspecific divergence of 2.16%.

Fourier shape morphometric analysis

Outline shape contours were obtained from 141 newly collected samples representing four *Pseudodon* species found in Indochina, including *P. cambodjensis* (n = 34), *P. vagulus* (n = 48), *P. vondembuschianus* (n = 42), and a new species (n = 13), as well as four type specimens for each taxon. The PCA yielded four effective principal components with eigenvalues that described more than 95% of the total variation between individuals. The PCA plot, with individuals grouped by species, showed shape variation among species, with the PC1 axis describing 80.84% and the PC2 axis describing 9.08% of the total variation (Fig. 3). Specimens of *P. vondembuschianus* clustered on the negative portion of PC1, separate from the other three species, which clustered in the positive portion and exhibited a considerable degree of morphological overlap. As visualized by the synthetic outlines, specimens on the negative portion of PC1 (i.e., *P. vondembuschianus*) exhibited a more elongated shell, a less convex ventral margin, and a lower posterior wing; whereas specimens on the positive portion (especially those of *P. vagulus* and *P. cambodjensis*) tended to have a sub-trigonal outline, a more convex ventral margin, and a higher posterior wing. In contrast to the PC1 axis, the PC2 axis showed less variation in shell shape between species, but showed a more prominent variation within each species. The majority of shape changes along the PC2 axis were related to the shape of the posterior end and the slope of the posterior margin. Specimens on the positive portion of PC2 exhibited a more rounded posterior end and a more curved posterior margin, whereas specimens on the negative portion exhibited a more pointed posterior end and a somewhat straight posterior margin.

The MANOVA revealed significant differences in shell morphology in all pairs of species (Wilk's Λ = 0.0963, $F_{30, 376.4}$ = 15.3, $p < 0.001$). On average, the LDA assigned 85.82% of individuals to their correct species. The most accurate classification was for *P. vondembuschianus* (97.67%). In contrast, *P. cambodjensis* showed the lowest accuracy rate (74.29%), with individuals incorrectly assigned to *P. vondembuschianus* (5.71%), *P. vagulus* (14.29%), and the new

TABLE 2. Average uncorrected p-distance of 660-bp COI gene fragment sequences (% ± S.D.) among *Pseudodon* species (below diagonal) and within each species (in bold).

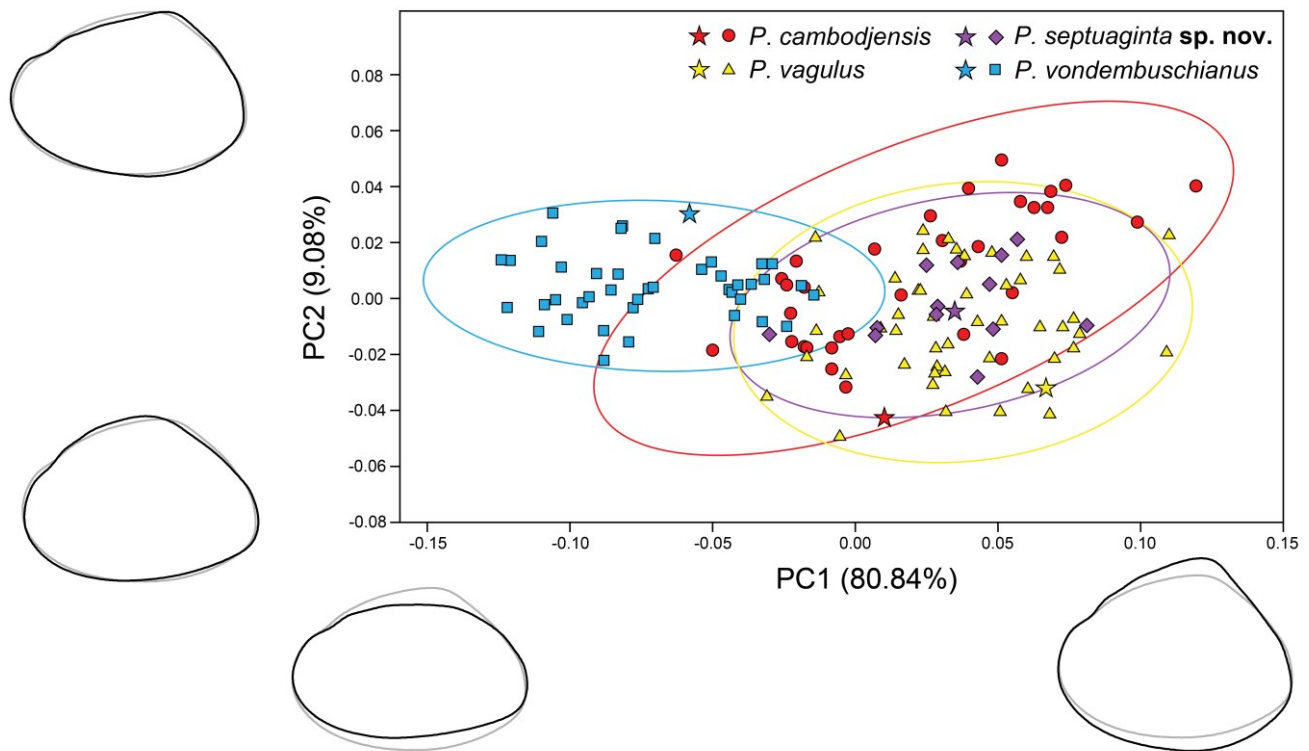| Taxa	1.	2.	3.	4.	5.	6.	7.
1. *P. cambodjensis*	**1.36 ± 0.85**						
2. *P. vagulus*	8.17 ± 0.44	**0.83 ± 0.54**					
3. *P. septuaginta* sp. nov.	7.65 ± 0.11	6.71 ± 0.31	**0.18 ± 0.15**				
4. *P. vondembuschianus*	8.09 ± 0.34	9.76 ± 0.35	8.21 ± 0.52	**2.16 ± 0.79**			
5. *P. inoscularis*	7.96 ± 0.40	10.56 ± 0.32	9.91 ± 0	9.05 ± 0.26	**0**		
6. *P. lenyanensis*	7.63 ± 0.29	9.44 ± 0.36	8.96 ± 0.16	8.89 ± 0.33	2.52 ± 0	**0.22 ± 0.19**	
7. *P. walpolei*	8.43 ± 0.38	9.18 ± 0.18	8.52 ± 0.11	11.03 ± 0.40	9.24 ± 0	8.07 ± 0.18	**1.68 ± 0**

FIGURE 3. Scatter plot based on principal component analysis (PCA) showing individual scores for the first two principal component (PC) axes, derived from 20 Fourier coefficients of shell shape variation in four *Pseudodon* species occurring in Indochina. Different symbols and colors correspond to each species, and star symbols indicate type specimens. Confidence intervals (95%) are depicted for each species. Contour shapes positioned along each axis illustrate the mean shell outline (gray lines) and the extreme negative and positive outline changes explained by each PC axis (black lines).

species (5.71%). The ability to differentiate between *P. vagulus* and the new species was moderate (average accuracy of 84.13%).

Systematics

Family Unionidae Rafinesque, 1820
Subfamily Gonideinae Ortmann, 1916
Tribe Pseudodontini Frierson, 1927
Subtribe Pseudodontina Frierson, 1927

Genus *Pseudodon* Gould, 1844

Anodon (*Pseudodon*) Gould, 1844: 161. Type species: *Anodon inoscularis* Gould, 1844 by original designation.
Monodontina Conrad, 1853: 269. Type species: *Margaritana vondembuschiana* Lea, 1840 by original designation.
Suborbiculus Simpson, 1900: 835. Type species: *Monocondylus orbicularis* Morelet, 1866 by original designation.
Diplopseudodon Haas, 1920: 313. Type species: *Pseudodon crassus* Drouët & Chaper, 1892 by original designation.

Diagnosis.– Shell medium, ovate to rounded subtrigonal, higher posteriorly, forming a posterior wing in some species, posterior margin rounded to truncated. One broad pseudocardinal tooth in each valve, weakly developed to moderately developed. Lateral teeth obsolete.

Distribution.– Lenya and Dawei river basins in Southern Myanmar, widespread in Indochina to the Malay Peninsula (Fig. 1; Brandt, 1974; Zieritz et al., 2016; Bolotov et al., 2023; Konopleva et al., 2023), the Greater Sunda Islands (Borneo, Java, and Sumatra; Brandt, 1974; Bolotov et al., 2020; Zieritz et al., 2024), and Nicobar Islands (Mörch, 1872; Bolotov et al., 2022).

Remarks.– Currently, the genus comprises nine extant species, namely *P. aeneolus* Drouët & Chaper, 1892, *P. cambodjensis* (Petit de la Saussaye, 1865), *P. inoscularis* (Gould, 1844), *P. lenyanensis* (Bolotov et al., 2020), *P. nicobaricus* (Mörch, 1872), *P. vagulus* (Fischer, 1891), *P. vondembuschianus* (Lea, 1840), *P. walpolei* (Hanley, 1871), and a new species described in this study, *P. septuaginta* sp. nov. Wu et al. (2024) proposed the transfer of *P. aeneolus* to *Cosmo-*

pseudodon Haas, 1920, basing their reclassification on its shell morphology. However, this opinion currently lacks molecular evidence for confirmation. Furthermore, the distribution of *P. aeneolus* in Borneo is geographically distant from the other two *Cosmopseudodon* species found in northern Vietnam and China (Wu et al., 2024). Therefore, in this study, *P. aeneolus* is retained within the genus *Pseudodon*.

The taxonomic accounts of the four Thai species are the focus of this study.

Pseudodon cambodjensis (Petit de la Saussaye, 1865)
(Figs 1–3, 4A–D)

Monocondylea cambodjensis Petit de la Saussaye, 1865: 16, pl. 4, fig. 4. Type locality: "Cambodje (Battambang)" [=Battambang Province, Cambodia].
Monocondylus orbicularis Morelet, 1866: 167. Type locality: not specified, but latter given by Morelet (1875: 339) as "Battambang" [=Battambang Province, Cambodia].

For a full list of the usage of the name, see Graf and Cummings (2025)

Type specimens.– Syntypes MNHN-IM-2000-34622 (3 specimens; Fig. 4A) of *Monocondylea cambodjensis*; "Cambodje (Battambang)" [=Battambang Province, Cambodia]. Syntype NHMUK 1893.2.4.1982 (1 specimen) of *Monocondylus orbicularis*; Battambang Province, Cambodia (see comment for the status of type series in Breure et al., 2018).

Materials examined.– **THAILAND** • 3 shells, MUMNH-UNI2191 to 2193; Nam Man River, Na Ho Subdistrict, Dan Sai District, Loei Province; 17°19'35.6"N, 101°8'54.5" E; E. Jeratthitikul, P. Prasankok, and K. Wisittikosol leg. • 1 shell, MUMNH-UNI0089; Yom River, Sam Ngam Subdistrict, Sam Ngam District, Phichit Province; 16°30'34.6" N, 100°12'09.8"E; E. Jeratthitikul and P. Prasankok leg. • 3 shells, MUMNH-UNI0573 to 0575; Lop Buri River, Sao Thong Subdistrict, Bang Pahan District, Ayutthaya Province; 14°29'30.4"N, 100°33'12.6"E; E. Jeratthitikul and P. Prasankok leg. • 8 shells, MUMNH-UNI2496 to 2500, 2128, 2129, 2092; Huai San Stream, Bang Khian Subdistrict, Chum Saeng District, Nakhon Sawan Province; 15°53'47.3"N, 100°13'09.27"E; E. Jeratthitikul leg. • 2 shells, MUMNH-UNI2900, 2908; Phetchaburi River, Tha Laeng Subdistrict, Tha Yang District, Phetchaburi Province; 12°57'01.8"N, 99°51'16.6"E; E. Jeratthitikul and K. Wisittikosol leg. • 2 shells, MUMNH-UNI2952, 2953; Phetchaburi River, Klat Luang Subdistrict, Tha Yang District, Phetchaburi

Province; 12°57'01.8"N, 99°51'16.6"E; E. Jeratthitikul, N. Phuhong, K. Macharoenboon, and R. Jhaijong leg. • 8 shells, MUMNH-UNI1810 to 1817; Ing River, Si Don Chai Subdistrict, Chiang Khong District, Chiang Rai Province; 20°08'08.2"N, 100°25'08.0"E; E. Jeratthitikul, A. Fanka, and K. Wisittikosol leg. • 1 shell, MUMNH-UNI0680; Kho Lueak Stream, Sa Pradu Subdistrict, Wichian Buri District, Phetchabun Province; 15°37'46.2"N, 101°06'01.3"E; E. Jeratthitikul and K. Wisittikosol leg. **CAMBODIA** • 3 shells, MUMNH-UNI2924 to 2926; Stung Prek Tnaot River, Chbar Mon Municipality, Kampong Speu Province; 11°27'40.15"N, 104°31'43.47"E; E. Jeratthitikul, T. H. Ng, P. B. Ngor, and A. Pholyotha leg. • 4 shells, MUMNH-UNI2767 to 2770; Kampong Chhnok Tru landing point, Tonle Sap Lake, Kampong Chhnok Tru, Chhnok Tru Commune, Boribo District, Kampong Chhnang Province; 12°04'23.6"N, 104°46'23.8"E; E. Jeratthitikul, T. H. Ng, P. B. Ngor, and A. Pholyotha leg. • 3 shells, MUMNH-UNI2637, 2765, 2766; Pursat River, Wat Loung Village, Lolork Sor Commune, Sampaov Meas District, Pursat Province; 12°30'20.1"N, 103°50'07.8"E; E. Jeratthitikul, T. H. Ng, P. B. Ngor, and A. Pholyotha leg. • 4 shells, MUMNH-UNI2659, 2762 to 2764; Stung Sen River, Kampong Samraung Village, Srayav Commune, Stung Saen District, Kampong Thom Province; 12°40'58.3"N, 104°54'33.1"E; E. Jeratthitikul, T. H. Ng, P. B. Ngor, and A. Pholyotha leg.

Diagnosis.– Shell medium to rather large, winged, ovate subquadrate, compressed to moderate inflated, moderately thick. Anterior margin rounded; dorsal margin curved, lower anteriorly and little shouldered, gradually elevated to posteriorly to form posterior wing (more developed in younger specimens; Fig. 4D); posterior margin slightly curved, posterior end slightly pointed to round; ventral margin curved. Umbo small, not elevated. Posterior ridge wide and obtuse, moderately elevated; posterior slope with two faint and curved lines running from umbo to posterior margin (sometimes invisible). Pseudocardinal teeth moderately developed, one on each valve: tooth on right valve more pronounced, smooth, wide base, tubercle-like; tooth on left valve smooth, hill-like to triangulate, more pointed. Lateral teeth obsolete. Anterior muscle scars well-developed: adductor muscle scar ovate, contiguous with pedal retractor and pedal protractor muscle scars; pedal retractor muscle scar rounded; pedal protractor muscle scar elongated, bean-shaped. Posterior adductor muscle scar less developed. Pallial line continuous, well-marked. Umbonal cavity moderately deep and wide, with one row of 4–6 muscle scars.
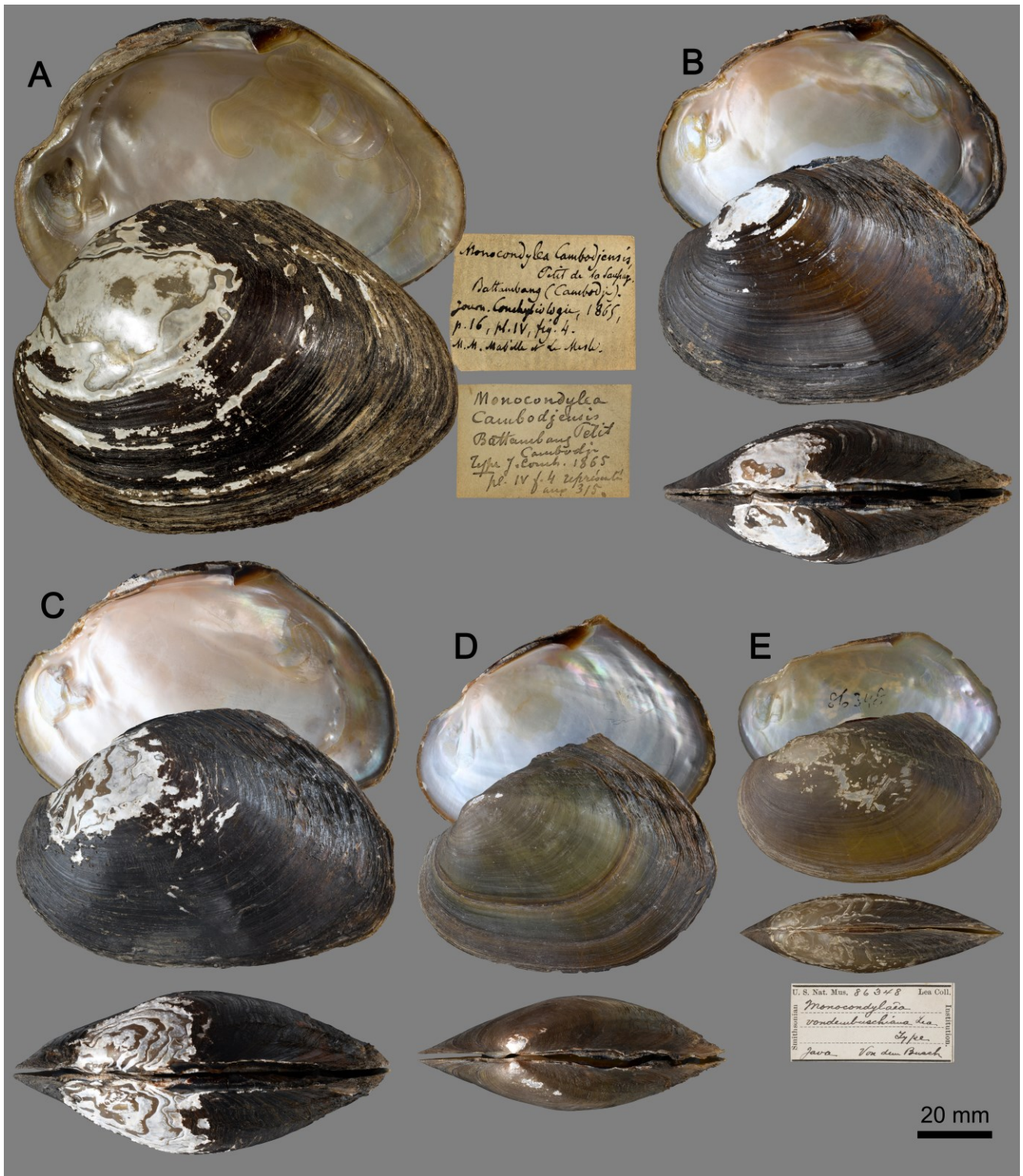
FIGURE 4. Shells of *Pseudodon* species showing the inner side of the right valve, the outer side of the left valve, and the dorsal view of both valves. **A–D.** *Pseudodon cambodjensis*. **A.** Syntype MNHN-IM-2000-34622 of *Monocondylea cambodjensis* Petit de la Saussaye, 1865, from Tonle Sap Basin, Battambang, Cambodia, with original labels. **B.** Sequenced specimen MUMNH-UNI2765 from Pursat River, Tonle Sap Basin, Pursat, Cambodia. **C.** Sequenced specimen MUMNH-UNI2900 from Phetchaburi River, Phetchaburi, Thailand. **D.** Sequenced specimen MUMNH-UNI2900 from Chao Phraya Basin, Nakhon Sawan, Thailand. **E.** Holotype USNM 86348 of *Margaritana vondembuschiana* Lea, 1840 from Java, Indonesia, with original label. Photographs: M. Caballer, under project RECOLNAT-ANR-11-INBS-0004 (**A**); C. Sucharit (**B–D**); USNM collection database (**E**).

Distribution.– Tonle Sap Lake and its tributaries in Cambodia; Chao Phraya, Pa Sak, Phetchaburi rivers in Thailand; tributaries of the Mekong River in northern Thailand; and the Malay Peninsula (Fig. 1; Brandt, 1974; Zieritz et al., 2016; Ng et al., 2020; this study).

Remarks.– A clade identified as '*P. vagulus*' in Zieritz et al. (2024) and Bolotov et al. (2023) should be recognized as *P. cambodjensis*.

Pseudodon vondembuschianus (Lea, 1840)
(Figs 1–3, 4E)

Margaritana vondembuschiana Lea, 1840: 288. Type locality: Java

For a full list of the synonyms and usage of the name, see Bolotov et al. (2023) and Graf and Cummings (2025).

Type specimen.– Holotype USNM 8648 (Fig. 4E); Java, Indonesia.

Materials examined.– **THAILAND** • 1 shell, MUMNH-UNI2093; Pat Stream, Fak Tha Subdistrict, Fak Tha District, Uttaradit Province; 17°59'24.2"N, 100°52'45.1"E; E. Jeratthitikul, P. Prasankok, and K. Wisittikosol leg. • 5 shells, MUMNH-UNI2559, 2560, 2864 to 2866; Khek Noi Stream, Khek Noi Subdistrict, Khao Kho District, Phetchabun Province; 16°49'32.6"N, 100°58'26.4"E; E. Jeratthitikul and C. Sucharit leg. • 1 shell, MUMNH-UNI0177; Kho Lueak Stream, Sa Pradu Subdistrict, Wichian Buri District, Phetchabun Province; 15°37'46.2"N, 101°04'23.6"E; E. Jeratthitikul and K. Wisittikosol leg. • 2 shells, MUMNH-UNI0288 to 0289; Pasak River, Na Yom Subdistrict, Mueang District, Phetchabun Province; 16°15'02.2"N, 101°07'36.4" E; E. Jeratthitikul and K. Wisittikosol leg. • 3 shells, MUMNH-UNI2511 to 2513; Taphoen Stream, Lat Ya Subdistrict, Mueang Kanchanaburi District, Kanchanaburi Province; 14°08'13.8"N, 99°22'59.5"E; E. Jeratthitikul and K. Wisittikosol leg. • 3 shells, MUMNH-UNI2905 to 2907; Phetchaburi River, Tha Laeng Subdistrict, Tha Yang District, Phetchaburi Province; 12°57'01.8"N, 99°51'16.6"E; E. Jeratthitikul and K. Wisittikosol leg. • 1 shell, MUMNH-UNI0299; Phrom Hot River, Han Sai Subdistrict, Aranyaprathet District, Sa Kaeo; 13°44'56.6"N, 102°25'37.6"E; E. Jeratthitikul leg. • 11 shells, MUMNH-UNI2878 to 2888; Phok Stream, Wang Thong Subdistrict, Wang Sombun District, Sa Kaeo Province; 13°20'15.3"N, 102°07'59.5"E; E. Jeratthitikul, P. Prasankok, and K. Wisittikosol leg. • 5 shells, MUMNH-UNI0800, 2532 to 2534, 2537; Huai Raeng Stream, Huai Raeng Subdistrict, Mueang District, Trat Province; 12°22'34.3"N, 102°34'55.2"E; E. Jeratthitikul and K. Wisittikosol leg. • 5 shells, MUMNH-UNI2910 to 2914; Phraphut Stream, Nong Ta Khong Subdistrict, Pong Nam Ron District, Chanthaburi Province; 15°02'39.21"N, 102°25'05.07"E; E. Jeratthitikul and K. Wisittikosol leg. • 5 shells, MUMNH-UNI2602 to 2606; Prasae River, Krasae Bon Subdistrict, Klaeng District, Rayong Province; 12°50'51.78"N, 101°38'38.85"E; E. Jeratthitikul and K. Wisittikosol leg. • 2 shells, MUMNH-UNI0771 to 0772; Chanthaburi River, Wang Saem Subdistrict, Makham District, Chanthaburi Province; 12°44'41.8"N, 102°09'30.7"E; E. Jeratthitikul and K. Wisittikosol leg. • 5 shells, MUMNH-UNI3042 to 3046; Songkhram River, Kham Lo Subdistrict, Chai Wan District, Udon Thani Province; 17°16'05.9"N, 103°17'52.5"E; E. Jeratthitikul leg. • 11 shells, MUMNH-UNI2005 to 2015; Kapo stream, Hong Charoen Subdistrict, Tha Sae District, Chumphon Province; 10°44'38.9"N, 99°12'38.6"E; E. Jeratthitikul and K. Wisittikosol leg. • 1 shell, MUMNH-UNI2915; Tha Nae Stream, Khao Pu Subdistrict, Si Banphot District, Phatthalung Province; 7°42'25.7"N, 99°50'28.2"E; R. Srisonchai leg. • 6 shells, MUMNH-UNI 2872 to 2877; Tum Stream, Thung Tam Sao Subdistrict, Hat Yai District, Songkhla Province; 6°53'48.9"N, 100°16'02.9"E; E. Jeratthitikul leg. • 5 shells, MUMNH-UNI0831 to 0835; Khlong Min Stream, Chawang Subdistrict, Chawang District, Nakhon Si Thammarat Province; 8°22'52.5"N, 99°31'22.3"E; E. Jeratthitikul and K. Wisittikosol leg. **LAOS** • 10 shells, MUMNH-UNI3162 to 3171; Tributary of Nam Lik River, Ban Don, Fuang District, Vientiane Province; 18°41'59.8"N, 102°07'27.1"E; E. Jeratthitikul, K. Inkhavilay, and C. Sucharit leg. • 5 shells, MUMNH-UNI2521 to 2525; Bunghona Market, 7 km N of Xe Bangfai River, Teoung, Kammoune Province; 17°08'12.2"N, 104°59'09.3"E; E. Jeratthitikul, K. Inkhavilay, P. Prasankok, and K. Wisittikosol leg. • 3 shells, MUMNH-UNI1897 to 1899; Huay Phong Stream, Xaisetha District, Attapeu Province; 14°48'39.4"N, 106°52'26.1"E; E. Jeratthitikul, K. Inkhavilay, and C. Sucharit leg.

Diagnosis.– Shell medium, winged or without wing, elongate ovate, compressed to rather inflated, thin to moderately thick. Anterior margin rounded; dorsal margin curved, lower anteriorly and little shouldered, gradually elevated posteriorly, posterior slightly high, posterior wing not prominent. Umbo small, slightly elevated. Posterior ridge wide and obtuse, slightly to moderately elevated; posterior slope with two curved fold lines running from umbo to posterior margin,

rather prominent. Pseudocardinal teeth less to moderately developed, one on each valve: tooth on right valve more pronounced, smooth, wide base, hill-like to rectangular; tooth on left valve smooth, wide base, hill-like, more pointed, or almost reduced. Lateral teeth absent or obsolete. Anterior muscle scars shallow: adductor muscle scar ovate or droplet-like, contiguous with pedal retractor and pedal protractor muscle scars; pedal retractor muscle scar rounded; pedal protractor muscle scar elongated or bean-shaped. Posterior adductor muscle scar less developed, almost invisible. Pallial line continuous, faint to rather clear. Umbonal cavity moderately deep to shallow, with one row of 2–4 muscle scars.

Distribution.– Widespread in Indochina (especially in Chao Phraya River and Mekong River basins) to the Malay Peninsula, Java, and Sumatra (Fig. 1; Brandt, 1974; Zieritz et al., 2016; Bolotov et al., 2023; Konopleva et al., 2023; this study).

Remarks.– *Pseudodon vondembuschianus* is common in Indochina. It has been found in high abundance in almost all of the examined drainages in Indochina, except in the north of Thailand (Fig. 1). Phylogenetic analysis revealed a degree of localization within certain clades, exhibiting phylogeographic patterns restricted to particular drainages. Consequently, some authors have proposed subspecific classifications for these populations, including *P. v. mekongi* (Bolotov et al., 2020) from the headwaters of the Phong River, northeastern Thailand; *P. v. laosica* (Bolotov et al., 2020) from the Mekong Basin in Laos; *P. v. tapienica* (Konopleva et al., 2023) from the Tapi River Basin, southern Thailand; and *P. v. thasaenica* (Konopleva et al., 2023) from the Tha Sae River Basin, southern Thailand (Bolotov et al., 2023; Konopleva et al., 2023; Jeratthitikul et al., 2024). However, with the inclusion of more specimens in the phylogenetic analyses in this study, there was insufficient support to indicate monophyly in some of these subspecies (Fig. 2). Therefore, we initially interpret these subspecific classifications as representing localized genetic variation. Further investigation with more comprehensive sampling across the taxa and over a larger geographic range are necessary to confirm this hypothesis.

Pseudodon vagulus (Fischer, 1891)
(Figs 1–3, 5A–D)

Unio subtrigonus Sowerby II, 1867: *Unio* pl. 58, species 292 (homonym of †*Unio subtrigonus* Noulet, 1846). Type locality: "Siam" [=Thailand].

Unio vagulus Fischer, 1891: 223 (new name for *Unio subtrigonus* Sowerby II, 1867).
Pseudodon cambodjensis tenerrimus Brandt, 1974: 270, pl. 20, fig. 29. Type locality: "Songkram River at Sri Songkram" [=Songkhram River, Si Songkhram District, Nakhon Phanom Province].

For a full list of the usage of the name, see Graf and Cummings (2025).

Type specimen.– Holotype NHMUK 1874.12.11.3. (Fig. 5A) of *Unio subtrigonus*; "Siam" [=Thailand]. Holotype SMF 188817/1 (Fig. 5B) of *Pseudodon cambodjensis tenerrimus* "Songkram River at Sri Songkram" [=Songkhram River, Si Songkhram District, Nakhon Phanom Province, Thailand].

Materials examined.– THAILAND • 2 shells, MUMNH-UNI2177, 2178; Nam Mong Stream, Nam Mong Subdistrict, Tha Bo District, Nong Khai Province; 17°53'29.1"N, 102°32'03.0"E; E. Jeratthitikul, P. Prasankok, and K. Wisittikosol leg. • 3 shells, MUMNH-UNI2211 to 2213; Nam Suai Stream, Thung Luang Subdistrict, Phon Phisai District, Nong Khai Province; 17°57'50.4"N, 102°57'57.4"E; E. Jeratthitikul, P. Prasankok, and K. Wisittikosol leg. • 1 shell, MUMNH-UNI2205; Luang River, Tao Hai Subdistrict, Phen District, Udon Thani Province; 17°37'13.4"N, 103°06'39.5"E; E. Jeratthitikul, P. Prasankok, and K. Wisittikosol leg. • 7 shells, MUMNH-UNI0819, 0820, 0911 to 0915; Songkhram River, Thung Fon Subdistrict, Thung Fon District, Udon Thani Province; 17°27'06.5"N, 103°16'50.4"E; E. Jeratthitikul, P. Prasankok, and K. Wisittikosol leg. • 14 shells, MUMNH-UNI2112, 2113, 2115, 2116, 2118 to 2127; Nam Som River, Non Thong Subdistrict, Na Yung District, Udon Thani Province; 17°57'54.6"N, 102°14'37.1"E; E. Jeratthitikul, P. Prasankok, and K. Wisittikosol leg. • 1 shell, MUMNH-UNI0586; Unnamed tributary of Mekong River, Khok Kong Subdistrict, Mueang Bueng Kan District, Bueng Kan Province; 18°20'22.4"N, 103°45'45.4"E; E. Jeratthitikul and K. Wisittikosol leg. • 6 shells, MUMNH-UNI0667 to 0672; Songkhram River, Tha Sa-at Subdistrict, Seka District, Bueng Kan Province; 17°55'56.3"N, 103°45'30.8"E; E. Jeratthitikul and K. Wisittikosol leg. • 1 shell, MUMNH-UNI2206; Nam Hee, Nong Thum Subdistrict, Seka District, Bueng Kan Province; 17°55'07.2"N, 103°55'33.4"E; E. Jeratthitikul, P. Prasankok, and K. Wisittikosol leg. • 9 shells, MUMNH-UNI2182 to 2190; Nam Mao Stream, Hat Phaeng Subdistrict, Si Songkhram District, Nakhon Phanom Province; 17°42'49.3"N, 104°14'49.3"E; E. Jeratthitikul, P. Prasankok, and K. Wisittikosol leg. • 4 shells, MUMNH-UNI2207 to

2210; Thuai River, Non Tan Subdistrict, Tha Uthen District, Nakhon Phanom Province; 17°33'43.7"N, 104°36'32.9"E; E. Jeratthitikul, P. Prasankok, and K. Wisittikosol leg. • 2 shells, MUMNH-UNI0901, 0902; Songkhram River, Chai Buri Subdistrict, Tha Uthen District, Nakhon Phanom Province; 17°38'58.5"N, 104°27'41.2"E; E. Jeratthitikul, P. Prasankok, and K. Wisittikosol leg. • 15 shells, MUMNH-UNI2159 to 2173; Songkhram River, Kham Ta Kla Subdistrict, Kham Ta Kla District, Nakhon Phanom Province; 17°51'56.4"N, 103°46'26.9"E; E. Jeratthitikul, P. Prasankok, and K. Wisittikosol leg. • 3 shells, MUMNH-UNI2608 to 2610; Songkhram River, Dong Mo Thong Subdistrict, Ban Muang District, Sakon Nakhon Province; 18°04'13.6"N, 103°30' 39.2"E; E. Jeratthitikul, P. Prasankok, and K. Wisittikosol leg. • 3 shells, MUMNH-UNI0347 to 0349; Non Stream, Charoen Sin Subdistrict, Charoen Sin District, Sakon Nakhon Province; 17°31'56.1"N, 103°33'39.0"E; E. Jeratthitikul, P. Prasankok, and K. Wisittikosol leg. • 10 shells, MUMNH-UNI2842 to 2851; Songkhram River, Kham Ta Kla Subdistrict, Kham Ta Kla District, Sakon Nakhon Province; 17°51'56.4"N, 103°46' 26.9"E; C. Sutcharit and K. Macharoenboon leg.

Diagnosis.– Shell medium-sized, winged, rounded triangular outline, compressed, moderately thick. Anterior margin rounded; dorsal margin slightly curved to straight; lower anteriorly and little shouldered, gradually elevated posteriorly to form posterior wing; posterior margin truncated to curved, posterior end angulated to round (protruded in older individuals); ventral margin curved. Posterior ridge wide and obtuse, not prominent; posterior slope with two faint and curved lines running from umbo to posterior margin, and lower one more pronounced. Pseudocardinal teeth weak to moderately developed, one on each valve: tooth on right valve more pronounced, smooth, hill-like to tubercle-like; tooth on left valve smooth, hill-like, more pointed. Lateral teeth obsolete. Anterior muscle scars shallow: adductor muscle scar ovate, contiguous with pedal retractor and pedal protractor muscle scars; pedal retractor muscle scar ovate; pedal protractor muscle scar elongated. Posterior adductor muscle scar less developed. Pallial line continuous, well-marked. Umbonal cavity moderate deep, with one row of 5–7 muscle scars.

Distribution.– Songkhram River Basin and tributaries of the Mekong River in northeastern Thailand, and Laos (Fig. 1; Brandt, 1974; Bolotov et al., 2023; this study).

Remarks.– *Unio subtrigonus* Sowerby II, 1867 was described based on a specimen collected from "Siam" [=Thailand], though the precise type locality was not mentioned. This name became a junior homonym which was later replaced by a new replacement name, *Unio vagulus* Fischer, 1891. However, this name was long considered a junior synonym of *P. cambodjensis* (see Haas, 1920; Brandt, 1974) until Bolotov et al. (2023) resurrected it as a valid species again. Interestingly, Bolotov et al. (2023) assigned a clade containing specimens from Tonle Sap in Cambodia, Thailand, and Malaysia as *P. vagulus*, while they also recognized a clade from the Nam Ngum River (Mekong River Basin, Laos) as *P. cambodjensis* s.s. Upon comparing newly collected specimens from tributaries of the Mekong River in the upper part of Khorat Plateau (i.e., Songkhram River and several drainages in Sakon Nakhon Basin) in Thailand with the type specimen (Fig. 5A), the newly collected materials (Fig. 5C, D) closely matched the type, particularly in regard to the prominent posterior wing and protruded posterior end. Consequently, we consider the clade from the upper part of Khorat Plateau as *P. vagulus*. Furthermore, specimen RMBH biv 0811 recognized as '*P. cambodjensis*' from the Nam Ngum River by Bolotov et al. (2023: fig 8C, D) was phylogenetically clustered within our *P. vagulus* clade. This specimen also exhibits conchological similarities to the less-winged morph collected from the Songkhram River in this study (Fig 5C).

In addition, our phylogenetic analyses confirmed that the *P. cambodjensis tenerrimus* Brandt, 1974 is a junior synonym of *P. vagulus* as suggested by Bolotov et al. (2023). Specifically, the topotypic specimen (Fig 5C) that exhibited conchological identity to the holotype (Fig 5B) was nested within the *P. vagulus* clade (Fig. 2).

Pseudodon septuaginta sp. nov.

https://zoobank.org/urn:lsid:zoobank.org:act: AC292F97-4265-4956-99E1-B946D793FCE2
(Figs 1–3, 5E, F)

Pseudodon cambodjensis tenerrimus—Brandt, 1974: 270 (in part).

Type materials.– Holotype MUMNH-UNI3423 (Fig. 5E, length 87.3 mm, height 58.3 mm, width 22.6 mm); Dom Yai River, Mueang Det Subdistrict, Det Udom District, Ubon Ratchathani Province, Thailand; 14°57' 35.9"N, 105°06'12.1"E; E. Jeratthitikul and K. Prasankok leg. Paratypes: 9 shells, MUMNH-UNI3418 to 3422, UNI3424 to 3427; same collection data as for holotype. • 3 shells, MUMNH-UNI2543, UNI2544, UNI2557 (Fig. 5F); Dom Yai River, Tha Pho Si
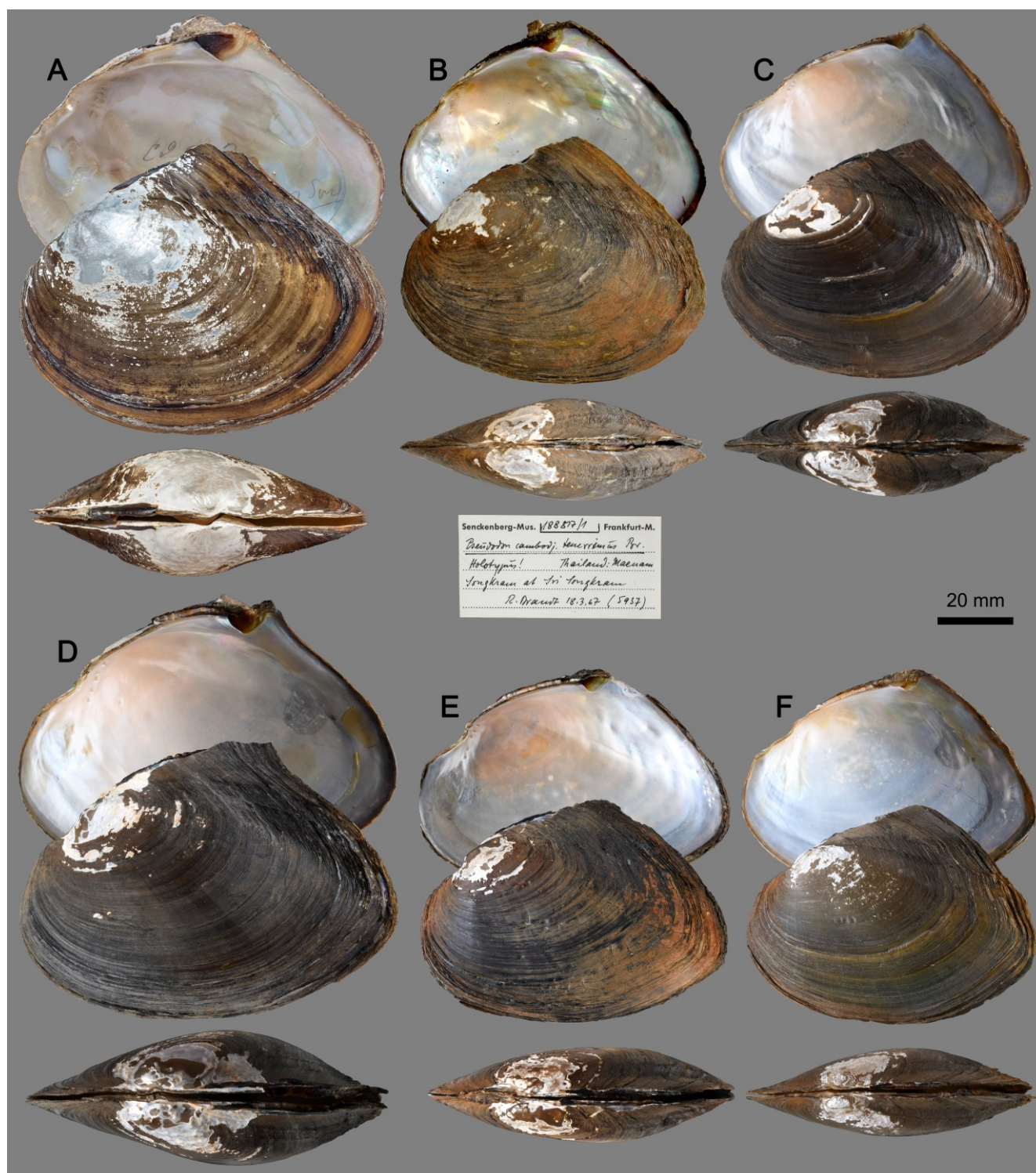
FIGURE 5. Shells of *Pseudodon* species showing the inner side of the right valve, the outer side of the left valve, and the dorsal view of both valves. **A–D.** *Pseudodon vagulus*. **A.** Holotype NHMUK 1874.12.11.3 of *Unio vagulus* Fischer, 1891 from "Siam" [=Thailand]. **B.** Holotype SMF 188817/1 of *P. cambodjensis tenerrimus* Brandt, 1974, from Songkhram River, Nakhon Phanom, Thailand, with label. **C.** Sequenced specimen MUMNH-UNI2209 from Thuai River, Nakhon Phanom, Thailand. **D.** Sequenced specimen MUMNH-UNI0902 from Songkhram River, Nakhon Phanom, Thailand. **E, F.** *Pseudodon septuaginta* sp. nov. **E.** Holotype MUMNH-UNI3423 from Dom Yai River, Ubon Ratchathani, Thailand and **F.** paratype MUMNH-UNI2557 from the type locality. Photographs: Kevin Webb, NHMUK Photographic Unit (**A**); C. Sucharit (**B–F**); label photo, S. Hof (**B**).

Subdistrict, Det Udom District, Ubon Ratchathani Province, Thailand; 14°49'43.9"N, 105°04'48.5"E; E. Jeratthitikul and K. Wisittikosol leg.

Other materials.– THAILAND • 1 shell, MUMNH-UNI1629; Dom Yai River, Mueang Det Subdistrict, Det Udom District, Ubon Ratchathani Province; 14°53'55.3"N 105°05'58.4"E; E. Jeratthitikul and K. Wisittikosol leg. • 4 shells, MUMNH-UNI3172, 3173, 3197, 3198; Pao River, Kamalasai Subdistrict, Kamalasai District, Kalasin Province; 16°20'25.5"N, 103°34'33.8"E; E. Jeratthitikul and K. Macharoenboon leg.

Measurements.– Shell length 63.3–88.2 mm (mean = 76.41 mm, n = 15), shell height 48.5–59.3 mm (mean = 55.86 mm, n = 15), shell width 46.2–55.3 mm (mean = 20.66 mm, n = 15).

Etymology.– The specific epithet "*septuaginta*" is derived from the Latin word meaning "seventy", and chosen to celebrate the occasion of the seventieth birthday of Her Royal Highness Princess Maha Chakri Sirindhorn of Thailand, who has long been interested in and promoted the study of taxonomy and diversity in Thailand.

Differential diagnosis.– The new species conchologically resembles *P. vagulus*, especially among younger individuals (Fig. 5). However, it can be distinguished from the latter species by several shell characteristics (Table 3), including a more compressed and thinner shell, shallower umbonal cavity, and lower posterior wing. The ventral margin of the new species is straight (vs. curved in *P. vagulus*), and the posterior margin is truncate (vs. angular to curved posterior margin with a protruded posterior end in some older individuals). Pseudocardinal teeth of the new species are also less developed compared to those of *P. vagulus*. The new species differs from its congeners by

having four fixed nucleotide substitutions in the COI gene fragments (Table 4).

The shell outline of the new species is similar to *Lannanaia kokensis* Jeratthitikul et al., 2024, a monotypic genus from the Mekong Basin, northern Thailand in having a subtrigonal shell outline and posterior wing present (Jeratthitikul et al., 2024). However, the new species can be distinguished by its larger shell size (63.3–88.2 mm vs. 57.1–57.2 mm), shouldered anterior end (vs. short anterior end with a tiny anterior wing), lower posterior wing (vs. higher and pointed posterior wing), more developed pseudocardinal teeth (vs. absent or present as very rudimentary broad pseudocardinal teeth), more prominent anterior muscle scars (vs. very shallow anterior muscle scars), and a rather clear pallial line (vs. very faint pallial line) (Jeratthitikul et al., 2024).

Description.– Shell rather thin, medium-sized, inequilateral, winged, sub-trigonal outline, rather compressed, rather high (average H/L ratio including posterior wing = 0.73, n = 15). Anterior margin rounded; dorsal margin slightly curved to straight, lower anteriorly and little shouldered, gradually elevated posteriorly to form posterior wing; posterior margin truncated, posterior end somewhat pointed; ventral margin slightly curved. Umbo tiny, not elevated, usually eroded. Posterior ridge wide and obtuse, not prominent; posterior slope with two faint and curved lines running from umbo to posterior margin; sometimes invisible. Periostracum thin, dark brown to dark olive-green, eroded part white to coppery-brown. Shell surface with fine growth lines.

Inner side of shell: ligament long, very narrow, dark brown in color. Pseudocardinal teeth weak to nearly absent, and one on each valve: on right valve, smooth, wide base, hill-like or triangulate and situated well anteriorly; on left valve less developed, smooth, hill-like, more pointed. Lateral teeth obsolete. Posterior end

TABLE 3. Conchological characteristics of four *Pseudodon* species occurring in Indochina.

Conchological feature	*P. vondembuschianus*	*P. cambodjensis*	*P. vagulus*	*P. septuaginta* sp. nov.
Shell shape	elongate ovate	rounded triangular outline	rounded triangular outline	sub-trigonal
Shell inflation	compressed to rather inflated	compressed	compressed	rather compressed
Shell thickness	thin to moderately thick	moderately thick	moderately thick	rather thin
Umbo shape	small, slightly elevated	tiny, not elevated	tiny, not elevated	tiny, not elevated
Posterior wing	not prominent	present to not prominent	present	present
Dorsal margin	slightly curved	slightly curved to straight	slightly curved to straight	slightly curved to straight
Ventral margin	curved to straight	curved	curved	slightly curved
Pseudocardinal teeth	hill-like to rectangular	hill-like to tubercle-like	hill-like to tubercle-like	hill-like or triangulate
Umbonal cavity	moderate deep to shallow	moderate deep	moderate deep	shallow

TABLE 4. Fixed nucleotide differences in COI sequences among *Pseudodon* species useful for species diagnosis. Nucleotide position based on sequence alignment of 660 bp of COI gene fragment in this study.

Taxon	Fixed nucleotide differences
P. cambodjensis	39A, 576C
P. vagulus	18A, 19C, 46C, 99A, 108C, 292C, 438C, 450C, 591C
P. septuaginta sp. nov.	66C, 117C, 465C, 627G
P. vondembuschianus	37C, 78A, 177A, 225G, 603C, 621A
P. inoscularis	345A, 471A, 501G
P. lenyanensis	501A, 597C
P. walpolei	54A, 333A, 486T, 492A, 559C, 643C

of hinge plate with wide V-shaped furrow. Anterior muscle scars shallow: adductor muscle scar ovate, contiguous with pedal retractor- and pedal protractor-muscle scars; pedal retractor muscle scar rounded; pedal protractor muscle scar elongated oval. Posterior adductor muscle scar ovate, almost invisible. Pallial line continuous, clear. Umbonal cavity shallow, with one row of 4–6 muscle scars. Nacre whitish blue, with orange tinge near umbo.

Small epithelial fold divides exhalant and inhalant apertures. Siphon apertures with strip of dark pigmentation running along aperture edge. Exhalant aperture slightly narrower than inhalant aperture, with one row of tubercular papillae running along aperture. Inhalant aperture with one row of papillae which vary in length and shape: shorter papillae with conical shape; longer papillae usually branched near tip to tiny papillae. Gills elongated and slightly ribbed; outer gills half as narrow as inner gills; anterior margin of inner gills slightly longer than outer gills. Labial palps narrow, elongate, pointed at tip. Glochidia unknown.

Distribution.– The new species is known only from the type locality in the Mun River Basin, northeastern Thailand (Fig. 1).

Habitat.– Living specimens were found in abundance buried in sandy or muddy riverbeds.

Remarks.– Specimens reported as '*P. cambodjensis tenerrimus*' by Brandt (1974) from the Mun River Basin (i.e., from Choen, Chi, Mun, and Pong rivers) should be included in the new species.

DISCUSSION

Species validity and phylogenetic relationship of *Pseudodon*

This study utilized the most comprehensive dataset of the genus *Pseudodon* to date, consisting of a nuclear gene marker (28S rRNA) and mitochondrial gene markers (COI and 16S rRNA), to infer the phylogenetic relationships and provide insights into the evolutionary history and biogeography of the genus. Our findings confirm the valid status of seven among the nine currently recognized extant *Pseudodon* species, and include the discovery of a new cryptic species, *P. septuaginta* sp. nov., from the Mekong River Basin in northeastern Thailand. All species examined in this study were consistently grouped into distinct clades with exceptionally high statistical support from both ML and BI analyses (BS = 95–100%, BPP = 1), reflecting their status as clearly separated evolutionary lineages. The pairwise genetic distances as expressed by uncorrected COI p-distance among *Pseudodon* species were 8.47% on average (range from 2.52 to 11.03%; Table 2). This value is relatively high compared to established thresholds for species delimitation in other Indochinese freshwater mussels, which range from 2.3 to 12.3% (Jeratthitikul et al., 2019a, 2019b, 2021a, 2021b, 2022, 2024; Konopleva et al., 2019; Jeratthitikul and Sutcharit, 2023). Moreover, morphometric analyses also confirmed significant differences in shell morphology among the four species inhabiting in Indochina. PCA showed that the first principal component (PC1) alone accounted for over 80% of the shape variation and distinguished *P. vondembuschianus* from other Indochinese species based on shell elongation and posterior wing development (Fig. 3). MANOVA further indicated statistically significant differences in shell morphology among all pairs of species studied.

The phylogenetic trees generated from both ML and BI analyses consistently revealed a monophyletic relationship for the genus (Fig. 2) and placed the Borneo-endemic taxon, *P. walpolei*, at a basal position to all *Pseudodon* members. This was followed by a clade from the West Indochina Subregion (river basins in Myanmar), preceding the major diversification of the genus in Indochina. Although the phylogenetic relationships among genera within the Pseudodontini remain largely uncertain (Bolotov et al., 2023; Jeratthitikul et al., 2024, 2025), previous studies have suggested a close relationship between *Pseudodon* and Mekong-endemic taxa such as *Namkongnaia* and *Isannaia*. These two genera exhibit a remarkably

elongate shell outline and lack a posterior wing (Jeratthitikul et al., 2021b, 2024). A similar combination of an elongate shell outline and a less developed posterior wing has been observed within the basal clade of *Pseudodon*, including *P. walpolei*, *P. lenyanensis*, *P. inoscularis*, and some populations of *P. vondembuschianus* (Figs 2, 3). This pattern leads to the hypothesis that the common ancestor of *Pseudodon* likely possessed an elongate shell, with the posterior wing being a derived character. Subsequently, a more pronounced posterior wing and a more rounded triangular shell outline appear to have evolved later in the evolutionary history of taxa inhabiting Indochina, such as *P. cambodjensis*, *P. vagulus*, and *P. septuaginta* sp. nov. (Figs 2–5).

Biogeography of *Pseudodon* in Indochina

Phylogenetic pattern revealed in this study suggests that the common ancestor of *Pseudodon* may have arisen in Borneo before spreading north to Myanmar and then eastward to Indochina (Fig. 2). A time-calibrated phylogeny from a previous study suggested that the divergence event of *Pseudodon* from its most closely related genus occurred around 54.7 million years ago (Mya) in the Early Eocene, somewhat earlier than the diversification of other genera in the Pseudodontini (Bolotov et al., 2023). This South-to-North colonization pattern differs significantly from *Pilsbryoconcha*, another genus in the tribe Pseudodontini that has a large distribution range covering both Indochina and the Greater Sunda Islands, which exhibit an opposite North-to-South colonization pattern. *Pilsbryoconcha* was hypothesized to have originated in the approximate location of the present-day Khorat Plateau basin in northeastern Thailand during the Eocene, before later spreading to the Chao Phraya River Basin with two taxa that extend their range southward to Java and Sumatra (Jeratthitikul et al., 2022). The oldest diversification event in *Pilsbryoconcha* can be traced back to 51.3 Mya, approximately in the same period of *Pseudodon* (Bolotov et al., 2023).

These contrasting biogeographic patterns among unionid fauna in Indochina challenge the previous concept of the former paleo-Mekong catchment as a center of radiation for the Pseudodontini (Bolotov et al., 2023). In fact, the phylogenetic pattern that is observed within *Pseudodon* appears to be a recurring colonization event within the larger tribe context. The unionid fauna of Borneo are considered unique and exhibit high levels of endemism (Zieritz et al., 2020, 2021, 2024). Recently, two endemic tribes, Schepmaniini Lopes-Lima et al., 2021 and Ctenodesmini Pfeiffer et al. 2021, were discovered (Zieritz et al., 2021). These two tribes show a sister group relationship with Indochina-endemic tribes: Schepmaniini with Pseudodontini, and Ctenodesmini with Contradentini Modell, 1942 and Rectidentini Modell, 1942. Within Pseudodontini, phylogenetic analysis by Jeratthitikul et al. (2024) placed the tribe Schepmaniini at the basal position, followed by the subtribe Indopseudodontina, which is endemic to Myanmar, and then the majority of the genera in Indochina. This phylogenetic pattern suggest that the Bornean taxa are relatively older than those in Indochina and likely supports Borneo as an evolutionary origin for unionid mussels in this region. A predominant distribution from Borneo to Indochina in Unionidae has been suggested to have occurred sometime in the late Cretaceous (Zieritz et al., 2021), possibly through the connection of the western Borneo and Indochinese paleo-drainage systems via Sundaland, which connected present-day western Borneo, eastern parts of Java and Sumatra, and the Thai-Malay Peninsula (Hall, 2013). It is plausible that after colonization in Indochina (i.e., paleo-Mekong drainages), the common ancestor of Pseudodontini underwent a rapid radiation at both genus and species levels, which is thought to have occurred during the period from Eocene to Miocene (Bolotov et al., 2023). However, further research incorporating broader taxon sampling and regional geological events is highly recommended to provide a more detailed understanding of the factors driving the overall biogeographic patterns of unionid mussels in Southeast Asia. Moreover, this hypothesis needs to be tested using robust biogeographic modeling approaches.

Discovery of cryptic species within the Khorat Plateau

Multiple lines of evidence have confirmed the validity of a cryptic lineage in northeastern Thailand as a new species, herein described as *P. septuaginta* sp. nov. This new species shares similar conchological features with its sister taxon, *P. vagulus*. However, these two species can be distinguished by several shell characters, including shell inflation, overall shell shape, and the pseudocardinal teeth (Table 3). Furthermore, both species exhibit a unique fixed nucleotide difference in the COI gene (Table 4), a highly useful marker for their differentiation (Wu et al., 2018), and are separated by a p-distance genetic divergence of 6.7% (Table 2). Moreover, *P. septuaginta* sp. nov. and *P. vagulus* exhibit a disjunct distribution across separate river basins. Based on the specimens examined in this study, *P. septuaginta* sp. nov. is found in the tributaries of the Mun River Basin, a large basin flowing west to east across the Khorat Plateau in northeastern Thailand (Fig. 1). In contrast, *P. vagulus* is distributed in Sakhon Nakhon Basin in the upper

region of the plateau, specifically within the Songkhram River Basin and several smaller rivers that drain into the Mekong River. This biogeographic separation between the upper and lower basins within the Khorat Plateau is independently supported across almost all examined unionid genera in the Rectidentini, Contradentini, and Pseudodontini (Muanta et al., 2019; Jeratthitikul et al., 2021a; Konopleva et al., 2021; Pfeiffer et al., 2021), suggesting consistent biogeographic patterns indicative of significant barriers between these two regions. Although the present-day Mekong River provides a thorough connection of all drainages on the Khorat Plateau, the proto-Mekong River is thought to have been divided into several independent paleo-drainages (Adamson et al., 2012). Consequently, the ancestral populations of *P. septuaginta* sp. nov. and *P. vagulus* likely dispersed to the Khorat Plateau before undergoing separation by inhabiting isolated drainage systems for an extended period. This limited gene flow would have promoted reproductive isolation and ultimately led to speciation. This vicariance speciation likely occurred after their divergence from the Chao Phraya lineage, as evidenced by the more recent divergence observed in the phylogenetic tree and the similarity in shell morphology between them.

Deep genetic divergence within *P. cambodjensis*

Another interesting biogeographic pattern has been found within *P. cambodjensis*. Phylogenetic analyses in this study revealed the existence of two subclades within the species (Fig. 2). One subclade consisted of specimens collected from the Tonle Sap Basin in Cambodia, the same basin as the type locality, as well as one specimen from Kelantan, Malaysia. The other subclade was mainly distributed in the Chao Phraya River Basin in central Thailand and the Phetchaburi River in western Thailand, along with two specimens from Perak and Kelantan, Malaysia. These two subclades were separated by a 2.08% uncorrected COI p-distance, which is relatively low to consider them distinct species (i.e., compared with a minimum of 2.52% divergence between *P. inoscularis* and *P. lenyanensis*), especially since there are no supporting morphological characters sufficient to distinguish them. Therefore, we have chosen to classify this as a case of deep genetic divergence rather than recognizing them as separate species or subspecies.

The genetic connection between the Tonle Sap Basin and the Chao Phraya Basin, as well as the drainages in the Malay Peninsula, has been documented in several unionid genera (Pfeiffer et al., 2021) and other freshwater taxa (i.e., de Bruyn and Mather, 2007; de Bruyn et al., 2013; Jamaluddin et al., 2021). This pattern may have been caused by extensive lowland

connections through the exposed Sundaland during periods of lower sea level (Attwood and Johnston, 2001; Adamson et al., 2012), followed by subsequent isolation when sea levels rose. Sea-level fluctuations in Southeast Asia have occurred since the Early Miocene until the most recent Last Glacial Maximum approximately 20,000 years ago (Hall, 2013). This coincides with the shallow genetic divergence observed within *P. cambodjensis*, suggesting that the separation likely occurred during a more recent event.

CONCLUSION

This study employed a comprehensive sample of specimens, molecular dataset, and morphometric analyses to elucidate the taxonomy and phylogenetic relationships of the *Pseudodon*, with an emphasis on the Indochinese populations. *Pseudodon* currently consists of nine extant species. The valid status of four Indochinese species has been confirmed by shell morphology and phylogenetic analyses, including the discovery of a new cryptic lineage, *P. septuaginta* sp. nov., from northeastern Thailand. The nominal *P. vagulus* was fixed to the clade distributed in the upper part of the Khorat Plateau, whereas *P. cambodjensis* was assigned to the populations in the Tonle Sap and Chao Phraya River basins, with some populations extending to the Malay Peninsula. Our phylogenetic analyses further supported the potential Bornean origin for the genus *Pseudodon*, followed by dispersal into Myanmar and later Indochina, and highlighted the role of vicariance due to paleo-drainage isolation in the Khorat Plateau for the speciation. The observed deep genetic divergence within *P. cambodjensis* likely resulted from recent separation facilitated by Sundaland land bridges and subsequent sea-level fluctuations. Moreover, the interesting phylogeographic pattern containing a localized clade within *P. vondembuschianus* suggests ongoing evolutionary processes and warrants further investigation. While this study provides significant insights into the evolutionary history and biogeographic pattern of *Pseudodon*, future research incorporating broader geographic sampling, utilizing more robust molecular markers, and integrating geological data will be crucial for a more complete understanding of the complex biogeographic patterns shaping unionid diversity in Southeast Asia.

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