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Original Article

The freshwater mussels (Bivalvia: Unionida) of Java: first island-wide assessment reveals new species, endemism, and urgent conservation needs

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ABSTRACT

The freshwater mussel (Bivalvia: Unionida) fauna of Java has never been examined comprehensively in a modern context, leading to a lack of a species inventory and knowledge on current species distributions and how these have been impacted by human activities over the past 70 years. In 2022/23, we surveyed 66 sites across 18 river basins of Java, and one site near the *Rectidens sumatrensis* type locality in Sumatra. Species were delineated and identified through an integrated morphological–molecular approach using *COI*-based phylogenetic and haplotype analyses. We found and sequenced 76 populations (= species-site occurrences) across 42 sites and 16 river basins, comprising eight native and one non-native species. Whilst confirming the presence of *Lens contradens*, *Physunio superbus*, *Pilsbryoconcha exilis*, *Pseudodon vondembuschianus* stat. rev., *Rectidens orientalis* comb. rev., and *Sinanodonta pacifica* (non-native), we provide the first records of *Lens lugens*, *Pilsbryoconcha linguaeformis*, and ***Pseudodon cokelatus* sp. nov.** *Rectidens sumatrensis* is absent from Java. Comparing our data to historical records indicates considerable population losses of most native species driven by the steep increase in urbanization, industrialization, mining, and other human activities. Conservation actions are urgently needed, particularly in the species-rich Bengawan Solo and Brantas River basins.

Keywords: endemic species; freshwater bivalves; freshwater mussels; Mollusca; Southeast Asia; Sundaland; threatened species; tropical rivers; Unionidae

INTRODUCTION

Freshwater mussels (Bivalvia: Unionida) are a globally distributed, threatened animal group, providing important ecosystem functions and services in rivers, lakes, and other freshwater environments, especially in the Global South (Zieritz *et al.* 2018a, 2022, Aldridge *et al.* 2023). Barring a limited number of records from the 19th and early 20th century, research on freshwater mussel diversity and distribution in the biodiversity hotspot Sundaland

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(= Malay Peninsula, Sumatra, Borneo, Java, and numerous smaller islands; Fig. 1A) had been neglected until recently. Since 2015, a series of studies focusing on the Malay Peninsula and parts of Borneo have profoundly changed our understanding of this fauna (Zieritz *et al.* 2016, 2018b, 2020, 2021, 2024b, Gallardo *et al.* 2018, Zieritz and Lopes-Lima 2018). Specifically, field surveys and integration of local ecological knowledge, and morphological, molecular, and environmental data, led to the detection of a new genus,

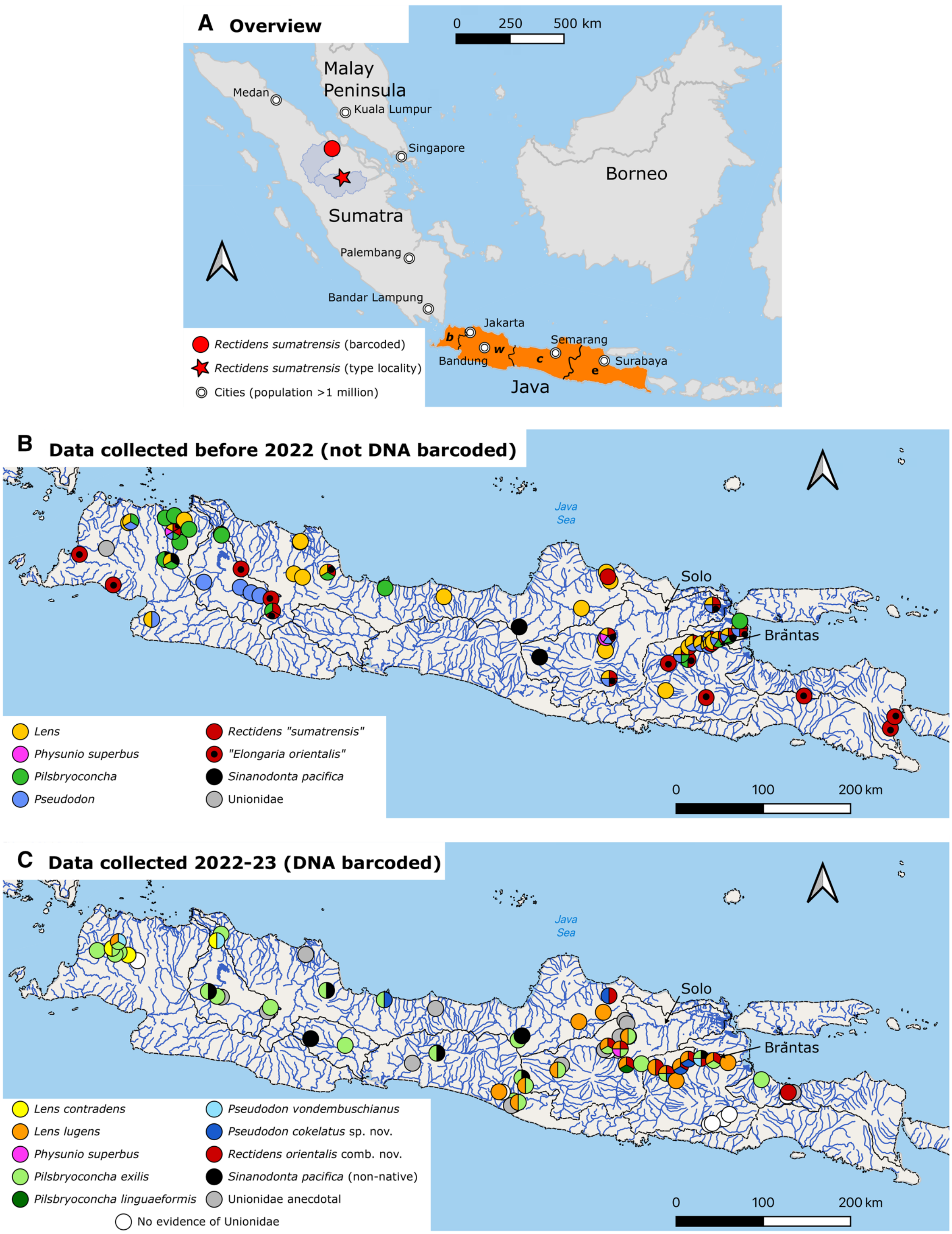

Figure 1. Maps of study area and relevant freshwater mussel (Bivalvia: Unionida) records. A, major land masses comprising the biodiversity hotspot Sundaland, showing study region (Java) in orange, including the major provinces Banten (***b***), West Java (***w***), Central Java (***c***), and East Java (***e***), and the *Rectidens sumatrensis* (Dunker, 1852) record from the type locality in Sumatra. B–C, freshwater mussel records (B) available from museum collections (Graf and Cummings 2025) and publications (< 1900 to 2015, i.e. Van Benthem Jutting 1953; Affandi *et al.* 2013a; Marwoto and Isnaningsih 2014; Bolotov *et al.* 2016), and (C) collected during fieldwork in 2022–23. HydroBASINS level 6 shown as dashed lines (Lehner & Grill 2013).

five new species, and ancient endemic lineages, and revealed considerable losses in species ranges and habitat due to the effects of deforestation, land-use conversion to palm oil monocultures, urbanization, and other human threats. However, for large parts of Sundaland, including the islands of Java and Sumatra, freshwater mussel diversity and distribution has never been examined in a modern context (Sahidin *et al.* 2021).

The freshwater mussels of Java are historically relatively well studied when compared to other parts of Sundaland. Available data are largely based on Van Benthem Jutting's (1953) study of this fauna across the island. Also noteworthy is Affandi *et al.*'s (2013a, b) survey of a section of the Brantas River, and Marwoto and Isnaningsih (2014) who provide records from a number of lakes. Based on these works and available museum records, six species in as many genera are currently considered native to Java, namely *Elongaria orientalis* (Lea, 1840), *Lens contradens* (Lea, 1838), *Physunio superbus* (Lea, 1843), *Pilsbryoconcha exilis* (Lea, 1838), *Pseudodon vondembuschianus* (Lea, 1840), and *Rectidens sumatrensis* (Dunker, 1852) (Graf and Cummings 2025). The type locality for these species is 'Java' apart from *R. sumatrensis*, with the type locality 'Danau Luar, Sumatra', and *Ph. superbus*, with the type locality 'New Holland' [but note that this type locality is probably incorrect, as it likely refers to Australia from where the type specimen was sent but not collected; see Lea (1838: 281)] (Table 1). All of the species appear to have a wide distribution across Java (Fig. 1B). In addition, *Sinanodonta pacifica* (Heude, 1878) was first introduced to Java from Taiwan around 1970 through fish parasitized by mussel larvae (Douda *et al.* 2025 and references therein).

Apart from three published DNA sequences of *Pi. exilis* from Bogor Botanical Garden (GenBank Accession Numbers MZ822408–10), our current understanding of the native freshwater mussels of Java is exclusively derived from species descriptions and identifications based on shell morphology, as no other DNA sequence data are available to date. This is problematic, as freshwater mussels display high morphological (phenotypic) plasticity within species and convergences among species (Zieritz *et al.* 2010, Keogh *et al.* 2025). As a result, inclusion of DNA sequence data has led to revisions of species inventories and the discovery of several new mussel taxa in other parts of Sundaland and beyond (Zieritz *et al.* 2016, 2018b, 2021, 2024b). In addition, available data from Java are generally outdated, and we therefore lack knowledge on current species distributions and how they have been impacted by human activities and environmental change over the past 70 years. Threats to the freshwater mussels of Java can thereby be expected to differ somewhat from other parts of Sundaland. Across large parts of Borneo, Sumatra, and the Malay Peninsula, industrial-scale oil palm plantations have replaced tropical rainforest and are arguably the biggest driver of freshwater mussel population loss (Zieritz *et al.* 2016, 2018b, 2020, 2021, 2024b, Gallardo *et al.* 2018). In contrast, due to its fertile, volcanic soil, Java is densely populated, a global hub for manufacturing industries and dominated by small-scale agriculture (predominantly rice) (Zieritz *et al.* 2024a).

The aim of this work is to provide the first comprehensive modern assessment of the diversity and distribution of the freshwater mussels of Java. Based on data and material collected through fieldwork conducted in 2022 and 2023, and subsequent integrated molecular and morphological analyses of specimens, we (i) provide a species inventory, (ii) describe distribution of species and haplotypes, (iii) assess changes in species distributions since Van Benthem Jutting (1953), (iv) identify the most prevalent threats to this fauna, and (v) provide recommendations for conservation.

MATERIALS AND METHODS

Field surveys

Fieldwork was conducted during 8–18 November 2022 and 30 May–4 July 2023. We surveyed 66 sites across 18 river basins emptying to the north, south, and west of Java (Fig. 1C, Table 1). In addition, we sampled *Rectidens* specimens from near the type locality of *R. sumatrensis* (= Danau Luar, Kampar River basin, Sumatra), i.e. at Rokan River (Fig. 1A). Survey methodology followed Zieritz *et al.* (2020). In brief, where possible, local residents living close to the river or lake were asked about the presence of mussels at the site. Mussels were then sampled by hand. Voucher specimens and tissue snips were collected and preserved in absolute ethanol and deposited at the Museum Zoologicum Bogoriense, Directorat of Scientific Collection Management (DIRI), National Research and Innovation Agency (BRIN). Except for vouchers, all specimens were returned to their habitat.

Species identification, and morphological and phylogenetic analysis

Collected specimens were identified to species level through an integrative morphological-molecular approach. DNA was extracted from foot tissue snips taken from 1–3 specimens per population (i.e. morpho-species per site) for DNA barcoding using the Qiagen DNeasy® Blood & Tissue kit following the manufacturer's protocol. A 658 bp fragment of the female lineages of mitochondrial cytochrome *c* oxidase subunit 1 (*COI*) was amplified and sequenced in both directions from all extracts using the standard primers LCO1490 and HCO2198 (Folmer *et al.* 1994) in 10 µL reactions containing 5.0 µL 10× Green Dye PCR Buffer, 0.5 µL 10 mmol L^{-1} of each primer, 1.0 µL DNA template, and 3.0 µL nuclease free water. Cycle parameters were initial denaturation at 95°C for 5 min, 35 cycles of denaturation at 95°C (50 s), annealing at 52°C (50 s), and extension at 72°C (50 s), and a final extension at 72°C for 5 min. Amplified DNA fragments were purified and sequenced by the commercial company Eurofins Genomics, Ebersberg, Germany. Sequences were assembled in MEGA X (Kumar *et al.* 2018) and deposited in GenBank (Accession Numbers in Supporting Information, Tables S1–S5).

COI phylogenies and species delineation

COI datasets were generated for each of the genera *Lens*, *Pilsbryoconcha*, *Pseudodon*, and *Rectidens*, as well as *Ph. superbus* and *S. pacifica*, for further phylogenetic analysis, phylogeographic interpretation, and species delineation (Supporting Information, Tables S1–S6). For each genus/species, the respective *COI* dataset included all newly sequenced individuals as well as previously published sequences available in GenBank. The *COI* datasets of the genera *Lens*, *Pilsbryoconcha*, *Pseudodon*, and *Rectidens* were analysed using the Maximum Likelihood (ML) method, using IQTREE v.3.0.1 (Minh *et al.* 2020); the *COI* datasets were thereby reduced to unique haplotypes for *Lens*, *Pilsbryoconcha*, and

Table 1. Freshwater mussel (Bivalvia: Unionida) species records per river basin in Java based on fieldwork conducted in 2022–23 and identified by integrated morphological and molecular (COI) analysis. River basins sorted by the location of the mouth in the first instance and from west to east in the second instance. See main text for museum acronyms

		West (Sunda Strait)	North (Java Sea)									South (Indian Ocean)					
Classification	**Type information**	**Liman**	**Cidurian-delta**	**Citarum**	**Bondet**	**Pemali-delta**	**Tuntang**	**Serang**	**Karanggeneng**	**Bengawan Solo**	**Brantas**	**Kali Rejoso**	**Kali Bujel-delta**	**Citanduy**	**Kali Serayu**	**Kali Progo**	**Opak**
Family Unionidae Rafinesque, 1820																	
Subfamily Gonideinae Ortmann, 1916																	
Tribe Contradentini Modell, 1942																	
Lens contradens (Lea, 1838)	Holotype USNM_85185, Java		•	•													
Lens lugens (Drouët & Chaper, 1892)[a]	Holotype MNHN_IM-2000-1701, Borneo		•					•		•	•					•	•
Physunio superbus (Lea, 1843)	Lectotype USNM_83934, New Holland (erroneous)									•							
Tribe Pseudodontini Frierson, 1927																	
Pilsbryoconcha exilis (Lea, 1838)	Figured syntype USNM_86726, Java	•	•	•	•	•	•			•	•	•		•	•		•
Pilsbryoconcha linguaeformis (Morelet, 1875)[a]	Holotype NHMUK_93-2-4-614, Cambodia									•							
Pseudodon vondembuschianus (Lea, 1840)	Holotype USNM_86348, Java		•	•							•						
Pseudodon cokelatus Zieritz, Sumaedi & Marwoto[a]	Holotype MZB. PEL_x884, Sungai Brantas at Sonobekel, Sungai Brantas River basin, Nganjuk Regency, East Java, Java					•			•		•						
Tribe Rectidentini Modell, 1942																	
Rectidens orientalis (Lea, 1840)	Holotype USNM_86058, Java								•	•	•		•				
Subfam. Unioninae Rafinesque, 1820																	
Sinanodonta pacifica (Heude, 1878)	Syntype USNM_472421, Ning-Kouo fou, China			•	•		•							•	•		•

[a]First record of the species in Java.

Rectidens (Supporting Information, Table S1, S3, S5). The best-fit models of nucleotide substitution and partitioning schemes were selected using ModelFinder (Kalyaanamoorthy *et al.* 2017). ML analyses were then performed with an initial tree search, followed by 10 independent runs and 10000 ultrafast bootstrap replicates. Sequences from *Solenaia emarginata*, *Pseudodon mekongi* (see below), *Namkongnaia inkhavilayi*, and *Hyriopsis bialata* were selected as outgroups for phylogenetic analyses of *Lens*, *Pilsbryoconcha*, *Pseudodon*, and *Rectidens*, respectively (Supporting Information, Tables S1, S3–S5).

Three different methods were applied to each of the *Lens*, *Pilsbryoconcha*, *Pseudodon*, and *Rectidens COI* datasets to determine the number of molecular operational taxonomic units (MOTUs). The Barcode Index Number (BIN) system was applied to each *COI* dataset without the outgroup using the Cluster Sequences tool as implemented in BOLD 4 (http://v4.boldsystems.org) (Ratnasingham and Hebert 2013). Automatic Barcode Gap Discovery (ABGD) (Puillandre *et al.* 2012) was applied to the *COI* dataset without the outgroup using the online version implemented in Spart explorer (https://spartexplorer.mnhn.fr), employing the default settings and the Kimura 2-parameter (K2P) distance matrix (Puillandre *et al.* 2021). The third method used haplotype network reconstructions in TCS 1.21 (Clement *et al.* 2000) with a statistical parsimony limit of 95%. MEGA X (Kumar *et al.* 2018) was used to estimate sequence divergence (uncorrected *p*-distance) and examine genetic differentiation between lineages. TCS 1.21 was also used to create haplotype networks for interpreting the phylogeography of *Ph. superbus* and *S. pacifica*, and the following clades of each phylogeny, *Lens contradens* + *L. micropterus* + *L. lugens*, *Pi. exilis*, *Pi. linguaeformis*, *Ps. cokelatus* + *Ps. walpolei*, *Ps. vondembuschianus* and *Rectidens*, with the same parameters as above.

Information on the synonymy of freshwater mussel species from Java is largely based on the MolluscaBase (MolluscaBase 2025) and MUSSELp databases (Graf and Cummings 2021, Graf and Cummings 2025).

Museum acronyms

NHMUK—Natural History Museum, London, United Kingdom; MNHN—Muséum national d'Histoire naturelle, Paris, France; MZB.PEL—Museum Zoologicum Bogoriense (Pelecypoda), Bogor, Indonesia; 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; SMF—Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main, Germany; UMMZ—University of Michigan Museum of Zoology, Ann Arbor, USA; USNM—National Museum of Natural History, Washington, USA; ZMB—Museum für Naturkunde, Berlin, Germany.

RESULTS

Summary of the dataset

Freshwater mussels were collected at 42 of the 66 sites and 16 of the 18 river basins surveyed (Fig. 1C, Table 1; Supporting Information, Tables S1–S6). In addition, anecdotal records for freshwater mussels were obtained from one site of each the Kali Jambe and the Kali Pangkalan, respectively as well as an additional 14 sites from other river basins; these anecdotal records are based on interviews with local people but could not be confirmed by us through physical sampling due to inaccessibility of the site at the time (usually due to high water). No evidence of mussels was found at the remaining eight sites surveyed.

We collected specimens and sequenced at least one specimen for 76 populations (= species-site occurrences), generating 88 novel *COI* sequences from Java. In addition, two *COI* sequences of *Rectidens* collected from Sumatra were generated. *COI*-barcoding and molecular phylogenetic analysis revealed that the dataset from Java comprised eight native species, i.e. *L. contradens*, *Lens lugens* (Drouët & Chaper, 1892), *Ph. superbus*, *Pi. exilis*, *Pilsbryoconcha linguaeformis* (Morelet, 1875), *Pseudodon vondembuschianus*, *Pseudodon cokelatus*, and *Rectidens orientalis* (Table 1). In addition, we recorded the non-native species *S. pacifica*. The highest species richness was found in the Bengawan Solo and the Sungai Brantas, each with a record of five species (Table 1, Fig. 1C).

Family Unionidae Rafinesque, 1820
Subfamily Gonideinae Ortmann, 1916
Tribe Contradentini Modell, 1942

Genus *Lens* Simpson, 1900

Lens specimens were collected from 21 sites, ranging from small irrigation channels to large rivers, and belonged to two species (Figs 1C, 2C; Supporting Information, Table S1). The majority of populations, i.e. 19 of 22 generated *COI* sequences for this genus, fell into the *L. lugens* clade, which is otherwise represented only from specimens collected from Borneo (Fig. 2A). All species delineation methods recovered that clade as a separate species from *L. micropterus*, which is restricted to the Mekong River basin (Pfeiffer *et al.* 2021). *Lens lugens* was collected from one site in the Cidurian basin in the west of Java but appears to be more common and widespread in the east of the island, having been collected from the Serang, the Bengawan Solo, the Brantas, the Kali Progo, and the Kali Opak River basins (Figs 1C, 2C, Table 1; Supporting Information, Table S1). The 19 *COI* sequences generated were distributed across nine haplotypes (Fig. 2A, B), with the geographical distribution of closely related haplotypes largely corresponding to river basins (Fig. 2C). Notable are the distinct haplotype compositions of the adjacent river basins of the Bengawan Solo and Brantas River (Fig. 2C).

The three other *Lens*-sequences fell into the *L. contradens* clade (Fig. 2A). *Lens contradens* was collected from one site in the Citarum River and two sites in the Cidurian basin, both in the western part of the island (Figs 1C, 2C, Table 1; Supporting Information, Table S1), with each sequence representing a separate haplotype (Fig. 2B, C). The *L. contradens* populations from Java were separated from other available sequences of this species by at least seven mutations; all of these were from the main Southeast Asian peninsula, with the most closely related haplotype (LCN8) being restricted to the Pahang River, Peninsular Malaysia (Fig. 2C). All species delineation methods recovered the four specimens from northwestern Peninsular Malaysia (River Muda and Perlis River basins) as a separate species, which we here refer to as *L.* cf. *contradens* (Supporting Information, Table S1). However, the clade comprising all *L. contradens* specimens from mainland Southeast Asia, including the *L.* cf. contradens clade, was poorly resolved, as indicated by a low support value and multiple polytomies (Fig. 2A).

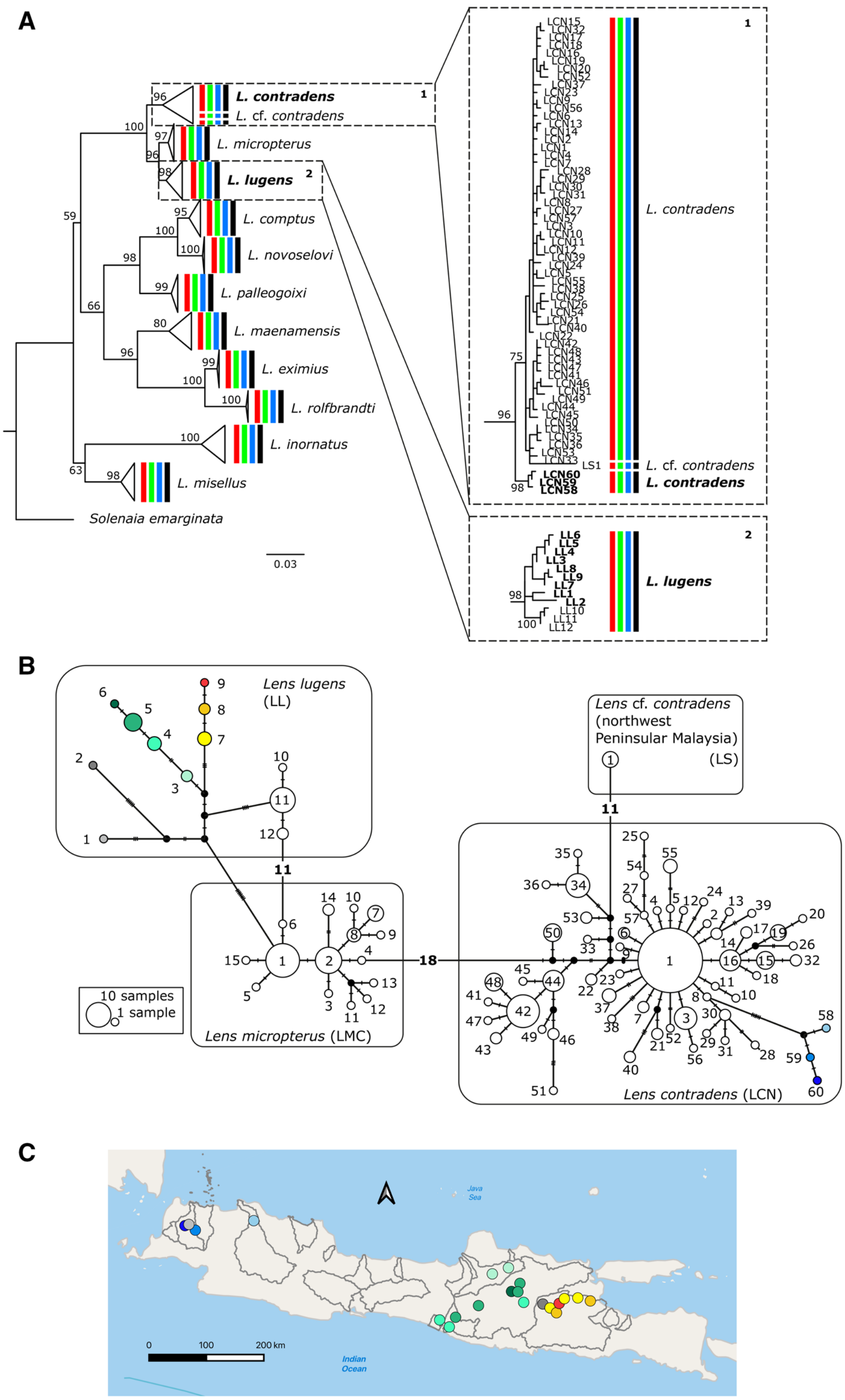

Figure 2. A, phylogenetic tree of *Lens*, and (B) haplotype network and (C) geographical distribution of haplotypes across freshwater basins in Java of the *L. contradens–lugens–micropterus* clade inferred from the COI dataset. Values at nodes indicate Maximum Likelihood ultrafast bootstrap values. Vertical bars correspond to molecular operational taxonomic units by various species delimitation methods: red—TCS (95%); green—ABGD; blue—BINS of BOLD; black—consensus. Haplotypes and taxa present in Java are bold. Map shows hydrobasins that were surveyed in the present study. Haplotypes present in Java are coloured; for details on location(s) of haplotypes, including those outside Java, see Supporting Information, Table S1.

Genus *Physunio* Simpson, 1900

Physunio specimens were collected only from a single site in the Bengawan Solo (Fig. 1C, Table 1; Supporting Information, Table S2). *COI*-barcoding confirmed that the species was *Ph. superbus.* The *COI* sequence from Java represented a new haplotype, which is separated from other known haplotypes from Thailand and the Malay Peninsula by at least nine mutations (Fig. 3). The uncorrected *p*-distance of the Javanese haplotype (PS7) to the most closely related haplotype from Thailand/Malay Peninsula (PS1) was 1.4%.

Tribe Pseudodontini Frierson, 1927

Genus *Pilsbryoconcha* Simpson, 1900

Pilsbryoconcha specimens were collected from 29 sites and belonged to two species. All but one of the 32 newly generated *COI* sequences for this genus fell into the *Pi. exilis* clade (Fig. 4A), which was found in a diversity of habitats, including irrigation and rice paddy channels, small to large rivers, and ponds across 12 different river basins distributed throughout the island (Figs 1C, 4C, Table 1; Supporting Information, Table S3). The 31 new *Pi. exilis* sequences were distributed across nine haplotypes, seven of which had not previously been detected and were therefore unique to Java (Fig. 4B). Haplotype PE14, detected in the Citarum basin, was also known from Peninsular Malaysia and the Chao Phraya basin, and haplotype PE21, detected in the Bengawan Solo and Brantas River basins, was also known from the Chao Phraya basin (Fig. 4B, C; Supporting Information, Table S3). Several haplotypes were widely distributed across the island, whilst others appeared to be restricted to specific regions (e.g. haplotype PE27 in the west, haplotype PE21 in the east). Previously published COI sequences of *Pi. exilis* from Java were restricted to specimens from a pond in the Botanical Gardens, Bogor, and fell into two haplotypes that were also present in mainland Southeast Asia (Fig. 4B; Supporting Information, Table S3).

The other *COI* sequence fell into the *Pi. linguaeformis* clade (Fig. 4A), which was detected only at a single site in the Bengawan Solo (Fig. 4B, C; Table 1; Supporting Information, Table S3). This species has so far been known only from mainland Southeast Asia, including Cambodia, Thailand, and Peninsular Malaysia (Supporting Information, Table S3). The haplotype from Java (PL7) was unique and most closely related to haplotypes from Peninsular Malaysia (Fig. 4B, C; Supporting Information, Table S3).

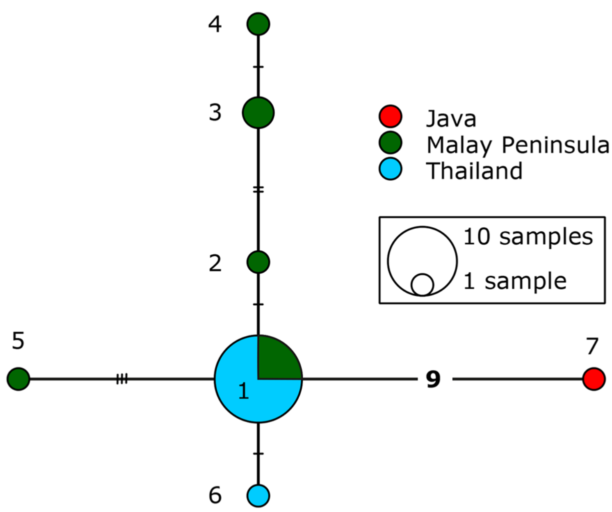

Figure 3. Haplotype network of *Physunio superbus* inferred from the COI dataset [see Supporting Information, Table S2 for full dataset and details on location(s) of haplotypes]. For details on location(s) of haplotypes, including those outside Java, see Supporting Information, Table S2.

Genus *Pseudodon* Gould, 1844

The 10 newly generated *COI* sequences for this genus fell into two different species-level clades, which we here recognize as *Ps. vondembuschianus* and *Ps. cokelatus* (Fig. 5A; Supporting Information, Table S4).

Pseudodon vondembuschianus has to date been considered to be a common and widely distributed species across Southeast Asia. However, none of the specimens collected from the type locality, Java, fall into this clade. In contrast, collected specimens from Java that fall into the clade currently considered as *Pseudodon cambodjensis* (Petit de la Saussaye, 1865) (= *Ps. vagulus sensu* Bolotov *et al.* 2023) (Zieritz *et al.* 2016, Pfeiffer *et al.* 2021, Jeratthitikul *et al.* 2025) morphologically conformed with the type specimen of *Ps. vondembuschianus* (type locality Java; Fig. 6). *Pseudodon vondembuschianus* (= *Ps. cambodjensis*) is therefore currently known from Java, the Malay Peninsula and the Mae Klong, Chao Phraya, and Mekong River basins in Indochina (Supporting Information, Table S4; Jeratthitikul *et al.* 2025). The species previously considered *Ps. vondembuschianus* (Bolotov *et al.* 2023, Jeratthitikul *et al.* 2025) is here considered to be *Ps. mekongi* (see Taxonomic account for detail). On Java, we found *Ps. vondembuschianus* in small to mid-sized rivers, including channelized rivers, in three different basins, i.e. Cidurian, Citarum, and Brantas River (Figs 1C, 5C). Each sequenced specimen from that species represented a unique haplotype, with the Javanese haplotypes forming a cluster in between haplotypes from the Malay Peninsula (PV1–3) and the Malay Peninsula and the Mekong River basin (PV8 + 9) (Fig. 5B; Supporting Information, Table S4).

The second *Pseudodon* species present in Java had not been detected previously and was here named *Ps. cokelatus* (Fig. 6). *Pseudodon cokelatus* was sister to *Ps. walpolei*, which is endemic to Borneo (Bolotov *et al.* 2023) (Fig. 5A) and from which it was separated by all species delineation methods except ASAP, separated by 3.9% (*COI* uncorrected *p*-distance). However, in our phylogenetic tree, based only on partial *COI*-sequences, the species was not recovered as a monophyletic clade (Fig. 5A). *Pseudodon cokelatus* was found in small streams to large rivers, including channelized and dredged rivers, in three basins, i.e. the Brantas River, Kali Karanggeneng, and Kali Malang in the Pemali delta, each with a unique haplotype composition (Fig. 5C; Supporting Information, Table S4).

Whilst no *Pseudodon* specimens were found in the Bengawan Solo, historical records indicate presence of at least one *Pseudodon* species in that river basin (e.g. lot SMF_14736) (Van Benthem Jutting 1953).

Tribe Rectidentini Modell, 1942

Genus *Rectidens* Simpson, 1900

Rectidens specimens were detected at 11 sites across four river basins, all in the eastern part of the island (Figs 1C, 7C, Table 1; Supporting Information, Table S5). The two newly generated *COI* sequences from specimens from near the *R. sumatrensis* type locality in Sumatra (Fig. 1A) formed a separate *R. sumatrensis* haplotype (RS10), which clustered with haplotype RS3, restricted to the Perak River basin, Malay Peninsula (Fig. 7A, B; Supporting Information, Table S5). All 17 newly generated *COI* sequences from Java, including morphotypes conforming with the type specimen of *Elongaria orientalis* (Fig. 8), clustered within the *Rectidens* clade and are here considered *R. orientalis* (Fig. 7A; see Taxonomic account for detail).

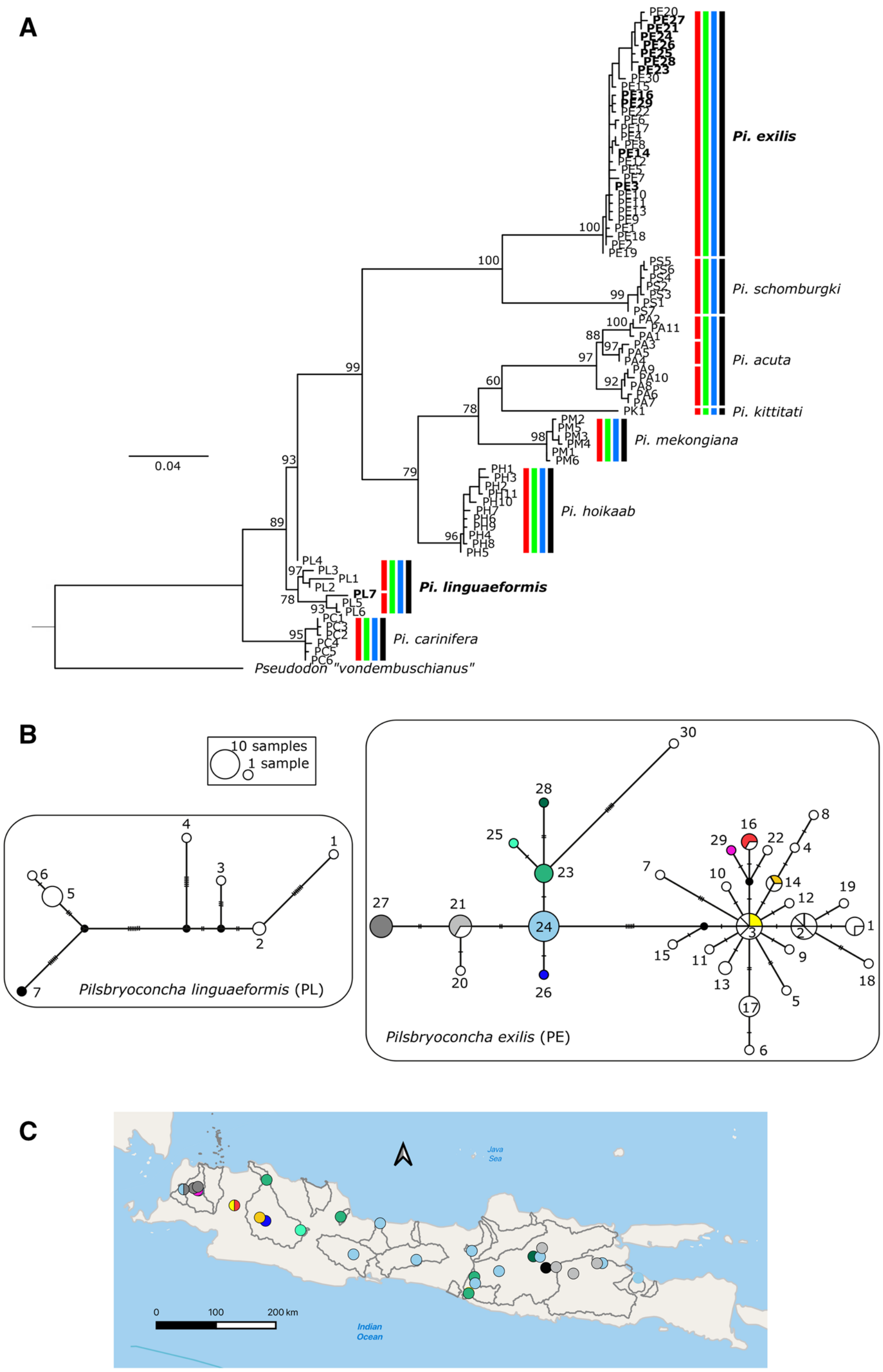

Figure 4. A, phylogenetic tree of *Pilsbryoconcha*, (B) haplotype networks of *Pi. linguaeformis* and *Pi. exilis*, and (C) geographical distribution of these haplotypes across freshwater basins in Java inferred from the COI dataset. Values at nodes indicate Maximum Likelihood ultrafast bootstrap values. Vertical bars correspond to molecular operational taxonomic units by various species delimitation methods: red—TCS (95%); green—ABGD; blue—BINS of BOLD; black—consensus. Haplotypes and taxa present in Java are bold. Map shows hydrobasins that were surveyed in the present study. Haplotypes present in Java are coloured; for details on location(s) of haplotypes, including those outside Java, see Supporting Information, Table S3.

The species exhibited extensive variability in shell morphology, including shape and dentition (Fig. 8). Habitats of *R. orientalis* ranged from small streams to large rivers, such as the mainstem Bengawan Solo and Brantas River. The 17 *COI* sequences were distributed across seven haplotypes (Fig. 7B). Of these, RS1 was the most common and the only one that was detected at more than one site (Fig. 7B).

Subfamily Unioninae Rafinesque, 1820
Tribe Anodontini Rafinesque, 1820

Genus *Sinanodonta* Modell, 1945
(**Fig. 9**)

Sinanodonta was collected at six sites from as many river basins in Java (Fig. 1, Table 1; Supporting Information, Table S6). Habitats

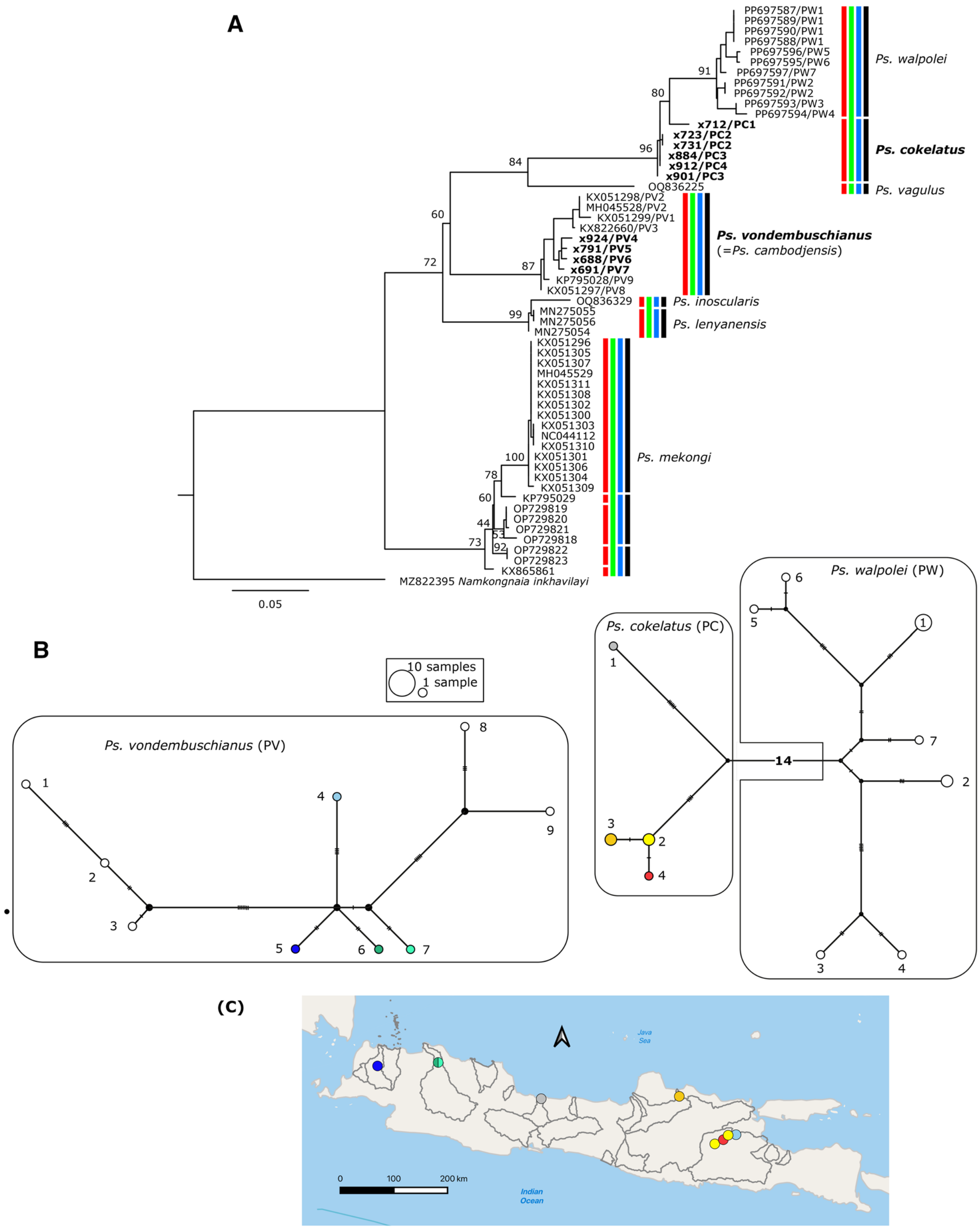

Figure 5. A, phylogenetic tree of *Pseudodon*, (B) haplotype networks of *Ps. vondembuschianus* and *Ps. cokelatus* + *Ps. walpolei*, and (C) geographical distribution of these haplotypes across freshwater basins in Java inferred from the COI dataset. Values at nodes indicate Maximum Likelihood ultrafast bootstrap values. Vertical bars correspond to molecular operational taxonomic units by various species delimitation methods: red—TCS (95%); green—ABGD; blue—BINS of BOLD; black—consensus. Specimens, haplotypes and taxa present in Java are bold. Map shows hydrobasins that were surveyed in the present study. Haplotypes present in Java are coloured; for details on location(s) of haplotypes, including those outside Java, see Supporting Information, Table S4.

included several fish ponds, a rice paddy channel, and a canal. All of the six newly generated *COI* sequences fell into haplotype 10, which is also known from Taiwan, where it is possibly native, as well as Malaysia, Singapore, the Philippines, Japan, Costa Rica, and the Indonesian island of Flores (Fig. 9).

TAXONOMIC ACCOUNTS

Pseudodon vondembuschianus (Lea,1840) stat. rev. (Fig. 6)

= *Margaritana vondenbuschiana* Lea, 1840: 288 (incorrect original spelling; holotype USNM_86348; type locality: Java).

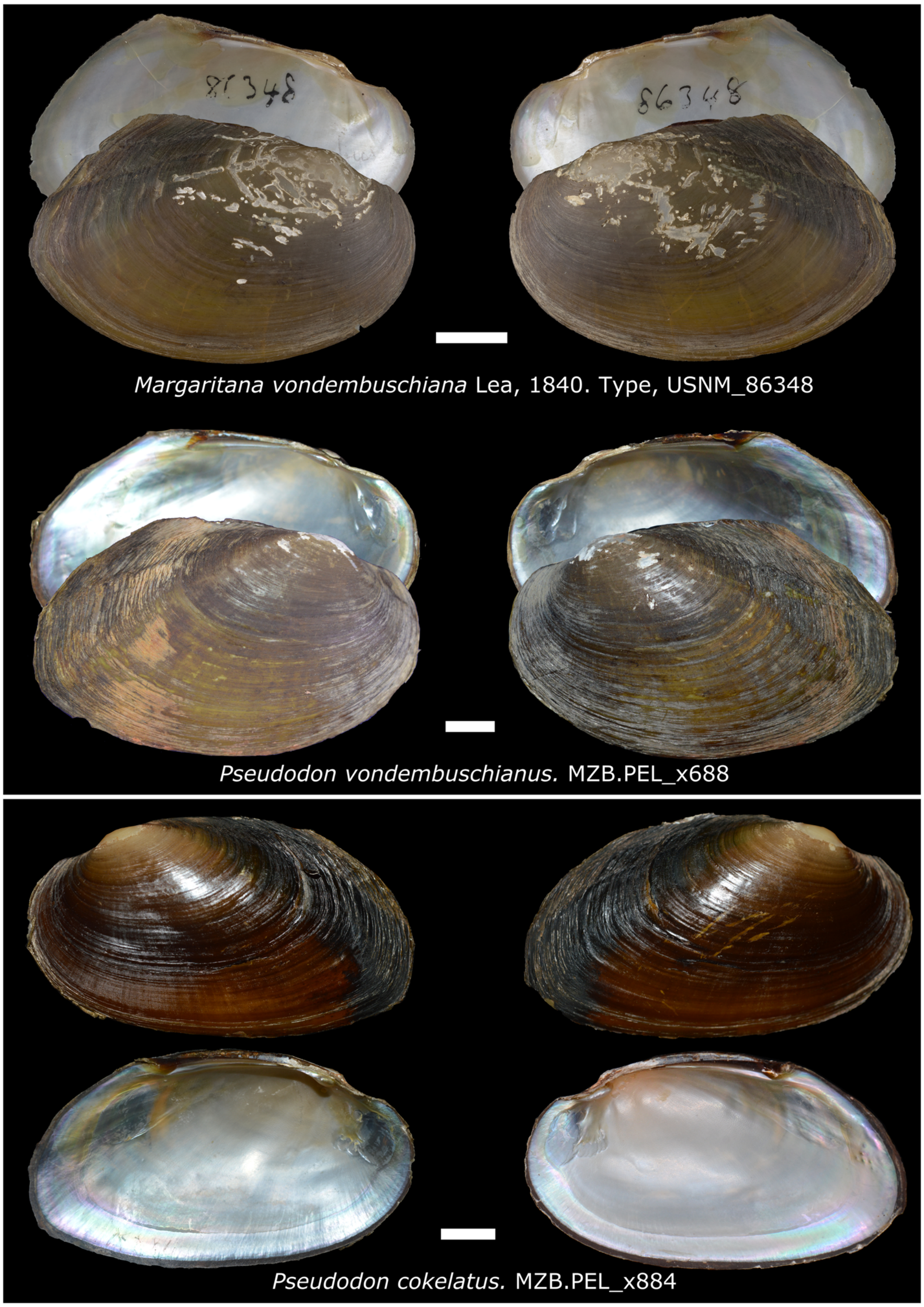

Figure 6. Type and sequenced specimen of *Pseudodon vondembuschianus* (Lea, 1840) (=*Margaritana vondembuschiana* Lea, 1840), and holotype of *Pseudodon cokelatus*, Sungai Brantas at Sonobekel, Sungai Brantas River basin, Nganjuk Regency, East Java, Java. See main text for museum acronyms. White bars indicate 1 cm scale.

= *Alasmodonta zollingeri* Mousson, 1849: 96, pl. 18, figs 1–2 [junior subjective synonym; syntype SMF_4685/1; type locality: Indonesia, 'aus der Gegend von Tjikoja' (Chikuya, 7.05° S, 108.83° E)].
= *Alasmodonta crispata* Mousson, 1849: 97, pl. 19, fig. 1 [junior subjective synonym; syntype SMF_316475/1; the protologue does not contain information on the type locality; Nagel (2025) assumed that the type series was sampled together with *Alasmodonta zollingeri* and that the type locality could be proposed as 'Indonesia, Chikuya (= Cikuya, Brebes Regency, Java), 7.05° S, 108.83° E'].
= *Monocondyloea planulata* Lea, 1859 (junior subjective synonym; holotype USNM_86351; type locality: Java).
= *Margaritana vondembuschiana* Lea, 1870: 73 (basionym; correct name for *Margaritana vondenbuschiana*).
= *Margaritana fragilis* Küster, 1862: 295, pl. 98, fig. 2 (junior subjective synonym; type: whereabouts unknown; type locality: Java).
= *Monocondylea cambodjensis* Petit de la Saussaye, 1865: 16, pl. 4, fig. 4 [new junior subjective synonym; syntypes MNHN_IM-2000-34622; type locality: 'Cambodje (Battambang)' (= Battambang Province, Mekong River basin, Cambodia)].

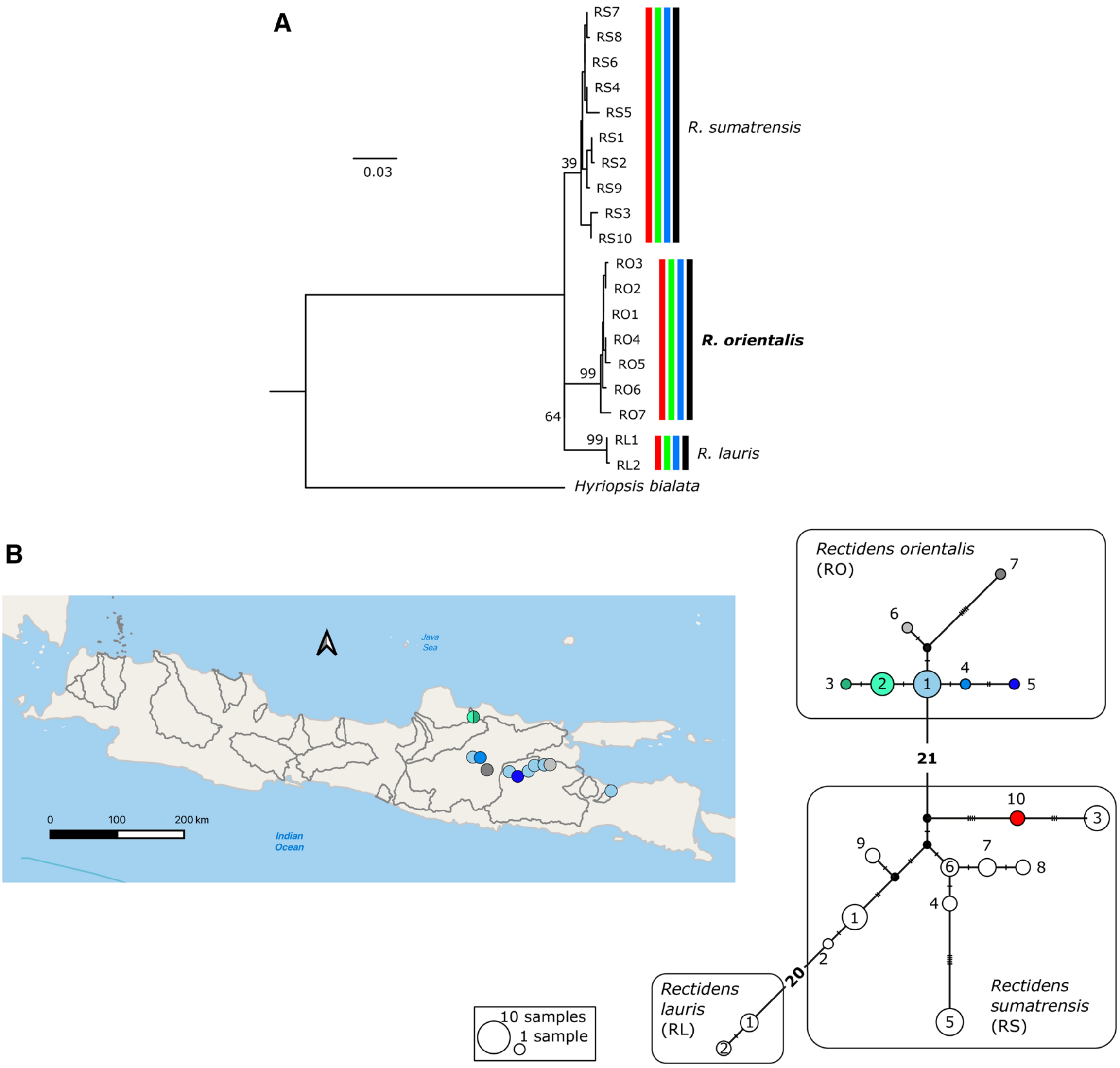

Figure 7. A, phylogenetic tree, and (B) haplotype network of *Rectidens* inferred from the COI dataset, including geographical distribution of these haplotypes across freshwater basins in Java. Values at nodes indicate Maximum Likelihood ultrafast bootstrap values. Vertical bars correspond to molecular operational taxonomic units by various species delimitation methods: red—TCS (95%); green—ABGD; blue—BINS of BOLD; black—consensus. Map shows hydrobasins that were surveyed in the present study. Taxa present in Java are bold. Haplotypes present in Java (RO1–7) and Sumatra (haplotype RS10) are coloured; for details on location(s) of haplotypes, including those outside Java, see Supporting Information, Table S5.

= *Monocondylus orbicularis* Morelet, 1866: 167 [new junior subjective synonym; syntype NHMUK_93-2-4-1982; type locality: 'Battambang, Siam' (= Battambang Province, Mekong River basin, Cambodia) based on the holotype's label and Morelet (1875: 339)].
= *Microcondylaea hageni* Strubell, 1897: 8 {junior subjective synonym; lectotype SMF_3580/1 [illustrated by Nagel (2025: 177, fig. 181)]; type locality: South Sumatra}.
= †*Unio trinilensis* Dubois, 1908: 1249, pl. 39, fig. b [junior subjective synonym; type: whereabouts unknown; type locality: 'Hauptknochenschicht' deposits at Trinil site, 7.3667° S, 111.3500° E, Middle Pleistocene (^{40}Ar/^{39}Ar maximum and minimum age of 0.54 and 0.43 Mya, respectively), Solo River valley, Ngawi Regency, East Java, Indonesia (Van Benthem Jutting 1937, Joordens *et al.* 2015, Bolotov *et al.* 2023)].
= *Pseudodon* (*Trigonodon*) *vandervlerki* Oostingh, 1935: 164, fig. 19 [junior subjective synonym; type: whereabouts unknown; type locality: Kali Glagah beds at Boemiajoe, approximately 7.2620° S, 108.9864° E, Early Pleistocene (age *c.* 1.8 Mya), Kaliglagah Formation, Bumiayu District, Brebes Regency, Central Java, Indonesia (Van Benthem Jutting 1937, Bolotov *et al.* 2023, Gibran *et al.* 2023).

Distribution: Widespread in Indochina (Mekong, Chao Phraya, and Mae Klong River basins), Malay Peninsula, Java and, probably, Sumatra (Zieritz *et al.* 2016, Bolotov *et al.* 2023, Jeratthitikul *et al.* 2025). There are two fossil subspecies from Java: †*Pseudodon vondembuschianus vandervlerki* Oostingh, 1935 (Early Pleistocene, Central Java) and †*Pseudodon vondembuschianus trinilensis* Dubois, 1908 (Middle Pleistocene of East Java) (Van Benthem Jutting 1937, Joordens *et al.* 2015, Bolotov *et al.* 2023).

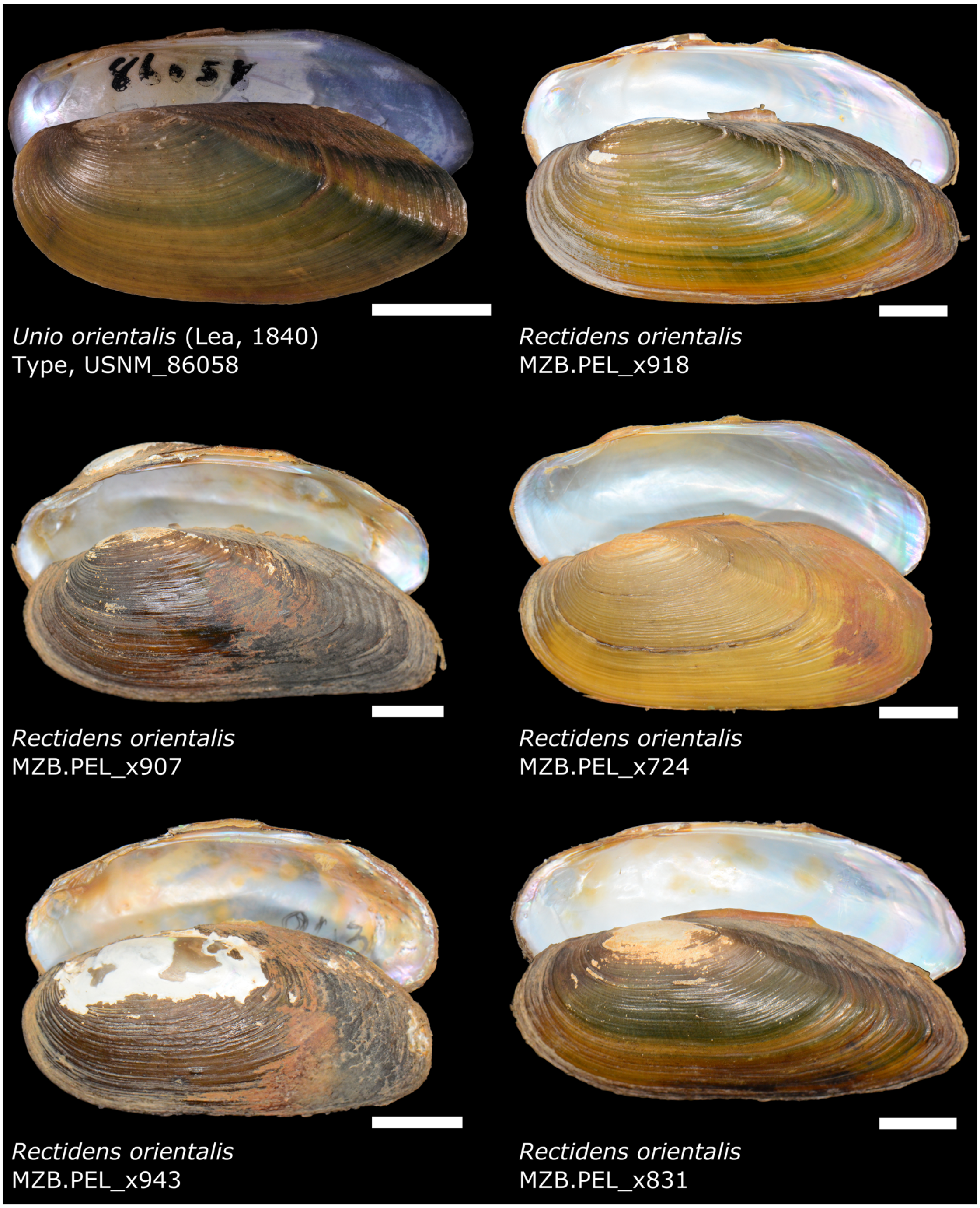

Figure 8. Type and sequenced specimens of *Rectidens orientalis*. See Supporting Information, Table S5 for detailed location information of specimens. See main text for museum acronyms. White bars indicate 1 cm scale.

Remarks: Here we show that topotypes of *Ps. vondembuschianus* from Java genetically cluster with the clade of *Ps. cambodjensis/Ps. orbicularis* (Fig. 5). Based on this data, we propose a new synonymy as follows: *Ps. vondembuschianus* (= *Ps. cambodjensis* syn. nov.; = *Ps. orbicularis* syn. nov.). In turn, several taxa from mainland Southeast Asia, previously linked to *Ps. vondembuschianus* as its sister species or subspecies (Bolotov *et al.* 2023, Jeratthitikul *et al.* 2025), are reconsidered as *Ps. mekongi* (see below).

Pseudodon mekongi (Bolotov *et al.* 2020) stat. rev. (= *Ps. vondembuschianus* auct. non Lea, 1840)

= *Monodontina mekongi* Bolotov *et al.*, 2020: 11, figs 3E, 5A (basionym; holotype RMBH_biv0122; type locality: headwater of the Phong River, 16.8616° N, 101.9105° E, Mekong Basin, Thailand).
= *Monodontina laosica* Bolotov *et al.*, 2020: 11, figs 3C, 5A (junior subjective synonym; holotype UMMZ_304650; type locality: *c.* 300 m upstream of the mouth of Houai Pin Stream, 14.7944° N,

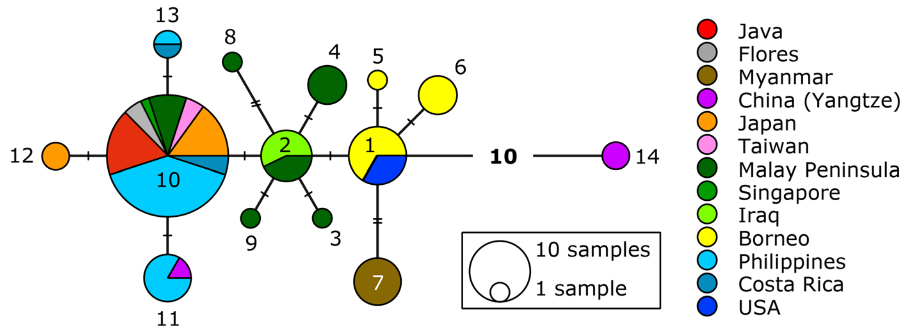

Figure 9. Haplotype network of *Sinanodonta pacifica* inferred from the COI dataset. For details on location(s) of haplotypes, including those outside Java, see Supporting Information, Table S6.

106.4842° E, a tributary of the Vang Ngao River, Mekong Basin, Laos).

= *Monodontina vondembuschiana tapienica* Konopleva *et al.*, 2022: 15, fig. 3A–L (junior subjective synonym; holotype RMBH_biv1272/1; type locality: Main Klong Min, Tapi River basin, Tambon Kaew San, Nabon District, Nakhon Si Thammarat Province, 8.2997° N, 99.5580° E, southern Thailand).

= *Monodontina vondembuschiana thasaenica* Konopleva *et al.*, 2022: 16, fig. 3M–T (junior subjective synonym; holotype RMBH_biv1321/1; type locality: Main Klong Thasae, Tha Taphao River Basin, nearby Wat Na Srang, Thasae District, Chumphon Province, 10.6753° N, 99.1737° E, southern Thailand).

Distribution: Widespread in Indochina, especially in the Mekong, Chao Phraya, and Bang Pakong River basins, and several basins in southern Thailand and the Malay Peninsula (Zieritz *et al.* 2016, Bolotov *et al.* 2020, Bolotov *et al.* 2023, Konopleva *et al.* 2022, Jeratthitikul *et al.* 2025). Presence in Sumatra uncertain.

Remarks: The recent taxonomic history of this clade is rather complicated. *Monodontina mekongi* (Phong River, Mekong Basin, Thailand) and *M. laosica* (Vang Ngao River, Mekong Basin, Laos) were described as separate species sister to *M. vondembuschiana* based on a sufficient genetic distance between these lineages (Bolotov *et al.* 2020). Two additional lineages from southern Thailand were considered subspecies of *M. vondembuschiana* (Konopleva *et al.* 2022). Later on, it was established that *Monodontina* was a synonym of *Pseudodon* (Bolotov *et al.* 2023). *Pseudodon vondembuschianus* was delineated to several subspecies such as the nominate subspecies (Malaysia, Java, and Sumatra), *Ps. vondembuschianus laosicus* (Bolotov *et al.*, 2020) (Mekong River basin in Laos), *Ps. vondembuschianus tapienicus* (Konopleva *et al.*, 2022) (Tapi River basin in southern Thailand), *Ps. vondembuschianus thasaenicus* (Konopleva *et al.*, 2022) (Tha Taphao River basin in southern Thailand), †*Ps. vondembuschianus vandervlerki* Oostingh, 1935 (Early Pleistocene, Central Java), and †*Ps. vondembuschianus trinilensis* (Dubois, 1908) (Middle Pleistocene of East Java) (Bolotov *et al.* 2023). Jeratthitikul *et al.* (2025) collected a large dataset of new DNA sequences from Indochina and found that the recent subspecies and *Ps. mekongi* do not show clear distinctiveness on phylogenetic trees. Based on this evidence, it was suggested to consider *Ps. mekongi*, *Ps. vondembuschianus laosicus*, *Ps. vondembuschianus tapienicus*, and *Ps. vondembuschianus thasaenicus* as synonyms of the widespread species *Ps. vondembuschianus* (Jeratthitikul *et al.* 2025). Here, we show that these taxa do not belong to *Ps. vondembuschianus* at all, being representatives of a separate species. The oldest available names for this species are *Ps. mekongi* and *Ps. laosicus*. These names were introduced in the same paper (Bolotov *et al.* 2020). Our First Reviser action on the precedence of simultaneous synonyms: *Ps. mekongi* over *Ps. laosicus*.

Pseudodon cokelatus Zieritz, Sumaedi & Marwoto, sp. nov. (Fig. 6)

ZooBank registration: urn:lsid:zoobank.org:act:7961F505-634C-4D6E-A54A-49505659E131.

Type and type locality: Holotype, MZB.PEL_x884. Indonesia: Sungai Brantas at Sonobekel, Sungai Brantas River basin, Nganjuk Regency, East Java, Java. 31 May 2023. Collectors: Marwoto M.R., Ghivany R.S., Zieritz A. (Fig. 6).

Type material: Paratypes, MZB.PEL_x882, MZB.PEL_x883, MZB.PEL_x885. Indonesia: type locality, same collecting date and collectors, three specimens.

Material examined: MZB.PEL_x712, MZB.PEL_x713, MZB.PEL_x714, MZB.PEL_x723, MZB.PEL_x729, MZB.PEL_x730, MZB.PEL_x731, MZB.PEL_x732, MZB.PEL_x882, MZB.PEL_x883, MZB.PEL_x884, MZB.PEL_x885, MZB.PEL_x901, MZB.PEL_x912, SMF_4685, USNM_86351.

Diagnosis: Morphologically and genetically similar to *Pseudodon walpolei* but differs from it by a less pronounced posterior wing. It can also be distinguished from *Ps. walpolei* based on a minimum of 21 nucleotide substitutions in the *COI* gene fragment. Different to the potential synonyms (i) *Alasmodonta crispata* Mousson, 1849, which has a more convex ventral margin, a straighter dorsal margin, and a higher shell in the posterior half compared to the rather parallel dorsal and ventral margins of *Ps. cokelatus*; (ii) *Alasmodonta zollingeri* Mousson, 1849, (iii) *Monocondyloea planulata* Lea, 1859, and (iv) *Margaritana fragilis* Küster, 1862, which all have a more pronounced posterior wing with two intermediate ridges, typical of *Ps. vondembuschianus*. In addition, the type specimen of *A. zollingeri* and presumably *A. crispata* was collected from Tjikoya (= Cikoya), Banten (see Taxonomic accounts for details), where we collected only *Ps. vondembuschianus*.

Description: Specimen length 46–73 mm; height 27–43 mm; width 14–20 mm. Shell elliptical, inequilateral, moderately thick, rounded anteriorly, slightly truncated posteriorly; dorsal margin slightly curved, ventral margin slightly curved or straight. The umbones slightly elevated, with two radial rows of nodulous sculpture. Marked muscle attachment scars drop shaped and confluent. Periostracum dark brown, smooth; nacre whitish. One short, moderately thick pseudocardinal in each valve.

Distribution: Known from the Pemali-delta, Kali Karanggeneng, and Sungai Brantas River basins in Central and East Java.

Etymology: The species is named after its dark brown colour using the Bahasa Indonesian word '*cokelat*', meaning 'brown'.

Rectidens orientalis (Lea,1840) comb. rev.

(Fig. 8)

= *Unio orientalis* Lea, 1840: 285 (basionym; holotype USNM_86058; type locality: Java).
= *Unio productus* Mousson, 1849: 93, pl. 17, figs 3–5 (unavailable name; homonym of *Unio productus* Conrad, 1836).
= *Margaron* (*Unio*) *productior* Lea, 1852: 29 (junior subjective synonym; new name for *Unio productus* Mousson, 1849).
= ? *Unio bithynicus* Kobelt, 1893: 96, pl. 179, fig. 1128 (junior subjective synonym; type: whereabouts unknown; type locality: 'im vorderen Kleinasien' [= in the eastern part of Asia Minor; probably erroneous]).

Distribution: Known only from Java.

Remarks: Simpson (1900) placed *Unio orientalis* in the genus *Nodularia* Conrad, 1853. Frierson (1911: 98) stated that '*Nodularia orientalis* Lea is placed by Mr Simpson in this genus, it is true, as he observes, with much doubt because of paucity of material. This shell, however, both by its geographical distribution as well as by its whole facies, belongs to the genus *Rectidens*'. Haas (1911) described a new genus, *Elongaria* Haas, 1911, for this species. Our new phylogenetic data inferred from topotypes of this species reveals that Frierson's hypothesis was correct and that the genus *Elongaria* becomes a junior subjective synonym of *Rectidens*.

The case of *Elongaria trompi* (Drouët & Chaper, 1892), the second species of this genus, is more complicated due to some morphological inconsistences and the lack of DNA sequences. This species is endemic to the Kapuas River basin on Borneo but has not been recorded there for over a century (Zieritz *et al.* 2024b). Pfeiffer *et al.* (2018) concluded that *Elongaria trompi* clearly resembles members of the subfamily Parreysiinae (especially Indochinellini) with which it shares a straight ventral margin and similar sculpturing on the shell disc. Conversely, Parreysiinae representatives seem to be confined to fragments of the former supercontinent Gondwana with a few dispersal events to Indochina (Bolotov *et al.* 2022, 2024b). At first glance, we can simply transfer this nominal species to *Rectidens*, but this action has little justification because of specific conchological traits. Meanwhile, it is the type species of the subgenus *Elongaria* (*Nannonaia*) Haas, 1913 (Haas 1913). In this situation, we choose to elevate *Nannonaia* stat. rev. to the full generic rank and to propose *Nannonaia trompi* (Drouët & Chaper, 1892) comb. rev. This taxonomic opinion needs to be checked in the future on the basis of DNA sequences, if this species has not become extinct due to a human-mediated loss of habitats (Zieritz *et al.* 2024b). This taxon is the name-bearing type of the tribe Nannonaiini Modell, 1942 (Pfeiffer *et al.* 2018) and may represent an ancient relict lineage, as do some other Bornean freshwater mussels (Zieritz *et al.* 2021, 2024b).

DISCUSSION

Freshwater mussel species inventory of Java

Our results have led to significant changes in our understanding of the freshwater mussel fauna of Java, with implications on taxa outside the study region. Specifically, we confirm the presence of *L. contradens*, *Ph. superbus*, *Pi. exilis*, and *Ps. vondembuschianus* in Java, provide records of four additional species, namely *L. lugens*, *Pi. linguaeformis*, *Ps. cokelatus*, and *R. orientalis*, and revise the taxonomic identity and distribution ranges of *Ps. vondembuschianus*, *Ps. mekongi*, *E. orientalis*, *E. trompi*, and *R. sumatrensis*. Two species, *Ps. cokelatus* and *R. orientalis*, are currently known only from Java.

Lens

Lens is represented by two species on Java. *Lens contradens* has a wide distribution across Southeast Asia, currently believed to range from the northern tributaries of the Mekong and Chao Phraya River basins to the eastern and western basins of the Malay Peninsula, Sumatra, and Java (Zieritz *et al.* 2016, Pfeiffer *et al.* 2021). As expected, the Javanese populations, restricted to the west of the island, are genetically distant from populations from mainland Southeast Asia. However, DNA sequences from Sumatra and Borneo—if the species is present on these islands—will be needed to provide a full understanding of the historical connections of populations across its whole distribution range. Addressing these questions will require dedicated surveys in yet unexplored areas of Sundaland, particularly in rivers of southern Sumatra and southern Borneo historically connected with Javanese river basins through the East Sunda palaeo-basin (Cheng and Faidi 2025). Resolving the phylogenetic history and ultimately, taxonomy of *L. contradens*, including *L.* cf. *contradens* and the clade representing only Javanese specimens, will additionally require a larger dataset comprising multiple genes.

Lens lugens was previously considered to be endemic to Borneo (Pfeiffer *et al.* 2021, Zieritz *et al.* 2024b), with DNA sequence data being available from 15 specimens across a site in the Batang Sadong River basin and several tributaries and sites of the Kapuas River basin (Supporting Information, Table S1) (Zieritz *et al.* 2024b). Our results reveal the presence of *L. lugens* in Java, where it is widely distributed. Based on currently available data, genetic variability of the species appears to be considerably higher in Java than in Borneo, but targeted surveys in southern Borneo and Sumatra are needed for a more complete understanding of the historical connections and origins of populations.

Physunio

Physunio superbus is widely distributed across Southeast Asia, from the Chao Phraya River in the north to the eastern basins of the Malay Peninsula, Sumatra and ultimately, Java in the south (Zieritz *et al.* 2016, Pfeiffer *et al.* 2021). No records of the genus are available from Borneo to date (Pfeiffer *et al.* 2021). On Java, *Ph. superbus* appears to be rare and possibly restricted to the Bengawan Solo, although there are historical records from Jakarta (e.g. lot SMF_14736) (Van Benthem Jutting 1953).

Pilsbryoconcha

Pilsbryoconcha is represented by two species on Java. *Pilsbryoconcha exilis* has a particularly wide distribution across Southeast Asia, ranging from the northern tributaries of the Chao Phraya and Mekong River basins in the north to the eastern and western basins of the Malay Peninsula, and Sumatra and Java in the south (Zieritz *et al.* 2016, Jeratthitikul *et al.* 2022). In Java, *Pi. exilis* is arguably the most common freshwater mussel species. Although some of the haplotypes restricted to or present in Java are visibly clustered in the network, several other haplotypes present in Java are shared across geographically distant locations (e.g. haplotype PE3 present across several river basins and ponds in Thailand, Malaysia, and Java), suggesting human dispersal either directly or via host fish.

The second species, *Pi. linguaeformis*, is currently known from the lower Mekong (specifically, Tonle Sap) in Cambodia, the Bang Pakong River in Thailand (Jeratthitikul *et al.* 2022), several basins of the Malay Peninsula (Zieritz *et al.* 2016), and the Bengawan Solo in Java. The considerable genetic distances among haplotype-clusters in the Bang Pakong and Mekong River basins in Indochina (PL2–4), the Malay Peninsula (PL5–6) and Java (PL7) indicate that these represent naturally distributed populations. However, human dispersal cannot be eliminated as a potential driver of this distribution and is indeed the likely reason for the presence of the 'Indochina' haplotype PL1 in a fish pond in Peninsular Malaysia (Zieritz *et al.* 2016).

Pseudodon

Following our revision of the taxonomic identity of *Ps. vondembuschianus* (= *Ps. cambodjensis*), this species has a disjunct distribution comprising the Mekong, Chao Phraya, and Mae Klong River basins (Bolotov *et al.* 2023, Jeratthitikul *et al.* 2025), several western and eastern basins of the Malay Peninsula (Zieritz *et al.* 2016), and several basins in western and eastern Java. Whilst Javanese haplotypes were clustered and distinct from haplotypes in mainland Southeast Asia, DNA sequences from Sumatra and Borneo—if present on these islands—will be needed to provide a full understanding of the historical connections within *Ps. vondembuschianus* across its distribution range. The nominal species *Microcondylaea hageni* Strubell, 1897 described from South Sumatra morphologically conforms to *Ps. vondembuschianus* and is considered its synonym (see Taxonomic account for detail).

The second *Pseudodon* species present in Java is new to science and currently considered endemic to the island, although future surveys in southern Borneo and Sumatra may reveal a wider distribution range. To date, *Ps. cokelatus* is only known from three river basins in central and eastern Java. Resolving the phylogenetic history of *Ps. cokelatus* in more detail and with higher support will require a larger dataset comprising multiple genes.

Rectidens (= *Elongaria syn. nov.*)

Our results revealed the presence of one *Rectidens* species present in Java, namely *R. orientalis*. The species exhibits considerable morphological plasticity in shell shape, including morphotypes that conform with the morphology of the *E. orientalis* type specimen. Our data additionally lead to a revised distribution range of *R. sumatrensis*, which spans Sumatra, the Malay Peninsula, and northern and northwestern Borneo (Zieritz *et al.* 2016, 2018b, 2020, 2024b). *Rectidens orientalis* may be endemic to Java, but data from southern Borneo and Sumatra will be needed to confirm this. Whilst our records are restricted to basins in East Java, historical records of *R.* '*sumatrensis*' and '*E. orientalis*' are available from several locations in West Java (Fig. 1A), indicating that the species has a wide natural distribution across the island.

Changes in distribution, environmental requirements, and threats

Comparing our data to available historical records, most of which are > 70 years old, indicates considerable changes in freshwater mussel species distribution across the island. This is particularly evident in western Java, where historical records collated by Van Benthem Jutting (1953) comprise all five native genera, including several records of *Pseudodon*, *Rectidens* (and '*Elongaria*'), and *Physunio* (Fig. 1B). In contrast, most of our records collected in 2022–23 in this region, which now includes the megacities of Jakarta and Bandung (Fig. 1A), are from *Pi. exilis* and the non-native *S. pacifica*, whilst *Rectidens* and *Physunio* were not collected at all (Fig. 1C). Our data also suggest population loss of certain species in central and eastern Java; for example, we did not detect *Pseudodon* in the Bengawan Solo despite historical records by Van Benthem Jutting (1953). In summary, our results indicate that most of the eight native freshwater mussel species of Java have been significantly impacted by anthropogenic activities over the past decades and are likely threatened in Java and in several cases, globally.

The underlying cause for the pronounced changes in freshwater mussel species distribution in Java is the dramatic human population increase over the past 70 years, resulting in rapid rates of urbanization, industrialization, mining, and other activities. For example, from 1950 to 2020, the total population of Greater Jakarta grew from about 1.5 to > 30 million, with the megacities Jakarta and Bandung being in the process of conurbation (Spreitzhofer 2009, Rustiadi *et al.* 2021). The three largest rivers of Java, namely the Bengawan Solo, Brantas, and Citarum, are heavily polluted with nutrients, heavy metals, microplastics, bacteria, oil, and other substances, predominantly stemming from domestic waste, industrial waste, and agriculture (Basuki *et al.* 2024). Gold mining, including illegal, artisanal small-scale gold mining (ASGM), is particularly common in West and Central Java (e.g. the River Tajum and Cigaru area) and has multiple environmental impacts, including pollution (including mercury and cyanide) and sedimentation, posing severe threats to both biodiversity and human health (Barkdull *et al.* 2019, Budianta 2021, Meutia *et al.* 2023, Dossou Etui *et al.* 2024). The rapid development of infrastructure has additionally resulted in a rapid increase in the mining of sand from rivers, including the Brantas River, resulting in the loss of substrate, deepening of the river channel, and general hydrological changes (Nawiyanto *et al.* 2020). As a combined result of these and other anthropogenic pressures, natural river and lake ecosystems across Java have been heavily degraded (Zieritz *et al.* 2024a), which has resulted in a loss of populations of most freshwater mussel species.

The only native freshwater mussel species of Java that appears to be able to survive in these heavily impacted ecosystems, including eutrophic ponds and canals, is *Pi. exilis*, which is now arguably the most common and widespread freshwater mussel in Java. As shown above, *Pi. exilis* appears to be commonly introduced to new habitats by humans and has been reported as a non-native invasive species in Bangladesh (Ollard *et al.* 2024) and Myanmar (Bolotov *et al.* 2024a), probably as a result of accidental introduction through fish hosts and its ability to establish populations in degraded habitats.

Conclusions and recommendations for conservation

Halting or at least slowing down the current rates of population losses of most freshwater mussel species in Java urgently requires targeted conservation and research actions. Arguably, these actions should be focused in the river basins of East Java, including the Brantas River and Bengawan Solo, which are particularly species rich and host several endemic species and haplotypes. One of the most important actions is the mitigation of pollution from industry, agriculture (including land-use conversion), mining, household waste, and other sources. As discussed by Nawiyanto *et al.* (2020), Meutia *et al.* (2023), Pambudi (2025), and others, relevant governmental policies and regulations, including those relating to Integrated Watershed Management, riparian buffers, water treatment, sand mining, and ASGM, are already in place but are frequently not implemented and enforced due to corruption, lack of resources for policing, and regulatory contradictions. Whilst it is beyond our expertise and scope of this article to recommend solutions for these problems, we stress the importance of actively involving local communities in conservation actions, starting from the planning stage (Basuki *et al.* 2024, Zieritz *et al.* 2024a).

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AUTHOR CONTRIBUTIONS

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SUPPLEMENTARY DATA

Supplementary data is available at *Zoological Journal of the Linnean Society* online.

CONFLICT OF INTEREST

None declared.

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DATA AVAILABILITY

DNA sequence data underlying this article are available in the GenBank Nucleotide Database at https://www.ncbi.nlm.nih.gov/nucleotide/, and can be accessed with the accession numbers available in this article. The GPS location data for freshwater mussel populations underlying this article cannot be shared publicly for conservation reasons. The data will be shared on reasonable request to the corresponding author. All other data underlying this article are available in the article and in its online supplementary data.

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