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# New records of freshwater mussels (Unionida, Unionidae and Mycetopodidae) from rivers, lakes, and lagoons in El Salvador, with notes on the expansion of invasive mollusc species

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**Abstract.** We examined 35 sites across 24 rivers, lakes, and lagoons in El Salvador and documented two native and one non-native freshwater mussel species in addition to the invasive *Corbicula*. Phylogenetic analyses supported the synonymy of *Nephronaias lempensis* Marshall, 1926, under *Nephronaias goascoranensis* (Lea, 1858). Mussel distributions were patchy; *Mycetopoda subsinuata* (Sowerby, 1868) occurred in soft, lentic habitats, whereas *N. goascoranensis* occupied a broader range. *Sinanodonta pacifica* (Heude, 1878), a non-native species, occurred in the upper Lempa basin, and *Corbicula* showed recent expansion. These results provide essential data for conservation planning.

**Keywords.** Biodiversity, Central America, distribution, DNA barcoding, *Mycetopoda*, *Nephronaias*, *Sinanodonta*

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## Introduction

Freshwater ecosystems support exceptional biodiversity relative to their surface area but face escalating anthropogenic pressures globally. Habitat modification and destruction, pollution, invasive species, and climate change have driven disproportionate declines in freshwater taxa compared to terrestrial and marine groups (Reid et al. 2019). These declines are especially concerning in Central America, where limited historical and contemporary data continue to hinder effective conservation planning for the region's unique assemblages and endemic species (Contreras-MacBeath et al. 2022). In El Salvador, a nationwide assessment of inland fish documented 101 species (McMahan et al. 2013), more than doubling the 45 species previously reported (Hildebrand 1925); however, only 4% of them (mainly Characidae and Heptapteridae) are primary freshwater taxa, and only one species is endemic to the country. Moreover, many Salvadoran rivers experience substantial contamination that reduces the abundance and integrity of freshwater macroinvertebrate communities (Sermeño-Chicas et al. 2010). Despite these known threats, holistic assessments for many freshwater taxa remain scarce, leaving critical gaps in taxonomy, distribution, and conservation status.

Freshwater mussels (Bivalvia, Unionida) are among the most imperilled aquatic organisms worldwide. As long-lived sedentary filter feeders, they provide essential ecosystem services, such as improving water quality, cycling and storing nutrients, and stabilizing sediment (Vaughn 2017). However, their obligatory parasitic larval stage, coupled with specialized habitat requirements, makes them particularly vulnerable to habitat alterations and fragmentation (Lopes-Lima et al. 2018). Currently, approximately 45% of freshwater mussel species are classified as near threatened, threatened, or extinct globally (Lopes-Lima et al. 2018). In well-studied regions such as North America, approximately 30 species have become extinct, and 199 of the remaining species (65% of extant North American species) are considered endangered, threatened, or vulnerable (Haag and Williams 2014). Similar trends and threats to freshwater mussels are likely widespread throughout Central America.

Central America forms a biogeographic bridge between the Nearctic and Neotropical regions, supporting a distinctive fauna composed of North American Unionidae and South American Mycetopodidae

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(Graf and Cummings 2021). However, systematic field surveys and biological research on this fauna have been sporadic, and many species are known only from their initial descriptions during the 19th and early 20th centuries. The scarcity of modern surveys and molecular analyses exemplifies a major shortfall in knowledge of taxonomy, species distributions, and evolutionary relationships across the region, which hinders assessments of species' conservation status (Hortal et al. 2015). Recent studies have started to address these gaps (Cummings et al. 2025; Martínez et al. 2026).

In El Salvador, *Nephronaias lempensis* Marshall, 1926 was the only mussel species originally described from the country, based on material collected by Hildebrand and Foster in the Río Lempa during the U.S. Bureau of Fisheries' nationwide assessments (Hildebrand 1925). *Nephronaias goascoranensis* (Lea, 1859) was described from the Río Goascorán along an international border between El Salvador and Honduras. A recent study reported that the range of this species extends eastward into the Río Nacaome and Río Choluteca drainages of Honduras (Martínez et al. 2026). Two additional species, *Nephronaias rowellii* (Lea, 1859) and *Mycetopoda subsinuata* (Sowerby, 1868), were later reported from El Salvador (Agudo-Padrón 2019). Although recent surveys did not detect any *N. rowellii*, the range of *M. subsinuata* has been shown to extend into the Río Choluteca drainage in Honduras (Martínez et al. 2026). All four species are currently listed as Endangered nationally (MARN 2023). However, no systematic surveys or molecular studies have been conducted to validate species identities in El Salvador, and the recent synonymization of *N. lempensis* with *N. goascoranensis* remains unvalidated (Cummings et al. 2025).

Here, we present the first comprehensive survey of freshwater mussels from El Salvador, combining field collections, DNA barcoding, and phylogenetic analyses to clarify species identities and distributions. Our study documents new national records and provides essential baseline data for future taxonomic, ecological, and conservation assessments on El Salvadoran and Central American mussel faunas.

## Study area

El Salvador lies within the Pacific basin of the Central American isthmus, with the Río Paz and Río Goascorán outlining portions of its western and eastern borders, and mountains and rivers delineating much of the northern frontier. The region's geological origin reflects the subduction of the Cocos Plate beneath the Caribbean Plate, a process that began near the end of the Tertiary period approximately five million years ago. This tectonic activity produced intense seismicity and volcanism throughout Central America (Rapprich et al. 2005). Magma rising from the mantle generated numerous volcanoes, several of which later collapsed into calderas following major and recurrent eruptions. Areas more distant from the subduction zone experienced extensive sedimentation and erosion from volcanic activity, forming flood plains that gradually emerged to create the modern Central American landmass (Bergoeing 2015). Consequently, active tectonic forces have been the primary drivers shaping the geomorphology of El Salvador (Bommer et al. 2002; Rapprich et al. 2005; Lexa et al. 2012; Bergoeing 2015).

El Salvador has a tropical climate with a dry season (November–April) and a wet season (May–October). These conditions support extensive tropical dry forest across much of the country, while higher elevations experience cooler temperatures and increased precipitation that sustain mountain forests. Annual rainfall ranges from ~1,500 mm along the coastal plain to more than 2,300 mm in upland regions, and evaporation occurs year-around (Buckalew et al. 1998). Climatic and topographic variation strongly influences the nation's hydrology. Twelve major hydrographic regions have been proposed for El Salvador, including the endorheic basins of Lago de Coatepeque and Lago de Ilopango–Río Jiboa system (McMahan et al. 2013; Figure 1). Numerous national protected areas encompass rivers, lagoons, and coastal ecosystems, all of which support significant aquatic biodiversity. Additionally, the country contains Ramsar Sites representing diverse aquatic habitats, including one artificial reservoir and three lagoons.

## Methods

Freshwater mussel surveys were conducted during the dry season between 2021 and 2026 in selected rivers, lakes, and lagoons across El Salvador, with particular focus on the Río Goascorán, Río Lempa, and Río Grande de San Miguel basins. Survey locations were chosen based on a combination of historical records (from past surveys and museum records), local observations (from fishermen,

communities, and citizen scientists), new sites identified through accessibility (e.g. proximity to bridge, parks, and public boat ramps, permission from landowners), and the presence of suitable habitat (e.g. stable gravel or gravel-sand substrates, riffles, bluff pools). Several sites were located within Ramsar-designated wetlands.

At each site, a minimum of two surveyors conducted timed searches by snorkelling, scuba, or wading. We employed a combination of visual and tactile methods, gently disturbing the substrate to locate buried or partially buried individuals. This approach is known to maximize species richness, including rare taxa (Vaughn et al. 1997). Surveys initially had a duration of at least 20 minutes, adjusted for habitat complexity and mussel density. Following each survey, we identified, measured, and counted all live mussels in the field before collecting mantle tissue clips for genetic analysis. We also recorded the presence of invasive bivalves, particularly *Corbicula* sp. (Venerida, Cyrenidae). Up to ~20 live individuals were preserved in 95% non-denatured ethanol and deposited at the Museo de Historia Natural de El Salvador (MUHNES, San Salvador, El Salvador). A subset of shell vouchers was sent to Shedd Aquarium (Chicago, IL, USA) for further examination and subsequently deposited at the Illinois Natural History Survey (INHS, Champaign, IL, USA).

We also incorporated opportunistic collections made prior to 2020 by the authors. Although these earlier samples did not follow the standardized protocol described above, they represent unpublished records that contribute distributional data. If available, tissue samples from these collections were also included in the molecular analyses.

For DNA barcoding, total DNA was extracted from mantle tissue clips preserved in 95% non-denatured ethanol using cetyltrimethylammonium bromide (CTAB)–chloroform extraction, followed by ethanol precipitation (Saghai-Maroof et al. 1984). Extracted DNA was diluted to approximately 10 ng/µL for use as a template in polymerase chain reactions (PCRs). Partial sequences of the cytochrome oxidase subunit 1 (*cox1*) gene were amplified with LCO22me2 and HCO700dy2 primers (Walker et al. 2006) producing sequences that are 658 base pairs (bp) in length. A PCR was conducted in a 10 µL reaction volume containing 5 µL of GoTaq Master Mix (Promega, Inc.), 0.25 µM of each forward and reverse primer, and 10 ng of template DNA, and proceeded for 35 cycles, with denaturation at 95°C for 1 min, annealing at 50 °C for 1 min, and extension at 72 °C for 1 min, with final extension at 72 °C for 10 min. The PCR products were visualized on 1.5% agarose gels and purified with exonuclease I and shrimp alkaline phosphatase (New England Biolabs, Ipswich, MA). Bidirectional Sanger sequencing was performed on a 3730xL DNA Analyzer (Thermo Fisher Scientific, Inc.) with BrightDye terminator kit (MCLAB, South San Francisco, CA). Sequencing preps were conducted at Shedd Aquarium's Molecular Ecology and Conservation Laboratory, and Sanger sequencing was conducted at the Field Museum's Pritzker DNA Laboratory for Molecular Systematics and Evolution.

The sequences were assembled with Geneious Prime v. 2025.2.2 (https://www.geneious.com) and aligned using MAFFT v. 7 (Katoh et al. 2019) along with samples collected from the Pacific drainages of Honduras (Martínez et al. 2026) and publicly available sequences in GenBank database (Table 1). The initial sequence alignment included all available sequences; subsequently, a subset of sequences was retained for phylogenetic analyses to reduce redundancy resulting from highly shared haplotypes. We used IQ-Tree (Nguyen et al. 2015) to determine the best substitution models for each codon positions of *cox1* and reconstructed a maximum-likelihood tree with 1000 ultrafast bootstrap replicates to evaluate branch supports.

# Results

We surveyed 35 sites across 24 waterbodies, of which 13 sites supported freshwater mussels. Mussel occurrence was patchy across the region, including the Río Lempa, Río Grande de San Miguel, and Río Goascorán basins, and more concentrated in the lower reaches (Figure 1). Although there was a historical museum record of *N. lempensis* in the Río Torola (Río Lempa tributary; MUHNES 90-815) and *N. rowellii* in the Río Paz along the El Salvador–Guatemala border (USNM 347898), we did not recover any individuals during the survey. Additionally, we confirmed the presence of the invasive *Corbicula* sp. at four sites in the following river basins: Río Grande de San Miguel, Río Sirama, and Río Goascorán (Figures 1, 2).

We examined ~658 bp of the *cox1* gene from 155 individuals, including 43 *M. subsinuata*, 91 *N. goascoranensis*, and 21 *S. pacifica*. Sequences generated in this study were submitted to GenBank (accession numbers PZ516483–PZ516637; Table 1). Phylogenetic analyses recovered three distinct lineages from El Salvador (Figure 3). *Mycetopoda subsinuata* from El Salvador (denoted as Msub in Figure 3)

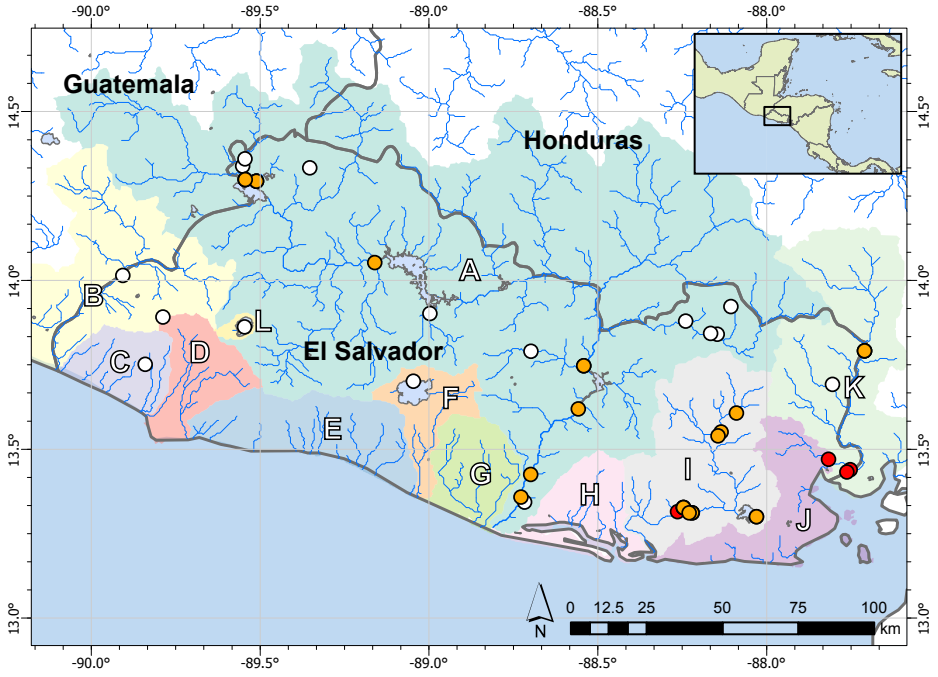


**Figure 1.** A map of sampled locations in El Salvador. Coloured circles correspond to the presence (orange) and the absence (white) of freshwater mussels and the presence of the invasive *Corbicula* sp. (red). Shaded, lettered areas correspond to the major river basins: A = Lempa, B = Paz, C = Cara Sucia–San Pedro, D = Grande de Sonsonate, E = Mandinga–Comalapa, F = Ilopango–Jiboa, G = Estero Jaltepeque, H = Bahía Jiquilisco, I = Grande de San Miguel, J = Sirama, K = Goascorán, L = Coatepeque.

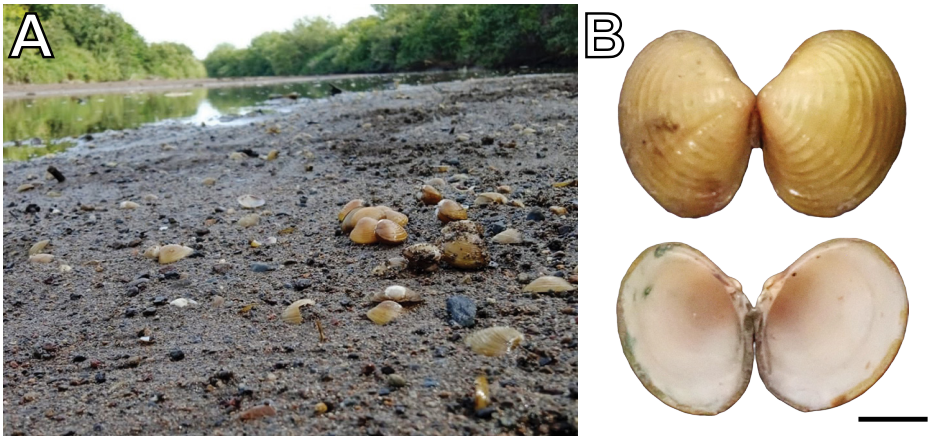


**Figure 2.** Shells of *Corbicula* sp. observed on the riverbank of the Río Goascorán (**A**), and the external and internal views of a specimen (**B**). Scale bar = 10 mm.

**Table 1.** List of species and sequences included in the phylogenetic analysis. GenBank accession numbers are provided. Asterisks (*) indicate sequences obtained for this study.

| Family | Species | *cox1* |
|---|---|---|
| Mycetopodidae | *Anodontites elongata* (Swainson, 1823) | MK761136 |
| Mycetopodidae | *Anodontites guanarensis* Marshall, 1927 | AF231741 |
| Mycetopodidae | *Anodontites trapesialis* (Lamarck, 1819) | KU873119 |
| Mycetopodidae | *Anodontites trigona* (Spix in Wagner, 1827) | AF231738 |
| Mycetopodidae | *Mycetopoda siliquosa* (Spix in Wagner, 1827) | JN243887 |
| Mycetopodidae | *Mycetopoda subsinuata* (Sowerby, 1868) | PX986872–PX986876 (Honduras)<br>*PZ516483–PZ516525 (El Salvador) |
| Unionidae | *Amblema plicata* (Say, 1817) | NC_050056 |
| Unionidae | *Cyrtonaias tampicoensis* (Lea, 1838) | PQ057767 |
| Unionidae | *Eurynia dilatate* (Rafinesque, 1820) | MN649035 |
| Unionidae | *Mesonaias explicate* (Morelet, 1849) | MK001769 |
| Unionidae | *Nephronaias goascoranensis* (Lea, 1858) | PX986877–PX986882 (Honduras)<br>*PZ516526–PZ516616 (El Salvador) |
| Unionidae | *Nephronaias tempisquensis* Pilsbry, 1920 | PQ057767 |
| Unionidae | *Pachynaias spheniopsis* (Morelet, 1849) | MK001773 |
| Unionidae | *Popenaias berezai* Inoue et al., 2020 | MT553859 |
| Unionidae | *Popenaias popeii* (Lea, 1857) | KP779878 |
| Unionidae | *Proronaias guatemalensis* (Simpson, 1900) | MK001760 |
| Unionidae | *Quadrula quadrula* (Rafinesque, 1820) | NC_013658 |
| Unionidae | *Reginaia ebenus* (Lea, 1831) | AY654999 |
| Unionidae | *Sinanodonta pacifica* (Heude, 1878) | MG591513<br>*PZ516617–PZ516637 (El Salvador) |

was indistinguishable from Honduran populations at the *cox1* gene and formed a sister relationship to *Mycetopoda siliquosa* (Spix in Wagner, 1827) from Peru. Specimens initially identified as *N. lempensis* from the Río Lempa and Río Grande de San Miguel (Nlem) clustered with *N. goascoranensis* from the Río Goascorán (Ngoa) and adjacent drainages in Honduras. This clade formed a broader clade comprising *N. lempensis*, *N. goascoranensis*, and *Nephronaias tempisquensis* Pilsbry, 1920 from the Río Tempisque in Costa Rica (GenBank accession PQ057767). In the upper Río Lempa watershed, we also detected the invasive *Sinanodonta pacifica* (Heude, 1878) (Swoo), which was genetically identical to a Malaysian haplotype (GenBank accession MG591513).

Based on field surveys and genetic evidence, we document two native and one non-native freshwater mussel species from El Salvador and clarify their taxonomic affinities. Note that the geographic coordinates provided in the New records were obscured due to the conservation status of the species.

**Taxonomy**

Class Bivalvia Linnaeus, 1758
Order Unionida Gray, 1854
Family Mycetopodidae Gray, 1840
Genus *Mycetopoda* d'Orbigny, 1835

***Mycetopoda subsinuata* (Sowerby, 1868)**

Figures 3, 4

**New records.** EL SALVADOR — Departamento de Cabañas • Río Titihuapa, [Pacific Ocean – Río Lempa drainage], El Vado, 16.5 air km SE of Sensuntepeque, El Salvador, ca. 800 m upstream of the Río Lempa confluence; 13.7500°, −088.5400°; 23.II.2022; J.E. Barraza et al. leg.; 18 spec., MUHNES90-838, 5 spec., INHS97008 • same locality and collectors; 19.III.2023; 1 spec., INHS97009 — Departamento de La Unión • Laguna de Olomega [Pacific Ocean – Río Grande de San Miguel drainage], Ramsar site Área Natural Protegida Laguna de Olomega, 15.2 air km NE of Chirilagua, El Salvador, eastside of Laguna de Olomega; 13.3000°, −088.0300°; 29.VII.2017; J.E. Barraza et al. obs. • Same locality; 21.III.2023; J.E. Barraza et al. leg.; 9 spec., INHS97010 — Departamento de San Miguel • Laguna El Jocotal [Pacific Ocean – Río Grande de San Miguel drainage], Ramsar site Área Natural Protegida Laguna El Jocotal, 11.5 air km ESE of El Tránsito, El Salvador; 13.3200°, −088.2500°; 21.V.2021; J.E. Barraza et al. leg.; 23 spec., MUHNES90-842, 3 spec., INHS97011 • same locality and collectors; 22.III.2023; 9 spec., INHS97012 — Departamento de Santa Ana • Río Ostúa [Pacific Ocean – Río Lempa – Río Desagüe – Lago de Güija drainage], Parque Nacional San Diego y San Felipe de las Barras, 10.8 air km WSW of Metapán, El Salvador, at a boat ramp near the mouth to Lago de Güija; 14.3000°, −089.5400°; 7.III.2024; J.E. Barraza et al. leg.; 1 spec., MUHNES90-830.

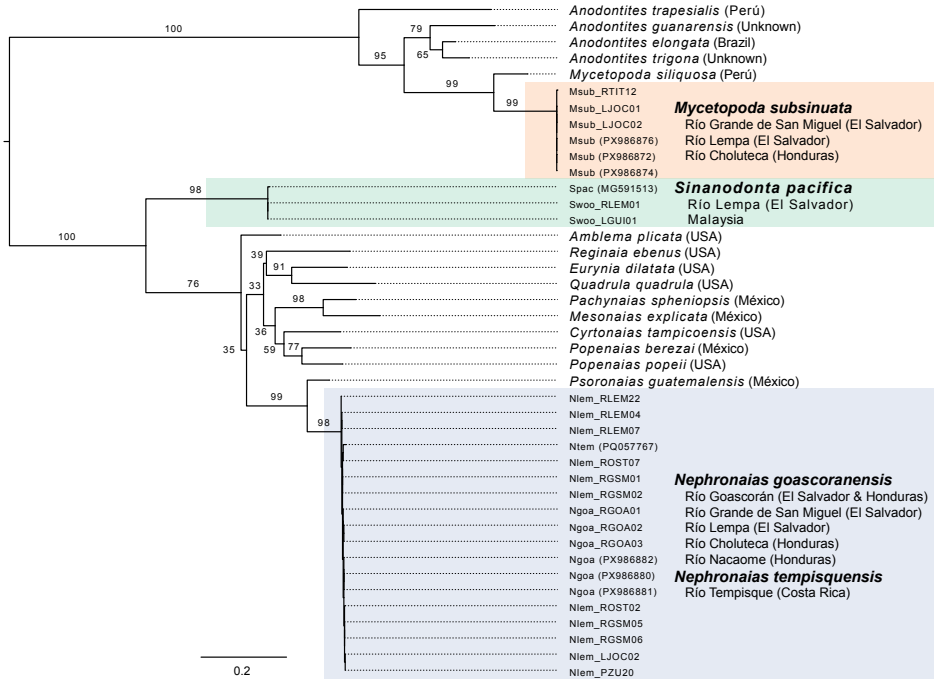


**Figure 3.** Phylogenetic tree reconstructed by maximum-likelihood analysis for the *cox1* sequence dataset. Bootstrap support values are shown for major clades along the nodes. The midpoint root was taken. Major clades are annotated by species, river basin, and country. Coloured box along clades corresponds to the species collected during the surveys.

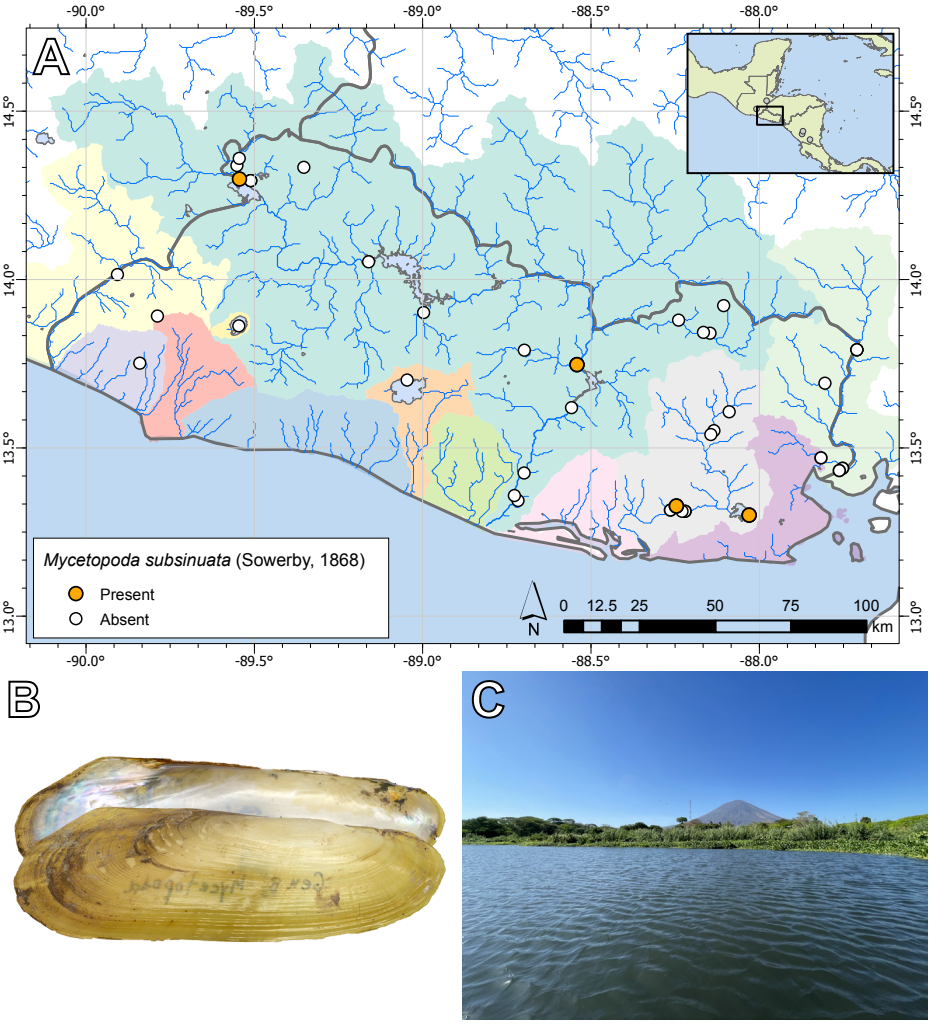


**Figure 4.** *Mycetopoda subsinuata*. **A.** Occurrence map. Coloured circles correspond to the presence (orange) and the absence (white) of *M. subsinuata*. Previous records (grey) of *M. subsinuata*, obtained from the Global Biodiversity Information Facility (https://www.gbif.org) and Cummings et al. (2025), are shown in the inset map. Coloured areas correspond to the major river basins (see Figure 1). **B.** External view, 89.2 mm in length. **C.** Laguna El Jocotal.

**Identification.** Specimens found during the survey match the original description of *Mycetopus subsinuatus* (Sowerby 1868), as well as images of museum specimens available on MUSSELp database (Graf and Cummings 2026). Shells are elongated, thin, and fragile, inequilateral, with the anterior margin broadly rounded and the posterior end elongated and somewhat truncated. The periostracum is yellowish to light brown, smooth to slightly clothlike, with fine concentric growth lines.

**Type locality.** Bogota, New Granada [Colombia] (Sowerby 1868).

**Presumed distribution.** Caribbean drainages of Colombia, and Caribbean and Pacific drainages of Panamá north to Guatemala and Honduras (Martínez et al. 2026). In El Salvador, *M. subsinuata* occurs in several tributaries of the upper to middle reaches of the Río Lempa, as well as lakes along the Río Grande de San Miguel.

**Remarks.** *Mycetopoda subsinuata* was predominantly found in soft to compact clay substrates with some amount of silt and mud along riverbanks and offshore lakes and lagoons at depths of 0.5–2 m. In Honduras, this species was reported from sand and muddy substrates in banks of the Río Choluteca (Martínez et al. 2026). The species was locally abundant and typically burrowed vertically into clay. In Laguna de Olomega, while only abundant recently dead shells were observed during the study, live individuals were observed as recently as 2017. This species also represents a new record from the Río Ostúa, a tributary of Lago de Güija. Although specimens are provisionally identified as *M. subsinuata*, lack of comparative material from the type locality warrants caution, and the taxonomic validity of El Salvador populations remains uncertain. *Mycetopoda subsinuata* (as *Mycetopoda siliquosa*) is currently listed as Endangered in El Salvador (MARN 2023).

Family Unionidae Rafinesque, 1820
Subfamily Ambleminae Rafinesque, 1820
Genus *Nephronaias* Cross & Fischer, 1894

***Nephronaias goascoranensis* (Lea, 1858)**
Figures 3, 5

**New records.** EL SALVADOR — Departamento de La Unión • Río Goascorán [Pacific Ocean drainage], 27.1 air km NE of Santa Rosa de Lima, El Salvador, off 2a Calle Oriente Road, sandy beach at Concepcion de Oriente; 13.7900°, −087.7100°; 13.III.2018; J.E. Barraza leg.; 1 spec., MUHNES90-843 • same locality and collector; 22.III.2023; 1 spec., INHS97013 • same locality and collector; 5.III.2024; 2 spec., INHS97014 — Departamento de Morazán • Río Seco [Pacific Ocean – Río Grande de San Miguel drainage], 10.4 air km S of San Francisco, El Salvador, at Ruta de La Paz [CA-7] bridge; 13.6100°, −088.0900°; 5.III.2024; J.E. Barraza et al. leg.; 8 spec., MUHNES90-827, 4 spec., MUHNES90-828, 4 spec., INHS97015 — Departamento de San Miguel • Laguna El Jocotal [Río Grande de San Miguel drainage], Ramsar site Área Natural Protegida Laguna El Jocotal, 11.5 air km ESE of El Tránsito, El Salvador, southside of Laguna El Jocotal; 13.3300°, −088.2500°; 25.IV.2022; J.E. Barraza and V. Melara leg.; 1 spec., MUHNES90-864, 6 spec., INHS97016 • Poza 1 [Río Grande de San Miguel drainage], 13.5 air km NW of Chirilagua, El Salvador, outlet of Laguna El Jocotal adjacent to the Río Grande de San Miguel; 13.3100°, −088.2200°; 17.III.2021; J.E. Barraza et al. leg.; 2 spec., MUHNES90-844, 2 spec., INHS97017 • same locality and collectors; 23.III.2023; 4 spec., MUHNES90-846, 10 spec., INHS97018 • Río Grande de San Miguel, 9.2 air km NE of San Miguel, El Salvador, downstream of a low water crossing [road to El Guayabal]; 13.5500°, −088.1300°; 21.IV.2022; J.E. Barraza et al. leg.; 1 spec., MUHNES 90-851, 2 spec., INHS97019 • Río Grande de San Miguel, 7.6 air km NE of San Miguel, El Salvador, downstream of a low water crossing [road to El Guayabal]; 13.5400°, −088.1400°; 21.III.2023; J.E. Barraza et al. leg.; 9 spec., MUHNES90-841, 2 spec., INHS97020 — Departamento de Santa Ana • Río Ostúa [Pacific Ocean

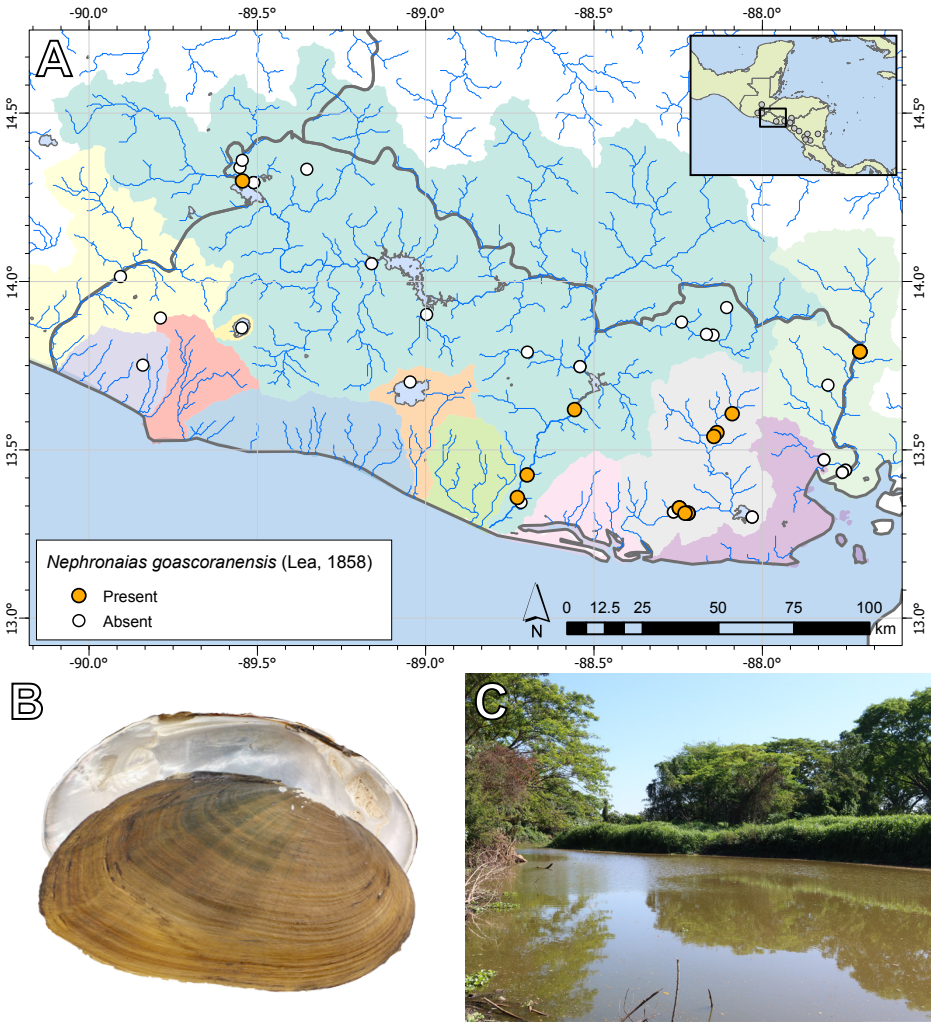


**Figure 5.** *Nephronaias goascoranensis*. **A.** Occurrence map. Coloured circles correspond to the presence (orange) and the absence (white) of *N. goascoranensis*. Previous records (grey) of *N. goascoranensis*, obtained from the Global Biodiversity Information Facility (https://www.gbif.org) and Cummings et al. (2025), are shown in the inset map. Coloured areas correspond to the major river basins (see Figure 1). **B.** External view, 49.3 mm in length. **C.** Poza 1 (Laguna El Jocotal outlet).

– Río Lempa – Río Desagüe – Lago de Güija drainage], Parque Nacional San Diego y San Felipe de las Barras, 10.8 air km WSW of Metapán, El Salvador, at a boat ramp near the mouth to Lago de Güija; 14.3000°, −089.5400°; 7.III.2024; J.E. Barraza et al. leg.; 4 spec., MUHNES90-832 — Departamento de Usulután • La Poza [Pacific Ocean – Río Lempa drainage], Área Natural Protegida Nancuchiname, 16.3 air km WNW of Jiquilisco, El Salvador, a cutoff pond ca. 130 m east of the Río Lempa; 13.3600°, −088.7300°; 31.V.2012; J.E. Barraza leg.; 2 spec., INHS97023 • same locality and collector; III.2014; 2 spec., INHS97022 • Río Lempa [Pacific Ocean drainage], 13.5 air km NNW of Berlin, El Salvador, a backwater pool below Central Hidroelectrica 15 de Septiembre dam; 13.6200°, −088.5600°; 19.III.2023; J.E. Barraza et al. leg.; 1 spec., MUHNES90-839, 1 spec., INHS97021 • Río Lempa [Pacific Ocean drainage], 17.4 air km NW of Jiquilisco, El Salvador, 1 air km N of the railroad bridge, at the type locality; 13.4300°, −088.6900°; 10.II.2024; J.E. Barraza leg.; 8 spec., MUHNES90-825, 8 spec., MUHNES90-826, 1 spec., INHS97024.

**Identification.** Specimens found during the survey closely resemble the original description of *Unio goascoranensis* Lea, 1858 and *Nephronaias lempensis* Marshall, 1926, and were obtained from the type localities of these species. Shells are oval to subelliptical, moderately thick, and somewhat inflated, with the anterior margin rounded and the posterior end biangulated and somewhat truncated to rounded. Left valve has pseudocardinal teeth and two divergent lateral teeth, while right valve has a single lateral tooth. The periostracum is dark brown, slightly clothlike, with distinct concentric growth lines. Young individuals have fine rays from the umbo. While individuals from the Río Lempa and Río Grande de San Miguel populations were initially identified as *N. lempensis* due to its proximity to the type locality, phylogenetic analyses confirmed these individuals genetically indistinguishable from *N. goascoranensis* from the Río Goascorán in El Salvador and Honduras. While shell morphology differs slightly between *lempensis* and *goascoranensis*, where *lempensis* tends to have compressed and thinner shells, considerable overlap in shell characters was observed among populations attributed to *lempensis* and *goascoranensis*.

**Type locality.** Río Goascorán, Honduras (Lea 1858).

**Presumed distribution.** Río Goascorán and adjacent Pacific drainages, including the Río Lempa and Río Grande de San Miguel in El Salvador, as well as the Río Nacaome and Río Choluteca in Honduras (Martínez et al. 2026).

**Synonym.** *Nephronaias lempensis* Marshall, 1926.

**Remarks.** *Nephronaias goascoranensis* primarily occurs in fine substrates ranging from gravel to mud along riverbanks, backwaters, riffles, and transitional riffle-pool habitats in both riverine and lentic environments. This species was often found floating in silt and soft mud where fine substrates dominate (e.g. Río Ostúa and Poza 1). It was locally abundant at several sites, except in the Río Goascorán near Concepcion de Oriente, where only three live individuals were found despite over six person-hours of searching during the study. In the Río Seco, numerous juveniles to subadults (10–30 mm long) were observed along riverbank pools near intermittent sections, with abundant dead shells found on adjacent gravel and sand bars. Occasional records also exist from oxbows and inundated wetlands along the Río Lempa. *Nephronaias goascoranensis* (including *N. lempensis*) is currently listed as Endangered in El Salvador (MARN 2023).

Subfamily Unioninae Rafinesque, 1820
Genus *Sinanodonta* Modell, 1945

***Sinanodonta pacifica* (Heude, 1878)**
Figures 3, 6

**New records.** EL SALVADOR — Departamento de Santa Ana • Lago de Güija [Pacific Ocean – Río Lempa – Río Desagüe drainage], Ramsar site Complejo Güija, 8.0 air km WSE of Metapán, El Salvador, at Caserio Las Conchas; 14.2900°, −089.5100°; 4.V.2021; J.E. Barraza and V. Melara leg.; 1 spec., MUHNES90-845, 3 spec., INHS97025 • same locality and collector; 3.V.2022; 4 spec., INHS97026 • Río Ostúa [Pacific Ocean – Río Lempa – Río Desagüe – Lago de Güija drainage], Parque Nacional San Diego y San Felipe de las Barras, 10.8 air km WSW of Metapán, El Salvador, at a boat ramp near the mouth to Lago de Güija; 14.2300°, −089.5400°; 7.III.2024; J.E. Barraza et al. leg.; 9 spec., MUHNES90-834 — Departamento de San Salvador • Río Lempa, Caserío Potrero Grande, San Salvador Norte; 14.0500°, −089.1600°; 4.VI.2024; J.E. Barraza obs.

**Identification.** Collected specimens match the description by Douda et al. (2024), and its identity was further confirmed via DNA barcoding.

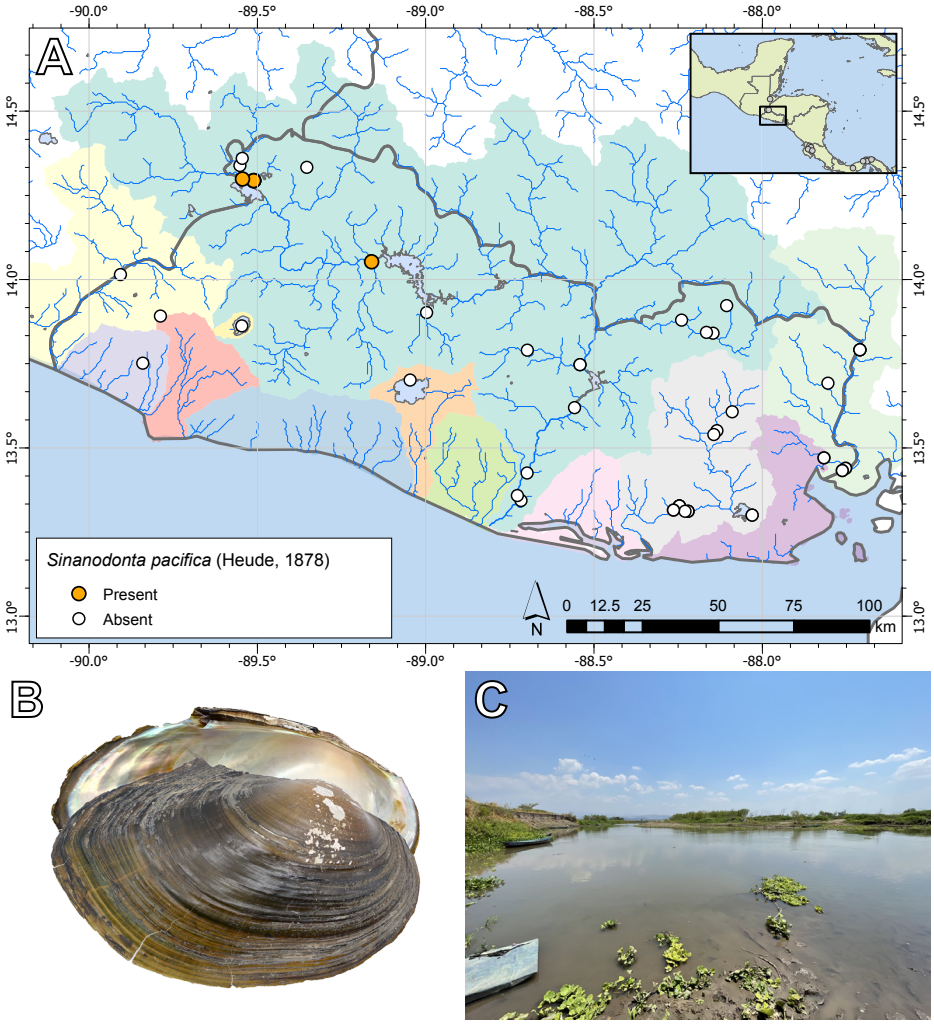


**Figure 6.** *Sinanodonta pacifica*. **A.** Occurrence map. Coloured circles correspond to the presence (orange) and the absence (white) of *S. pacifica*. Previous records (grey) of *S. pacifica*, obtained from the Global Biodiversity Information Facility (https://www.gbif.org) and Cummings et al. (2025), are shown in the inset map. Coloured areas correspond to the major river basins (see Figure 1). **B.** External view, 92.5 mm in length. **C.** Río Ostúa.

**Type locality.** La rivière de Ning-kouo-fou (Ngan-houé), China.

**Presumed distribution.** Native range in eastern China and Taiwan. Widely introduced in East Asia as well as Central America, and Iraq (Graf and Cummings 2026). In El Salvador, *S. pacifica* currently occurs in the upper reach of the Río Lempa including Lago de Güija.

**Remarks.** Initially thought of as the invasive *Sinanodonta woodiana* (Lea, 1834), recent review indicates the presence of multiple invasive *Sinanodonta* lineages (Douda et al. 2024); *S. pacifica* represents a tropical lineage in Central America. *Sinanodonta pacifica*, widely reported from Central America, was likely introduced primarily via the tilapia aquaculture trades (Bauer et al. 2021). In El Salvador, this species established highly abundant populations in the upper Río Lempa basin particularly in Lago de Güija and its tributaries.

# Discussion

We confirmed the presence of two native and one non-native freshwater mussel species and an invasive *Corbicula* sp. in El Salvador based on field surveys and DNA barcoding. *Sinanodonta pacifica* and *Corbicula* sp. represent newly verified invasive species in the country. Mussels were found in three river basins, including the Lempa, Grande de San Miguel, and Goascorán basins; however, species richness and distributions differed markedly and were patchy among sites. The upper Río Lempa supported the highest diversity of native species but also the densest *S. pacifica* populations. Despite historical records, no mussels were recovered from the Río Paz, and local residents reported that they have not observed mussels there in recent years.

*Nephronaias goascoranensis* was previously known from Pacific drainages of Honduras (Martínez et al. 2026) and only the easternmost portion of El Salvador. Our genetic evidence extends its distribution westward to the Río Lempa, encompassing populations previously identified as *N. lempensis*. This

finding supports the proposed synonymy of *N. lempensis* with *N. goascoranensis* (Cummings et al. 2025) and refines the species' distribution to span from the Río Lempa (El Salvador) southeast to the Río Choluteca (Honduras). Despite this apparent range expansion, we recommend retaining its Endangered status due to its fragmented distribution and vulnerability. We did not detect individuals at historical sites such as the Río Torola and La Poza Nancuchiname (oxbow lake off the Río Lempa) during our surveys despite being reported frequently a decade ago. This indicates a potential localized extirpation at these sites. In the middle reach of the Río Lempa, dam-regulated flows have created unstable, coarse substrates unsuitable for this species, which typically occupies gravel or finer substrates and moderate to slow currents. Currently, known mainstem populations persist only in a backwater pool immediately below the dam, protected from periodic discharge, and farther downstream in the coastal plain.

*Mycetopoda subsinuata* occupied distinct habitats characterized by soft to compact clay substrates, where individuals burrow vertically and anchor using their large mushroom-shaped foot. Consequently, the species is typically found along riverbanks, backwaters, and lentic environments where fine sediments accumulate. *Mycetopoda subsinuata* occasionally co-occurs with *N. goascoranensis* in some locations (Laguna El Jocotal and the Río Ostúa, a tributary of Lago de Güija), but *N. goascoranensis* exhibited a broader substrate preference and has a much wider distribution. In Central America, *M. subsinuata* is currently recognized from Guatemala south to Nicaragua. Although this species is locally abundant, their distribution is sporadic. Such soft-bottom habitats are highly vulnerable to sedimentation, pollution, hydrological alteration and climate variability. *Mycetopoda subsinuata* is listed as Endangered in El Salvador (MARN 2023), and we recommend maintaining this status while developing a recovery plan and long-term monitoring program for this species.

Taxonomic challenges persist within the genera *Nephronaias* and *Mycetopoda*. *Nephronaias* is the most species-rich genus among Central American mussels (Cummings et al. 2025), but reliable identification remains challenging due to morphological plasticity, overlapping characters, vague original descriptions, and a lack of recent specimens. In addition to the synonymy of *N. lempensis* with *N. goascoranensis*, Cummings et al. (2025) also proposed to synonymize several taxa from Pacific drainages of Guatemala under *N. goascoranensis*, and our molecular data suggests that *N. tempisquensis* from Pacific drainages of Costa Rica may also warrant re-evaluation. Broader phylogenetic analyses incorporating material from southern Mexico to Costa Rica are needed to clarify species boundaries and evolutionary relationships of *Nephronaias*. Furthermore, during the surveys, we did not recover *N. rowellii*, previously reported from the Río Paz and Lago de Güija. *Nephronaias rowellii* was originally described from the Río Chagres (Panamá), and its distribution is now restricted to the Chagres basin (Cummings et al. 2025). Therefore, we conclude that the original reports were likely misidentified individuals due to similar shell morphologies among *Nephronaias* species. Additionally, a lack of comparative specimens from the type locality of *M. subsinuata* makes the taxonomic identity of El Salvadoran populations uncertain. This underscores the need for broader taxon sampling and multilocus analyses for future revisionary work.

The high abundance and dominance of *S. pacifica* in the upper Río Lempa basin pose a significant threat to native mussel communities and freshwater ecosystem integrity. In Lago de Güija, *S. pacifica* co-occurred with invasive gastropods, such as *Melanoides tuberculata* (Müller, 1774) and *Tarebia granifera* (Lamarck, 1822), forming dense populations that now dominate benthic communities. *Sinanodonta pacifica* was likely introduced through aquaculture activities, particularly tilapia farming, like the invasion in other parts of Central America in the early 2000s (Bauer et al. 2021), and its range has recently expanded downstream into reservoir systems. This species also became one of the commonly harvested freshwater mussel species in Central America. Local communities harvest this species for food, and its perceived economic value has prompted attempts to intentionally propagate it locally. However, this initiative was halted by environmental authorities in El Salvador due to the lack of safeguarding measures. Prior to the invasion, Lago de Güija supported native mussel species such as *N. goascoranensis*, which now appear to have been displaced and restricted to tributaries of the lake. Immediate management actions, including control and mitigation measures, prevention of further spread, and community education on invasive species, are urgently needed.

The invasive *Corbicula* sp. currently appears restricted to coastal regions of the Río Goascorán and adjacent rivers, as well as Laguna El Jocotal. It was first observed in the lower Río Goascorán in early 2024 and rapidly established dense populations. More recently, it was observed in Laguna El Jocotal (mid 2025) and the Río Sirama (early 2026), raising concerns over rapid expansion. As with *S. pacifica*, close monitoring and prevention of further spread are urgently needed.

This study presents the first systematic, genetically informed assessment of freshwater mussels in El Salvador, integrating field surveys and DNA barcoding to clarify species diversity, distributions,

and taxonomy. Our results expand the known distribution of native taxa and highlight the invasive *S. pacifica* and *Corbicula* sp. as a growing conservation concern. These findings provide critical baseline data for future taxonomic, ecological, and conservation research and support efforts to safeguard El Salvador's rapidly declining freshwater biodiversity. Moreover, this study is significant within the broader Central American context, where freshwater biodiversity remains poorly documented and taxonomic uncertainty continues to hinder conservation.

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# Additional information

**Conflict of interest**

The authors declare that no competing interests exist.

**Ethical statement**

No ethical statement is reported.

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**Author contributions**

JEB, YQ, CRK, and KI conceived the idea for the study. JEB, VM, YQ, CRK, and KI conducted field surveys. KI performed genetic analyses. All authors contributed to the design and writing of the manuscript.

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**Data availability**

All data that support the findings of this study are available in the main text and sequences generated in this study are available at the NCBI GenBank (accession numbers PZ516483–PZ516637).

# References

**Agudo-Padrón AI** (2019) Los moluscos no marinos ocurrentes en la República de El Salvador, América Central: una breve revisión panorámica introductoria de su actual conocimiento. Bioma 5: 48–53.

**Bauer WG, Stewart DT, Céspedes RQ, Valverde SA, Easy RH** (2021) DNA barcoding evidence of the tropical invasive lineage of *Sinanodonta woodiana* in Costa Rica. Neotropical Naturalist 5: 1–8.

**Bergoeing JP** (2015) Geomorphology of Central America. Elsevier, New York, USA, 162 pp. https://doi.org/10.1016/c2014-0-03241-8

**Bommer JJ, Benito MB, Ciudad-Real M, Lemoine A, López-Menjívar MA, Madariaga R, Mankelow J, Méndez de Hasbun P, Murphy W, Nieto-Lovo M, Rodríguez-Pineda CE, Rosa H** (2002) The El Salvador earthquakes of January and February 2001: context, characteristics and implications for seismic risk. Soil Dynamics and Earthquake Engineering 22: 389–418. https://doi.org/10.1016/s0267-7261(02)00024-6

**Buckalew JO, Knowles RB, Waite L, James M, Laprevote J** (1998) Water resources assessment of El Salvador. U.S. Army Corps of Engineers, Washington, D.C., USA, 71 pp.

**Contreras-MacBeath T, Ardón DA, Quintana Y, Angulo A, Lyons T, Lardizabal C, McMahan CD, Elías DJ, Matamoros WA, Barraza JE, González R, Fuentes-Montejo CE, Ambruster JW, Carrasco JC, Brito Rodriguez M** (2022)

Freshwater fishes of Central America: distribution, assessment, and major threats. Diversity 14: 793. https://doi.org/10.3390/d14100793

**Cummings KS, Graf DL, Pfeiffer JM, Tiemann JS** (2025) Freshwater Mussels of Central America. CRC Press, Boca Ranton, Florida, USA, 508 pp. https://doi.org/10.1201/9781003314448

**Douda K, Zieritz A, Vodáková B, Urbańska M, Bolotov IN, Marková J, Froufe E, Bogan AE, Lopes-Lima M** (2024) Review of the globally invasive freshwater mussels in the genus *Sinanodonta* Modell, 1945. Hydrobiologia 852: 1243–1273. https://doi.org/10.1007/s10750-023-05457-3

**Graf DL, Cummings KS** (2021) A 'big data' approach to global freshwater mussel diversity (Bivalvia: Unionoida), with an updated checklist of genera and species. Journal of Molluscan Studies 87: eyaa034. https://doi.org/10.1093/mollus/eyaa034

**Graf DL, Cummings KS** (2026) MUSSEL Project. http://musselpdb.org. Accessed on: 2026-02-24.

**Haag WR, Williams JD** (2014) Biodiversity on the brink: an assessment of conservation strategies for North American freshwater mussels. Hydrobiologia 735: 45–60. https://doi.org/10.1007/s10750-013-1524-7

**Hildebrand SF** (1925) Fishes of the Republic of El Salvador, Central America. Bulletin of the Bureau of Fisheries 41: 237–287.

**Hortal J, de Bello F, Diniz-Filho JAF, Lewinsohn TM, Lobo JM, Ladle RJ** (2015) Seven shortfalls that beset large-scale knowledge of biodiversity. Annual Review of Ecology, Evolution, and Systematics 46: 523–549. https://doi.org/10.1146/annurev-ecolsys-112414-054400

**Katoh K, Rozewicki J, Yamada KD** (2019) MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. Briefings in Bioinformatics 20: 1160–1166. https://doi.org/10.1093/bib/bbx108

**Lea I** (1858) Description of four new fresh-water molluscs, from the Isthmus of Darien and Honduras. Proceedings of the Academy of Natural Sciences of Philadelphia 10: 118.

**Lexa J, Šebesta J, Chavez JA, Hernández W, Pécskay Z** (2012) Geology and volcanic evolution in the southern part of the San Salvador Metropolitan Area. Journal of GEOsciences 56: 106–140. https://doi.org/10.3190/jgeosci.088

**Lopes-Lima M, Burlakova LE, Karatayev AY, Mehler K, Seddon M, Sousa R** (2018) Conservation of freshwater bivalves at the global scale: diversity, threats and research needs. Hydrobiologia 810: 1–14. https://doi.org/10.1007/s10750-017-3486-7

**MARN** (2023) Listado Oficial de Especies de Vida Silvestre Amenazadas o en Peligro de Extinctión. Diario Oficial Tomo No 441 (Acuerdo No 257). Ministerio de Medio Ambiente y Recursos Naturales (MARN), San Salvador, El Salvador, 36–58.

**Martínez DE, Matamoros WA, Lardizabal CC, Soto Venegas KA, Quintana Y, Inoue K** (2026) New records of freshwater mussels (Unionida, Unionidae and Mycetopodidae) from rivers, lakes, and lagoons in Honduras. Check List 22: 224–236. https://doi.org/10.15560/22.2.224

**McMahan CD, Matamoros WA, Alvarez Calderon FS, Henriquez WY, Recinos HM, Chakrabarty P, Barraza E, Herrera N** (2013) Checklist of the inland fishes of El Salvador. Zootaxa 3608: 440–456. https://doi.org/10.11646/zootaxa.3608.6.2

**Nguyen LT, Schmidt HA, von Haeseler A, Minh BQ** (2015) IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. Molecular Biology and Evolution 32: 268–274. https://doi.org/10.1093/molbev/msu300

**Rapprich V, Hernández W, Erban V** (2005) Geology of the Metapán volcanic field NW El Salvador. Revista Geológica de América Central 33: 61–74. https://doi.org/10.15517/rgac.v0i33.4236

**Reid AJ, Carlson AK, Creed IF, Eliason EJ, Gell PA, Johnson PTJ, Kidd KA, MacCormack TJ, Olden JD, Ormerod SJ, Smol JP, Taylor WW, Tockner K, Vermaire JC, Dudgeon D, Cooke SJ** (2019) Emerging threats and persistent conservation challenges for freshwater biodiversity. Biological Reviews 94: 849–873. https://doi.org/10.1111/brv.12480

**Saghai-Maroof MA, Soliman KM, Jorgensen RA, Allard RW** (1984) Ribosomal DNA spacer-length polymorphisms in barley: Mendelian inheritance, chromosomal location, and population dynamics. Proceedings of the National Academy of Sciences of the United States of America 81: 8014–8018. https://doi.org/10.1073/pnas.81.24.8014

**Sermeño-Chicas JM, Cervantes LS, Springer M, Cienfuegos MRP, Pérez D, Flores AWR, Linares AYA** (2010) Determinación de la calidad ambiental de las aguas de los ríos de El Salvador, utilizando invertebrados acuáticos: índice biológico a nivel de familias de invertebrados acuáticos en El Salvador (IBF-SV-2010). Universidad de El Salvador, San Salvador, El Salvador, 40 pp.

**Sowerby GB II** (1868) Monograph of the genus *Mycetopus*. Conchologica Iconica 16: 1–4.

**Vaughn CC** (2017) Ecosystem services provided by freshwater mussels. Hydrobiologia 810: 15–27. https://doi.org/10.1007/s10750-017-3139-x

**Vaughn CC, Taylor CM, Eberhard KJ** (1997) A comparison of the effectiveness of timed searches vs. quadrat sampling in mussel surveys. In: Cummings KS, Buchanan AC, Mayer CA, Naimo TJ (Eds.) Conservation and management of freshwater mussels II: initiatives for the future. Proceedings of the Upper Mississippi River Conservation Committee (UMRCC) Symposium, Rock Island, Illinois, USA, 157–162.

**Walker JM, Curolé JP, Wade DE, Chapman EG, Bogan AE, Watters GT, Hoeh WR** (2006) Taxonomic distribution and phylogenetic utility of gender-associated mitochondrial genomes in the Unionoida (Bivalvia). Malacologia 48: 265–282.