Zootaxa 4816 (4): 457–490
https://www.mapress.com/j/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.4816.4.3
http://zoobank.org/urn:lsid:zoobank.org:pub:7683A3B0-5833-49B6-A7CE-675D116DBC67

A new species of freshwater mussel in the genus *Popenaias* Frierson, 1927, from the Gulf coastal rivers of central Mexico (Bivalvia: Unionida: Unionidae) with comments on the genus

KENTARO INOUE[1,2], KEVIN S. CUMMINGS[3], JEREMY S. TIEMANN[3,8], THOMAS D. MILLER[4], NATHAN A. JOHNSON[5], CHASE H. SMITH[6] & CHARLES R. RANDKLEV[1,7]

[1]*Natural Resources Institute, Texas A&M University, College Station, Texas, USA*
[2]*Daniel P. Haerther Center for Conservation and Research, John G. Shedd Aquarium, Chicago, IL, USA*
kinoue@sheddquarium.org, https://orcid.org/0000-0001-6087-3290
[3]*Illinois Natural History Survey, Prairie Research Institute, University of Illinois, Champaign, Illinois, USA, kscummin@illinois.edu,*
[4]*Environmental Science Center, Laredo Community College, Laredo, Texas, USA, tmiller@laredo.edu,*
[5]*Wetland and Aquatic Research Center, U.S. Geological Survey, Gainesville, Florida, USA*
najohnson@usgs.gov, https://orcid.org/0000-0001-5167-1988
[6]*Biology Department, Baylor University, Waco, Texas, USA.*
Chase_Smith1@baylor.edu, https://orcid.org/0000-0002-1499-0311
[7] *crandklev@ag.tamu.edu, https://orcid.org/0000-0002-6755-1507*
[8] *jtiemann@illinois.edu, https://orcid.org/0000-0001-7635-1403*

Abstract

The Gulf coastal drainages of central Mexico are a faunal transition zone between North and South America and harbor a unique assemblage of freshwater mussels (Bivalvia: Unionida). However, little information is available regarding the taxonomy, distribution, and evolutionary history of the Mexican mussel fauna due to limited sampling over the last 100 years. To address these knowledge gaps, we evaluated species-level diversity in the genus *Popenaias* Frierson, 1927, in Mexican Gulf coastal drainages as part of a larger effort to inform conservation efforts for members of this genus both in Mexico and the United States of America. Based on our analyses, we describe *Popenaias berezai* **n. sp.** from the Río Valles of the Río Pánuco basin, San Luis Potosí, Mexico. We also provide presumptive distributional range, phylogenetic structure, and molecular and morphological diagnoses of the new species and provide comments on the other species currently in *Popenaias*. Our findings highlight the high levels of endemism among freshwater mussels in Mexican Gulf coastal drainages and will help guide impending conservation actions for *P. popeii*, which is listed as "endangered" in the United States.

Key words: Mollusca, Fourier shape morphometrics, biodiversity, phylogenetics, species delimitation, endemic species

Introduction

The Gulf coastal drainages of Mexico south of the Rio Grande are a transition zone between the Nearctic and Neotropic realms and harbor unique assemblages of aquatic biota (Miller & Smith 1986). Freshwater mussels (Bivalvia: Unionida) have high species diversity in the Nearctic and Neotropic regions of North, Central, and South America (Graf & Cummings 2007; Bogan & Roe 2008; Lopes-Lima *et al.* 2018). The mussel fauna of Central America is highly endemic and is comprised of species in both Unionidae (94 spp.) and Mycetopodidae (8 spp.; Graf & Cummings 2007). However, outdated taxonomy (Frierson 1927; Haas 1969) combined with a lack of systematic sampling continues to stymie efforts to better understand the distribution and evolutionary history of the mussel fauna in Mesoamerica (Bogan & Roe 2008; Pfeiffer *et al.* 2018; Pfeiffer *et al.* 2019a; Pfeiffer *et al.* 2019b).

At 98,227 km^2, the Río Pánuco basin is one of the largest in Mesoamerica and is the third-largest watershed in Mexico after the Rio Grande (= Río Bravo del Norte in Mexico; 870,000 km^2) and Río Usumacinta (112,550 km^2) (Hudson *et al.* 2005). Early surveys for freshwater mussels in the Río Pánuco basin were conducted by Anson A. Hinkley from 1907–1909 (Pilsbry 1910; Pilsbry & Hinkley 1910). Hinkley collected mussels and other molluscs

Accepted by N. Malchus: 11 Jun. 2020; published: 20 Jul. 2020

at 41 sites in the Mexican states of San Luis Potosí and Tamaulipas (Pilsbry & Hinkley 1910). Based on Hinkley's survey, Pilsbry (1910) listed 17 mussel species and subspecies from the Río Pánuco basin, including seven new taxa. Additionally, multiple unpublished survey efforts in the Río Pánuco made it one of the only Mesoamerican basins that has been robustly sampled, and based on those efforts, appears to be a biodiversity hotspot for freshwater molluscs. However, the taxonomy and systematics of taxa attributed to this basin have not been assessed using modern molecular and morphometric techniques.

The genus *Popenaias* Frierson, 1927, as currently understood, contains three species: *Popenaias popeii* (Lea, 1857), *Popenaias metallica* (Say, 1831), and *Popenaias tehuantepecensis* (Crosse & Fischer, 1893) (Graf & Cummings 2007). *Popenaias popeii* was thought to have a large distribution, ranging from the Rio Grande and its tributaries in Mexico and the United States, south to northern Veracruz (Johnson 1999; Randklev *et al.* 2018). Currently, there are only four substantial populations remaining in the United States: the Black River (a tributary of the Pecos River in Eddy County, New Mexico), the Devils River (a tributary of the Rio Grande in Val Verde County, Texas), and the Rio Grande, both in the Lower Canyons (Brewster and Terrell counties, Texas) and downstream near Laredo (Webb County, Texas) (Randklev *et al.* 2018). Three live individuals have been reported from the Pecos River, a tributary of the Rio Grande; however, it appears this population has disappeared due to water quality and quantity issues (Inoue *et al.* 2014; Randklev *et al.* 2018; Hart *et al.* 2019). In Mexico, a fifth population was recently discovered in the Río San Diego, a tributary of the Rio Grande (D. Berg, pers. comm. 2018); however, detailed information on the distribution of *P. popeii* in Gulf coastal rivers south of the Rio Grande remains unknown. *Popenaias popeii* is currently ranked as "critically endangered" by the International Union for the Conservation of Nature (IUCN) (Bogan 1996), considered "threatened" by the state of Texas (Texas Parks and Wildlife Department 2020), "endangered" by the state of New Mexico (Carman 2007), and is listed as "endangered" under the U.S. Endangered Species Act (USFWS 2018).

The name *Popenaias metallica* has been applied by some previous researchers to one of the *Popenaias* species in Mexican Gulf coastal rivers (Haas 1969); however, the dubious type locality of "Mexico….Lake Chalco?" Mexico City, Mexico [19.26351, -98.97017] (Binney 1858, p. 134), and the absence of type specimens makes it difficult if not impossible to determine the validity of *P. metallica*. While the type specimens are presumedly lost, there are two specimen lots from Lake Chalco (AMNH 29105, n = 2 and AMNH 31036, n = 1) identified as *P. metallica*, representing the only unionids known from the type locality of *P. metallica*. However, it is unlikely that the population is still extant because the lake has been drained. Regarding its placement in the genus *Popenaias*, given that all of the known specimens in the genus are known from Gulf of Mexico tributaries, it is questionable that *Unio metallicus* Say, 1831 is a member of *Popenaias*.

Pilsbry (1910) described a subspecies of "*P. metallica"* (as *Lampsilis metallica ganina*) from the Río Gallinas of the Río Pánuco and we recognize *Popenaias ganina* (Pilsbry, 1910**) n. comb.** for those specimens previously referred to as *Lampsilis metallica ganina* (see Systematics below). Furthermore, *Unio cuprinus* Lea, 1831 is often treated as a junior synonym of *P. metallica* (e.g., Haas, 1969). However, due to the lack of a specific type locality ("Mexico") this could be one of about a dozen different species.

Another taxon, *Popenaias tehuantepecensis*, is thought to occur in southern Pacific coastal rivers of Oaxaca, Mexico. This species was described as *Unio tehuantepecensis* by Crosse & Fischer (1893, p. 297) from "prope Santa Efigenia, in isthmo Tehuantepec dicto, provinciae Oajaca, reipublicae Mexicanae," which would place it in the Pacific Basin at approximately Río Novillero, Santa Efigenia, Isthmus of Tehuantepec, Oaxaca, Mexico [16.40387, -94.21612]. However, due to its disjunct distribution and the limited number of specimens in museum collections, the taxonomic validity (including its placement in *Popenaias*) and distribution of *P. tehuantepecensis* are uncertain (see Systematics below).

The objective of this study is to resolve phylogenetic relationships and evaluate species-level diversity in *Popenaias* to better understand the evolutionary history of the group and support conservation efforts for *P. popeii* in the United States. We conducted fieldwork in the Río Pánuco basin in San Luis Potosí, Mexico, in 2017 and 2018. Based on our field data and existing museum records, we use a holistic approach to evaluate the taxonomic validity of *Popenaias* species in Mexican Gulf coastal rivers, particularly in the Río Pánuco basin. We first delineate species boundaries within *Popenaias* by reconstructing phylogenetic trees, and subsequently use Fourier shape morphometrics to examine morphological differences between the species. From these results, we formally describe *Popenaias berezai* **n. sp.** from the Río Valles, San Luis Potosí, Mexico, and further revise systematics within the *Popenaias*. Our findings highlight the high level of endemism in the Gulf coastal drainages of central Mexico and will help guide impending conservation actions for the federally endangered *P. popeii* (USFWS 2018).

Materials and methods

Specimen sampling and genetic data collection. We collected genetic samples (mucus swabs or mantle tissue biopsies) and photo vouchers of specimens that were identified as *Popenaias* from six rivers in the Río Pánuco basin, San Luis Potosí, Mexico, during reconnaissance surveys conducted in 2017 and 2018. Additionally, we collected fresh animals from a subset of the specimens to document shell and soft anatomy characteristics and to designate the type series for the species description. A total of 214 *Popenaias* specimens were collected from the Río Amajac (including the Río Claro, a tributary; n = 88), Río Gallinas (n = 21), Río Huichihuayán (n = 2), Río Tampaón (n = 12), Río Tancuilín (n = 21), and Río Valles (n = 70; Fig. 1; Appendix). All genetic samples and vouchered specimens were preserved in 95% ethanol and deposited at Texas A&M Natural Resources Institute, Dallas (NRI), Illinois Natural History Survey, Champaign (INHS), or the Universidad Autónoma de Tamaulipas, Victoria (UAT uncatalogued). Furthermore, we included 39 individuals of *P. popeii* from four locations in the Rio Grande basin (Devils River, two locations in the Lower Canyons of the Rio Grande, and lower Rio Grande near Laredo, TX; Fig. 1; Appendix). The Lower Canyons and lower Rio Grande individuals (n = 31) of *P. popeii* were collected in 2015–2017 prior to its listing as "endangered" under the U.S. Endangered Species Act (USFWS 2018) and non-lethal mantle clips were taken from the Devils River individuals (n = 8) in September 2018. Here, we use a subset of specimens for molecular and morphometric analyses.

In addition, specimens from the following institutions were examined for mapping and taxonomic accounts: Australian Museum of Natural History, Sydney (AMS), American Museum of Natural History, New York (AMNH), Academy of Natural Sciences of Drexel University, Philadelphia (ANSP), Carnegie Museum of Natural History, Pittsburgh (CM), Field Museum of Natural History, Chicago (FMNH), Illinois Natural History Survey, Champaign (INHS), Museum of Comparative Zoology, Harvard, Cambridge (MCZ), North Carolina Museum of Natural Sciences, Raleigh (NCSM), British Museum of Natural History, London (NHMUK), Texas A&M Natural Resources Institute, Dallas (NRI), Ohio State University Museum of Biological Diversity, Columbus (OSUM), Florida Museum of Natural History, Gainesville (UF), University of Michigan Museum of Zoology, Ann Arbor (UMMZ), Smithsonian National Museum of Natural History, Washington D.C. (USNM), and the Zoological Museum für Naturkunde, Berlin (ZMB). Museum acronyms follow Sabaj (2019). Additional data from published sources or online searches that we believe plausible are added to the range maps. Latitudinal and longitudinal coordinates for specimens not collected by the authors are estimates derived from the textual descriptions of the label data and are indicated by brackets. Numbers in parentheses following museum catalogue numbers represent the number of specimens in the lot.

We extracted total DNA using cetyltrimethylammonium bromide (CTAB)/chloroform extraction followed by ethanol precipitation (Saghai-Maroof *et al.* 1984). Extracted DNA was diluted to 10 ng/µL and used as a template in polymerase chain reaction (PCR) that amplified the mitochondrial DNA (mtDNA) cytochrome oxidase I (*cox1*) and 16S ribosomal RNA (*16S*) genes and the nuclear DNA (nDNA) adenine nucleotide translocase (*ANT*) gene. We used the *cox1* primers described by Walker *et al.* (2006), the *16S* primers described by Lydeard *et al.* (1996), and the *ANT* primers described by Audzijonyte & Vrijenhoek (2010). We followed the recommended thermal conditions for PCR provided in the original literature. The PCR products were visualized using 1% agarose gel electrophoresis and purified with exonuclease I and shrimp alkaline phosphatase (New England Biolabs, Ipswich, MA). We employed Eurofins Genomics (Louisville, KY) for DNA sequencing. Sequences were assembled and aligned using SeqMan Pro v14.0 (DNASTAR, Madison, WI), and an open-reading-frame was verified for *cox1* and *ANT* genes. Ambiguous sequences on the 3' and the 5' ends were trimmed. We used MAFFT v7.429 (Katoh & Standley 2013) to perform multiple sequence alignment.

Phylogenetic analyses and estimate of genetic diversity. Phylogenetic inference was performed using Bayesian inference (BI), maximum likelihood (ML), and maximum parsimony (MP) analyses based on a concatenated dataset (*cox1*, *16S*, and *ANT*; GenBank accession numbers: MT553859–MT553983 for *cox1*, MT561579–MT561701 for *16S*, MT558866–MT558910 for *ANT*; Appendix). Additionally, we included 24 species from the tribes Amblemini, Lampsilini, and Popenaiadini to evaluate phylogenetic relationships (Table 1). We used *Quadrula quadrula* (Rafinesque, 1820) (Quadrulini) as the outgroup based on previous phylogenetic assessments (Lopes-Lima *et al.* 2017; Pfeiffer *et al.* 2019a; Smith *et al.* 2019). Phylogenetic analyses were performed with MrBayes v3.2.6 (Ronquist *et al.* 2012), IQ-Tree v1.6.5 (Nguyen *et al.* 2015), and MPBoot v1.1.0 (Hoang *et al.* 2018b).

TABLE 1. List of outgroup sequences used in this study. GenBank accession numbers are provided.

Tribe	Species	*cox1*	*16S*	*ANT*
Amblemini	*Amblema elliottii*	AY654991	AY655029	
Amblemini	*Amblema neislerii*	KT285617	MK001787	
Amblemini	*Amblema plicata*	KT285618	MK001786	
Amblemini	*Reginaia ebenus*	KF035133		
Amblemini	*Reginaia rotulata*	KT285641	MK001789	
Lampsilini	*Actinonaias ligamentina*	AF156517	AY655027	MK672134
Lampsilini	*Cyrtonaias explicata* (1)	MK001769	MK001801	
Lampsilini	*Cyrtonaias explicata* (2)*	MK001770	MK001802	
Lampsilini	*Cyrtonaias tampicoensis*	MT553984	MT561702	MT558911
Lampsilini	*Cyrtonaias tampicoensis*	MT553985		MT558912
Lampsilini	*Cyrtonaias tampicoensis*	MT553986		MT558913
Lampsilini	*Cyrtonaias tampicoensis*	MT553987	MT561703	MT558914
Lampsilini	*Cyrtonaias tampicoensis*	MT553988	MT561704	MT558915
Lampsilini	*Cyrtonaias tampicoensis*	MT553989	MT561705	
Lampsilini	*Cyrtonaias tampicoensis*	MT553990	MT561706	
Lampsilini	*Cyrtonaias tampicoensis*	MT553991		MT558916
Lampsilini	*Cyrtonaias tampicoensis*	MT553992		MT558917
Lampsilini	*Cyrtonaias tampicoensis*	MT553993		
Lampsilini	*Epioblasma triquetra*	AF156528	DQ208546	
Lampsilini	*Glebula rotundata*	KT285642	MK001808	MT558918
Lampsilini	*Lampsilis cardium*	KP795038	KP795057	MK672139
Lampsilini	*Ligumia recta*	AF156516	AF385134	
Lampsilini	*Pachynaias spheniopsis* (1)	MK001773	MK001805	
Lampsilini	*Pachynaias spheniopsis* (2)	MK001774	MK001806	
Lampsilini	*Potamilus alatus*	KP795037	KP795056	
Lampsilini	*Ptychobranchus fasciolaris*	AF156517	JX311498	
Lampsilini	*Sphenonaias microdon* (1)	MK001771	MK001803	
Lampsilini	*Sphenonaias microdon* (2)	MK001772	MK001804	
Lampsilini	*Truncilla truncata*	AF156513	AY655080	
Lampsilini	*Villosa iris*	AF156524	AF385133	
Popenaiadini	*Psoronaias semigranosa* (1)***	MK001758	MK001775	
Popenaiadini	*Psoronaias semigranosa* (2)	MK001759	MK001776	
Popenaiadini	*Psorula guatemalensis* (1)	MK001760	MK001777	
Popenaiadini	*Psorula guatemalensis* (2)	MK001761	MK001778	
Popenaiadini	*Psorula percompressa*	MK001762	MK001779	
Popenaiadini	*Psorula profunda*	MK001763	MK001780	
Popenaiadini	*Psorula rudis* (1)	MK001765	MK001782	
Popenaiadini	*Psorula rudis* (2)	MK001764	MK001781	
Popenaiadini	*Psorula usumasintae* (1)***	MK001766	MK001783	
Popenaiadini	*Psorula usumasintae* (2)**	MK001767	MK001784	
Quadrulini	*Quadrula quadrula*	AF231757	AY238485	

* *Cyrtonaias explicata* (2) is genetically identical to *Cyrtonaias explicata* (1); ** *Psorula usumasintae* (2) is genetically identical to *Psorula rudis* (2); *** *Psoronaias semigranosa* (1) and *Psorula usumasintae* (1) are genetically identical to *Psorula rudis* (1).

Prior to the phylogenetic analyses, we used MetaPIGA v3.1 (Helaers & Milinkovitch 2010) to identify unique haplotypes and evaluate substitution saturations. We only used unique haplotypes for the phylogenetic analyses and used Kakusan4 (Tanabe 2011) to estimate the best-fit model of nucleotide substitution for *16S* and each codon position of *cox1* and *ANT*. In MrBayes, two simultaneous Markov chain Monte Carlo (MCMC) runs (each chain containing three heated and one cold chain) were executed for 2×10^6 generations, with trees sampled every 1000 generations. Convergence of the two independent runs was monitored using the potential scale reduction factors (PSRF) of each parameter and the average standard deviation of split frequencies.

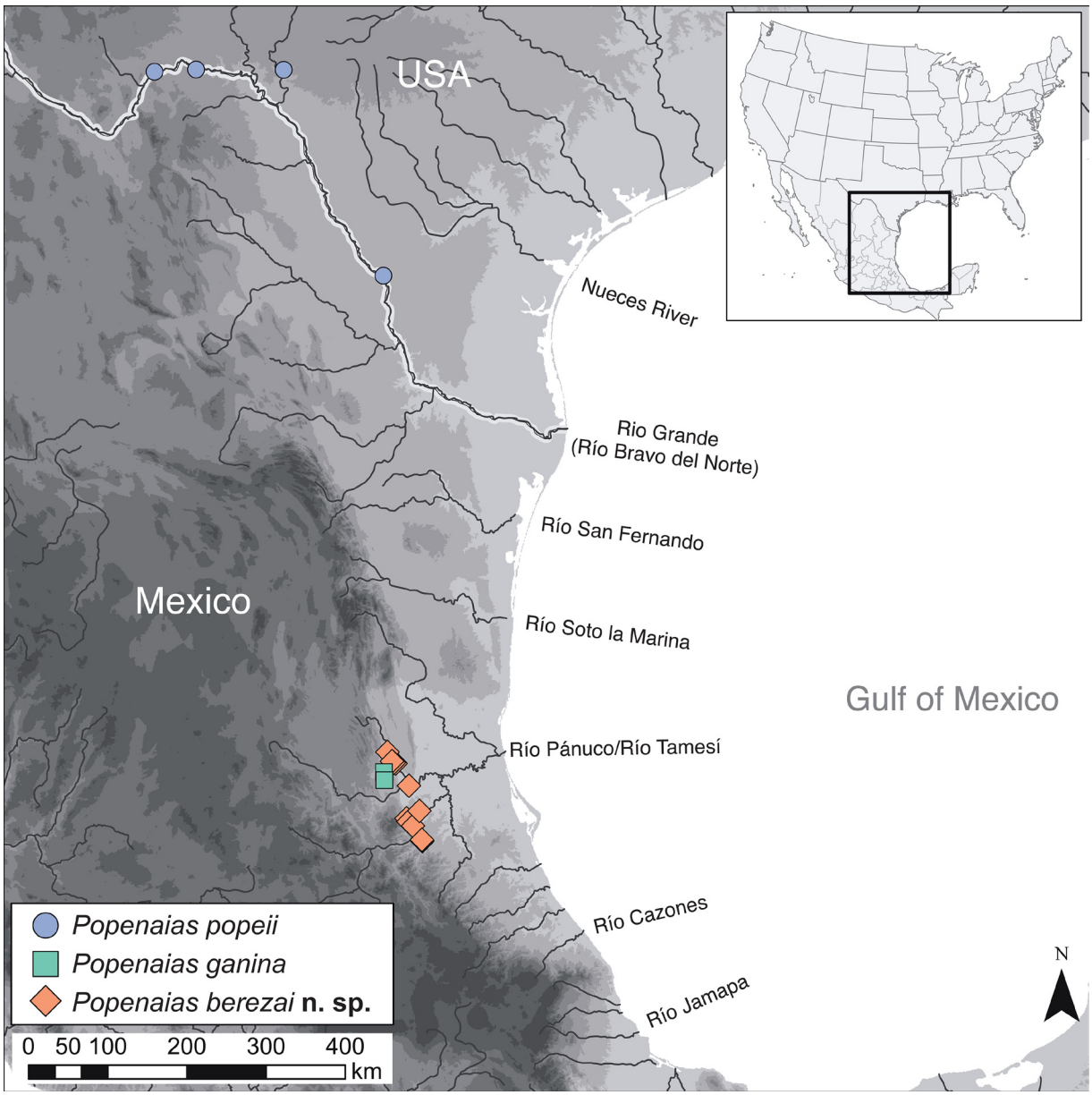

FIGURE 1. Collection localities for *Popenaias* species for molecular and morphometric analyses used in this study. Colored symbols represent target species (blue circles, *Popenaias popeii*; green squares, *P. ganina*; orange diamonds, *P. berezai* **n. sp.**). Shading indicates elevation where darker colors represent higher altitude.

We used Tracer v1.7 (Rambaut *et al.* 2018) to assess the convergence of both MCMC runs by plotting the log-likelihood scores for each sampled point. When the likelihood values reached plateau with sufficient effective sample sizes (ESS > 200), we considered the Markov chain stationary. Accordingly, we discarded the first 25% of trees as burn-in, a 50% majority rule consensus tree was estimated for remaining trees.

For the ML analysis, we used ModelFinder (Kalyaanamoorthy *et al.* 2017) implemented in IQ-Tree to estimate the best-fit substitution models for each gene and codon partition. We used 1000 ultrafast bootstrap replicates to

calculate nodal support values (Hoang *et al.* 2018a). For the MP analysis, we used default function in MPBoot to reconstruct a cladogram. We used 1000 ultrafast bootstrap replicates to calculate nodal support values. We used MEGA v7.0.16 (Kumar *et al.* 2016) to estimate pairwise genetic divergence (uncorrected p-distance) between pairs of species (i.e., *Popenaias ganina*, *P. popeii*, and *P. berezai* **n. sp.**) separately for each locus (i.e., *cox1*, *16S*, and *ANT*).

Morphometric analyses. We conducted Fourier shape morphometrics to compare shell shapes among *Popenaias* species. Digital photographs of the right valve were taken during field collections and of vouchered specimens with a Canon EOS7D SLR camera (Appendix). The outline of each shell was extracted by cropping the image in Adobe Photoshop CC v2015.0.0 (Adobe Systems). Using the cropped shell images, the shell outline was described by 20 Fourier coefficients using SHAPE v1.3 (Iwata & Ukai 2002).

We examined morphological variation within and among species through principal component analysis (PCA) and canonical variate analysis (CVA). While both analyses simplified description of variation among individuals, CVA requires *a priori* assignments to group individuals (i.e., *Popenaias ganina*, *P. popeii*, and *P. berezai* **n. sp.**). We plotted PCA and CVA with the first two axes. Additionally, we used multivariate analysis of variance (MANOVA) and discriminant function analysis (DFA) to determine how frequently principal component (PC) scores correctly distinguished between groups. We retained the first five PC axes, which contained >90% of total variation, for the analyses. We created a confusion matrix based on the DFA by calculating proportions of correct group assignments. Statistical analyses were performed using the software PAST v2.17 (Hammer *et al.* 2001).

Results

The BI, ML, and MP phylogenies based on the concatenated gene dataset show similar tree topologies and nodal supports (Figs 2 and 3). Convergence of the two MrBayes runs is supported by the PSRF value for each parameter equal to 1.000 and the average of the standard deviation of split frequencies (0.0113). Popenaiadini is recovered as a monophyletic clade with strong nodal supports with the exception of the MP analysis (posterior probability (PP) = 100%, ML bootstrap support (MLBS) = 96%, MP bootstrap support (MPBS) = 70%; Figs 2 and 3). *Popenaias* is resolved as sister to a clade consisting of species in the genera *Psoronaias* Fischer & Crosse, 1894, and *Psorula* Haas, 1930, and nominal species in *Psoronaias* and *Psorula* formed a shallow clade (Figs 2 and 3). Within *Popenaias*, *P. popeii* is recovered as sister to a clade of *P. ganina* from the Río Gallinas and *P. berezai* **n. sp.** from the Río Valles (PP = 100%, MLBS = 99%, MPBS = 99%; Figs 2 and 3).

Mean pairwise genetic divergence among species range from 0.0904 between *Popenaias ganina* and *P. berezai* **n. sp.** (range 0.0858–0.0978) to 0.1176 between *P. ganina* vs. *P. popeii* (0.1133–0.1246) for the *cox1* gene and ranged from 0.0264 between *P. ganina* and *P. berezai* **n. sp.** (0.0262–0.0300) to 0.0671 between *P. popeii* and *P. berezai* **n. sp.** (0.0624–0.0726) for the *16S* gene (Table 2). For the nDNA *ANT* gene, genetic divergence among species is relatively low (range 0.0022–0.0082; Table 2).

TABLE 2. Pairwise genetic divergences (uncorrected p-distance) between species for each mitochondrial DNA gene below diagonal (top = *cox1*, bottom = *16S*) and nuclear DNA gene above diagonal (*ANT*). Minimum and maximum divergences and the mean divergence in parentheses are shown.

	Popenaias popeii	*Popenaias ganina*	*Popenaias berezai* **n. sp.**
Popenaias popeii	—	0.0081–0.0085 (0.0082)	0.0060–0.0085 (0.0073)
Popenaias ganina	0.1133–0.1246 (0.1176) 0.0605–0.0685 (0.0616)	—	0–0.0040 (0.0022)
Popenaias berezai **n. sp.**	0.1063–0.1155 (0.1106) 0.0624–0.0726 (0.0671)	0.0858–0.0978 (0.0904) 0.0262–0.0300 (0.0264)	—

External shell morphologies are statistically different among *Popenaias* species (Table 3; Fig. 4). The PCA based on Fourier morphometrics yields the first two eigenvalues that describe 79.5% of the total variation among individuals (Fig. 4A). The PC1 axis describes 69.8% of the total variation and represents elongation of shells along the posterior-anterior axis and the PC2 axis describes 9.7% of the total variation and represents the presence/absence of arcuation on the ventral margin.

TABLE 3. Confusion matrix with percentage of individuals in an *a priori* species classification (rows) that are assigned to the predicted species (columns) based on a discriminant function analysis for Fourier shape morphometrics. The *a priori* species classification includes *Popenaias popeii* (n = 31), *P. ganina* (n = 21), and *P. berezai* **n. sp.** (n = 195). Diagonal values indicate the percentage of correctly predicted species assignments.

	Popenaias popeii	*Popenaias ganina*	*Popenaias berezai* **n. sp.**
Popenaias popeii	96.8	0	3.2
Popenaias ganina	0	100	0
Popenaias berezai **n. sp.**	1.0	8.2	90.8

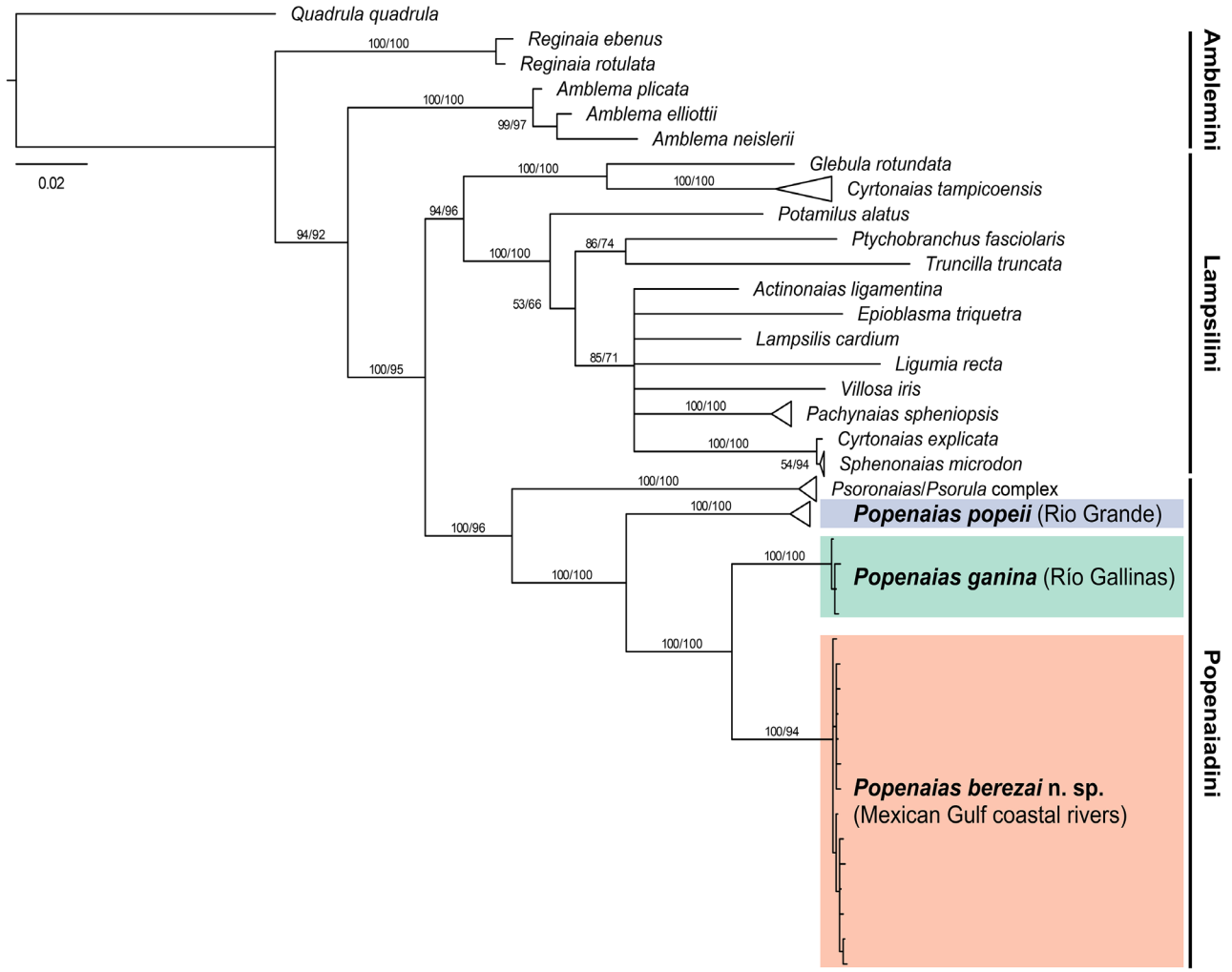

FIGURE 2. Phylogenetic tree reconstructed by Bayesian inference (BI) for the concatenated mitochondrial and nuclear DNA (*cox1*, *16S*, and *ANT*) sequence dataset. Nodal supports (i.e., posterior probability values from BI analysis and ultrafast bootstrap support values from maximum likelihood analysis) are shown as percentages along the branches. The tree is rooted with *Quadrula quadrula*. Major clades are annotated. Colored box along clades corresponds to the target taxa (blue, *Popenaias popeii*; green, *P. ganina*; orange, *P. berezai* **n. sp.**).

Popenaias popeii has a relatively elongated shell outline when compared with other species of *Popenaias*, with some individuals exhibiting a concave ventral margin (Fig. 4A). *Popenaias berezai* **n. sp.** shows a larger morphological variation relative to other *Popenaias* species examined and has an elongated shell outline with a wider posterior margin. *Popenaias ganina* has a relatively oval shell outline and concave ventral margin.

The CVA plot shows similar patterns of clustering to PCA among species (Fig. 4B). The MANOVA revealed that shell morphologies are significantly different among species (Wilk's $\Lambda = 0.2466$; $F_{10, 476} = 48.26$; $P < 0.001$). Mean *a priori* correct assignment of individuals to groups was 96% and ranges from 91.2% to 100% ($P < 0.001$; Table 3).

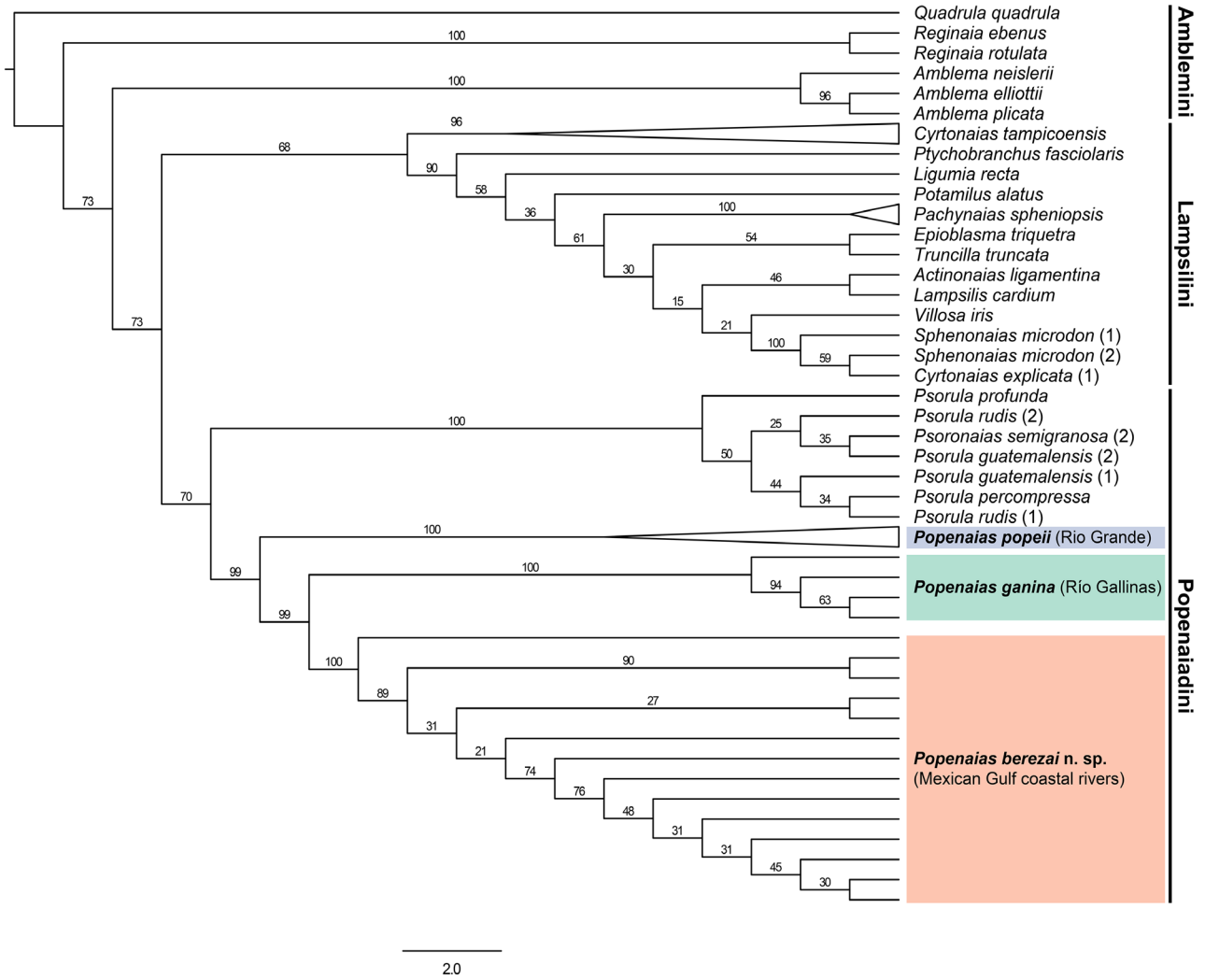

FIGURE 3. Maximum parsimony cladogram for the concatenated mitochondrial and nuclear DNA (*cox1*, *16S*, and *ANT*) sequence dataset. Bootstrap support values are shown in percent along the branches. The tree is rooted with *Quadrula quadrula*. Major clades are annotated. Colored box along clades corresponds to the target taxa: blue, *Popenaias popeii*; green, *P. ganina*; orange, *P. berezai* **n. sp.**

Systematics

Class Bivalvia Linnaeus, 1758

Order Unionida Gray, 1854

Family Unionidae Rafinesque, 1820

Tribe Popenaiadini Heard & Guckert, 1970

Genus *Popenaias* Frierson, 1927

Popenaias berezai Inoue *et al.* n. sp.

(Figs 5, 6, 7, 8A, 9A)

Common name: Mexico Hornshell

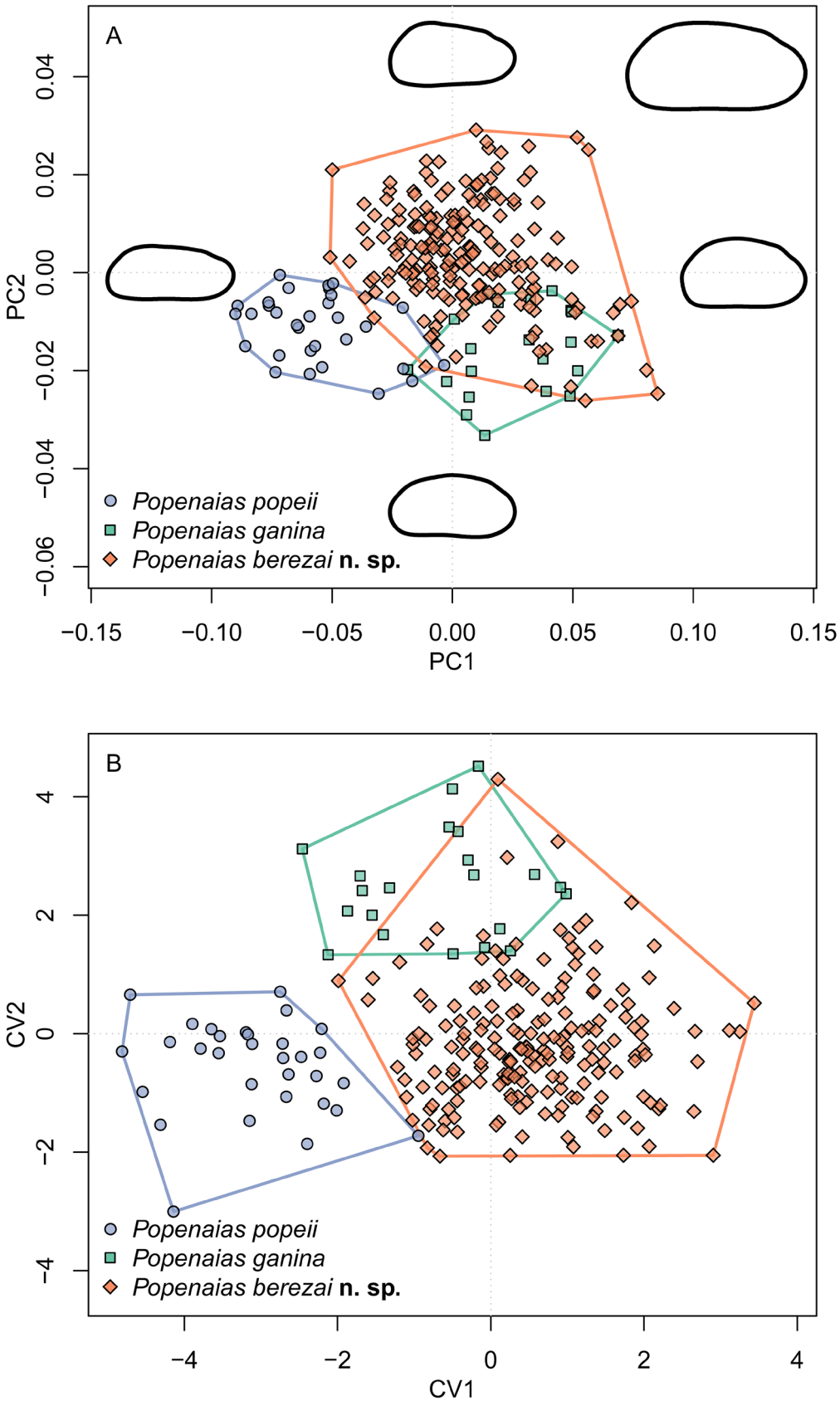

FIGURE 4. Biplots from principal component analysis (PCA; A) and canonical variate analysis (CVA; B) of Fourier shape morphometrics. Colors and shapes of points correspond to species: blue circles, *Popenaias popeii*; green squares, *P. ganina*; orange diamonds, *P. berezai* **n. sp.** Polygons enclose convex hulls of each species. Outlined shell shapes represent a mean shape (top-right) and ±2 × SD on PC1 and PC2 axes.

Type locality: Río Valles (Gulf of Mexico—Río Pánuco—Río Tampaón), Estación Micos, 20 km NW of Ciudad Valles, San Luis Potosí, Mexico, 22.11417, -99.16166.

Type specimens: *Holotype*: CNMO 8037 (ex. INHS 90397.5). *Paratypes*: from the type locality, CNMO 8038 (3), FMNH 344800 (3), INHS 90397 (9), NHMUK 20191101 (3), NRI 9603 (3), UF 548816 (3), USNM 1617023 (3); Río Claro (Río Pánuco—Río Moctezuma—Río Amajac), 5.5 km SE of Tamazunchale, San Luis Potosí, Mexico, 21.22150, -98.75573, INHS 90134 (3); Río Amajac (Río Moctezuma), 5.1 km SE of Tamazunchale, San Luis Potosí, Mexico, 21.22728, -98.75437, CNMO 8039 (2), FMNH 344801 (2), INHS 90152 (10), NHMUK 20191102 (2), NRI 9604 (2), UF 548817 (2), USNM 1617024 (2); Río Huichihuayán (Río Moctezuma), Huichihuayán, Ejido Tazaquil, San Luis Potosí, Mexico, 21.47269, -98.95768, INHS 90167 (1); Río Tancuilín (Río Moctezuma—Río Axtla), Jalpilla, 5.5 km S of Axtla de Terrazas, San Luis Potosí, Mexico, 21.39008, -98.87544, CNMO 8040 (2), FMNH 344802 (2), INHS 90175 (9), NHMUK 20191103 (2), NRI 9605 (2), UF 548818 (2), USNM 1617025 (2); Río Tampaón (Río Pánuco), Álvaro Obregón (Pujal), at confluence of the ríos Valles and Tampaón, San Luis Potosí, Mexico, 21.84489, -98.94373, INHS 90183 (12); Río Huichihuayán (Río Moctezuma), Rt. 120, 9 km WSW of Axtla de Terrazas, 12 km NNE of Xilitla, San Luis Potosí, Mexico, 21.43633, -98.93345, INHS 90192 (2); Río Amajac (Río Moctezuma), Temamatla, San Luis Potosí, Mexico, 21.23664, -98.76189, CNMO 8041 (5), FMNH 344803 (5), INHS 90199 (33), NHMUK 20191103 (5), NRI 9606 (5), UF 548819 (5), USNM 1617026 (5).

Synonymy

Unio (*Graphonaias*) *popei* Lea, 1857—Fischer & Crosse 1894:605.
Unio (*Nephronaias*) *popei* Lea, 1857—von Martens 1900:504.
Unio (sec. *Elliptio*) *popeii* (Lea, 1857)—Simpson 1900:738 [in part]; Simpson 1914:700 [in part].
Lampsilis popei (Lea, 1857)—Pilsbry 1910:535 [in part].
Elliptio popei (Lea, 1857)—Ortmann 1912:271.
Elliptio (*Popenaias*) *popei* (Lea)—Frierson 1927:38 [in part]; Haas 1929:330 [in part].
Nephronaias (*Popenaias*) *popei* (Lea, 1857)—Haas 1969:201 [in part].
Popenaias popeii (Lea, 1857)—Graf & Cummings 2007 [in part]; Pfeiffer *et al.* 2019a:108.
Note: "[in part]" indicates that the author(s) mentioned Mexican specimens of *Popenaias berezai* (herein) as *popeii* in their publications.

Other material examined (North to South):

Río Soto la Marina drainage. **Tamaulipas:** Río Soto la Marina, 6.5 km SW of Padilla, near Guemez, [23.93784, -98.93584], MCZ 295008 (2); Río Purificación, near Padilla, [24.01667, -98.78333], MCZ 295009 (8); Río Purificación, 27–28 km NE of Victoria, Presa Vicente Guerrero, [24.04069, -98.90226], INHS 89431 (6) (ex. OSUM uncat.).

Río Carrizal drainage. Tamaulipas: Río Carrizal, at Mex. Rt. 180 in Nuevo Progreso, [23.16598, -97.95372], USNM 1282588 (39), USNM 1283216 (8), UF 231218 (1).

Río Pánuco drainage. San Luis Potosí: Río Valles, (without locality), ANSP 48095 (3), NHMUK 1910.9.30.176 (4), FMNH 59275 (3), MCZ 21084 (6), MCZ 99988 (3), UF 93148 (15), ZMB 61687 (3); Río Valles, Valles, [21.98293, -99.01849], ANSP 985544 (16), CM 61.4493 (1), CM 61.4494 (1), FMNH 21855 (2), FMNH 67916 (5), INHS 21695 (14), INHS 21696 (11), INHS 21699 (10), INHS 21769 (1), MCZ 68500 (2), MCZ 69853 (1), MCZ 99977 (5), MCZ 295010 (8), NCSM 103876 (4), UF 229539 (2), UF 270526 (2), UF 270527 (5), UMMZ 66449 (5), USNM 207439 (3); Río Valles, Willis Ranch, about halfway between Valles and Pujal, [21.90403, -98.97669], ANSP 98543 (6), ANSP 98556 (1), INHS 21694 (4), INHS 21701 (8), MCZ 99982 (3), UF 93182 (1); Río Valles, ~3 km W Micos, [22.13971, -99.21375], ANSP 985545 (9), INHS 21693 (4), INHS 21698 (4), INHS 21703 (5), UF 93150 (5), UMMZ 66448 (2), UMMZ 66450 (3), UMMZ 108003 (5); Río Valles, Falls of the Valles, below Valles, [21.93722, -98.98936], INHS 21702 (8); Río Valles, Micos, [22.10047, -99.15292], MCZ 99979 (4), UF 270525 (2); Río Valles, 2.5 km N Plantas Hidroelectrica de Micos, [22.10343, -99.15654], USNM 1282578 (16); Arroyo los Gatos (Río Valles), Nuevo Morelos, [22.53333, -99.20000], USNM 1282592–1282594 (75); Río Moctezuma, Taman, 13 km SSW Tamazunchale, [21.23313, -98.87915], NCSM 63677 (8); Río Moctezuma, Tamazunchale, [21.26205, -98.78887], NCSM 100791 (2); Río Axtla, Comoca, 74 km S Valles, [21.42220, -98.88951], NCSM 63674 (1); Río Huichihuayán, 8 km NE Xilitla, Mexico Federal Hwy 120, [21.43623, -98.93393], USNM 1282587 (25), USNM 1282580–1282582 (36); Tampamolón Creek, Tampamolón, [21.54667, -98.74895], INHS 21697 (1);

Río Coy, 28 km SSE Valles, [21.74975, -98.95738], INHS 21700 (2); Arroyo Choy, 0.3 km W of Tamuin, at Mex. Fed. Hwy. 70, [21.99902, -98.80659], USNM 1282579 (2); Río Estero, at Mex. Rt. 110, [22.00833, -98.74167], USNM 1282577 (7).

Tamaulipas: Río Pánuco, Tampico, [22.20780, -97.84820], ANSP 93808 (2), UF 93172 (2); Río Tamesí, Hwy 80, 1.6 km W Magiscatzin, [22.79737, -98.71302], NCSM 63678 (8); Río Guayalejo, 30 km ENE Ciudad Mante, [22.79739, -98.71284], AMS 102101 (2), MCZ 288422 (1), MCZ 288427 (2); stream, at Rt. Mex. 80, 5 km E of Ciudad Mante [22.72031, -98.91831] USNM 1282595 (1); Río Guayalejo, 5 km NE junction of Mex. Rt. 85 and the road to Xicotencatl, [22.94966, -98.99817], USNM 1282590 (14); Río Guayalejo, near Magiscatzin, [22.79781, -98.71434], MCZ 361552 (1); Río Sabinas, Hwy 85, 18 km E Gómez Farías, [23.03147, -99.09294], NCSM 63676 (5), UMMZ 191827 (3), USNM 1282589 (5); ditch, 2 km NW El Limon, [22.85672, -99.01875], AMS 102114 (3); creek flowing into Río Frio ca. 0.8 km above bridge of Rt. Mex. 85, [22.84290, -99.02595], USNM 1282591 (15).

Veracruz: Río Tempoal, Rt. Mex. Rt. 105 between Tempoal and Platon Sanchez, [21.41667, -98.39167], USNM 1282604–1282605 (22); Río Tempoal, Tempoal, [21.53388, -98.38657], NCSM 63675 (4).

Río Cazones drainage. Veracruz: Río Cazones, 4 km WSW Poza Rica, [20.49933, -97.51849], AMS 102106 (5), MCZ 288438 (4); Arroyo Pital, near Pital y Mozutla (S of Tuxpan), [20.63333, -97.40000], FMNH 49614 (1); Arroyo Totolapa, Totolapa, 3.2 km NW Poza Rica de Hidalgo, [20.56620, -97.47761], NCSM 103877 (1); unnamed creek, 4.5 km NNW Poza Rica de Hidalgo, [20.58657, -97.44797], MCZ 288426 (1); just N Poza Rica de Hidalgo, [20.57289, -97.49233], USNM 1282600–1282602 (100); Poza Rica de Hidalgo, [20.52437, -97.48333], USNM 1282603 (3).

Río Jamapa drainage. Veracruz: Río Jamapa, (without locality), [19.06977, -96.13124], ANSP 142600 (1).

Comparative diagnosis: *Popenaias berezai* has similar conchological characters to *P. ganina* and *P. popeii*; however, the majority of *P. berezai* individuals have an elongated shape and nearly straight ventral margin compared to *P. ganina* (Figs 4 and 8). *Popenaias berezai* has a wide posterior margin and metallic pink to copper-colored nacre compared to *P. popeii* (Figs 4 and 8). Additionally, *P. berezai* is distinguished from other species of *Popenaias* by 26 diagnostic nucleotides in *cox1*, eight diagnostic nucleotides in *16S*, and two diagnostic heterozygous loci in *ANT* (Table 4).

Shell description: Shell length to 80 mm. Shell outline elongate subtrapezoidal (Fig. 5). Posterior ridge biangulate. Dorsal and ventral margins almost parallel and nearly straight. Umbo broad, even with hinge line or elevated slightly above. Umbo cavity wide, shallow. Shells thin to thick.

Periostracum texture subglossy to clothlike, brown to dark gray or black, with faint thin rays (when present; Fig. 5). Faint irregular corrugations sometimes present on posterior-central disk. Nacre color typically fine metallic pink to copper color and iridescent posteriorly.

Left valve with two thin lateral teeth, straight to slightly curved; two triangular, compressed pseudocardinal teeth (Fig. 6). Right valve with single thin and relatively long lateral tooth, and one compressed triangular, serrated pseudocardinal tooth.

Soft anatomy description: Mantle tan to off-white, sometimes lighter outside of pallial line; mantle wall usually with black, brown and white mottling adjacent to incurrent and excurrent apertures (Fig. 7).

Apertures with dark shades of tan and grey, or black distally, often multicolor. Supra-anal aperture pursed with mantle bridge separating supra-anal and excurrent apertures. Margin of supra-anal aperture smooth and shorter than excurrent aperture. Excurrent aperture bearing reduced, off-white to dark conical, single stalk papillae. Incurrent aperture larger than excurrent aperture and bearing larger papillae, particularly in gravid females.

Papillae are conical, elongate and vary from simple, bifid, and trifid within a single individual; in gravid females, elongation may be extreme such that papillae take on an arborescent appearance.

Gills creamy white to tan, may show streaks of dark pigmentation posteriorly in non-gravid and partially gravid individuals (Fig. 7). Female outer gill marsupial, entire gill is utilized to brood glochidia except the extreme posterior portion and is distended or pad-like when gravid.

Labial palps creamy-white to off-white and often translucent, pointed distally and almost spade-like or boot-shaped in appearance (Fig. 7). Visceral mass usually pearly white, often with tan areas dorsally. Foot off-white to tan and may show dendritic coloration with both colors.

Distribution: *Popenaias berezai* appears to occur in the ríos Soto la Marina, Carrizal, Pánuco (except the Río Gallinas), Cazones, Tecolutla, and Jamapa drainages (north to south) in San Luis Potosí, Tamaulipas, and Veracruz, Mexico (Fig. 9A). However, whether this is the full extent of its distribution is currently unknown.

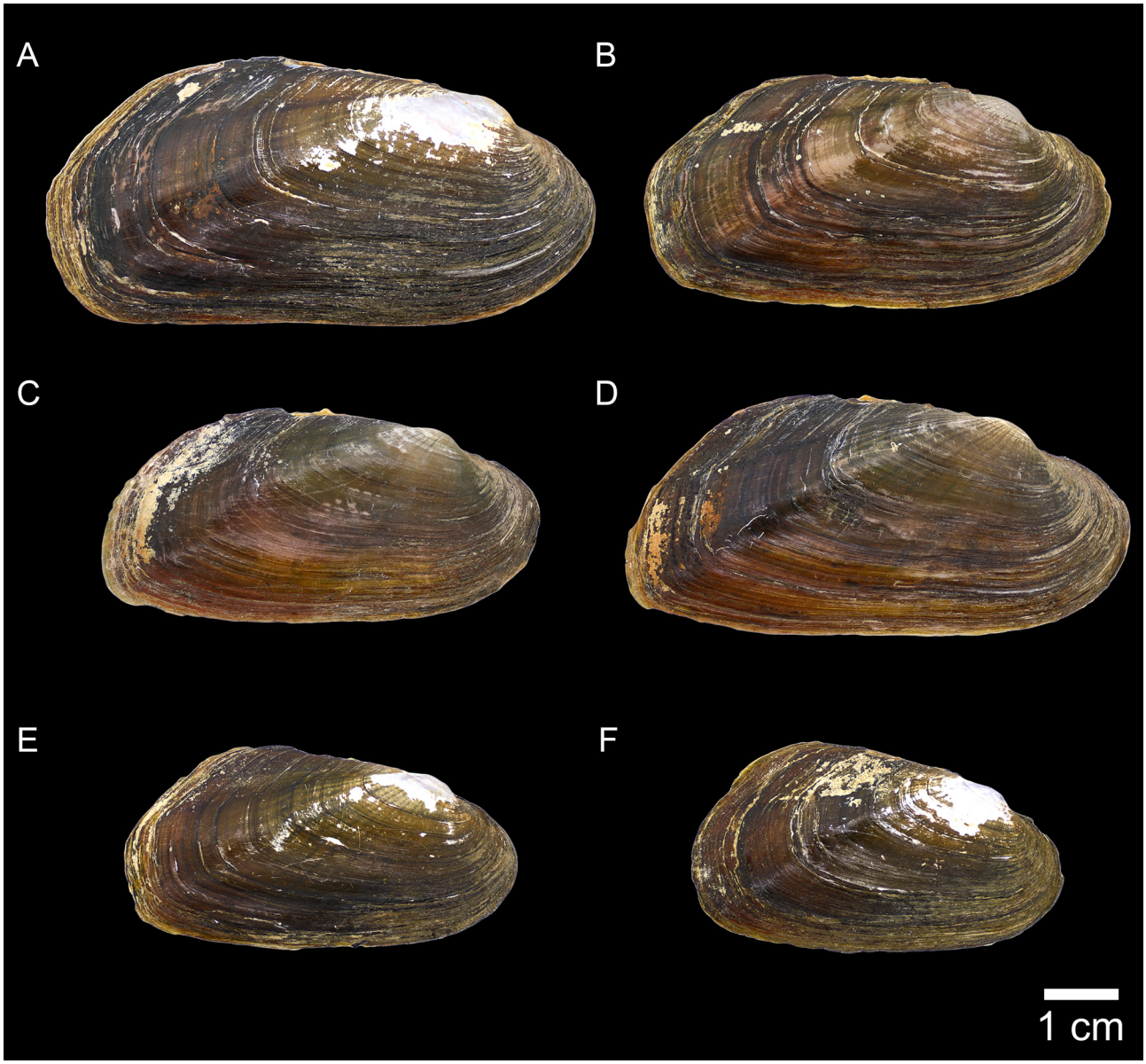

FIGURE 5. Right valve external views of *Popenaias berezai* **n. sp.** (A–F). (A) Holotype (CNMO 8037, ex. INHS 90397.5), 73 mm length, from the Río Valles, Estación Micos, 20 km NW of Ciudad Valles, San Luis Potosí, Mexico; (B) Paratype (INHS 90397.1), 62 mm, from the locality same as A; (C) Paratype (INHS 90183.3), 59 mm, from the Río Tampaón (Río Pánuco) Álvaro Obregón (Pujal), at confluence of the ríos Valles and Tampaón; (D) Paratype (INHS 90183.1), 67 mm length, from the locality same as C; (E) Paratype (INHS 90175.3), 53 mm, from the Río Tancuilin, 0.5 km south of Jalpilla, San Luis Potosí, Mexico; (F) Paratype (INHS 90175.2), 50 mm, from the locality same as E. White bar denotes 1 cm scale.

Etymology: The specific epithet *berezai* is in honor of Mr. Daniel J. Bereza. Dan Bereza was born Danylo Jaroslav Illyich Bereza on 22 October 1950 in Philadelphia, Pennsylvania. He attended St. Nicholas parochial school and then Central High School in Philadelphia, Pennsylvania. Dan was a member of the Philadelphia Shell Club since about the age of 10. He volunteered for Tucker Abbott at the Department of Malacology at the ANSP. From 1973–1974, Dan was a grant-supported staff member in the Department of Malacology and a 1st year graduate student at Jefferson Medical University. In the late 1970s and early 1980, Bereza and colleagues collected at over 100 sites in the Pánuco drainage and elsewhere in central Mexico. Dan Bereza died on June 4, 2007, at the age of 56. His brother and sister donated his collection of unionids (including soft parts) to the Smithsonian National Museum of Natural History, Washington, D.C., where they are available for study (Luebke & Graf 2013; M.G. "Jerry" Harasewych, pers. comm., 2019).

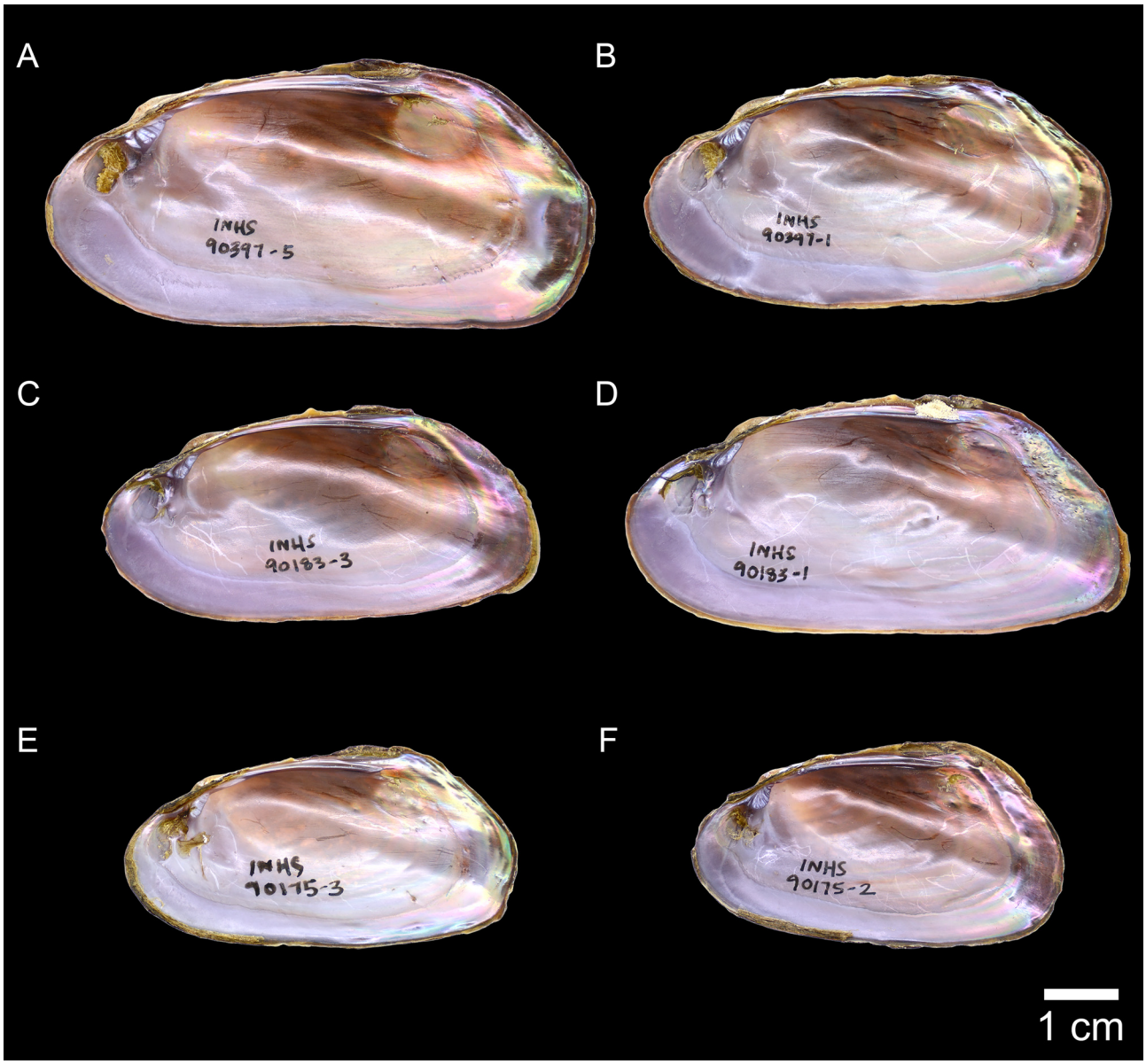

FIGURE 6. Right valve internal views of *Popenaias berezai* **n. sp.** Localities correspond to those of Fig. 5. (A) Holotype (CNMO 8037, ex. INHS 90397.5); (B) Paratype (INHS 90397.1); (C) Paratype (INHS 90183.3); (D) Paratype (INHS 90183.1); (E) Paratype (INHS 90175.3); (F) Paratype (INHS 90175.2). Scale bar 1 cm.

Remarks: Some previous researchers placed *Unio veraepacis* Tristram, 1863, in the synonymy of *P. popeii* s.l. (Frierson 1927; Howells *et al.* 1996). Prior to 1914, *U. veraepacis* was considered as a valid taxon (Lea 1870; Fischer & Crosse 1894; Simpson 1900; von Martens 1900). Simpson (1900, p. 738) stated that "Only a Latin description was given by Tristram, and the species is not identifiable. It is probably close to *U. popeii*, and may possibly be that." Simpson (1914, p. 701) stated that "*Unio verae-pacis* Tristram is probably a synonym" of *Unio popeii* and placed it there as *Unio* (sec. *Elliptio*) *popeii* Lea, 1857. However, Simpson did not include the supposed type locality of *U. veraepacis* (Lago de Peten in the Usumacinta basin, Guatemala) in the range he gave for *P. popeii*, which he stated as "South Texas; northeast Mexico" (Simpson 1914, p. 700).

Simpson's (1914) placement of *U. veraepacis* was followed by Frierson (1927), and Howells *et al.* (1996, p. 93) who stated "probably." Similarly, Haas (1929, p. 329) recognized *U. veraepacis* as valid as *Elliptio* (*Nephronaias*) *verae-pacis* (Tristram) but with the qualifier that "Daß ich *ravistellus* und *verae-pacis* für nahe verwandt halte, sagte ich bereits und ich halte es keineswegs für augeschlossen, daß die zweite nur eine Form aus der Variationsbreite der ersten darstellt." [translated: That I believe *ravisellus* and *verae-pacis* to be closely related has already been said, and I do not at all exclude [the possibility] that the second represents only one form from the variation of the first."] Like Simpson, Haas later changed his mind and placed *U. veraepacis* in the synonymy of *P. popeii* (Haas 1969).

Von Martens' (1900) opinion that *U. veraepacis* was a variation of *Unio ravistellus* Morelet, 1849, described from Lago de Izabal in the Gulf of Honduras drainage, has merit. Although von Martens (1900) gave measurements and a figure of "Tristram's type" (NHMUK 1901.6.22.1537), the specimen is highly eroded and almost unidentifiable. It does appear that it might have come from the same lot as other syntypes of *U. ravistellus* (MNHN-IM-2000-1767). Given that the southernmost limit of *P. berezai* is in the Río Jamapa in Veracruz, Mexico, we agree with von Martens that *U. veraepacis* is a synonym of *U. ravistellus* (= *Nephronaias ravistella*).

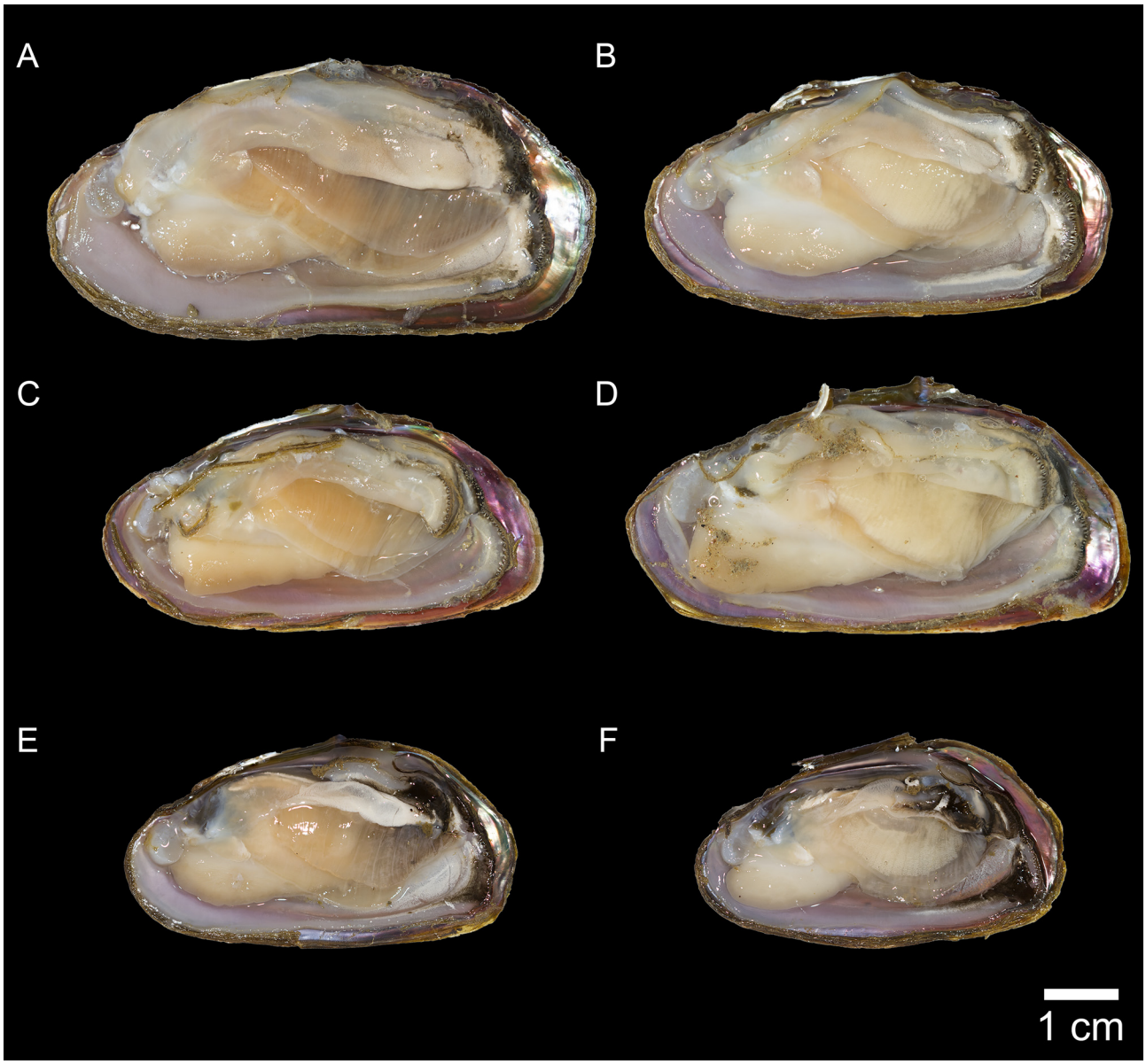

FIGURE 7. Soft anatomy of *Popenaias berezai* **n. sp.** Localities correspond to those of Fig. 5. (A) Holotype, non-gravid (CNMO 8037, ex. INHS 90397.5); (B) Paratype, gravid individual (INHS 90397.1); (C) Paratype, non-gravid (INHS 90183.3); (D) gravid individual (INHS 90183.1); (E) Paratype, non-gravid (INHS 90175.3); (F) Paratype, gravid individual (INHS 90175.2). Scale bar 1 cm.

***Popenaias ganina* (Pilsbry, 1910) new combination**
(Figs. 8B, 9B)

Common name: Gallinas Hornshell

Original combination: *Lampsilis metallica ganina* Pilsbry, 1910. Unionidae of the Panuco River system, Mex-

ico. Proceedings of the Academy of Natural Sciences of Philadelphia 61(3):532–539 + 3 plates. Page 539, pl. 27, fig. 6.

Verbatim type locality: "Ganina River, three miles southwest of San Dieguito"

Type locality: Río Gallinas (Gulf of Mexico—Río Pánuco— Río Tampaón), 4.5 km SW of San Dieguito, San Luis Potosí, Mexico, [21.98691, -99.25485].

Type specimens: *Lectotype*: ANSP 99523a designated by Johnson & Baker (1973:156, as the holotype). *Paralectotypes*: all from the type locality, ANSP 99523 (4), INHS 82200 (3), MCZ 189371 (15) (Johnson 1956:116, as cotypes).

Synonymy:

Lampsilis semirasa Pilsbry, 1910. Unionidae of the Panuco River system, Mexico. Proceedings of the Academy of Natural Sciences of Philadelphia 61(3):532–539 + 3 plates. Page 534, pl. 26, figs. 7–9.
Lampsilis (*Proptera*) *metallicus* var. *ganinus* Pilsbry, 1909—Simpson 1914:180.
Elliptio (*Popenaias*) *metallicus-ganinus* (Pilsbry, 1909)—Frierson 1927:38, sp. 152a.
Elliptio (*Popenaias*) *metallicus* (Say) var. *ganinus* (Pilsbry)—Haas 1929:330.
Elliptio (*Popenaias*) *metallicus* (Say) var. *regalis* Pilsbry—Haas 1929:330 [*nomen nudem*].
Nephronaias (*Popenaias*) *metallica* (Say, 1831)—Haas 1969:202 [in part].
Popenaias metallica (Say, 1831)—Graf & Cummings 2007:308 [in part].

Material examined:

Río Pánuco drainage. San Luis Potosí: Río Gallinas, (without locality), San Luis Potosí, [22.01667, -99.26667], MCZ 361553 (3), MCZ 361554 (3), UF 229377(1), UF 270381(3), UF 29535(1), ZMB 61692 (2); Río Gallinas, 4.5 air km SW of San Dieguito, [21.98691, -99.25485], FMNH 68134 (6), FMNH 68204 (3), UMMZ 66451 (4), UMMZ 91164 (8), UMMZ 91174 (11); Río Gallinas, 1 km S Ejido el Jabali, [21.87500, -99.24834], UF 283780 (1); Río Gallinas, 5 km SW San Dieguito, [21.98691, -99.25485], UF 93147 (5), UMMZ 66447 (6); Río Gallinas, N of Rascon, [21.98646, -99.25507], INHS 21753–21756 (26), INHS 21764–21766 (21), INHS 21768 (5), UF 270380 (2), UF 284051 (2), UF 283714 (1), UF 283720 (3), USNM 207435 (3), USNM 207437 (2); tributary to Río Gallinas, N of Rascon, [22.00041, -99.26419], ANSP 99524 (4), INHS 21767 (8), UF 270359 (3), UF 93149 (7); Arroyo Tamasopo, 4 km SW El Rascon, [21.95355, -99.27315], AMS 102129 (3); Río Gallinas, at road to Estacion Rascon, ca. 5.5 km N of the junction with Mex. Rt. 70, [21.99167, -99.25000], USNM 1282575 (11); Arroyo San Nicolas, Estacion Rascon-Damian Carmona road bridge, [22.00779, -99.26294], USNM 1282583–1282586 (171), USNM 1282576 (10).

Comparative diagnosis: *Popenaias ganina* resembles its sister taxon *P. berezai*; however, *P. ganina* has a relatively oval shape and reniform ventral margin compared to *P. berezai* (Figs 4 and 8). *Popenaias ganina* resembles *P. popeii*, but specimens of *P. ganina* are typically less elongate and has a dark metallic colored nacre (Figs. 4 and 8). *Popenaias ganina* appears to be not syntopic with other *Popenaias* species. Additionally, *P. ganina* is distinguished from other members of *Popenaias* by 31 diagnostic nucleotides in *cox1*, six diagnostic nucleotides in *16S*, and one diagnostic homozygous locus in *ANT* (Table 4).

Shell description: Shell length to 80 mm. Shell outline slightly elongate subtrapezoidal but more reniform (Fig. 8B). Posterior ridge somewhat biangulate. Dorsal margin straight or slightly arched, ventral margin concave in the middle or straight. Umbo broad, even with hinge line or elevated slightly above. Umbo cavity wide, shallow to moderately deep. Shells thin to thick.

Periostracum texture subglossy to clothlike, brown to dark gray or black, with indistinct darker or greenish rays (when present). Nacre color typically dark metallic purple to copper color and iridescent posteriorly (Fig. 8B).

Left valve with two thin lateral teeth, straight to slightly curved; two triangular, compressed pseudocardinal teeth. Right valve with single thin and relatively long lateral tooth, and one compressed triangular, serrated pseudocardinal tooth.

Distribution: *Popenaias ganina* was thought to occur in the southern Gulf coastal rivers of Mexico from the Río Pánuco basin south to Tabasco. Based on our sampling within the Río Pánuco basin and molecular findings, *P. ganina* appears to be endemic to the Río Gallinas of the Río Pánuco basin (Fig. 9B). Previous records of the species outside of the basin were likely misidentified due to their similar shell morphologies to other *Popenaias* species.

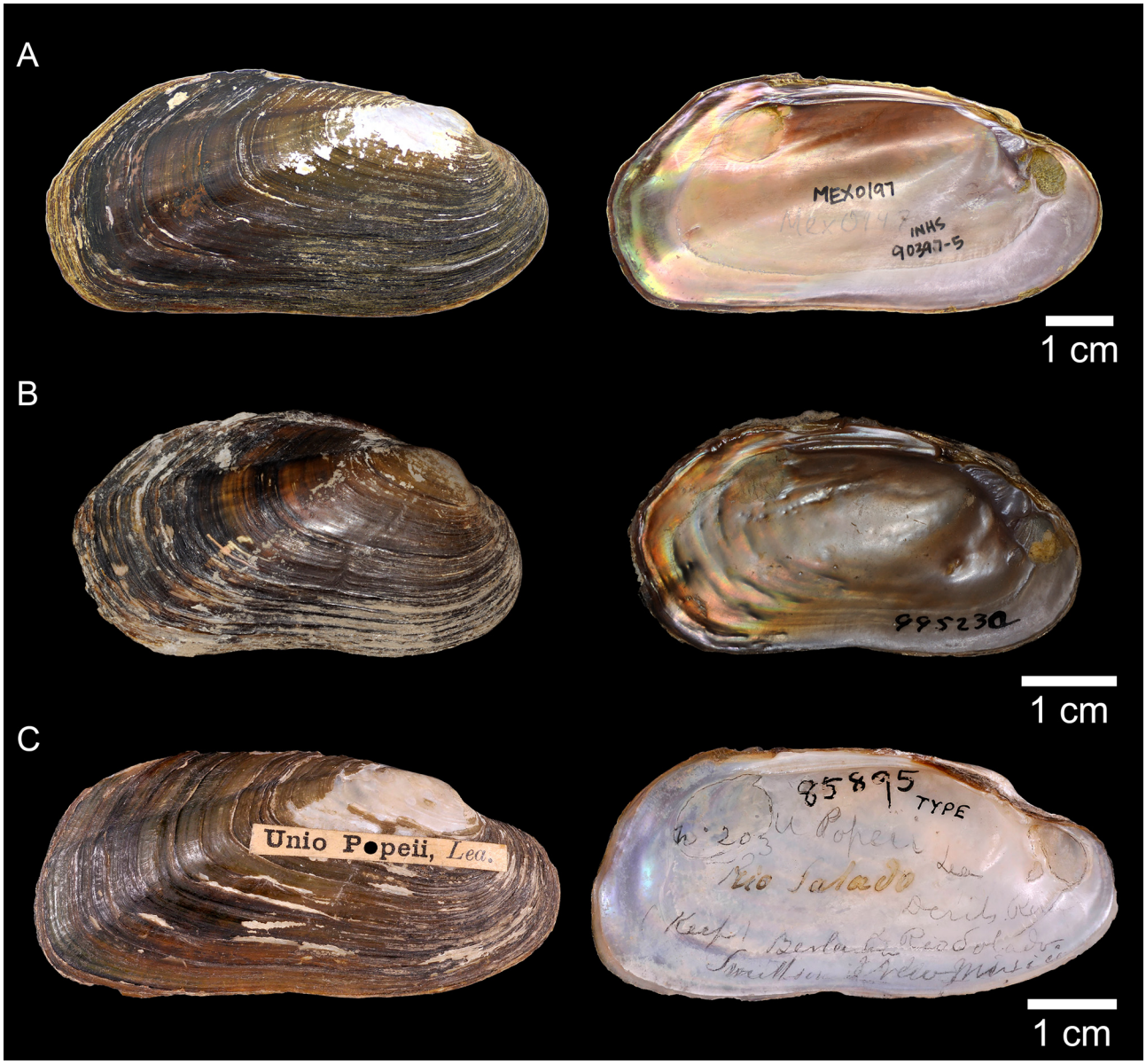

FIGURE 8. Right valve external shells. (A) *Popenaias berezai* **n. sp.**, Río Valles, San Luis Potosí, Mexico, Holotype CNMO 8037, ex. INHS 90397.5; (B) *Popenaias ganina*, Río Gallinas, San Luis Potosí, Mexico, Lectotype ANSP 99523a; (C) *Popenaias popeii*, Río Salado, Nuevo León, Mexico, Lectotype USNM 85895.

Popenaias popeii **(Lea, 1857)**

(Figs. 8C, 9C)

Common name: Texas Hornshell.

Original combination: *Unio popeii* Lea, 1857. Description of six new species of fresh water and land shells of Texas and Tamaulipas, from the collection of the Smithsonian Institution. Proceedings of the Academy of Natural Sciences of Philadelphia 9:101–102. Not figured. Figured in Lea (1860:372, pl. 66, fig. 197).

Verbatim type locality: "Devils River and Río Salado, Texas."

Type locality: Río Salado (Gulf of Mexico—Rio Grande), 6 air km SSE of Anáhuac, Nuevo León, Mexico, [27.19444, -100.10917].

Type specimens: *Lectotype*: USNM 85895, designated and the type locality fixed by Johnson (1974:115, as the "figured holotype"; 1999:21, 62, pl. 6, fig. 1, as *P. popei* and incorrectly as USNM 85859). *Paralectotypes*: from the type locality, USNM 85895b (2).

Synonymy:
Unio popei Lea, 1857—Sowerby 1868:pl. 81, sp. 430; Singley 1893:322.
Margaron (*Unio*) *popeii* Lea, 1857—Lea 1870:57.
Unio (sec. *Elliptio*) *popeii* (Lea, 1857)—Simpson 1900:738 [in part]; Simpson 1914:700 [in part].
Lampsilis popei (Lea, 1857)—Pilsbry 1910:535 [in part].
Elliptio (*Popenaias*) *popei* (Lea, 1857)—Frierson 1927:38, sp. 151 [in part]; Haas 1929:330.
Elliptio (sec. *Popenaias*) *popei* (Lea, 1857)—Thiele 1934:829.
Nephronaias (*Popenaias*) *popeii* (Lea, 1857)—Haas 1969:201 [in part].
Popenaias popei (Lea, 1857)—Heard & Guckert 1970:339; Burch 1975:14; Turgeon *et al.* 1988:32; Williams *et al.* 1993:13; Howells *et al.* 1996:93; Johnson 1999:21 [in part]; Haag 2012:71.
Popenaias popeii (Lea, 1857)—Turgeon *et al.* 1998:36; Campbell *et al.* 2005:155; Zanatta & Murphy 2006:197; Graf & Cummings 2007:308 [in part]; Chapman *et al.* 2008:306; Campbell & Lydeard 2012:15; Inoue *et al.* 2013:195; Inoue *et al.* 2015:1911; Williams *et al.* 2017:42; Inoue *et al.* 2018:Table S2; Burlakova *et al.* 2019:349.

Material examined:

Rio Grande drainage. USA: New Mexico: North Spring River (Pecos River), Roswell, Chaves County, [33.40393, -104.52264], ANSP 91432 (1), USNM 168765 (1); Pecos River, T23S, R28E, sec. 24, Eddy County, [32.29598, -104.04306], USNM 487417 (4); Pecos River, Malaga Bend, Eddy County, [32.21443, -103.98203], USNM 592723 (1); Pecos River, under Bataan Bridge, Carlsbad, Eddy County, [32.44633, -104.25631], USNM 758208 (4); Black River (Pecos River), a 7 km stretch between Black River Village and Carlsbad Irrigation District dam, Eddy County, [32.20196, -104.25060], NCSM 35330 (1); Black River, ~1.2 km N and 3 km downstream John D. Forehand Road, Davis Ranch, Eddy County, [32.22940, -104.21040], NCSM 45778 (16).

USA: Texas: Las Moras Creek, Fort Clark, Kinney County, [29.30583, -100.42167], MCZ 295007 (2), USNM 308943 (28), USNM 130175 (1), USNM 151538 (5), UF 269336; Pecos River, at bridge ~ 8 km S of Pandale, Val Verde County, [30.12909, -101.57358], ANSP 346884 (1); Pecos River, about 8 km SW of Pandale and 0.5 km N of Bed Rock Crossing on road from Pandale to Langtry, Val Verde County, [30.11944, -101.54491], USNM 709228 (1); Pecos River, Val Verde County, [29.69944, -101.37111], ANSP 85268 (1); Pecos River, near Barstow, Ward County, [31.42691, -103.38907], USNM 464732 (1); Devils River, Val Verde County, [29.45889, -101.05917], USNM 118394 (2), USNM 252546 (2), USNM 464728 (2), USNM 25735 (1); Devils River, Comstock, Val Verde County, [29.68417, -101.17306], ANSP 341891 (25); Devils River, 27.0 air km NE of Comstock, Val Verde County, 29.87025, -100.99365, NRI 8696 (8); Rio Grande, Black Gap Wildlife Management Area, Brewster County, 29.73578, -102.66024, NRI 8106 (2); Rio Grande, Terrell County, 29.79975, -102.12611, NRI 8204 (1); Rio Grande, La Bota Ranch, 12.6 air km NNW of Laredo, Webb County, 27.61248, -99.55182, NRI 8265 (1); NRI 8385 (6).

Mexico: Coahuila: Canon Espantoso, S of San Vicente, near Cuatro Cienegas, [26.95000, -101.93333], USNM 533951 (1); Río Sabinas, W of Río Villa de San Juan on Hwy 20, [27.92305, -101.30583], INHS 29013 (3).

Mexico: Nuevo León: Río Salado de Nadadores, 8 km SW Progresso, [27.19636, -101.23419], USNM 1283220 (3); Río Salado, [26.84499, -99.58374], USNM 120920 (1).

Comparative diagnosis: *Popenaias popeii* resembles other *Popenaias* species but is more elongate in shape and has a straighter ventral margin (Figs 4 and 8). *Popenaias popeii* is endemic to the Rio Grande basin and appears to not be syntopic with other *Popenaias* species. Additionally, *P. popeii* is distinguished from other members of *Popenaias* by 46 diagnostic nucleotides in *cox1*, 27 diagnostic nucleotides in *16S*, and three diagnostic homozygous loci in *ANT* (Table 4).

Shell description: Shell length to 120 mm. Shell outline elongate subtrapezoidal (Fig. 8C). Dorsal and ventral margins almost parallel. Dorsal margin straight, ventral margin straight to slightly concave in the middle. Posterior ridge flat to broadly rounded and may appear double. Posterior slope flat to slightly to concave. Umbo low, sharp, even with hinge line or elevated slightly above. Umbo sculpture (when present) faint double-looped ridges. Umbo cavity shallow and broad. Shell thin to slightly thick.

Periostracum subglossy, brown to dark gray or black, some, particularly smaller individuals, may have green rays (Fig. 8C). Nacre color typically white, iridescent posteriorly, occasionally light salmon pink or orange on umbo cavity.

Left valve with two thin lateral teeth, straight to slightly curved; two triangular, compressed pseudocardinal teeth. Right valve with single thin and relatively long lateral tooth, and one compressed triangular pseudocardinal tooth.

TABLE 4. Diagnostic nucleotide sites of mitochondrial DNA cytochrome c oxidase I (*cox1*) and 16S rRNA (*16S*) and nuclear DNA adenine nucleotide translocase (*ANT*) genes of *Popenaias berezai* **n. sp.**, *P. ganina*, and *P. popeii*. Bold letters represent diagnostic sites observed in samples from pooled populations. Hyphens (-) represent gaps in *16S* gene.

	cox1																													
																	1	1	1	1	1	1	1	1	1	1	1	1	2	2
	1	1	2	3	3	4	4	5	5	6	7	7	8	8	8	9	0	0	1	2	2	4	5	5	6	6	7	9	0	0
	6	9	8	5	7	6	9	2	8	1	0	6	2	5	8	1	3	9	2	1	7	2	4	7	3	6	2	0	5	8
Popenaias berezai **n. sp.**	G	G	A	**C**	G	A	**C**	**G**	**C**	G	A	G	G	**G**	G	G	T	**A**	A	A	**A**	T	C	T	T	A	G	T	T	**T**
Popenaias ganina	G	G	**G**	T	**A**	A	T	A	T	G	A	**A**	**A**	A	G	G	T	G	**G**	**G**	G	T	**T**	**C**	T	A	**A**	T	T	**C**
Popenaias popeii	**A**	**A**	A	T	G	**G**	T	A	T	**A**	**T**	G	G	A	**A**	**A**	**C**	G	A	A	G	**C**	C	T	**C**	**G**	G	**A**	**A**	**A**
	cox1																													
	2	2	2	2	2	2	2	2	2	2	2	2	3	3	3	3	3	3	3	3	3	3	3	3	3	4	4	4	4	4
	2	4	4	5	5	6	6	7	8	8	8	9	0	0	0	0	1	1	2	3	3	4	4	6	8	0	0	2	3	3
	3	1	4	0	6	2	5	1	3	7	9	0	1	2	4	7	0	6	5	1	4	3	6	7	2	1	6	1	0	3
Popenaias berezai **n. sp.**	T	G	G	T	T	G	**G**	**A**	T	T	G	**C**	**G**	T	**A**	G	A	**A**	T	G	G	**A**	**A**	**C**	G	T	T	**C**	G	G
Popenaias ganina	**C**	G	G	T	**G**	G	A	G	T	**C**	**A**	T	**T**	**C**	G	G	**G**	G	**A**	**A**	G	G	G	T	G	**C**	**C**	T	G	**A**
Popenaias popeii	T	**A**	**A**	**C**	C	**A**	A	G	**C**	T	G	T	**C**	T	G	**A**	A	G	T	G	**T**	G	G	T	**A**	T	T	T	**A**	G
	cox1																													
	4	4	4	4	4	4	4	4	4	4	4	4	5	5	5	5	5	5	5	5	5	5	5	5	5	5	6	6	6	6
	3	4	4	5	6	6	7	8	8	8	9	9	0	0	1	2	2	3	3	5	5	5	6	8	8	9	0	0	2	2
	6	2	8	4	0	9	9	1	2	7	3	9	2	8	1	3	9	2	8	0	6	7	5	3	6	8	1	4	2	5
Popenaias berezai **n. sp.**	T	T	T	T	**G**	G	C	G	A	C	G	T	G	G	A	**T**	A	T	G	G	C	T	**C**	**C**	T	T	**C**	G	**T**	T
Popenaias ganina	T	**C**	**C**	T	A	G	C	G	A	C	G	**C**	G	G	**G**	A	**G**	T	G	G	C	T	T	T	T	**C**	T	G	**C**	T
Popenaias popeii	**C**	T	T	**C**	A	**A**	**T**	**A**	**G**	**T**	**A**	T	**A**	**A**	A	A	A	**A**	**A**	**A**	**T**	**C**	T	T	**A**	T	T	**A**	**G**	**A**
	cox1												16S																	
	6	6	6	6	6	6	6	6	6	6	6	6							1	1	1	1	1	1	1	1	1	2	2	2
	2	3	3	3	4	2	3	3	3	4	5	5		1	1	1	4	5	0	2	2	3	3	4	6	7	9	3	4	5
	8	1	4	7	3	8	1	4	7	3	2	8	7	0	2	6	6	0	4	4	8	0	9	1	5	5	5	8	2	1
Popenaias berezai **n. sp.**	T	G	**C**	G	A	T	G	**C**	G	A	**T**	T	T	C	C	T	**G**	**C**	C	**C**	**T**	G	C	C	T	A	T	-	C	T
Popenaias ganina	T	**A**	T	G	A	T	**A**	T	G	A	C	**C**	**C**	C	C	T	A	T	C	T	**G**	G	C	C	T	A	T	-	C	**C**
Popenaias popeii	**A**	G	T	**A**	**G**	**A**	G	T	**A**	**G**	C	T	T	**T**	**T**	**C**	A	T	**T**	T	**A**	**A**	**T**	**T**	**C**	**G**	**C**	**T**	**T**	T
	16S																					ANT								
	2	2	2	2	2	3	3	3	3	3	3	3	3	3	3	3	3	3	3	4		1	1	2						
	6	6	6	6	9	0	1	1	1	1	2	2	2	2	2	3	3	4	4	1	8	0	6	7						
	0	1	3	9	6	0	4	6	7	8	1	2	5	6	7	2	9	0	9	0	8	6	6	7						
Popenaias berezai **n. sp.**	C	A	-	A	T	T	C	**T**	C	A	C	**A**	**G**	A	T	C	T	**C**	T	G	**R**	C	A	**Y**						
Popenaias ganina	C	**G**	-	A	T	T	C	C	C	A	-	-	A	**G**	T	C	T	**T**	T	G	**A**	C	A	T						
Popenaias popeii	**T**	A	**C**	**T**	**C**	**C**	**A**	C	**A**	**G**	C	-	A	A	**G**	**G**	**C**	**A**	**C**	**A**	G	**T**	**G**	T						

Distribution: *Popenaias popeii* was thought to occur as far south as Veracruz, Mexico (Johnson 1999); however, the current study revealed that the species is endemic to the Rio Grande drainage in Mexico and the United States (Fig. 9C), reducing its presumptive range. In the Rio Grande proper, it is known from near the confluence with the Río Conchos and adjacent tributaries to Falcon Breaks, now inundated by Lake Falcon. It is also known from the Black River, Pecos River, Devils River, and Las Moras Creek in New Mexico and Texas, United States, and the Río San Diego and Río Salado (also called the Río Salado de Nadadores) in Chihuahua, Coahuila, and Nuevo León, Mexico (Fig. 9C). Extant populations are known from the Lower Canyons near Big Bend National Park, middle Rio Grande near Laredo, Texas, Devils River, Canyonlands of the lower Pecos River, and the Black River near Malaga, New Mexico, United States, and Río San Diego, Coahuila, Mexico (Randklev *et al.* 2018; D. Berg, pers. comm., 2018). As a result of the restricted range and few extant populations, *P. popeii* was listed as "endangered" under the U.S. Endangered Species Act (USFWS 2018).

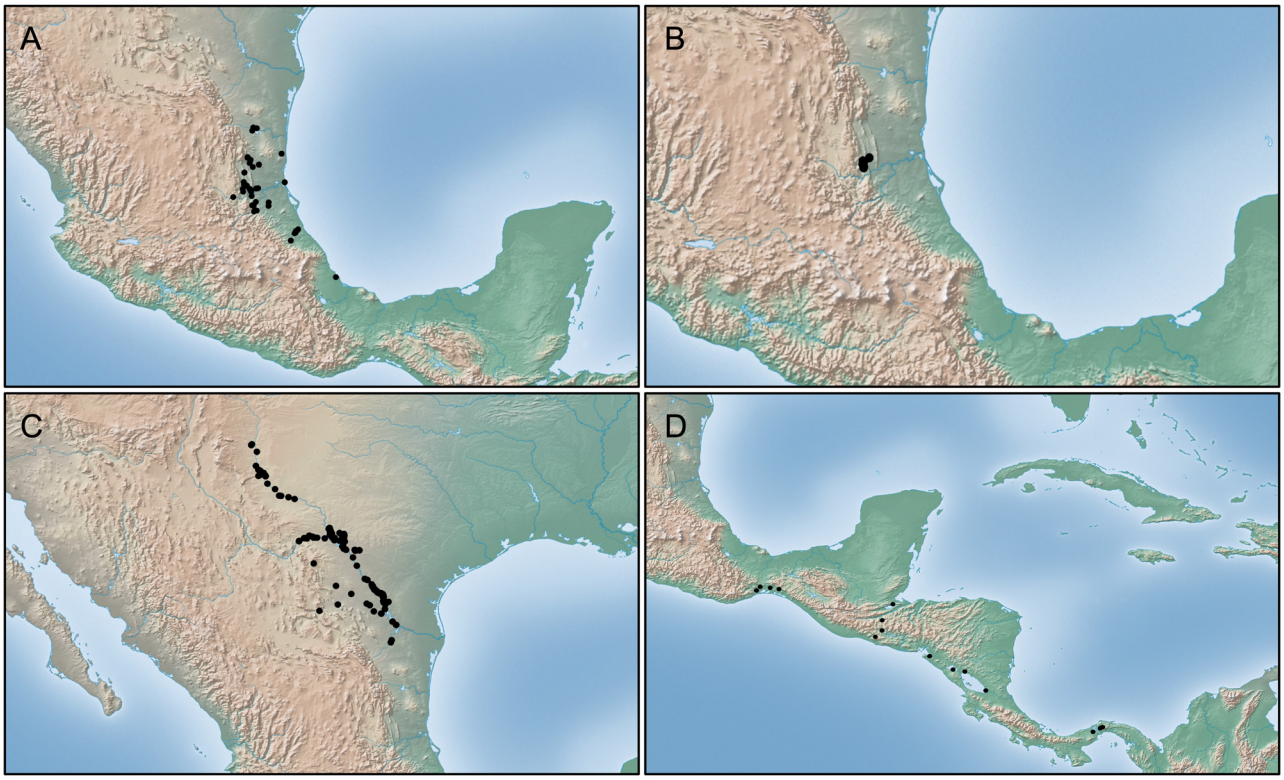

FIGURE 9. Presumptive historic and current distributional ranges of (A) *Popenaias berezai* **n. sp.** in Mexican Gulf coastal rivers, (B) *Popenaias ganina* in the Río Gallinas of the Río Pánuco basin, (C) *Popenaias popeii* in the Rio Grande basin of Mexico and the United States, and (D) *Popenaias tehuantepecensis* including *Nephronaias rowellii* (Lea, 1859) in Central America.

Popenaias tehuantepecensis (Crosse & Fischer, 1893)

(Fig. 9D)

Original Combination: *Unio tehuantepecensis* Crosse & Fischer, 1893. Diagnoses molluscorum novorum, Republicae Mexicanae incolarum. Journal de Conchyliologie 41:293–297. Page 296. Not figured. Figured in Fischer & Crosse 1894:618, pl. 65, figs. 3, 3a and 4.

Verbatim Type Locality: "prope Santa Efigenia, in isthmo Tehuantepec dicto, provinciae Oajaca, reipublicae Mexicanae"

Type locality: Río Novillero (Pacific Ocean), Santa Efigenia, Isthmus of Tehuantepec, Oaxaca, Mexico, [16.40387, -94.216116].

Type specimens: Syntypes, MNHN-IM-2000-1799 (n = 11, 2 of which were figured as noted above).

Synonymy:

Unio (*Sphenonaias*) *tehuantepecensis* Crosse & Fischer, 1893 —Fischer & Crosse 1894:618, pl. 645, figs. 3–4; von

Martens 1900:501.
Nephronaias tehuantepecensis (Crosse & Fischer, 1893)—Simpson 1900:594; Simpson 1914:267.
Nephronaias (*Popenaias*) *tehuantepecensis* (Crosse & Fischer, 1893)—Haas 1969:202.
Popenaias tehuantepecensis (Crosse & Fischer, 1893)—Graf & Cummings 2007:308.

Material examined (all Pacific drainages):

Mexico, (without locality), UMMZ 107978 (1); Southern Mexico, (without locality), UMMZ 107977 (1); Oaxaca, Mexico, (without locality) MNHN uncat. (3); Rio Tehuantepec, Tehuantepec, Oaxaca, Mexico [16.33010, -95.23510], AMNH 30269 (3), MCZ 361571 (2), UF 231214 (3), NCSM 62217 (5), ZMB uncat. (3); Laguna Dolores, Oaxaca, Mexico, [16.46837, -94.61511], MNHN uncat. (6); Rio Perros, Perros, 4.9 km SSE Ixtepec, Oaxaca, Mexico, [16.52057, -95.06719], NCSM 5816 (9).

Distribution: *Popenaias tehuantepecensis* was thought to occur in southern Pacific coastal rivers of Mexico. This species was described as *Unio tehuantepecensis* by Crosse & Fischer (1893) from the Pacific Basin at approximately Río Novillero, Santa Efigenia, Isthmus of Tehuantepec, Oaxaca, Mexico. *Unio tehuantepecensis* was considered valid by von Martens (1900) and Simpson (1900, 1914). Frierson (1927) synonymized it with *Elliptio* (*Sphenonaias*) *callosus* (Lea, 1841), a taxon of dubious identity originally described from near Columbus, Ohio but thought to be a Mexican species by Simpson (1900) and Frierson (1927). However, there are no data to support that assertion and it is doubtful that *Unio callosus* Lea, 1841 was collected in Mexico and we consider it to be a synonym of *Unio ligamentina* Lamarck, 1819. Haas (1929) synonymized *Unio tehuantepecensis* with *Elliptio* (*Nephronaias*) *goascoranensis* (Lea, 1858), described from "Hab. — River Goascoran, Honduras, Pacific Slope." In his worldwide revision of freshwater mussels, Haas (1969) considered *tehuantepecensis* as valid and placed it in *Popenaias* as *Nephronaias* (*Popenaias*) *tehuantepecensis* (Crosse & Fischer, 1893) along with *popeii* and *metallica*. Why Haas placed it in *Popenaias* is unknown; however, based upon the examination of shell morphology, the taxon could be a member of numerous Central American genera. It had not been treated since Haas (1969) and was recognized as valid in the most recent global checklist of freshwater mussels (Graf & Cummings, 2007). However, due to its disjunct distribution and the limited number of specimens in museum collections, the taxonomic validity (including its placement in *Popenaias*) and distribution of *P. tehuantepecensis* are uncertain. An examination of the syntypes and other specimens in the NCSM, UMMZ, and ZMB identified as *Popenaias tehuantepecensis* strongly suggest it is likely synonymous with *Nephronaias rowellii* (Lea, 1859).

Discussion

Our examination of multi-locus sequence data of Gulf coastal members of *Popenaias* reveals that *P. popeii* in the sense of previous authors is not monophyletic. So far, *P. popeii* was thought to occur in the Rio Grande basin south to Mexican Gulf coastal rivers of northern Veracruz, including the Río Pánuco basin (Pilsbry 1910; Johnson 1999). However, inference from distributional, molecular, and morphological data strongly suggest that the individuals originally identified as *P. popeii* in the Río Pánuco basin are a distinct species. Specifically, our results support three geographically isolated clines that are diagnosable using morphological characters (e.g., shell outline, ventral margin, and nacre color) and multi-locus sequence data: *P. berezai* **n. sp.**, *P. ganina*, and *P. popeii*.

Based on our findings, we conclude that the distribution of *P. popeii* is restricted to the main stem and tributaries of the Rio Grande in Mexico and the United States, which substantially reduces the presumed range of the species. The distribution of *P. popeii* in the United States is relatively well-known (Inoue *et al.* 2014; Randklev *et al.* 2018); however, the extent and status of populations in Mexican tributaries remains poorly understood. Thus far, only one extant population in the Río San Diego, Coahuila, Mexico, is known from Mexican tributaries of the Rio Grande (D. Berg, pers. comm., 2018). Because *P. popeii* has been federally listed as "endangered" in the United States (USFWS 2018), robust survey efforts in Mexican tributaries of the Rio Grande are needed to understand the full extent of *P. popeii* distribution in the Rio Grande basin and to develop effective species recovery strategies.

Popenaias berezai **n. sp.** and *P. ganina* both occur within the Río Pánuco basin; however, the two species do not co-occur there. *Popenaias berezai* **n. sp.**, occurs throughout the basin, including tributaries of the Río Moctezuma (including the ríos Amajac, Huichihuayán, Tancuilín, and their tributaries) and Río Tampaón (including the Río Valles but excluding the Río Gallinas). Based on historical records and museum specimens, we hypothesize that

the species is present from the Río Soto la Marina in Tamaulipas south to the Río Jamapa in Veracruz. However, future studies with comprehensive field surveys and molecular validation are warranted to further characterize its true distribution.

To our knowledge, *P. ganina* is endemic to the Río Gallinas, a tributary of the Río Tampaón (Río Pánuco basin). Interestingly, the populations of *P. ganina* in the Río Gallinas are geographically close to localities of *Popenaias berezai* **n. sp.** in the Río Valles (*ca.* 20 km straight). The Río Gallinas is known to harbor unique assemblages of fish communities including several endemic cichlid and cyprinid species (Schönhuth *et al.* 2008; De la Maza-Benignos *et al.* 2014). The presence of unique aquatic communities is likely derived from the isolation of the Río Gallinas, where the 102 m waterfall Cascada de Tamul is located at the confluence of the Río Gallians and Río Santa María, forming the Río Tampaón. As the central portion of the Río Pánuco basin drains the mountains of the Sierra Madre Oriental, deeply incised valleys create waterfalls when headwaters and tributaries join (Hudson *et al.* 2005). As allopatry is a critical driver in the diversification of aquatic taxa (Seehausen & Wagner 2014), including freshwater mussels (Inoue *et al.* 2019; Smith *et al.* 2019), physiographic isolation appears to have largely shaped the geographically disparate patterns of biodiversity within the Río Pánuco basin.

To date, generating a well-resolved phylogeny for Mesoamerican mussels has been hindered by a lack of updated distributional information and availability of genetic material from the region. The problem with identifying mussels morphologically can be well illustrated by examining the confusion surrounding species in Gulf coastal rivers of eastern Mexico (the present study; Pfeiffer *et al.* 2019a). Although the current study sheds light on some of the hidden biodiversity in Mesoamerican mussels, further studies integrating genomic and morphometric techniques are integral towards a better understanding of their diversity and evolution in Mesoamerica.

Acknowledgements

We thank David Berg, Amy Burden, Michael Hart, Steven Hein, Anna Pieri, and Ned Strenth for sharing specimens and help in the field and laboratory. We especially thank Aaron Koch, Heather Warman, Enrique Aguado, and Charlie Morones from SUP Kentucky and Kayak Huasteca for taking very good care of us while in Mexico. Edna Naranjo assisted with permit acquisition. We thank Eduardo Gonzalez, Enrique Corona, and Pablo Gonzalez at the Universidad Autónoma de Tamaulipas for logistical support and assistance in the field. We thank Chris Harper, Gary Pandolfi, and Susan Oetker (U.S. Fish and Wildlife Service) for funding (F17AC01008); without their support this study could not have happened. Samples were collected under TE79165C-0 (USFWS permit for *P. popeii*) and SGPA/DGVS/002175/18 (Mexico *Popenaias*). Thanks also go to Jerry Harasewych for the biographical information on Dan Bereza.

We would like to thank the following curators and collection managers for allowing us access to examine specimens under their care: Winston Ponder (AMS); Gary Rosenberg and Paul Callomon (ANSP); Kathie Way and Jon Ablett (NHMUK); Tim Pearce (CM); Rüdiger Bieler, Jochen Gerber, and Marty Pryzdia (FMNH); Adam Baldinger and Richard Johnson (MCZ); Art Bogan and Jamie Smith (NCSM); Tom Watters (OSUM); John Slapcinsky and Fred Thompson (UF); Diarmaid O'Foighil and Taehwan Lee (UMMZ); Robert Hershler, Ellen Strong, Tim Coffer, and John Pfeiffer (USNM); and Thomas von Rintelen and Mathias Glaubrecht (ZMB). Finally, we thank John Pfeiffer, Steve Walsh, the editor, and one anonymous referee for helpful comments on an earlier draft of this manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

References

Audzijonyte, A. & Vrijenhoek, R.C. (2010) Three nuclear genes for phylogenetic, SNP and population genetic studies of molluscs and other invertebrates. *Molecular Ecology Resources*, 10 (1), 200–204. https://doi.org/10.1111/j.1755-0998.2009.02737.x

Binney, W.G. (1858) *The complete writings of Thomas Say on the conchology of the United States*. H. Bailliere Co., New York, 252 pp.

Bogan, A.E. (1996) *Popenaias popeii*. *The IUCN Red List of Threatened Species*, 1996, e.T17992A7641578. https://doi.org/10.2305/IUCN.UK.1996.RLTS.T17992A7641578.en

Bogan, A.E. & Roe, K.J. (2008) Freshwater bivalve (Unioniformes) diversity, systematics, and evolution: status and future

directions. *Journal of the North American Benthological Society*, 27 (2), 349–369.
https://doi.org/10.1899/07-069.1

Burch, J.B. (1975) *Freshwater Unionacean Clams (Mollusca, Pelecypoda) of North America*. Malacological Publications, Hamburg, Michigan, 204 pp.

Burlakova, L.E., Campbell, D. & Karatayev, A.Y. (2019) Status of rare endemic species: molecular phylogeny, distribution and conservation of freshwater molluscs *Truncilla macrodon* and *Truncilla cognata* in Texas. *Malacologia*, 62 (2), 345–363.
https://doi.org/10.4002/040.062.0210

Campbell, D.C. & Lydeard, C. (2012) The genera of Pleurobemini (Bivalvia: Unionidae: Ambleminae). *American Malacological Bulletin*, 30 (1), 19–38.
https://doi.org/10.4003/006.030.0102

Campbell, D.C., Serb, J.M., Buhay, J.E., Roe, K.J., Minton, R.L. & Lydeard, C. (2005) Phylogeny of North American amblemines (Bivalvia: Unionoida): prodigious polyphyly proves pervasive across genera. *Invertebrate Biology*, 124 (2), 131–164.
https://doi.org/10.1111/j.1744-7410.2005.00015.x

Carman, S.M. (2007) Texas hornshell *Popenaias popeii* recovery plan. New Mexico Department of Game and Fish, Santa Fe, 57 pp.

Chapman, E.G., Gordon, M.E., Walker, J.M., Lang, B.K., Campbell, D., Watters, G.T., Curolé, J.P., Piontkivska, H. & Hoeh, W.R. (2008) Evolutionary relationships of *Popenaias popeii* and the early evolution of lampsiline bivalves (Unionidae): phylogenetic analyses of DNA and amino acid sequences from F and M mitochondrial genomes. *Malacologia*, 50 (1–2), 303–318.
https://doi.org/10.4002/0076-2997-50.1-2.303

Crosse, H. & Fischer, P. (1893) Diagnoses molluscorum novorum, Republicae Mexicanae incolarum. *Journal de Conchyliologie*, 41, 293–297.

De la Maza-Benignos, M., Ornelas-García, C.P., Lozano-Vilano, M. de L., García-Ramírez, M.E. & Doadrio, I. (2014) Phylogeographic analysis of genus *Herichthys* (Perciformes: Cichlidae), with descriptions of *Nosferatu* new genus and *H. tepehua* n. sp. *Hydrobiologia*, 748 (1), 201–231.
https://doi.org/10.1007/s10750-014-1891-8

Fischer, P. & Crosse, H. (1894) Études sur les mollusques terrestres et fluviatiles du Mexique et du Guatemala. *Mission Scientifique au Mexique et dans l'Amérique Central, Recherches Zoologiques*, 2 (15), 489–576.

Frierson, L.S. (1927) *A Classification and Annotated Check List of the North American Naiades*. Baylor University Press, Waco, Texas, 111 pp.

Graf, D.L. & Cummings, K.S. (2007) Review of the systematics and global diversity of freshwater mussel species (Bivalvia: Unionoida). *Journal of Molluscan Studies*, 73 (4), 291–314.
https://doi.org/10.1093/mollus/eym029

Haag, W.R. (2012) *North American Freshwater Mussels: Natural History, Ecology, and Conservation*. Cambridge University Press, Cambridge, 505 pp.
https://doi.org/10.1017/CBO9781139048217

Haas, F. (1929) Bemerkungen über mittelamerikanische Najaden. *Senckenbergiana*, 11, 310–344.

Haas, F. (1969) Superfamilia Unionacea. *Das Tierrich, Berlin*, 88, 1–663.

Hammer, Ø., Harper, D.A.T. & Ryan, P.D. (2001) PAST: Paleontological statistics software package for education and data analysis. *Palaeontologia Electronica*, 4 (1), 1–9.

Hart, M.A., Miller, T.D. & Randklev, C.R. (2019) Salinity tolerance of a rare and endangered unionid mussel, *Popenaias popeii* (Texas Hornshell) and its implications for conservation and water management. *Ecotoxicology and Environmental Safety*, 170, 1–8.
https://doi.org/10.1016/j.ecoenv.2018.11.031

Heard, W.H. & Guckert, R.H. (1970) A re-evaluation of the recent Unionacea (Pelecypoda) of North America. *Malacologia*, 10 (2), 333–355.

Helaers, R. & Milinkovitch, M.C. (2010) MetaPIGA v2.0: maximum likelihood large phylogeny estimation using the metapopulation genetic algorithm and other stochastic heuristics. *BMC Bioinformatics*, 11, 379.
https://doi.org/10.1186/1471-2105-11-379

Hoang, D.T., Chernomor, O., von Haeseler, A., Minh, B.Q. & Vinh, L.S. (2018a) UFBoot2: improving the ultrafast bootstrap approximation. *Molecular Biology and Evolution*, 35 (2), 518–522.
https://doi.org/10.1093/molbev/msx281

Hoang, D.T., Vinh, L.S., Flouri, T., Stamatakis, A., von Haeseler, A. & Minh, B.Q. (2018b) MPBoot: fast phylogenetic maximum parsimony tree inference and bootstrap approximation. *BMC Evolutionary Biology*, 18 (1), 11.
https://doi.org/10.1186/s12862-018-1131-3

Howells, R.G., Neck, R.W. & Murray, H.D. (1996) *Freshwater Mussels of Texas*. Texas Parks and Wildlife Department, Austin, Texas, 218 pp.

Hudson, P.F., Hendrickson, D., Benke, A.C., Varela-Romero, A., Rodiles-Hernández, R. & Minckley, W.L. (2005) Rivers of Mexico. *In*: Benke, A.C. & Cushing, C.E. (Eds.), *Rivers of North America*. Elsevier Academic Press, Burlington, Massachusetts, pp. 1030–1084.

https://doi.org/10.1016/B978-012088253-3/50026-2
Inoue, K., Harris, J.L., Robertson, C.R., Johnson, N.A. & Randklev, C.R. (2019) A comprehensive approach uncovers hidden diversity in freshwater mussels (Bivalvia: Unionidae) with the description of a novel species. *Cladistics*, 36 (1), 88–113. https://doi.org/10.1111/cla.12386
Inoue, K., Hayes, D.M., Harris, J.L., Johnson, N.A., Morrison, C.L., Eackles, M.S., King, T.L., Jones, J.W., Hallerman, E.M., Christian, A.D. & Randklev, C.R. (2018) The Pleurobemini (Bivalvia : Unionida) revisited: molecular species delineation using a mitochondrial DNA gene reveals multiple conspecifics and undescribed species. *Invertebrate Systematics*, 32 (3), 689–702.
https://doi.org/10.1071/is17059
Inoue, K., Lang, B.K. & Berg, D.J. (2013) Development and characterization of 20 polymorphic microsatellite markers for the Texas hornshell, *Popenaias popeii* (Bivalvia: Unionidae), through next-generation sequencing. *Conservation Genetics Resources*, 5 (1), 195–198.
https://doi.org/10.1007/s12686-012-9766-7
Inoue, K., Lang, B.K. & Berg, D.J. (2015) Past climate change drives current genetic structure of an endangered freshwater mussel species. *Molecular Ecology*, 24 (8), 1910–1926.
https://doi.org/10.1111/mec.13156
Inoue, K., Levine, T.D., Lang, B.K. & Berg, D.J. (2014) Long-term mark-and-recapture study of a freshwater mussel reveals patterns of habitat use and an association between survival and river discharge. *Freshwater Biology*, 59 (9), 1872–1883.
https://doi.org/10.1111/fwb.12389
Iwata, H. & Ukai, Y. (2002) SHAPE: a computer program package for quantitative evaluation of biological shapes based on elliptic Fourier descriptors. *The Journal of Heredity*, 93 (5), 384–385.
https://doi.org/10.1093/jhered/93.5.384
Johnson, R.I. (1956) The types of Naiades (Mollusca: Unionidae) in the Museum of Comparative Zoology. *Bulletin of the Museum of Camparative Zoology*, 115 (4), 102–142.
Johnson, R.I. (1974) Lea's unionid types or recent and fossil taxa of Unionacea and Mutelacea introduced by Isaac Lea, including the location of all the extant types. *Museum of Comparative Zoology, Harvard University, Special Occasional Publication*, 2, 1–159.
https://doi.org/10.5962/bhl.title.141075
Johnson, R.I. (1979) The types of Unionacea (Mollusca: Bivalvia) in the Museum of Zoology, University of Michigan. *Malacological Review*, 12 (1–2), 29–36.
Johnson, R.I. (1999) Unionidae of the Rio Grande (Rio Bravo del Norte) system of Texas and Mexico. *Occasional Papers on Mollusks*, 6, 1–66.
Johnson, R.I. & Baker, H.B. (1973) The types of Unionacea (Mollusca: Bivalvia) in the Academy of Natural Science of Philadelphia. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 125, 145–186.
Kalyaanamoorthy, S., Minh, B.Q., Wong, T.K.F., von Haeseler, A. & Jermiin, L.S. (2017) ModelFinder: fast model selection for accurate phylogenetic estimates. *Nature Methods*, 14 (6), 587–589.
https://doi.org/10.1038/nmeth.4285
Katoh, K. & Standley, D.M. (2013) MAFFT multiple sequence alignment software version7: Improvements in performance and usability. *Molecular Biology and Evolution*, 30 (4), 772–780.
https://doi.org/10.1093/molbev/mst010
Kumar, S., Stecher, G. & Tamura, K. (2016) MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution*, 33 (7), 1870–1874.
https://doi.org/10.1093/molbev/msw054
Lamarck, J. (1819) *Histoire Naturelle des Animaux sans vertèbres. Vol. 6*. Verdière, Libraire, Paris, 343 pp.
Lea, I. (1831) Observations on the Naïades, and descriptions of new species of that and other families. *Transactions of the American Philosophical Society*, 4, 63–121.
https://doi.org/10.2307/1004831
Lea, I. (1841) Continuation of paper on fresh water and land shells. *Proceedings of the American Philosophical Society*, 2, 30–34.
Lea, I. (1857) Description of six new species of fresh water and land shells of Texas and Tamaulipas, from the collection of the Smithsonian Institution. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 9, 101–102.
https://doi.org/10.5962/bhl.title.166580
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.
Lea, I. (1859) Descriptions of twenty-one new species of exotic Unionidæ. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 11, 151–154.
Lea, I. (1860) New Unionidæ of the United States and northern Mexico. *Journal of the Academy of Natural Sciences*, 4, 327–374.
Lea, I. (1870) *A synopsis of the family Unionidae*. Henry C. Lea, Philadelphia, Pennsylvania, 184 pp.
https://doi.org/10.5962/bhl.title.13200
Lopes-Lima, M., Bolotov, I.N., Do, V.T., Aldridge, D.C., Fonseca, M.M., Gan, H.M., Gofarov, M.Y., Kondakov, A.V., Prie,

V., Sousa, R., Varandas, S., Vikhrev, I.V., Teixeira, A., Wu, R.W., Wu, X., Zieritz, A., Froufe, E. & Bogan, A.E. (2018) Expansion and systematics redefinition of the most threatened freshwater mussel family, the Margaritiferidae. *Molecular Phylogenetics and Evolution*, 127, 98–118.
https://doi.org/10.1016/j.ympev.2018.04.041

Lopes-Lima, M., Froufe, E., Do, V.T., Ghamizi, M., Mock, K.E., Kebapci, U., Klishko, O., Kovitvadhi, S., Kovitvadhi, U., Paulo, O.S., Pfeiffer, J.M., III, Raley, M., Riccardi, N., Sereflisan, H., Sousa, R., Teixeira, A., Varandas, S., Wu, X., Zanatta, D.T., Zieritz, A. & Bogan, A.E. (2017) Phylogeny of the most species-rich freshwater bivalve family (Bivalvia: Unionida: Unionidae): Defining modern subfamilies and tribes. *Molecular Phylogenetics and Evolution*, 106, 174–191.
https://doi.org/10.1016/j.ympev.2016.08.021

Luebke, C.M. & Graf, D.L. (2013) Curation of the Daniel J. Bereza collection of freshwater mollusks at the Smithsonian National Museum of Natural History: Phase I. *In*: *University of Wisconsin Stevens-Point College of Letters and Sciences Undergraduate Research Symposium*. University of Wisconsin Stevens-Point College, Stevens Point, Wisconsin, pp. 1–62.

Lydeard, C., Mulvey, M. & Davis, G.M. (1996) Molecular systematics and evolution of reproductive traits of North American freshwater Unionacean mussels (Mollusca: Bivalvia) as inferred from 16S rRNA gene sequences. *Philosophical Transactions: Biological Sciences*, 351 (1347), 1593–1603.
https://doi.org/10.1098/rstb.1996.0143

Von Martens, E. (1890–1901) *Biologia Centrali-Americana*, *Land and freshwater Mollusca.* Published for the editors by R. H. Porter, London, 675 pp.

Miller, R.R. & Smith, M.L. (1986) Origin and geography of the fishes of Central Mexico. *In:* Hocutt, C.H. & Wiley, E.O. (Eds.), *The zoogeography of North American freshwater fishes*. John Wiley & Sons, Inc., New York, pp. 487–517.

Morelet, A. (1849) *Testacea Novissima Insulæ Cubanæ et Americæ Centralis 1*. J.-B. Baillière, Paris, 31 pp.
https://doi.org/10.5962/bhl.title.11067

Nguyen, L.T., Schmidt, H.A., von Haeseler, A. & Minh, B.Q. (2015) IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution*, 32 (1), 268–274.
https://doi.org/10.1093/molbev/msu300

Ortmann, A.E. (1912) Notes upon the families and genera of the najades. *Annals of the Carnegie Museum*, 8 (2), 222–365.

Pfeiffer, J.M., Atkinson, C.L., Sharpe, A.E., Capps, K.A., Emery, K.F. & Page, L.M. (2019a) Phylogeny of Mesoamerican freshwater mussels and a revised tribe-level classification of the Ambleminae. *Zoologica Scripta*, 48 (1), 106–117.
https://doi.org/10.1111/zsc.12322

Pfeiffer, J.M., Breinholt, J.W. & Page, L.M. (2019b) Unioverse: A phylogenomic resource for reconstructing the evolution of freshwater mussels (Bivalvia, Unionoida). *Molecular Phylogenetics and Evolution*, 137, 114–126.
https://doi.org/10.1016/j.ympev.2019.02.016

Pfeiffer, J.M., Sharpe, A.E., Johnson, N.A., Emery, K.F. & Page, L.M. (2018) Molecular phylogeny of the Neartic and Mesoamerican freshwater mussel genus *Megalonaias*. *Hydrobiologia*, 811 (1), 139–151.
https://doi.org/10.1007/s10750-017-3441-7

Pilsbry, H.A. (1910) Unionidae of the Panuco River system, Mexico. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 61 (3), 532–539.

Pilsbry, H.A. & Hinkley, A.A. (1910) Melaniidae of the Panuco River system, Mexico. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 61 (3), 519–531.

Rafinesque, C.S. (1820) Monographie des coquilles bivalves fluviatiles de la Riviére Ohio, contenant douze genres et soixante-huit espèces. *Annales générales des Sciences Physiques, Bruxelles*, 5 (5), 287–322.

Rambaut, A., Drummond, A.J., Xie, D., Baele, G. & Suchard, M.A. (2018) Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. *Systems Biology*, 67 (5), 901–904.
https://doi.org/10.1093/sysbio/syy032

Randklev, C.R., Miller, T., Hart, M., Morton, J., Johnson, N.A., Skow, K., Inoue, K., Tsakiris, E.T., Oetker, S., Smith, R., Robertson, C. & Lopez, R. (2018) A semi-arid river in distress: Contributing factors and recovery solutions for three imperiled freshwater mussels (Family Unionidae) endemic to the Rio Grande basin in North America. *Science of the Total Environment*, 631–632, 733–744.
https://doi.org/10.1016/j.scitotenv.2018.03.032

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61 (3), 539–542.
https://doi.org/10.1093/sysbio/sys029

Sabaj, M.H. (2019) Standard symbolic codes for institutional resource collections in herpetology and ichthyology: An Online Reference. Version 7.1. 21 March 2019. American Society of Ichthyologists and Herpetologists, Washington, D.C. Electronically accessible. Available from: http://www.asih.org (accessed 17 June 2020)

Saghai-Maroof, M.A., Soliman, K.M., Jorgensen, R.A. & Allard, R.W. (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

Say, T. (1831) *New terrestrial and fluviatile shells of North America. (cont.). The Disseminator. Series 2. 1 (29)*. New Harmony,

Indiana, no pagination.
Schönhuth, S., Doadrio, I., Dominguez-Dominguez, O., Hillis, D.M. & Mayden, R.L. (2008) Molecular evolution of southern North American Cyprinidae (Actinopterygii), with the description of the new genus *Tampichthys* from central Mexico. *Molecular Phylogenetics and Evolution*, 47 (2), 729–756.
https://doi.org/10.1016/j.ympev.2007.11.036
Seehausen, O. & Wagner, C.E. (2014) Speciation in Freshwater Fishes. *Annual Review of Ecology, Evolution, and Systematics*, 45 (1), 621–651.
https://doi.org/10.1146/annurev-ecolsys-120213-091818
Simpson, C.T. (1900) Synopsis of the naiades, or pearly fresh-water mussels. *Proceedings of the United State National Museum*, 22, 501–1044.
https://doi.org/10.5479/si.00963801.22-1205.501
Simpson, C.T. (1914) *A descriptive catalogue of the naiades, or pearly fresh-water mussels. Parts I–III*. Bryant Walker, Detroit, Michigan, 1540 pp.
https://doi.org/10.5962/bhl.title.10910
Singley, J.A. (1893) Contributions to the Natural History of Texas. Part I. Mollusca: A preliminary list of the land, fresh water, and marine Mollusca of Texas. *Geological Survey of Texas*, 4th Annual Report, 299–343. [1892]
Smith, C.H., Johnson, N.A., Inoue, K., Doyle, R.D. & Randklev, C.R. (2019) Integrative taxonomy reveals a new species of freshwater mussel, *Potamilus streckersoni* sp. nov. (Bivalvia: Unionidae): implications for conservation and management. *Systematics and Biodiversity*, 17 (4), 331–348.
https://doi.org/10.1080/14772000.2019.1607615
Sowerby, G.B. (1868) Genus *Unio*. *Conchologica Iconica*, 16, 61–96.
Tanabe, A.S. (2011) Kakusan4 and Aminosan: Two programs for comparing nonpartitioned, proportional and separate models for combined molecular phylogenetic analyses of multilocus sequence data. *Molecular Ecology Resources*, 11 (5), 914–921.
https://doi.org/10.1111/j.1755-0998.2011.03021.x
Texas Parks and Wildlife Department (2020) Threatened and endangered nongame species. Chapter 65. *In*: *Wildlife Subchapter G. Rule §65.175*. Texas Secretary of State, Austin, Texas. [Adopted rules]
Thiele, J. (1934) Scaphopoda; Bivalvia; Cephalopoda. *In*: *Handbuch der systematischen Weichtierkunde. Teil 3*. Gustav Fischer, Jena, pp. 779–1022.
Tristram, H.B. (1863) Supplemental catalogue of terrestrial and fluviatile mollusks collected in Guatemala by O. Salvin, Esq., M.A., F.Z.S. *Proceedings of the Zoological Soceity of London*, 1863, 411–414.
Turgeon, D.D., Bogan, A.E., Coan, E.V., Emerson, W.K., Lyons, W.G., Pratt, W.L., Roper, C.F.E., Scheltema, A., Thompson, F.G. & Williams, J.D. (1988) *Common and Scientific Names of Aquatic Invertebrates from the United States and Canada: Mollusks*. American *Fisheries Society Special Publication 16*. American Fisheries Society, Bethesda, Maryland, 277 pp.
Turgeon, D.D., Quinn, J.F., Jr., Bogan, A.E., Coan, E.V., Hochberg, F.G., Jr., Lyons, W.G., Mikkelsen, P.M., Neves, R.J., Roper, C.F.E., Rosenberg, G., Roth, B., Scheltema, A., Thompson, F.G., Vecchione, M. & Williams, J.D. (1998) *Common and Scientific Names of Aquatic Invertebrates from the United States and Canada: Mollusks. American Fisheries Society Special Publication 26. 2nd Edition.* American Fisheries Society, Bethesda, Maryland, 528 pp.
USFWS (US Fish and Wildlife Service) (2018) Endangered and threatened wildlife and plants; endangered species status for Texas hornshell. *Federal Register*, 83 (28), 5720–5735.
Walker, J.M., Curolé, J.P., Wade, D.E., Chapman, E.G., Bogan, A.E., Watters, G.T. & Hoeh, W.R. (2006) Taxonomic distribution and phylogenetic utility of gender-associated mitochondrial genomes in the Unionoida (Bivalvia). *Malacologia*, 48 (1–2), 265–282.
Williams, J.D., Bogan, A.E., Butler, R.S., Cummings, K.S., Garner, J.T., Harris, J.L., Johnson, N.A. & Watters, G.T. (2017) A revised list of the freshwater mussels (Mollusca: Bivalvia: Unionida) of the United States and Canada. *Freshwater Mollusk Biology and Conservation*, 20 (2), 33–58.
https://doi.org/10.31931/fmbc.v20i2.2017.33-58
Williams, J.D., Warren, M.L. Jr., Cummings, K.S., Harris, J.L. & Neves, R.J. (1993) Conservation status of freshwater mussels of the United States and Canada. *Fisheries*, 18 (9), 6–22.
https://doi.org/10.1577/1548-8446(1993)018<0006:CSOFMO>2.0.CO;2
Zanatta, D.T. & Murphy, R.W. (2006) Evolution of active host-attraction strategies in the freshwater mussel tribe Lampsilini (Bivalvia: Unionidae). *Molecular Phylogenetics and Evolution*, 41 (1), 195–208.
https://doi.org/10.1016/j.ympev.2006.05.030

APPENDIX. List of specimen information [species; source; DNA code, collected waterbody, GenBank accession numbers for cytochrome c oxidase I (*cox1*), 16S ribosomal RNA (*16S*), and adenine nucleotide translocase (*ANT*); morphometrics] used in molecular and morphometric analyses. "X" in the Morph column indicates an availability in morphometric analyses. CNMO, Universidad Nacional Autónoma de México; INHS, Illinois Natural History Survey; NRI, Texas A&M Natural Resources Institute Freshwater Mussel Collection; UAT, uncatalogued specimens deposited at the Universidad Autónoma de Tamaulipas; photo-only, external shell photo was taken in the field.

Species	Source	DNA Code	Waterbody	*cox1*	*16S*	*ANT*	Morph
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal1-C460	RVal1_Psp002	Río Valles, San Luis Potosí, Mexico	MT553859	MT561579	MT558866	X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal1-C461	RVal1_Psp003	Río Valles, San Luis Potosí, Mexico	MT553860	MT561580	MT558867	X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal1-C462	RVal1_Psp004	Río Valles, San Luis Potosí, Mexico	MT553861	MT561581	MT558868	X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal1-C463	RVal1_Psp005	Río Valles, San Luis Potosí, Mexico	MT553862	MT561582	MT558869	X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal1-C464	RVal1_Psp006	Río Valles, San Luis Potosí, Mexico	MT553863	MT561583		X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal1-C465	RVal1_Psp007	Río Valles, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal1-C466	RVal1_Psp008	Río Valles, San Luis Potosí, Mexico	MT553864	MT561584		X
Popenaias berezai **n. sp.**	UAT (uncat.) Asp-RVal1-C624	RVal5_Asp013	Río Valles, San Luis Potosí, Mexico	MT553865	MT561585		X
Popenaias berezai **n. sp.**	UAT (uncat.) Asp-RVal5-NT001	RVal5_Asp022	Río Valles, San Luis Potosí, Mexico	MT553866	MT561586		X
Popenaias berezai **n. sp.**	UAT (uncat.) Asp-RVal5-NT002	RVal5_Asp023	Río Valles, San Luis Potosí, Mexico	MT553867	MT561587		X
Popenaias berezai **n. sp.**	UAT (uncat.) Asp-RVal5-NT003	RVal5_Asp024	Río Valles, San Luis Potosí, Mexico	MT553868	MT561588		X
Popenaias berezai **n. sp.**	UAT (uncat.) Asp-RVal5-NT004	RVal5_Asp025	Río Valles, San Luis Potosí, Mexico	MT553869	MT561589		X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal5-C603	RVal5_Psp001	Río Valles, San Luis Potosí, Mexico	MT553870	MT561590	MT558870	X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal5-C604	RVal5_Psp002	Río Valles, San Luis Potosí, Mexico	MT553871	MT561591	MT558871	X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal5-C605	RVal5_Psp003	Río Valles, San Luis Potosí, Mexico	MT553872	MT561592	MT558872	X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal5-C606	RVal5_Psp004	Río Valles, San Luis Potosí, Mexico	MT553873	MT561593		X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal5-C607	RVal5_Psp005	Río Valles, San Luis Potosí, Mexico	MT553874	MT561594		X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal5-C608	RVal5_Psp006	Río Valles, San Luis Potosí, Mexico	MT553875	MT561595		X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal5-C609	RVal5_Psp007	Río Valles, San Luis Potosí, Mexico	MT553876	MT561596		X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal5-C610	RVal5_Psp008	Río Valles, San Luis Potosí, Mexico	MT553877	MT561597		X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal5-C611	RVal5_Psp009	Río Valles, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal5-NT001	RVal5_Psp010	Río Valles, San Luis Potosí, Mexico	MT553878	MT561598		X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal5-NT002	RVal5_Psp011	Río Valles, San Luis Potosí, Mexico	MT553879	MT561599		X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal5-NT003	RVal5_Psp012	Río Valles, San Luis Potosí, Mexico	MT553880	MT561600		X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal5-NT004	RVal5_Psp013	Río Valles, San Luis Potosí, Mexico	MT553881	MT561601		X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal5-NT005	RVal5_Psp014	Río Valles, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal5-NT006	RVal5_Psp015	Río Valles, San Luis Potosí, Mexico	MT553882	MT561602		X

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APPENDIX. (Continued)

Species	Source	DNA Code	Waterbody	*cox1*	*16S*	*ANT*	Morph
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal5-NT007	RVal5_Psp016	Río Valles, San Luis Potosí, Mexico	MT553883	MT561603		X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal6-NT001	RVal6_Psp001	Río Valles, San Luis Potosí, Mexico	MT553884	MT561604	MT558873	X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal6-NT002	RVal6_Psp002	Río Valles, San Luis Potosí, Mexico	MT553885	MT561605	MT558874	X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal6-NT003	RVal6_Psp003	Río Valles, San Luis Potosí, Mexico	MT553886	MT561606	MT558875	X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal6-NT004	RVal6_Psp004	Río Valles, San Luis Potosí, Mexico	MT553887	MT561607	MT558876	X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal6-NT005	RVal6_Psp005	Río Valles, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal6-NT006	RVal6_Psp006	Río Valles, San Luis Potosí, Mexico	MT553888	MT561608		X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal6-NT007	RVal6_Psp007	Río Valles, San Luis Potosí, Mexico	MT553889	MT561609		X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal6-NT008	RVal6_Psp008	Río Valles, San Luis Potosí, Mexico	MT553890	MT561610		X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal6-NT009	RVal6_Psp009	Río Valles, San Luis Potosí, Mexico	MT553891	MT561611		X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal6-NT010	RVal6_Psp010	Río Valles, San Luis Potosí, Mexico	MT553892	MT561612		X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal6-NT011	RVal6_Psp011	Río Valles, San Luis Potosí, Mexico	MT553893	MT561613		X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal6-NT012	RVal6_Psp012	Río Valles, San Luis Potosí, Mexico	MT553894	MT561614		X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal6-NT013	RVal6_Psp013	Río Valles, San Luis Potosí, Mexico	MT553895	MT561615		X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal6-NT014	RVal6_Psp014	Río Valles, San Luis Potosí, Mexico	MT553896	MT561616		X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal6-NT015	RVal6_Psp015	Río Valles, San Luis Potosí, Mexico	MT553897	MT561617		X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal6-NT016	RVal6_Psp016	Río Valles, San Luis Potosí, Mexico	MT553898	MT561618		X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal7-NT001	RVal7_Psp001	Río Valles, San Luis Potosí, Mexico	MT553899	MT561619	MT558877	X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal7-NT002	RVal7_Psp002	Río Valles, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal7-NT003	RVal7_Psp003	Río Valles, San Luis Potosí, Mexico	MT553900	MT561620	MT558878	X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal7-NT004	RVal7_Psp004	Río Valles, San Luis Potosí, Mexico	MT553901	MT561621	MT558879	X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal7-NT005	RVal7_Psp005	Río Valles, San Luis Potosí, Mexico	MT553902	MT561622		X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal7-NT006	RVal7_Psp006	Río Valles, San Luis Potosí, Mexico	MT553903	MT561623		X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal7-NT007	RVal7_Psp007	Río Valles, San Luis Potosí, Mexico	MT553904	MT561624		X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal7-NT008	RVal7_Psp008	Río Valles, San Luis Potosí, Mexico	MT553905	MT561625		X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal7-NT020	RVal7_Psp020	Río Valles, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal7-NT021	RVal7_Psp021	Río Valles, San Luis Potosí, Mexico	MT553906			X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal7-NT022	RVal7_Psp022	Río Valles, San Luis Potosí, Mexico	MT553907	MT561626		X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal7-NT023	RVal7_Psp023	Río Valles, San Luis Potosí, Mexico	MT553908	MT561627		X

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APPENDIX. (Continued)

Species	Source	DNA Code	Waterbody	*cox1*	*16S*	*ANT*	Morph
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal7-NT024	RVal7_Psp024	Río Valles, San Luis Potosí, Mexico	MT553909	MT561628		X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal7-NT025	RVal7_Psp025	Río Valles, San Luis Potosí, Mexico	MT553910	MT561629		X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal7-NT026	RVal7_Psp026	Río Valles, San Luis Potosí, Mexico	MT553911	MT561630		X
Popenaias berezai **n. sp.**	UAT (uncat.) Psp-RVal7-NT027	RVal7_Psp027	Río Valles, San Luis Potosí, Mexico	MT553912	MT561631		X
Popenaias berezai **n. sp.**	INHS90397.01	Morph-only	Río Valles, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90397.02	Morph-only	Río Valles, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90397.03	Morph-only	Río Valles, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90397.04	Morph-only	Río Valles, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	CNMO 8037	Morph-only	Río Valles, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90397.06	Morph-only	Río Valles, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90397.07	Morph-only	Río Valles, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90397.08	Morph-only	Río Valles, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90397.09	Morph-only	Río Valles, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90397.10	Morph-only	Río Valles, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90134.01	RCla_Psp001	Río Claro, San Luis Potosí, Mexico	MT553913	MT561632	MT558880	X
Popenaias berezai **n. sp.**	INHS90134.02	RCla_Psp002	Río Claro, San Luis Potosí, Mexico	MT553914	MT561633	MT558881	X
Popenaias berezai **n. sp.**	INHS90134.03	RCla_Psp003	Río Claro, San Luis Potosí, Mexico	MT553915	MT561634	MT558882	X
Popenaias berezai **n. sp.**	INHS90152.01	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90152.02	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90152.03	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90152.04	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90152.05	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90152.06	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90152.07	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90152.08	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90152.09	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90152.10	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90152.11	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90152.12	Morph-only	Río Amajac, San Luis Potosí, Mexico				X

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APPENDIX. (Continued)

Species	Source	DNA Code	Waterbody	*cox1*	*16S*	*ANT*	Morph
Popenaias berezai **n. sp.**	INHS90152.13	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90152.14	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90152.15	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90152.16	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90152.17	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90152.18	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90152.19	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90152.20	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90152.21	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90152.22	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.01	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.02	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.03	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.04	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.05	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.06	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.07	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.08	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.09	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.10	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.11	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.12	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.13	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.14	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.15	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.16	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.17	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.18	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.19	Morph-only	Río Amajac, San Luis Potosí, Mexico				X

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APPENDIX. (Continued)

Species	Source	DNA Code	Waterbody	*cox1*	*16S*	*ANT*	Morph
Popenaias berezai **n. sp.**	INHS90199.20	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.21	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.22	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.23	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.24	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.25	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.26	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.27	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.28	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.29	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.30	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.31	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.32	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.33	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.34	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.35	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.36	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.37	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.38	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.39	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.40	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.41	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.42	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.43	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.44	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.45	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.46	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.47	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.48	Morph-only	Río Amajac, San Luis Potosí, Mexico				X

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APPENDIX. (Continued)

Species	Source	DNA Code	Waterbody	*cox1*	*16S*	*ANT*	Morph
Popenaias berezai **n. sp.**	INHS90199.49	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.50	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.51	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.52	RAma_Psp001	Río Amajac, San Luis Potosí, Mexico	MT553916	MT561635	MT558883	X
Popenaias berezai **n. sp.**	INHS90199.53	RAma_Psp002	Río Amajac, San Luis Potosí, Mexico	MT553917	MT561636	MT558884	X
Popenaias berezai **n. sp.**	INHS90199.54	RAma_Psp003	Río Amajac, San Luis Potosí, Mexico	MT553918	MT561637	MT558885	X
Popenaias berezai **n. sp.**	INHS90199.55	RAma_Psp004	Río Amajac, San Luis Potosí, Mexico	MT553919	MT561638		X
Popenaias berezai **n. sp.**	INHS90199.56	RAma_Psp005	Río Amajac, San Luis Potosí, Mexico	MT553920	MT561639		X
Popenaias berezai **n. sp.**	INHS90199.57	RAma_Psp006	Río Amajac, San Luis Potosí, Mexico	MT553921	MT561640		X
Popenaias berezai **n. sp.**	INHS90199.58	RAma_Psp007	Río Amajac, San Luis Potosí, Mexico	MT553922	MT561641		X
Popenaias berezai **n. sp.**	INHS90199.59	RAma_Psp008	Río Amajac, San Luis Potosí, Mexico	MT553923	MT561642		X
Popenaias berezai **n. sp.**	INHS90199.60	RAma_Psp009	Río Amajac, San Luis Potosí, Mexico	MT553924	MT561643		X
Popenaias berezai **n. sp.**	INHS90199.61	RAma_Psp010	Río Amajac, San Luis Potosí, Mexico	MT553925	MT561644		X
Popenaias berezai **n. sp.**	INHS90199.62	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90199.63	Morph-only	Río Amajac, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90167.01	RHui_Psp001	Río Huichihuyán, San Luis Potosí, Mexico	MT553926	MT561645	MT558886	X
Popenaias berezai **n. sp.**	INHS90192.01	RHui_Psp002	Río Huichihuyán, San Luis Potosí, Mexico	MT553927	MT561646	MT558887	X
Popenaias berezai **n. sp.**	INHS90175.01	RTan_Psp001	Río Tancuilín, San Luis Potosí, Mexico	MT553928	MT561647	MT558888	X
Popenaias berezai **n. sp.**	INHS90175.02	RTan_Psp002	Río Tancuilín, San Luis Potosí, Mexico	MT553929	MT561648	MT558889	X
Popenaias berezai **n. sp.**	INHS90175.03	RTan_Psp003	Río Tancuilín, San Luis Potosí, Mexico	MT553930	MT561649	MT558890	X
Popenaias berezai **n. sp.**	INHS90175.04	RTan_Psp004	Río Tancuilín, San Luis Potosí, Mexico	MT553931	MT561650	MT558891	X
Popenaias berezai **n. sp.**	INHS90175.05	RTan_Psp005	Río Tancuilín, San Luis Potosí, Mexico	MT553932	MT561651		X
Popenaias berezai **n. sp.**	INHS90175.06	RTan_Psp006	Río Tancuilín, San Luis Potosí, Mexico	MT553933	MT561652		X
Popenaias berezai **n. sp.**	INHS90175.07	RTan_Psp007	Río Tancuilín, San Luis Potosí, Mexico	MT553934	MT561653		X
Popenaias berezai **n. sp.**	INHS90175.08	RTan_Psp008	Río Tancuilín, San Luis Potosí, Mexico	MT553935	MT561654		X
Popenaias berezai **n. sp.**	INHS90175.09	RTan_Psp009	Río Tancuilín, San Luis Potosí, Mexico	MT553936	MT561655		X
Popenaias berezai **n. sp.**	INHS90175.10	RTan_Psp010	Río Tancuilín, San Luis Potosí, Mexico	MT553937	MT561656		X

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APPENDIX. (Continued)

Species	Source	DNA Code	Waterbody	*cox1*	*16S*	*ANT*	Morph
Popenaias berezai **n. sp.**	INHS90175.11	Morph-only	Río Tancuilín, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90175.12	Morph-only	Río Tancuilín, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90175.13	Morph-only	Río Tancuilín, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90175.14	Morph-only	Río Tancuilín, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90175.15	Morph-only	Río Tancuilín, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90175.16	Morph-only	Río Tancuilín, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90175.17	Morph-only	Río Tancuilín, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90175.18	Morph-only	Río Tancuilín, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90175.19	Morph-only	Río Tancuilín, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90175.20	Morph-only	Río Tancuilín, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90175.21	Morph-only	Río Tancuilín, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90183.01	RTam_Psp001	Río Tampaón, San Luis Potosí, Mexico	MT553938	MT561657	MT558892	X
Popenaias berezai **n. sp.**	INHS90183.02	RTam_Psp002	Río Tampaón, San Luis Potosí, Mexico	MT553939	MT561658	MT558893	X
Popenaias berezai **n. sp.**	INHS90183.03	RTam_Psp003	Río Tampaón, San Luis Potosí, Mexico	MT553940	MT561659	MT558894	X
Popenaias berezai **n. sp.**	INHS90183.04	RTam_Psp004	Río Tampaón, San Luis Potosí, Mexico	MT553941	MT561660	MT558895	X
Popenaias berezai **n. sp.**	INHS90183.05	RTam_Psp005	Río Tampaón, San Luis Potosí, Mexico	MT553942	MT561661		X
Popenaias berezai **n. sp.**	INHS90183.06	RTam_Psp006	Río Tampaón, San Luis Potosí, Mexico	MT553943	MT561662		X
Popenaias berezai **n. sp.**	INHS90183.07	RTam_Psp007	Río Tampaón, San Luis Potosí, Mexico	MT553944	MT561663		X
Popenaias berezai **n. sp.**	INHS90183.08	RTam_Psp008	Río Tampaón, San Luis Potosí, Mexico	MT553945	MT561664		X
Popenaias berezai **n. sp.**	INHS90183.09	RTam_Psp009	Río Tampaón, San Luis Potosí, Mexico	MT553946	MT561665		X
Popenaias berezai **n. sp.**	INHS90183.10	Morph-only	Río Tampaón, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90183.11	Morph-only	Río Tampaón, San Luis Potosí, Mexico				X
Popenaias berezai **n. sp.**	INHS90183.12	Morph-only	Río Tampaón, San Luis Potosí, Mexico				X
Popenaias ganina	UAT (uncat.) Firi-RGal3-C488	RGal3_Firi002	Río Gallinas, San Luis Potosí, Mexico	MT553947	MT561666		X
Popenaias ganina	UAT (uncat.) Firi-RGal3-C490	RGal3_Firi004	Río Gallinas, San Luis Potosí, Mexico	MT553948	MT561667		X
Popenaias ganina	UAT (uncat.) Firi-RGal3-C493	RGal3_Firi007	Río Gallinas, San Luis Potosí, Mexico	MT553949	MT561668		X
Popenaias ganina	UAT (uncat.) Psp-RGal3-C481	RGal3_Psp001	Río Gallinas, San Luis Potosí, Mexico	MT553950		MT558896	X
Popenaias ganina	UAT (uncat.) Psp-RGal3-C482	RGal3_Psp002	Río Gallinas, San Luis Potosí, Mexico	MT553951	MT561669	MT558897	X
Popenaias ganina	UAT (uncat.) Psp-RGal3-C483	RGal3_Psp003	Río Gallinas, San Luis Potosí, Mexico	MT553952	MT561670	MT558898	X

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APPENDIX. (Continued)

Species	Source	DNA Code	Waterbody	*cox1*	*16S*	*ANT*	Morph
Popenaias ganina	UAT (uncat.) Psp-RGal3-C484	RGal3_Psp004	Río Gallinas, San Luis Potosí, Mexico	MT553953	MT561671	MT558899	X
Popenaias ganina	UAT (uncat.) Psp-RGal3-C485	RGal3_Psp005	Río Gallinas, San Luis Potosí, Mexico	MT553954	MT561672		X
Popenaias ganina	UAT (uncat.) Asp-RGal4-C562	RGal4_Asp017	Río Gallinas, San Luis Potosí, Mexico	MT553955	MT561673		X
Popenaias ganina	UAT (uncat.) Asp-RGal4-C564	RGal4_Asp019	Río Gallinas, San Luis Potosí, Mexico	MT553956	MT561674		X
Popenaias ganina	UAT (uncat.) Asp-RGal4-C565	RGal4_Asp020	Río Gallinas, San Luis Potosí, Mexico	MT553957	MT561675		X
Popenaias ganina	UAT (uncat.) Psp-RGal4-C540	RGal4_Psp001	Río Gallinas, San Luis Potosí, Mexico	MT553958	MT561676	MT558900	X
Popenaias ganina	UAT (uncat.) Psp-RGal4-C545	RGal4_Psp006	Río Gallinas, San Luis Potosí, Mexico	MT553959	MT561677	MT558901	X
Popenaias ganina	UAT (uncat.) Psp-RGal4-C546	RGal4_Psp007	Río Gallinas, San Luis Potosí, Mexico	MT553960	MT561678	MT558902	X
Popenaias ganina	UAT (uncat.) Psp-RGal4-C547	RGal4_Psp008	Río Gallinas, San Luis Potosí, Mexico	MT553961	MT561679	MT558903	X
Popenaias ganina	UAT (uncat.) Psp-RGal4-C548	RGal4_Psp009	Río Gallinas, San Luis Potosí, Mexico	MT553962	MT561680		X
Popenaias ganina	UAT (uncat.) Psp-RGal4-C549	RGal4_Psp010	Río Gallinas, San Luis Potosí, Mexico	MT553963	MT561681		X
Popenaias ganina	UAT (uncat.) Psp-RGal4-C550	RGal4_Psp011	Río Gallinas, San Luis Potosí, Mexico	MT553964	MT561682		X
Popenaias ganina	UAT (uncat.) Psp-RGal4-C551	RGal4_Psp012	Río Gallinas, San Luis Potosí, Mexico	MT553965	MT561683		X
Popenaias ganina	UAT (uncat.) Psp-RGal4-C553	RGal4_Psp014	Río Gallinas, San Luis Potosí, Mexico	MT553966	MT561684		X
Popenaias ganina	UAT (uncat.) Psp-RGal4-C554	RGal4_Psp015	Río Gallinas, San Luis Potosí, Mexico	MT553967	MT561685		X
Popenaias popeii	NRI8106.1	Ppop_RG01	Rio Grande, Brewster Co., Texas, USA				X
Popenaias popeii	NRI8106.2	Ppop_RG02	Rio Grande, Brewster Co., Texas, USA				X
Popenaias popeii	NRI8204.1	Ppop_RG03	Rio Grande, Terrell Co., Texas, USA	MT553968	MT561686	MT558904	X
Popenaias popeii	NRI8265.1	Ppop_RG04	Rio Grande, Webb Co., Texas, USA	MT553969	MT561687	MT558905	X
Popenaias popeii	NRI8385.1	Ppop_RG05	Rio Grande, Webb Co., Texas, USA	MT553970	MT561688		X
Popenaias popeii	NRI8385.2	Ppop_RG06	Rio Grande, Webb Co., Texas, USA	MT553971	MT561689	MT558906	X
Popenaias popeii	NRI8385.3	Ppop_RG07	Rio Grande, Webb Co., Texas, USA	MT553972	MT561690		X
Popenaias popeii	NRI8385.4	Ppop_RG08	Rio Grande, Webb Co., Texas, USA	MT553973	MT561691		X
Popenaias popeii	NRI8385.5	Ppop_RG09	Rio Grande, Webb Co., Texas, USA	MT553974	MT561692		X
Popenaias popeii	NRI8385.6	Ppop_RG10	Rio Grande, Webb Co., Texas, USA	MT553975	MT561693		X
Popenaias popeii	Photo only	Morph-only	Rio Grande, Webb Co., Texas, USA				X
Popenaias popeii	Photo only	Morph-only	Rio Grande, Webb Co., Texas, USA				X
Popenaias popeii	Photo only	Morph-only	Rio Grande, Webb Co., Texas, USA				X
Popenaias popeii	Photo only	Morph-only	Rio Grande, Webb Co., Texas, USA				X

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APPENDIX. (Continued)

Species	**Source**	**DNA Code**	**Waterbody**	***cox1***	***16S***	***ANT***	**Morph**
Popenaias popeii	Photo only	Morph-only	Rio Grande, Webb Co., Texas, USA				X
Popenaias popeii	Photo only	Morph-only	Rio Grande, Webb Co., Texas, USA				X
Popenaias popeii	Photo only	Morph-only	Rio Grande, Webb Co., Texas, USA				X
Popenaias popeii	Photo only	Morph-only	Rio Grande, Webb Co., Texas, USA				X
Popenaias popeii	Photo only	Morph-only	Rio Grande, Webb Co., Texas, USA				X
Popenaias popeii	Photo only	Morph-only	Rio Grande, Webb Co., Texas, USA				X
Popenaias popeii	Photo only	Morph-only	Rio Grande, Webb Co., Texas, USA				X
Popenaias popeii	Photo only	Morph-only	Rio Grande, Webb Co., Texas, USA				X
Popenaias popeii	Photo only	Morph-only	Rio Grande, Webb Co., Texas, USA				X
Popenaias popeii	Photo only	Morph-only	Rio Grande, Webb Co., Texas, USA				X
Popenaias popeii	Photo only	Morph-only	Rio Grande, Webb Co., Texas, USA				X
Popenaias popeii	Photo only	Morph-only	Rio Grande, Webb Co., Texas, USA				X
Popenaias popeii	Photo only	Morph-only	Rio Grande, Webb Co., Texas, USA				X
Popenaias popeii	Photo only	Morph-only	Rio Grande, Webb Co., Texas, USA				X
Popenaias popeii	Photo only	Morph-only	Rio Grande, Webb Co., Texas, USA				X
Popenaias popeii	Photo only	Morph-only	Rio Grande, Webb Co., Texas, USA				X
Popenaias popeii	Photo only	Morph-only	Rio Grande, Webb Co., Texas, USA				X
Popenaias popeii	NRI8696.1	Ppop_DV01	Devils River, Val Verde Co., Texas, USA	MT553976	MT561694	MT558907	
Popenaias popeii	NRI8696.2	Ppop_DV02	Devils River, Val Verde Co., Texas, USA	MT553977	MT561695	MT558908	
Popenaias popeii	NRI8696.3	Ppop_DV03	Devils River, Val Verde Co., Texas, USA	MT553978	MT561696	MT558909	
Popenaias popeii	NRI8696.4	Ppop_DV04	Devils River, Val Verde Co., Texas, USA	MT553979	MT561697	MT558910	
Popenaias popeii	NRI8696.5	Ppop_DV05	Devils River, Val Verde Co., Texas, USA	MT553980	MT561698		
Popenaias popeii	NRI8696.6	Ppop_DV06	Devils River, Val Verde Co., Texas, USA	MT553981	MT561699		
Popenaias popeii	NRI8696.7	Ppop_DV07	Devils River, Val Verde Co., Texas, USA	MT553982	MT561700		
Popenaias popeii	NRI8696.8	Ppop_DV08	Devils River, Val Verde Co., Texas, USA	MT553983	MT561701		