



# New records of the Mountain Mullet, *Dajaus monticola* (Bancroft, 1834), and an overview of historical records in Texas

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## Abstract

*Dajaus monticola* (Bancroft, 1834) is an amphidromous species of mugilid known from South and Central America and the islands of the Caribbean but is rarely collected in Gulf coast states of the United States. Two new records of *D. monticola* collected from the Gulf of Mexico (Brazoria Co.) and the Brazos River (Washington Co.) are reported from Texas. The rare occurrence of *D. monticola* in Texas is discussed and diagnostic characters used to distinguish this species from other mugilids found in Texas are reevaluated.

## Keywords

Amphidromy, Brazos River, Gulf of Mexico, Mugiliformes.

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## Introduction

Members of the family Mugilidae, or grey mullets, are an economically important group of teleost fishes (79 species; Fricke Eschmeyer and Fong 2019) that are distributed across the globe (Durand et al. 2012). They primarily reside in marine coastal waters, from temperate to tropical climates, although there are a few species which occasionally travel to or permanently reside in freshwaters (Ghasemzadeh and González-Castro 2015). All members of this family share a similar body plan with only minor morphological differences which have made distinguishing closely related species relatively challenging (Thomson 1997, Ghasemzadeh and González-Castro 2015). As a result, systematic studies based solely on morphological characters are often conflicting and, with the recent inclusion of molecular studies, have been

shown to overlook a large number of evolutionarily distinct lineages (Durand et al. 2012, McMahan et al. 2013).

The Mountain Mullet, *Dajaus monticola* (Bancroft, 1834), is a freshwater mugilid typically found in high gradient, high flow streams reaching elevations of up to 1500 m, hence the common name (Cruz 1987, Miller et al. 2005, Matamoros et al. 2009). The Mountain Mullet is an amphidromous species (Smith and Kwak 2014), meaning spawning occurs in freshwater, typically coinciding with the rainy season, and fertilized eggs are washed out to sea where they hatch and develop in the marine environment before returning to freshwater rivers and streams as juveniles of 20–50 mm standard length (SL) (Anderson 1957). They are distributed along both the Pacific and Atlantic slopes of Central and southern North America. In the Pacific they range from Southern California (United States of America [USA])

down to Ecuador. In the Atlantic their range extends as far north as the coast of North Carolina (USA) southward to the coasts of Venezuela in South America and throughout the islands of the West Indies (Matamoros et al. 2009, McMahan et al. 2013). Despite this extensive range, they are rarely collected in the Gulf Coast states of the USA (Suttkus 1956, Schlicht 1959, Loftus et al. 1984, Matamoros et al. 2009). Recently, molecular studies have shown 4 distinct haplogroups of *D. monticola* (McMahan et al. 2013, Durand et al. 2017). Two haplogroups occur sympatrically among Pacific drainages, 1 haplogroup extends from the Caribbean northwards to the southeastern coast of the USA and 1 haplogroup is restricted to the Gulf Coast drainages of Mexico's eastern coast. To date there is no genetic data available for individuals of *D. monticola* collected from Texas.

Herein we report on 2 new records of *Dajaus monticola* from Texas, USA, including a specimen from the Gulf of Mexico (Brazoria Co.) earlier misidentified as a specimen of *Mugil* Linnaeus, 1758 and a specimen collected more recently from the Brazos River (Washington Co.). These 2 records represent only the 27<sup>th</sup> and 28<sup>th</sup> reported occurrence of *D. monticola* in the state of Texas. To better understand the occurrence and distribution of this species in Texas, we attempted to examine all available museum vouchered specimens collected within the state to reconfirm identification. We also compare a mitochondrial cytochrome c oxidase subunit 1 (COI) gene segment obtained from the recently collected specimen of *D. monticola* from the Brazos River to those available from other studies (Durand et al. 2017) in order to determine haplogroup membership. Finally, we provide an overview of diagnostic characters that can be used to distinguish *D. monticola* from the other 2 species of mullet commonly encountered in the freshwaters of Texas: the Striped Mullet *Mugil cephalus* Linnaeus, 1758 and the White Mullet *Mugil curema* Valenciennes, 1836.

## Methods

The newly collected specimen of *Dajaus monticola* was collected in the Brazos River (Washington Co., Texas) during a routine sampling trip on 4 November, 2016. Fishes were sampled along the edge of a sandbar using a 4.6 × 1.8 m seine. Collected fishes were euthanized with an overdose of MS222, fixed in a solution of 10% formalin and transferred to 70% EtOH for storage. Before fixation in formalin, a tissue sample (right pelvic fin) was taken from the euthanized specimen and preserved in 95% EtOH. All specimens and associated tissues were deposited at the Biodiversity Research and Teaching Collections, Texas A&M University, College Station, TX, USA (TCWC). An additional specimen of *D. monticola* (TCWC 16904.16), which was previously misidentified as *Mugil* sp., was discovered while reexamining lots of mugilids at the TCWC.

Previous records of *Dajaus monticola* collected

within the state boundary of Texas were obtained from the Fishes of Texas website (Hendrickson et al. 2015) or the literature (Schlicht 1959, Pezold and Edwards 1983) and visualized using ArcMap v. 10.5.1 (ESRI 2013). When possible, specimens from previous collections were reexamined, either in person or via photographs, in order to reconfirm the original identification, especially in specimens smaller than approximately 45 mm SL. This was accomplished using characters listed in the key to the family Mugilidae in Hubbs et al. (2008). Select specimens of *D. monticola* (TCWC 8875.04, TCWC 19764.01), *Mugil cephalus* (TCWC 10228.1, TCWC 14702.01) and *M. curema* (TCWC 19717.08, TCWC 16400.11) were also examined to determine the SL at which the characteristics most commonly used to distinguish between the 3 species become useful. Photographs of specimens or parts thereof were obtained either using a Zeiss SteReo Discovery V20 microscope equipped with a Zeiss Axiocam MRc5 digital camera or a Canon EOS 60D. Digital images were processed using Adobe Photoshop and Illustrator CC 2018 (Adobe Systems Inc., San Jose, CA, USA).

Genomic DNA was extracted from the right pelvic fin of a single individual of *Dajaus monticola* using a DNeasy Tissue Extraction Kit (Qiagen, Inc., Valencia CA, USA) following the manufacturer's protocols. A portion of the mitochondrial COI gene was amplified using polymerase chain reaction (PCR) and the primers LCO1490 and HCO2198 (Folmer et al. 1994). PCR conditions consisted of an initial denaturation at 94 °C for 4 min followed by 35 cycles of 94 °C for 30 s, 41 °C for 1 min and 72 °C for 1 min 30 s, followed by a final extension of 72 °C for 10 min and were performed in 25.0 µl containing 12.5 µl of GoTaq Green Master Mix (Promega, Madison, WI, USA), 10.95 µl of nuclease-free water, 300ng of template DNA, and 10 µM each of forward and reverse primer. Amplified PCR product was sequenced using the high-throughput sequence facilities at Yale University (New Haven, CT, USA). Obtained sequences were checked for accuracy of base determination and assembled using GENIOUS v. 11.1.4 (Kearse et al. 2012). The final sequence has been deposited on GenBank under accession number MK950847. An additional 37 COI sequences were downloaded from GenBank and aligned against the sequence generated as part of this study in MAFFT (Katoh and Standley 2013). The resulting aligned data set (38 sequences, each 650 bp) was viewed in Mesquite v. 3.51 (Maddison and Maddison 2018) to check for spurious stop codons. Relationships among *D. monticola* COI haplotypes were examined using a minimum spanning haplotype network (Bandelt et al. 1999) that was constructed and viewed in PopART (Leigh and Bryant 2015).

**Institutional Abbreviations.** ANSP, Academy of Natural Sciences of Drexler University, Philadelphia, PA, USA; MARIS, Multistate Aquatic Resources Information System, USGS, USA; TNHC, Texas Natural History Collections, University of Texas, Austin, Tx, USA; TU, Tulane Museum of Natural History, Tulane University,



**Figure 1.** *Dajaus monticola*, TCWC 20062.01, 34.7 mm SL; Brazos River, Washington Co., Texas, USA.

New Orleans, LA, USA.

## Results

**New records.** USA, Texas, Brazoria County, Gulf of Mexico (29.0697, -95.1251), Kole M. Kubicek & Kevin W. Conway (collectors), 12 October 2013 (1 specimen, 29.7 mm SL, TCWC 16904.16). USA, Texas, Washington County, Brazos River (30.3605, -96.1551), Kole M. Kubicek & Amanda K. Pinion (collectors), 04 November 2016 (1 specimen, 34.7 mm SL [Fig. 1], TCWC 20062.01).

At the site of collection of the most recent specimen (TCWC 20062.01), the Brazos River is characterized by sandbars and the occasional stretch of gravel. The specimen was collected over a substrate of sand at a depth of approximately 1 m, immediately adjacent to a sandbar. The collection site is located in a stretch of the river characterized as a lowland floodplain river with a sandy bottom and a silty, turbid composition. This stands in contrast to the rocky, high gradient and high elevation rivers and streams the species is known for in Central and South America.

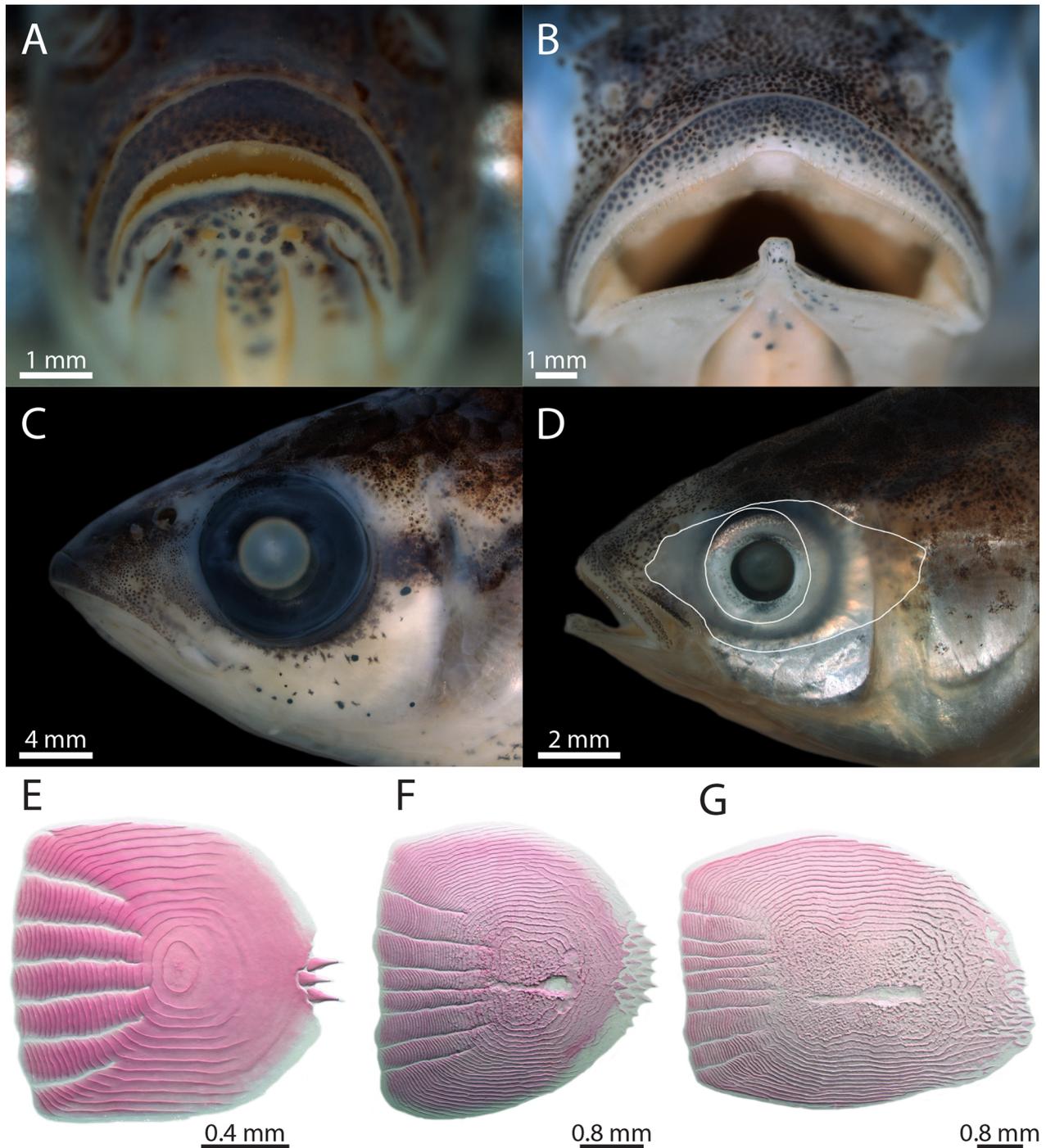
**Material examined.** *Dajaus monticola*, USA, Texas, Jefferson County, Sabine Lake (29.865, -93.9253), 22 November 1958 (1 specimen, photograph only [PO], 39.1 mm SL, TU 22052). USA, Texas, Liberty County, Trinity River (30.2763, -94.7982), 12 November 1966 (1 specimen, 35.5 mm SL, TCWC 1610.01). USA, Texas, Liberty County, Long King Creek (30.6040, -94.9585), 12 November 1966 (4 specimens, 38.4–47.4 mm SL, TCWC 1611.01). USA, Texas, Madison County, Youngs Creek (31.0308, -95.7110), 12 November 1966 (1 specimen, 41.5 mm SL, TCWC 1636.01). USA, Texas, Brazos County, Brazos River (30.6280, -96.5439), 27 September 1993 (1 specimen, 34.6 mm SL, TCWC 7542.03). USA, Texas, Victoria County, Guadalupe River (28.6337, -96.9551), 18 October 1999 (1 specimen, 28.9 mm SL, ANSP 186789). USA, Texas, Gonzales County, Guadalupe River (29.4287, -97.3837), 24 June 2013 (1 specimen, PO, 139.0 mm SL, MARIS 1921820.0). USA, Texas, Hidalgo County, Rio Grande (26.1366, -98.3343), 13 March 2012 (2 specimens, 92.1–111.7 mm SL, TNHC 11716). USA, Texas, Hidalgo County, Rio Grande (26.0236, -97.7311), 14 January 1993 (3 specimens,

41.4–46.7 mm SL, TNHC 24842). USA, Texas, Hidalgo County, Rio Grande (26.1316, -98.3310), 12 April 1993 (2 specimens, 129.0–152.0 mm SL, TNHC 24934). USA, Texas, Bell County, Lampassas River (31.0176, -97.5249), 25 March 2002 (3 specimens, 73.4–306.0 mm SL, TNHC 28665). USA, Texas, Williamson County, Brushy Creek (30.5263, -97.5668), 13 December 2008 (5 specimens, 114.5–125.7 mm SL, TNHC 51645). USA, Texas, Brazos County, Little Brazos River (30.6409, -96.5206), 13 December 2008 (1 specimen, 59.5 mm SL, TNHC 51814). USA, Texas, Victoria County, Guadalupe River (28.8971, -97.1384), 28 October 1999 (1 specimen, 102.5 mm SL, TNHC 54299). USA, Texas, Gonzales County, Guadalupe River (29.4845, -97.4481), 26 October 1999 (5 specimens, 47.0–57.8 mm SL, TNHC 54306). USA, Texas, Brazoria County, Brazos River (29.3504, -95.5829), 23 December 2004 (1 specimen, 34.4 mm SL, TNHC 68281). USA, Texas, Brazoria County, Brazos River (29.3504, -95.5829), 14 November 2004 (1 specimen, 33.0 mm SL, TNHC 68387). Trinidad and Tobago, Sangre Grande, unnamed river (10.8310, -61.0634), 27 May 2018 (7 specimens, 47.5–141.0 mm SL, TCWC 19764.01). Costa Rica, Province Limon, Laguna Tortuguero (10.5394, -83.5028), 15 August 1996 (5 specimens, 23.0–36.0 mm SL, TCWC 8875.04).

*Mugil cephalus*, USA, Texas, Travis County, Austin Bayou, April 1956 (23 specimens, 31.0–41.4 mm SL, TCWC 10228.01). USA, Texas, Washington County, Coles Creek (30.3483, -96.1675), 02 August 2006 (9 specimens, 77.0–105.3 mm SL, TCWC 14702.01). USA, Texas, Brazoria County, Chocolate Bayou (29.0819, -95.9447), 17 November 2000 (7 specimens, 80.1–109.8 mm SL, TCWC 12308.08). USA, Texas, Calhoun County, San Antonio Bay (28.3901, -96.7085), 18 May 2018 (14 specimens, 24.0–40.7 mm SL, TCWC 19717.19).

*Mugil curema*, USA, Texas, Calhoun County, San Antonio Bay (28.3901, -96.7085), 18 May 2018 (73 specimens, 22.0–46.0 mm SL, TCWC 19717.08). USA, Texas, Brazoria County, Christmas Bay (29.0484, -95.1649), 12 October 2013 (1 specimen, 72.5 mm SL, TCWC 16400.11).

**Identification.** The specimen was identified using the key by Hubbs et al. (2008: 32) to the Mugilidae occurring in the freshwaters of Texas. Our identification is based



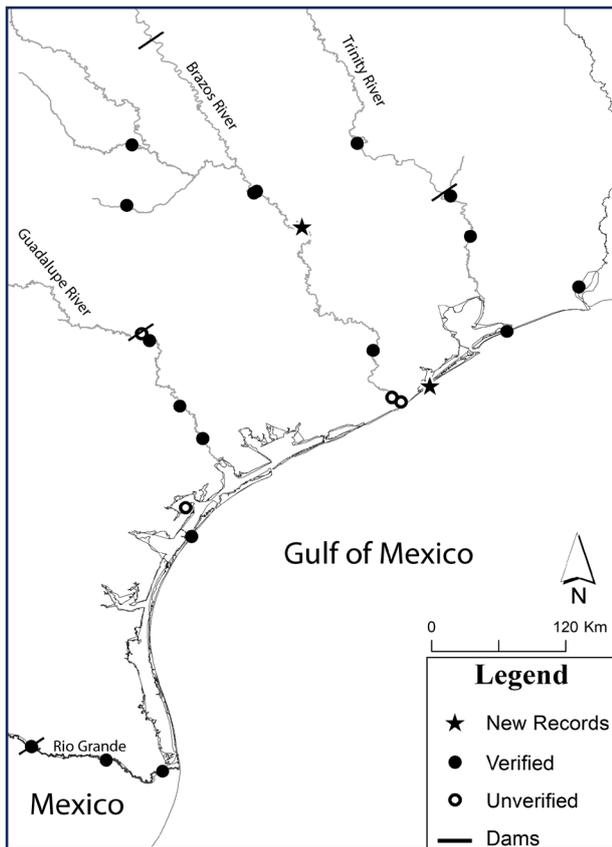
**Figure 2.** Diagnostic characters of *Dajaus monticola* and *Mugil* spp. **A, B.** Shape of mouth and presence/absence of a symphyseal knob; mouth in anterior view: **(A)** *D. monticola* (TCWC 20062.01, 34.7 mm SL); **(B)** *M. curema* (TCWC 19717.08, 46.0 mm SL). **C, D.** Presence/absence of adipose eyelid (outlined in white when present); head in lateral view: **(C)** *D. monticola* (TCWC 19764.01, 47.5 mm SL); **(D)** *M. curema* (TCWC 19717.08, 46.0 mm SL). **E–G.** Scales showing the earliest formation of ctenii observed: **(E)** *D. monticola* (TCWC 8875.01, 23.0 mm SL); **(F)** *M. curema* (TCWC 19717.08, 46.0 mm SL); **(G)** *M. cephalus* (TCWC 12308.08, 109.8 mm SL).

on external morphological features, including: (1) lower jaw rounded, without a symphyseal knob in *D. monticola* (Fig. 2A) vs lower jaw angular, with a prominent symphyseal knob in *Mugil* spp. (Fig. 2B); (2) scales ctenoid in *D. monticola* (Fig. 2E) vs scales cycloid in young, ctenoid in adults in *Mugil* spp. (Fig. 2F, G). The segment of the COI gene obtained from the Brazos River specimen of *Dajaus monticola* (GenBank accession # MK950847) is identical to those available on GenBank from several

individuals (GenBank JQ935845.1–JQ935849.1), further corroborating our identification.

## Discussion

The distribution of all 28 records of *Dajaus monticola* in Texas is provided in Figure 3. Of the 26 previously reported records, 18 were available for reexamination with 17 confirmed to be *D. monticola*. Only a single



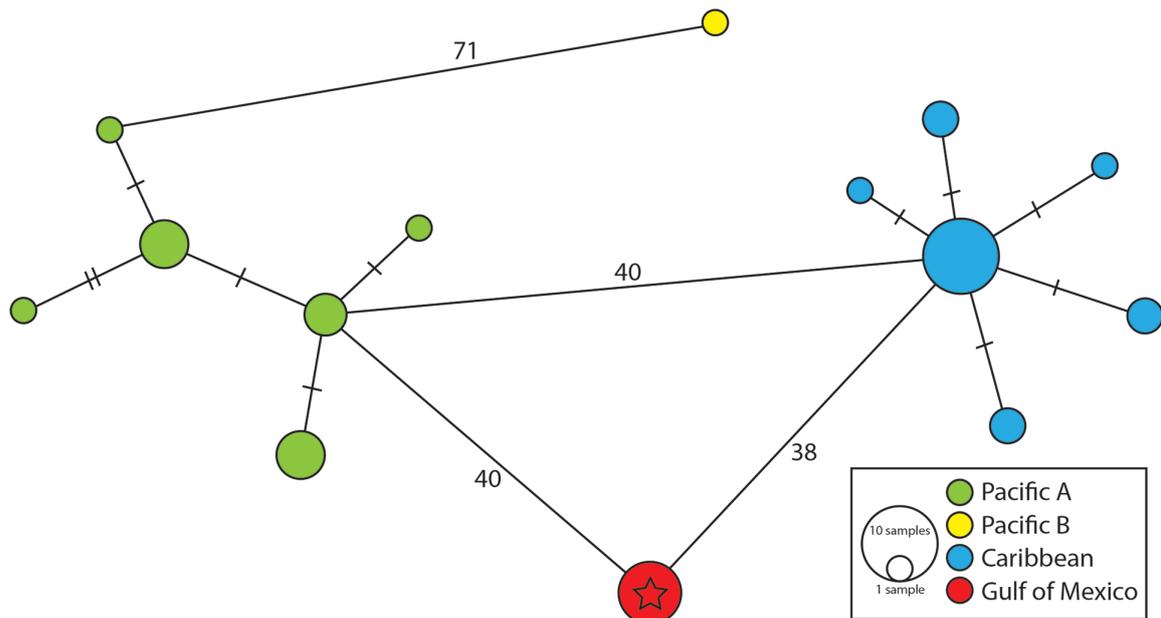
**Figure 3.** Localities of *Dajaus monticola* collected in Texas based on museum vouchered material in collections and from the literature (Pezold and Edwards 1993, Schlicht 1994). New localities indicated by stars. Verified localities indicated by black circles. Unverified localities indicated by open circles.

record (TCWC 14702.01) was misidentified and instead keyed out to *Mugil cephalus*. Four records, despite not being available for examination, were determined to be

correctly identified based on the detailed description of the specimens provided from the literature (Schlicht 1959, Pezold and Edwards 1983). The remaining 4 records were unavailable for examination and remain to be verified.

Including the 2 new records reported herein, there are 23 confirmed records of *D. monticola* in Texas. These records are represented by individuals ranging in size from smaller juveniles (28.9 mm SL; ANSP 186789) to adults (309.0 mm SL; TNHC 28665). Most of the reported collection events resulting in these specimens occurred inland in major rivers and their tributaries, with only 9 from coastal estuaries or the lower courses of rivers close to the delta. Of note, individuals were only collected upstream in 4 of the 7 major rivers that drain directly into the Gulf of Mexico: the Rio Grande, Guadalupe, Brazos, and Trinity rivers. The lowest barrier or impoundment on each of these rivers (Anzaluduas Dam, Rio Grande; Gonzalez Hydro Station, Guadalupe River; Lake Whitney Dam, Brazos River; Lake Livingston Dam, Trinity River) is located far upstream of the gulf, potentially allowing any juveniles of *D. monticola* that enter these rivers to migrate farther inland. This is supported by the collection localities of all previous records being downstream of these barriers except for 1 individual on the Trinity River which was collected in 1966, prior to the completion of Lake Livingston Dam in 1969.

The COI haplotype network recovered the same four discrete haplogroups (Fig. 4) that were found in previous studies (McMahan et al. 2013, Durand et al. 2017), each of which was separated by a substantial number of single nucleotide polymorphisms. The individual collected recently from the Brazos River (TCWC 20062.01) belongs to the Gulf of Mexico haplogroup and



**Figure 4.** Minimum spanning haplotype network of 38 COI sequences of *Dajaus monticola* (see Appendix). Circle sizes are proportional to haplotype frequencies. Nucleotide changes are indicated by thin bars/numbers on lines connecting haplotypes. Colours correspond to geographic location. Star indicates position of sequence obtained from TCWC 20062.01.

possessed the same haplotype as 5 individuals collected in the Río Guayalejo in Tamaulipas, Mexico (GenBank JQ935845.1–JQ935849.1). This finding is not surprising given that this haplogroup comprises individuals collected from a location that is geographically the closest to Texas within the dataset. A similar result was found for individuals collected on the western coast of Florida which, similar to Texas, has 26 known records (Matamoros et al. 2009). McMahan et al. (2013) determined that cytochrome b sequences obtained from individuals collected in Florida belonged to the Caribbean haplogroup and hypothesized that they were likely migrants from Cuba, an idea that had been suggested previously by Anderson (1957). This hypothesis would also account for the paucity of records from the remaining three U.S. Gulf Coast states, which are located between Texas and Florida and farther away from potential source populations in Mexico or the Caribbean (Louisiana,  $n = 6$ ; Mississippi,  $n = 4$ ; Alabama,  $n = 0$ ; Matamoros et al. 2009).

Taking into account the amphidromous life history of *D. monticola* and the relatively few specimens that have been collected from Gulf Coast rivers in Texas to date, it does appear likely that those collected in Texas are migrants that may have drifted northward from Mexican Gulf coast source populations by chance. The timing of collections may further support this as 16 of the 23 verified collections occurred between August and January, a time period offset by 3 months from the rainy season in Central America which typically occurs from May to October (Darnell 1962, Magaña et al. 1999). The spawning of *D. monticola* in Caribbean drainages has been reported to be seasonal (Cruz 1987, Phillip 1993, Aiken 1998) and often in association with increased levels of precipitation (Erdman 1972, Phillip 1993), though see Chicas (2001) and Matamoros et al. (2009) for reports of *D. monticola* possibly spawning year-round in some portions of the range. If populations along the Gulf Coast of Mexico also exhibit this pattern, it is likely that the individuals collected during this time, which range in size from 28.9–125.7 mm SL, were young of the year based on the growth rate suggested by Anderson (1957). Additionally, *D. monticola* has been collected only in 12 of the 61 years that have passed since the first specimen was collected from Texas in 1958. In all but three of these years, there were multiple collections reported (2–3) suggesting that there is a higher prevalence of *D. monticola* “drifters” during certain years which may increase the likelihood of collection. Although there is no evidence to suggest the occurrence of reproducing populations in Texas, juveniles of *D. monticola* that have entered rivers in Texas appear to be capable of surviving for an undetermined period of time, as multiple individuals over 100 mm SL have been collected. As such, it is important to continue to monitor the presence of *D. monticola* in Texas in order to gain a better understanding of their abundance and what role, if any, they play in the freshwater ichthyofaunal communities of Texas.

Distinguishing individuals of *D. monticola* from

individuals of the two other species of mullet (*Mugil cephalus* and *Mugil curema*) found in Texas coastal and freshwaters can be challenging due to their similarity in external morphology, particularly at smaller sizes (<45 mm SL) when diagnostic features may not be present (Thomson 1997). Currently there are 3 external morphological characters that are regularly used to distinguish between the 3 species: (1) shape of the lower jaw and presence of symphyseal knob; (2) presence of an adipose eyelid; and (3) presence of ctenoid scales. The presence and degree of development of the symphyseal knob is a common character used to distinguish between some genera of mugilids (Thomson 1997). The lower jaw of *D. monticola* is rounded in shape and lacks a symphyseal knob (Fig. 2A) while in species of *Mugil* the lower jaw is angled and a prominent symphyseal knob is present (Fig. 2B). This character was consistent in all examined individuals with the symphyseal knob visible in even the smallest individuals of *M. cephalus* (24.0 mm SL, TCWC 19717.19) and *M. curema* (22.0 mm SL, TCWC 19717.08) examined. Most members of Mugilidae are noted to have an adipose eyelid, a deposit of fatty tissue located anterior and posterior to the orbit that may cover a portion of the outer margin of the eye in some species (Thomson 1954). *Dajaus monticola* does not possess an adipose eyelid (Fig. 2C) whereas in species of *Mugil* an adipose eyelid is present (Fig. 2D). The adipose eyelid is obvious in individuals at approximately 42 mm SL in both *M. cephalus* and *M. curema* but was noticeable in some individuals as small as 38 mm SL. Ctenoid scales are present in many species of Mugilidae; however, in some species the scales do not become ctenoid until later developmental stages when larger body sizes are reached (Jacot 1920, Thomson 1954). Ctenoid scales are present in all 3 mugilid species in Texas; however, in species of *Mugil* they are cycloid initially and do not become ctenoid until they reach larger sizes (Jacot 1920). In *D. monticola* ctenoid scales were obvious in the smallest specimen examined (23.0 mm SL, TCWC 8875.01). Interestingly, in the scales of *M. curema*, ctenii begin to appear in individuals of about 43 mm SL while in *M. cephalus* they do not begin to form until a much larger size of approximately 110 mm SL. To our knowledge this difference in timing of the formation of ctenii between *M. cephalus* and *M. curema* has not been previously reported.

Based on this information, the most consistent character to use to distinguish individuals of *D. monticola* from individuals of *M. cephalus* and *M. curema* is the shape of the lower jaw and the presence of a symphyseal knob. If the specimen is smaller than about 42 mm SL, then the presence/absence of ctenoid scales can also be utilized reliably to confirm the identification as *D. monticola*. The presence/absence of ctenoid scales can still be useful for identifying *D. monticola* specimens up to approximately 110 mm SL; however, this should only be for specimens collected in localities where *M. curema* does not occur. The presence/absence of the adipose

eyelid can only be utilized to distinguish *D. monticola* from *M. cephalus* and *M. curema* in specimens larger than about 42 mm SL. Finally, individuals of *M. curema* and *M. cephalus* can be distinguished from each other between about 42 and 110 mm SL by the presence or absence of ctenoid scales, respectively. However, the validity of this character in populations of both of these species outside of Texas remains to be verified given that both *M. cephalus* and *M. curema* have previously been shown to consist of multiple distinct evolutionary lineages (Durand 2012, 2017), which may exhibit differences in scale characters. Given that these lineages were discovered only recently through the analysis of genetic data, a thorough morphological investigation between these lineages, particularly focusing on characters that change through ontogeny, like those shown herein, may help to resolve the current systematic confusion associated with this globally distributed family of morphologically conserved fishes.

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## Authors' Contributions

All authors participated in field work and wrote the manuscript; KMK and AKP identified specimens and prepared figures; KMK compiled information on characters.

## References

- Aiken KA (1998) Reproduction, diet and population structure of the Mountain Mullet, *Agonostomus monticola*, in Jamaica, West Indies. *Environmental Biology of Fishes* 53 (3): 347–352. <https://doi.org/10.1023/A:1007440424424>
- Anderson WW (1957) Larval forms of freshwater mullet (*Agonostomus monticola*) from the open ocean off the Bahamas and south Atlantic coast of the United States. *U.S. Fish and Wildlife Service, Fishery Bulletin* 57: 415–425.
- Bandelt HJ, Forster P, Röhl A (1999) Median-joining networks for inferring intraspecific phylogenies. *Molecular Biology and Evolution* 16 (1): 37–48. <https://doi.org/10.1093/oxfordjournals.molbev.a026036>
- Chicas FA (2001) Juvenile fish in a tidal pool, Terraba-Sierpe Forest Preserve, Puntarenas, Costa Rica. *Revista de Biología Tropical* 49: 307–314.
- Cruz GA (1987) Reproductive biology and feeding habits of Cuyamel, *Joturus pichardi* and Tepemechin, *Agonostomus monticola* (Pisces: Mugilidae) from Rio Platano, Mosquitia, Honduras. *Bulletin of Marine Science* 40 (1): 63–72.
- Darnell RM (1962) Fishes of the rio Tamesí and related coastal lagoons in east-central Mexico. *Publications of the Institute of Marine Sciences* 8: 299–365.
- Durand JD, Hubert N, Shen KN, Borsa P (2017) DNA barcoding Grey Mullet. *Reviews in Fish Biology and Fisheries* 27 (1): 233–243. <https://doi.org/10.1007/s11160-016-9457-7>
- Durand JD, Shen KN, Chen WJ, Jamandre BW, Blel H, Diop K, Nirchio N, Garcia de León FJ, Whitfield AK, Chang CW, Borsa P (2012) Systematics of the Grey Mullet (Teleostei: Mugiliformes: Mugilidae): molecular phylogenetic evidence challenges two centuries of morphology-based taxonomy. *Molecular Phylogenetics and Evolution* 64 (1): 73–92. <https://doi.org/10.1016/j.ympev.2012.03.006>
- Erdman DS (1972) *Inland Game Fishes of Puerto Rico*. Department of Agriculture, Commonwealth of Puerto Rico, San Juan, Puerto Rico, 96 pp.
- ESRI (2013) ArcMAP Desktop, Release 10.5. 1.
- Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology* 3 (5): 294–299.
- Fricke R, Eschmeyer WN, Fong JD (2019) Species by Family/Subfamily. <http://research.calacademy.org/research/ichthyology/catalog/SpeciesByFamily.asp>. Accessed on: 2019-03-02.
- Ghasemzadeh J, González-Castro M (2015) Morphology and morphometry based taxonomy of Mugilidae. In Crosetti D, Blaber S (Eds) *Biology, Ecology and Culture of Grey Mullet (Mugilidae)*. CRC Press, Florida, 10–30.
- Hendrickson DA, Cohen AE (2015) Fishes of Texas Project Database (version 2.0). <http://doi.org/10.17603/C3WC70>. Accessed on: 2019-02-28.
- Hubbs C, Edwards RJ, Garrett GP (2008) An annotated checklist of the freshwater fishes of Texas, with keys to identification of species. 2nd edition. Texas Academy of Science, Edinburg, 87 pp. <http://hdl.handle.net/2152/6290>
- Jacot AP (1920) Age, growth and scale characters of the mullets, *Mugil cephalus* and *Mugil curema*. *Transactions of the American Microscopical Society* 39 (3): 199–229. <https://www.jstor.org/stable/3221748>
- Katoh K, Standley DM (2013) MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* 30 (4): 772–780. <https://doi.org/10.1093/molbev/mst010>
- Kearse M, Moir R, Wilson A, Stones-Havas S, Cheung M, Sturrock S, Buxton S, Cooper A, Markowitz S, Duran C, Thierer T, Ashton B, Meintjes P, Drummond A (2012) Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* 28 (12): 1647–1649. <https://doi.org/10.1093/bioinformatics/bts199>
- Leigh JW, Bryant D (2015) popart: full-feature software for haplotype network construction. *Methods in Ecology and Evolution* 6 (9): 1110–1116. <https://doi.org/10.1111/2041-210X.12410>
- Loftus WF, Kushlan JA, Voorhees SA (1984) Status of the Mountain Mullet in southern Florida. *Florida Scientist* 47 (4): 256–263. <http://www.jstor.org/stable/24319847>
- Maddison WP, Maddison DR (2018) Mesquite: a Modular System for Evolutionary Analysis. Version 3.51 <http://www.mesquiteproject.org>
- Magaña V, Amador JA, Medina S (1999) The midsummer drought over Mexico and Central America. *Journal of Climate* 12 (6): 1577–1588. [https://doi.org/10.1175/1520-0442\(1999\)012<1577:TMDOM A>2.0.CO;2](https://doi.org/10.1175/1520-0442(1999)012<1577:TMDOM A>2.0.CO;2)
- Matamoros WA, Schaefer J, Mickle P, Arthurs W, Ikoma RJ, Ragsdale R (2009) First record of *Agonostomus monticola* (family: Mugilidae) in Mississippi freshwaters with notes of its distribution in the southern United States. *The Southeastern Naturalist* 8 (1): 175–179. <https://doi.org/10.1656/058.008.0116>
- McMahan CD, Davis MP, Domínguez-Domínguez O, García-de-León FJ, Doadrio I, Piller KR (2013) From the mountains to the sea: phylogeography and cryptic diversity within the Mountain Mullet, *Agonostomus monticola* (Teleostei: Mugilidae). *Journal of Biogeography* 40 (5): 894–904. <https://doi.org/10.1111/jbi.12036>

- Miller RR (2005) *Freshwater Fishes of Mexico*. University of Chicago Press, Chicago, xxvi + 490 pp.
- Pezold FL, Edwards RJ (1983) Additions to the Texas marine ichthyofauna, with notes on the Rio Grande estuary. *The Southwestern Naturalist* 28 (1): 102–105. <https://www.jstor.org/stable/3670603>
- Phillip, DAT (1993) Reproduction and feeding of the Mountain Mullet, *Agonostomus monticola*, in Trinidad, West Indies. *Environmental Biology of Fishes* 37: 47–55. <https://doi.org/10.1007/BF00000711>
- Schlicht FG (1959) First record of the Mountain Mullet, *Agonostomus monticola* (Bancroft), in Texas. *The Texas Journal of Sciences* 11: 181–182.
- Smith WE, Kwak TJ (2014) A capture–recapture model of amphidromous fish dispersal. *Journal of Fish Biology* 84 (4): 897–912. <https://doi.org/10.1111/jfb.12316>
- Suttikus RD (1956) First record of the Mountain Mullet, *Agonostomus monticola* (Bancroft), in Louisiana. *Proceedings of the Louisiana Academy of Sciences* 29: 43–46.
- Thomson JM (1954) The Mugilidae of Australia and adjacent seas. *Marine and Freshwater Research* 5 (1): 70–131. <https://doi.org/10.1071/MF9540070>
- Thomson JM (1997) The Mugilidae of the world. *Memoirs of the Queensland Museum* 41 (3): 457–562.

## Appendix

**Table A1.** GenBank accession numbers and locality information for 38 COI sequences available for *D. monticola*.

GenBank Accession #	Country	Water body	GenBank Accession #	Country	Water body
MK950847	USA	Brazos River	JQ935845.1	Mexico	Rio Guayalejo
JQ060398.1	Venezuela	La Trilla River	JQ935846.1	Mexico	Rio Guayalejo
FN545593.1	Cuba	Manglarito stream	JQ935847.1	Mexico	Rio Guayalejo
FN545594.1	Cuba	Manglarito stream	JQ935848.1	Mexico	Rio Guayalejo
JF911702.1	Venezuela	La Trilla River	JQ935849.1	Mexico	Rio Guayalejo
JQ060399.1	Venezuela	La Trilla River	JQ060395.1	Mexico	Rio Presidio
JQ060400.1	Honduras	Guanaja Isl.	JQ060396.1	El Salvador	Rio Jiboa
JQ060401.1	Panama	Rio Changuinola	JQ060397.1	El Salvador	Rio El Zonte
JQ060402.1	Guadeloupe	Bourceua	MG496129.1	Nicaragua	Rio Casares
MG496128.1	Nicaragua	Rio Grande de Matagalpa	MG496130.1	Nicaragua	Rio Brico
MG496133.1	Costa Rica	Rio Sixaola	MG496131.1	Costa Rica	Rio Salama Nuevo
MG936869.1	Panama	Rio Cascajal	MG936866.1	Panama	Rio Chiriqui Viejo
MG936870.1	Panama	Rio Cocle del Norte	MG936867.1	Panama	Rio Tuira
MG936872.1	Panama	Rio Cascajal	MG936868.1	Panama	Rio Charare, Rio Tuira
MG936873.1	Panama	Rio Azucar	MG936871.1	Panama	Rio Santa Maria
MG936876.1	Panama	Rio Acla	MG936874.1	Panama	Rio Cocle del sur
MG936877.1	Panama	Rio Changuinola	MG936875.1	Panama	Rio Tuira
MG496132.1	Costa Rica	Rio San Juan	MG936878.1	Panama	Rio Santa Maria
HQ131880.1	—	—	JQ060403.1	Mexico	Rio Presidio