Species Status Assessment Addendum for the Roundtail Chub (*Gila robusta*) in the Lower Colorado River Basin

Photo Credit: Randy Babb

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1.0 Introduction

1.1 Background

In 2003, the U.S. Fish and Wildlife Service (hereafter "we", "our") received a petition from the Center for Biological Diversity (CBD) requesting that we list both the headwater chub (*Gila nigra*) and a DPS of the roundtail chub (*Gila robusta*) in the Lower Colorado River basin as an endangered or threatened species under the Endangered Species Act of 1973, as amended (Act). After several subsequent 12-month findings, lawsuits, and court-orders, in 2022 we found that listing the Lower Colorado River roundtail chub DPS was not warranted (87 FR 19657). This finding was informed by a Species Status Assessment (SSA) (Service 2022, entire). As part of the SSA, we reviewed the taxonomy of the roundtail chub. There has been considerable uncertainty in the scientific literature regarding the taxonomy of *Gila* in the Lower Colorado River basin, specifically relationship between the roundtail chub, headwater chub, and Gila chub (*Gila intermedia*). The Gila chub has been listed as endangered with critical habitat sine 2002 (70 FR 66664). In our recent SSA, we reviewed information that indicated a lack of differentiation between the three species, although there was also contrary information as well. We concluded that that the available information did not support recognizing the Gila chub or headwater chub as distinct taxonomic entities and instead should be classified as roundtail chub. We noted this in our 12-month finding for the roundtail chub and issued an advanced notice of proposed rulemaking to delist the Gila under the justification that it was not a listable entity (87 FR 19657).

Since publication of that finding, additional research has published that continues to address the taxonomy of *Gila* in the Lower Colorado River basin. This addendum evaluates new science and information that has become available since the publication of our 2022 SSA (Service 2022, entire). For simplicity, we do not restate the contents of the 2022 SSA unless our assessment of the new information resulted in an update to our analysis or was necessary for understanding the new information. Comparing and contrasting the new information with our previous analysis will require familiarity with the content of the 2022 SSA. The information in this addendum, taken alongside the information in the 2022 SSA, together comprise our current, 2025, "Lower Colorado River Basin Roundtail Chub SSA".

1.2 Addendum Scope

Our 2022 SSA evaluated the biological status and future viability of the roundtail chub in the Lower Colorado River basin. Based on our interpretation of the taxonomic status of *Gila*, we included populations previously designated as Gila chub as part of the assessment for roundtail

chub. Thus, the current and future resiliency of populations that have been considered Gila chub is embedded in that assessment.

For this addendum, we focus specifically on the taxonomic information relevant to *Gila* in the Lower Colorado River basin. The basis for the delisting of Gila chub was based solely on taxonomy and whether it constituted a listable entity. Therefore, we will not be revisiting other aspects of the SSA, such as threats, current population status, or future resiliency of these populations. We will also not be reviewing recovery criteria and whether the Gila chub qualifies for delisting based on species recovery (Service 2015, entire).

2.0 Taxonomy of *Gila*

2.1 Taxonomy of *Gila* in the Lower Colorado River basin

The genus *Gila* was first described by Baird and Girard (1853a, pp. 368-369) within the family Cyprinidae, which is a diverse group of freshwater fishes often referred to as the carp or minnow family. Members of the genus *Gila* occur in basins throughout western North America and are commonly referred to as the chubs. There are 23 accepted species names under the genus *Gila* (Page et al. 2023, p. 70). Some of the first specimens used to define this genus were collected from the Colorado River basin (Baird and Girard 1853b, pp. 388-389) and one of the first species to be described was the roundtail chub (*Gila robusta*) (1853a, p. 369). Since then, a plethora of genus and species names have been applied to fishes in the Colorado River basin that are now recognized as *Gila*. Over time, many genus and species names have been synonymized (reviewed by Copus et al. 2018, pp. 3-6). There are seven nominal taxa in the Colorado River basin (*G. cypha*, *G. elegans*, *G. intermedia*, *G. jordani*, *G. nigra*, *G. robusta*, and *G. seminuda*) that together constitute the *G. robusta* species complex (Copus et al. 2018, p. 1). The term "*G. robusta* complex" has been applied to these species due their propensity to hybridize and the difficultly in delineating species boundaries (Gerber et al. 2001, p. 2028).

For a variety of hydrological, geological, biogeographical, ecological, evolutionary, and political factors, there has traditionally been a division between the Upper and Lower Colorado River basins, demarcated by the Glen Canyon Dam. This same division has also been applied to characterize fish faunas and the taxonomy of *Gila* in the Colorado River basin. Within the Lower Colorado River basin, there have been fifteen species names and seven genus names applied to fishes in the *G. robusta* complex (Copus et al. 2018, p. 5). These various names have been synonymized and currently only three valid species names are recognized for *Gila* in the Lower Colorado River basin (Copus et al. 2018, pp. 4-6; Page et al. 2023, p. 70). As noted, the roundtail chub was one of the first species described for the entire genus and the type specimen is believed to have been collected from the Zuni River in New Mexico (Copus et al. 2018, p. 3-

4), which is a tributary of the Little Colorado River and traditionally considered part of the Lower Colorado River basin. The roundtail chub has the widest distribution of any *Gila* and in the Lower Colorado River basin it is known from the Little Colorado, Bill Williams, and Gila River basins.

The Gila chub (*G. intermedia*) was first described as *Tigoma intermedia* by Girard (1856, p. 42) and underwent numerous taxonomic placements but was later treated as a subspecies of *G. robusta* (Miller 1945, p. 109). Rinne (1969, entire) recognized *G. intermedia* as a distinct species and described its range as a series of populations distributed in central and southern Arizona within the Gila River basin. The headwater chub (*G. nigra*) (Cope and Yarrow 1875, p, 663) had a similar taxonomic history, eventually becoming synonymized under *G. intermedia* (Rinne 1969, entire). Many authors accepted this synonymy until Minckley and DeMarais (2000, p. 254) resurrected the name *G. nigra* to apply to what they recognized as a distinct species previously classified as *G. robusta grahamii*. The moniker *G. nigra* has since applied to populations occupying tributaries of the Gila and Verde (itself a tributary of the Gila River) Rivers.

2.2 Taxonomic inference based on phenotypic data

Since the beginning of the formal Linnean taxonomic system, phenotype has been the primary tool used by taxonomists to delineate species. A phenotype is the physical traits expressed by an organism; taxonomists then use similarities in these traits to group individuals into species. Common characters used in ichthyology to delineate species include number of fin rays, number of gill rakers, body shape, mouth position, and scale patterns.

The original descriptions of *Gila* species were based on qualitative descriptions of phenotypes, including numerical counts of fin rays (Baird and Girard 1853a, p. 869; Baird and Girard 1853b, p. 389; Cope and Yarrow 1875, p. 663). There are no definitive, diagnostic characters that are unique among *G. robusta*, *G. intermedia*, and *G. nigra*. None of the three putative species co-occur in the same waterways, meaning at local scales they are allopatric (Minckley and DeMarais 2000; p. 251). However, the three species do not occupy geographically cohesive portions of the Lower Colorado River basin. The locations of populations classified as each species are disjunct across the basin, particularly for *G. intermdia* and *G. nigra*. In other words, the putative species boundaries do not correspond to cohesive geographic boundaries, such as subbasins. *G. intermedia* and *G. nigra* tend to occur in upper portions of a watershed; in fact, in some streams, populations of these species are separated from *G. robusta* by a waterfall alone (Marsh et al. 2017, p. 49). This has been hypothesized as a consequence of Pliocene variance events that resulted in morphologically similarly groups being isolated in different subbasins (Douglas et al. 1999, entire). There are also no differences in habitat associations among the

three species (Minckley and DeMarais 2000, p. 252) and environmental gradients are not highly correlated with morphological variation (Douglas et al. 1999, p. 243).

This geographic context is important for interpreting the disparate findings of studies that have investigated phenotypic differentiation among these three species. Minckley and DeMarais (2000, pp. 253-255) developed an identification key based on the means of meristic characters produced by other studies (Rinne 1976, entire; DeMarais 1986, entire; Douglas et al. 1999, entire), which has served as the basis for recognizing them as distinct entities. In their analysis, they grouped individuals by the purported species assignments prior to analyzing the data. Since no characters or counts of characters (e.g., lateral line scales, anal fin rays, dorsal fin rays, post-Weberian vertebrae) were diagnostic, they had to compare groups by the mean values due to the extensive overlap between specimens assigned to each species.

The prior grouping of individuals into the three putative species is important context, as other studies that have attempted to differentiate the three species on a rangewide-scale based on phenotypic characters have failed to do so. In other words, when *Gila* samples are compared without *a priori* assignment based on collection location or putative species assignment, biologists have been unable to identify three phenotypically discrete groups. Carter et al. (2018, entire) gathered data on a variety of morphological and meristic characters from *Gila* specimens in the Lower Colorado River basin and then used multivariate tests to determine whether they formed distinct groups. They found the three putative species displayed significant overlap in multivariate space. Although Carter et al. (2018, pp. 285-286) did identify three weakly supported phenotypic groupings, they constituted a mix of populations from each of the assumed species. They also performed a field test of the Minckley and DeMarais (2000) identification key using multiple independent observers: they reported a correct identification rate of 54 percent (Carter et al. 2018, p. 286). Based on the lack of phenotypic differentiation and inconsistency in presumed species keys, Carter et al. (2018, p. 289) concluded that there was not sufficient evidence that there are three distinct species of *Gila* in the Lower Colorado River basin.

Similar findings are echoed in other studies. Copus et al. (2018, pp. 12-15) found extensive overlap among phenotypic variables between the three species. Although they found the type specimens for the three species did differ, fresh specimens could not be reliably assigned to the presumed species based on phenotypic characters. Moran et al. (2017, pp. 307-309) also failed to reliably identify specimens based on the Minckley and DeMarais (2000) key and were unable to differentiate among the three species when comparing specimens across multivariate space. However, when they *a priori* grouped specimens by presumed species and ran multivariate tests designed to maximize differences between groups, they found more pronounced distinction among the three groups (Moran et al. 2017, pp. 310-311).

These various studies emphasize a similar theme: phenotypic overlap among *Gila* in the Lower Colorado River basin is extensive and the interpretation of phenotypic groupings depends on prior assignment of samples. In other words, when specimens are grouped according to putative species, differences are observed between these groups (e.g., Minckley and DeMarais 2000, entire; Moran et al. 2017, pp. 310-311). When specimens are compared irrespective of their presumed species assignment, phenotypic variation does not correspond to the three putative species groups (Carter et al. 2018, entire; Copus et al. 2018, pp. 12-15; Moran et al. 2017, pp. 307-309). This then creates a paradox, as the three species can only be differentiated phenotypically when specimens are assigned to one of those species. Such was noted by Page et al. (2017, pp. 458-459) in their review of the information related to *Gila* taxonomy in the Lower Colorado River basin. They concluded that the available phenotypic data do not indicate that populations within the Lower Colorado River basin *G. robusta* complex do not constitute more than one species.

2.3 Taxonomic inference based on genetic data

Over the past several decades, developments in molecular biology and genetics have facilitated the generation novel information critical to understanding the evolutionary history of biodiversity. *Gila* in the Lower Colorado River basin are no exception and several studies have used genetic information to investigate the relationships between these species.

The first studies were based analyses of allozyme (i.e., protein) markers and found that genetic divergence did not parallel morphological divergence between *G. robusta* and *G. intermedia* (DeMarais 1992, pp. 131-151). There was higher genetic differentiation between populations of *G. intermedia* than between it and *G. robusta*. Sequencing of mitochondrial haplotypes (i.e., sequences of DNA with the mitochondria of a cell) found that no haplotypes were unique to any of the three species and failed to recover any distinct clades that corresponded to *G. nigra* or *G. intermedia* (Schwemm 2006, entire). In fact, the partitioning of genetic variation was more pronounced among populations of *Gila* in the Lower Colorado River than among the three putative species (Schwemm 2006, p. 19). Phylogenetic analysis of mitochondrial and nuclear DNA sequences of *Gila* species across western North America found that *G. robusta*, *G. nigra*, and *G. intermedia* formed a single phylogenetic clade (Schönhuth et al. 2014, pp. 215-217). The same analysis found no support for either three of the species (*G. robusta*, *G. nigra*, and *G. intermedia*) to form a distinct species group on its own (Schönhuth et al. 2014, p. 219).

Analysis of nuclear microsatellite DNA further replicated these findings, failing to identify distinct genetic groups that corresponded to the three species (Dowling et al. 2015, pp. 12-14). Again, they found genetic differentiation was more pronounced between populations than the putative species (Dowling et al. 2015, p. 9). Marsh et al. (2017, entire) were able to differentiate

between populations of *G. robusta* and *G. nigra* in Fossil Creek, Arizona, using microsatellite markers. However, the scale of the study was restricted to a single stream and compared *Gila* that occurred above and below a waterfall. The differences they observed could have reflected population-level differentiation and too limited to make taxonomic-level inferences.

A recent suite of studies that have sequenced large portions of the nuclear genome provide contrasting insights into taxonomic relationships. These studies have used high-throughput DNA sequencing to generate thousands of variable markers across the genome. The first was Copus et al. (2018, entire), who also generated mitochondrial DNA sequences to accompany the nuclear DNA analysis. Regardless of marker type, they failed to recover any distinct clades that corresponded to the three species in their phylogenetic analyses. Instead, they found that the clades they did observe grouped populations by watershed (Copus et al. 2018, pp. 15-17).

Chafin et al. (2021, entire) also generated thousands of nuclear DNA markers and tested several hypotheses regarding the evolution of *Gila* in the Colorado River basin, with an emphasis on populations in the lower basin. They found three distinct genetic clades in the lower basin that generally corresponded to the three putative species. Populations assigned to same species fell within the same phylogenetic clade. However, statistical support for these three clades was low relative to the clades formed by other *Gila* species. In other words, there was not strong statistical support that the three species represented distinct monophyletic groups. Their conclusion was that the three species rapidly diversified following their initial divergence, resulting in incomplete lineage sorting that masked the underlying differentiation between them (Chafin et al. 2021, pp. 8-12).

The latest study generated a draft genome for *G. robusta* and aligned DNA sequences generated from *Gila* samples collected across the Lower Colorado River basin to identify variable markers (Suchocki et al. 2023, entire). Like Copus et al. (2018), they found that the putative species did not form distinct genetic groups: instead, populations had closer genetic affinity those inhabiting the same watershed (Suchocki et al. 2023, pp. 4-5). Patterns of genetic variation were better explain by watersheds, not species groups (Suchocki et al. 2023, p. 3). They also tested different analytical approaches, examining genetic variation when samples were initially group by *a priori* species assignment compared to not. As with the phenotypic studies (e.g., Moran et al. 2017, entire), when they performed analyses that maximized differences between groups, they were able to recover the three putative species (Suchocki et al. 2023, pp. 6-7). They concluded that the species are only recoverable when the geographical context (i.e., initial species assignment of populations) is used in the analysis. Blinded sampling (i.e., no initial assignment) fails to recover the three species and reveals patterns of genetic differentiation correspond to watershed opposed to purported taxonomy (Suchocki et al. 2023, p. 9).

3.0 Synthesis

As noted by nearly all researchers investigating the systematics of *Gila* species, the taxonomic situation is complicated and problematic (Holden and Stalnaker 1970, pp. 418-419; Minckley 1973, pp. 102-103; Minckley and DeMarais 2000, p. 251; Gerber et al. 2001, p. 2028; Schönhuth *et al*. 2014, p. 210 ; Copus *et al.* 2018, p. 2; Chafin *et al.* 2021, p. 7) and ongoing genetic and morphologic analyses of chubs in the Gila River basin continue to yield conflicting results (Page et al. 2017, entire; Copus *et al.* 2018, entire; Chafin *et al.* 2021, entire; Suckocki et al. 2023, entire). There are several conclusions that can be drawn based on the available evidence. First, there are no clear diagnostic phenotypic or genetic characters that distinguish between the three species. Second, the species can only be differentiated from each other when specimens are grouped into putative species assignments (Moran et al. 2017, pp. 310-311; Suchocki et al. 2023, p. 9). Accurate taxonomic assignment of specimens is therefore dependent on knowledge regarding the location of collection. Third, much of the genetic variation observed among Lower Colorado River basin *Gila* is partitioned by watershed (Schwemm 2006, p. 19; Dowling et al. 2015, p. 9; Suckocki et al. 2023, pp. 3). Populations within the same subbasin are more similar to each other than populations that occur outside that basin, meaning genetic differences are more tied to geography than nominal taxonomy. These findings indicate that at best, the differences between the three *Gila* species are subtle and not readily apparent to even skilled observers (e.g., Carter et al. 2018, entire). Multiple studies have shown that patterns of variation, whether phenotypic or genetic, do not fit into the three species model proposed by Minckley and DeMarais (2000, entire).

A variety of hypotheses have been proposed to explain the disparities between the observed patterns of phenotypic and genetic variation and the proposed three species taxonomy. Two of the most cited are incomplete lineage sorting and hybridization. Incomplete lineage sorting occurs when gene trees (i.e., sequences in the genome) have not yet diverged to mirror the true species trees (Chafin et al. 2021, p. 8). Often cited when patterns observed with genetic data do not match purported taxonomic relationships, incomplete lineage sorting cannot explain the inherent lack of differentiation among the three *Gila* species and lack of diagnostic characters. Also, the SVDQuartets method used by Chafin et al. (2021, p. 13) that recovered low statistical support for the three clades is robust to incomplete lineage sorting. Hybridization has been proposed as a mechanism to explain the similarity of populations among the three species (Minckley and DeMarais 2000, p. 253; Dowling et al. 2015, p. 15). However, genomic data have failed to identify signals of past hybridization among the three Lower Colorado River basin *Gila* species (Copus et al. 2017, p. 15-16; Chafin et al. 2021, p. 5). Patterns of morphological variation are also not correlated with natural in-stream barriers, which is a proxy for hybridization potential (Douglas et al. 1999, p. 243). Other hypotheses proposed include inadequate and/or biased sampling, as well as disagreements over methodology (Carter et al.

2018, p. 289; Chafin et al. 2021, p. 12; Suchocki et al. 2023, pp. 9-10). All of these hypotheses are meant to explain the discrepancy between the observed data and the proposed taxonomy, when a simpler hypothesis is that the proposed three species taxonomy does not reflect the real underlying evolutionary and genetic relationships of *Gila* in the Lower Colorado River basin.

To this point, in 2015 the Arizona Game and Fish Department asked the American Fisheries Society and American Society of Ichthyology and Herpetology Joint Committee on the Names of Fishes (AFS/ASIH) to review the taxonomic status of the *G. robusta* complex in the Lower Colorado River basin. In 2017, the AFS/ASIH published a joint report on the taxonomy of *Gila* in the Lower Colorado River basin (Page et al. 2017, entire). They concluded that the available evidence did not support species-level status for *G. nigra* and *G. intermedia* and they collapsed the three into *G. robusta*, recognizing only a single species (Page et al. 2017, p. 459). Recently, the AFS/ASIH published the latest edition of the accepted scientific names of North American fishes. They list *G. intermedia* and *G. nigra* as valid scientific names, while noting the taxonomic uncertainty of the *G. robusta* complex (Page et al. 2023, pp. 70, 224). However, inclusion of *G. intermedia* and *G. nigra* on this list reflects that the names themselves are considered valid according to taxonomic convention, not that the species themselves are valid entities.

The taxonomy of *Gila* in the Lower Colorado River basin has been in a state of flux since the first species were described (Copus et al. 2018, pp. 1-6) and will likely continue to change in the future. At this point, the available evidence does not indicate that the Gila and headwater chub are distinct taxonomic entities. Minckley and DeMarais (2000, entire) defined these two species based on a particular analysis of phenotypic data. Subsequent studies have failed to recover these two species using alternative analyses and could not even successfully assign individuals collected in the field to the supposed correct species using the Minckley and DeMarais taxonomic key (Moran et al. 2017, entire; Carter et al. 2018, entire). Genetic studies have also failed to identify three distinct entities (Schwemm 2006, entire; Dowling et al. 2015, entire; Copus et al. 2018, entire; Suchocki et al. 2023, entire), except for analyses that intentionally group populations into purported species assignments (Chafin et al. 2021, entire; Suchocki et al. 2023, pp. 6-7). In conclusion, *G. intermedia* (Gila chub) and *G. nigra* (headwater chub) are not valid taxonomic entities and populations previously assigned to those two species should be reclassified as *G. robusta* (roundtail chub).

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