Zootaxa 5249 (5): 501–539
https://www.mapress.com/zt/

Article

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

https://doi.org/10.11646/zootaxa.5249.5.1
http://zoobank.org/urn:lsid:zoobank.org:pub:F146B808-9D5B-477F-9E73-09A8DFDBFA31

Taxonomy of the Speckled Dace Species Complex (Cypriniformes: Leuciscidae, *Rhinichthys*) in California, USA

PETER B. MOYLE[1*], NICHOLAS BUCKMASTER[2] & YINGXIN SU[3]
[1]*Center for Watershed Sciences & Department of Wildlife, Fish and Conservation Biology, University of California, 425 LaRue Road, Davis CA 95626 USA .*
[2]*California Department of Fish & Wildlife,787 Main Street, Bishop, CA 93514 USA. Nick.buckmaster@wildlife.ca.gov*
[3]*Department of Animal Science, University of California, Davis, 1 Shields Avenue, Davis CA 95616 USA. syxsu@ucdavis.edu*
[*]*Corresponding author. pbmoyle@ucdavis.edu; https://orcid.org/0000-0002-4825-4865*

Abstract

The Speckled Dace, *Rhinichthys osculus* (Girard), is a small species of fish (Cypriniformes, Leuciscidae) that has the widest geographic range of any freshwater dispersing fish in western North America. The dynamic geologic history of the region has produced many isolated watersheds with endemic fish species. However, Speckled Dace from these watersheds cannot be differentiated readily by morphometrics and meristics. This has led to the widely accepted hypothesis that the dace's adaptability and ability to cross geologic barriers has resulted in interbreeding among neighboring populations, maintaining the dace as a single species. We investigate this hypothesis by looking at Speckled Dace populations in California which are the result of at least three separate colonization events of isolated watersheds. We synthesize results from taxonomic, genetic, and zoogeographic studies in combination with the findings of a recent genomics study, to show that there are distinctive evolutionary lineages within the Speckled Dace complex. These lineages are used to designate multiple species and subspecies. We back up these designations by examining how well these lineages fit with the geologic history of the isolated basins they inhabit and with the presence of other endemic fishes. We conclude the following nine taxa can be recognized within the Speckled Dace complex in California.

Santa Ana Speckled Dace, *Rhinichthys gabrielino* new species
Desert Speckled Dace, *Rhinichthys nevadensis* (Gilbert) new combination
    Lahontan Speckled Dace, *R. nevadensis robustus (*Gilbert) new combination
    Amargosa Speckled Dace, *Rhinichthys nevadensis nevadensis (*Gilbert)
    Long Valley Speckled Dace, *R. nevadensis caldera* new subspecies
Western Speckled Dace, *Rhinichthys klamathensis* (Evermann and Meek)
    Klamath Speckled Dace, *R. klamathensis klamathensis* new combination
    Sacramento Speckled Dace, *R. klamathensis achomawi* new subspecies
    Warner Speckled Dace, *R. klamathensis goyatoka* new subspecies

Key words: cryptic species, genomics, Great Basin fishes, endangered species, desert fishes

Introduction

The Speckled Dace, *Rhinichthys osculus*, as recognized today, is a single species of small fish in the family Leuciscidae. The Leuciscidae (order Cypriniformes) was formerly a subfamily within the family Cyprinidae which is now a separate family in the suborder Cyprinoidei, to which the Leuciscidae also belongs (Stout *et al.* 2016; Tan & Armbuster 2018). Species which comprise the Leuciscidae are widely distributed in North America and Eurasia (Yang *et al.* 2015, Schönhuth *et al.* 2018).

The Speckled Dace is purported to have the widest geographic range of any freshwater dispersing fish in western North America. It inhabits streams, rivers, springs, lakes, and other freshwater habitats, from northern Mexico and southern California through the Great Basin and southwestern Canada (Moyle 2002, Wydoski and Whitney 2003, Smith *et al.* 2002, 2017). Much of their range encompasses the arid Great Basin, where many isolated populations

Accepted by J. Armbruster: 1 Feb. 2023; published: 6 Mar. 2023

exist. Populations are found in diverse habitats, including warm outflows and pools of desert springs, large rivers, and cold lakes. Most inhabit small to medium-sized streams. The morphology is variable (within limits) and the variability tends to be more related to habitat than to evolution in isolation. Thus, narrow caudal peduncles and large pectoral fins are found on fish in fast-moving streams and while thick caudal peduncles and smaller fins are found in quiet-water populations (Sada *et al.* 1995, Smith *et al.* 2002, 2017, Page and Burr 2011). Regardless, most forms are clearly recognizable as Speckled Dace (Figure 1).

The taxon apparently diverged from an ancestral population in the upper Columbia Basin about 6.3 million years ago (Smith and Dowling 2008, Smith *et al.* 2017). About 3.6 million years ago, there was a major split into two clades, a northwest clade, that included the Columbia and California regions, and a Colorado clade (Smith and Dowling 2008). Dace subsequently followed connections among major drainage systems west of the Rocky Mountains or were carried to distant locales via tectonics (geologic plates), to become distributed throughout western North America; they arrived in Los Angeles area streams about 1.9 million years ago (Smith and Dowling 2008). The southern ends of these distributional pathways are mostly in California, which is edged by the Pacific Ocean. Speckled Dace arrived in California by three known pathways: the Colorado Basin (to the Los Angeles region), the Lahontan basin (to the eastern Sierras and to the Amargosa basin), and the northern Great Basin (via the ancestral Snake River). The latter led to colonization of the Klamath and Sacramento river systems, as well as the Warner Basin (Oakey *et al.* 2004). Given the apparent independent evolutionary history of Speckled Dace in each of the diverse geologic basins it inhabits, it is not surprising that multiple species or subspecies have been described from western North America (Table 1). Most are now subsumed under *R. osculus* because of the lack of meristic and morphometrc distinctiveness (Smith *et al.* 2002).

Moyle (2002) and Moyle *et al.* (2015) list seven dace taxa as present in California, all considered to be subspecies of *R. osculus* although five are not formally described. A recent genome-based analysis (Su *et al.* 2022) shows that there are three lineages of dace in California that can be recognized as distinct population segments; these lineages are more or less in concordance with lineages described in Oakey *et al.* (2004). Formal recognition is important because species/subspecies that lack scientific names are much less likely to be the focus of conservation actions under federal and state Endangered Species Acts. This is especially true if the lineages are regarded as just populations of one widely distributed species. The purpose of this study is to examine the taxonomy of Speckled Dace in California and to describe the three species (one new, two elevated to species level) and six subspecies (three new) that we found to be present. To do this, we (a) discuss the history of Speckled Dace taxonomy in California, (b) describe how we determined species and subspecies, (c) summarize the new genomic findings (Su *et al.* 2022) that supports the revised taxonomy in this study and (d) present a revision of the taxonomy of dace populations in California. We focus on California because it is an immense state with diverse habitats that have been the end point of colonization events as dace spread slowly from their presumptive ancestral home in the Columbia River basin. By and large, the geographic boundaries of the state coincide with physical boundaries (mountain ranges, ocean, deserts) so it can be treated as a natural, as well as a political, geographic entity. Most freshwater fishes native to the state are endemic to it (Moyle 2002). It is also a place of intense competition between native fish and people for water, so dace and other small fishes are constantly under threat of extinction (Moyle 2002, Moyle *et al.* 2011, 2015). Giving recognition to scattered but isolated forms will help to assure their preservation, as well as the preservation of the distinctive habitats in which they live.

Taxonomic History

Speckled Dace are fairly easy to recognize as small (adult length typically 5–8 cm), active cyprinoid fishes that have bluntly pointed snouts, tiny subterminal mouths, small eyes (relative to head size), fine scales, and thick caudal peduncles (Figure 1). Tiny, barely visible, maxillary barbels and a frenum on the upper jaw occur to varying degrees. Coloring is highly variable, but most individuals have lateral spotting and/or blotching on the body, often coalescing into a vague lateral band. The band usually becomes a black stripe on the head, running below or through the eye and over the snout (Moyle 2002).

Despite commonality of appearance across its vast range, the Speckled Dace is best referred to as the Speckled Dace complex, which is made up of multiple species and subspecies. One underlying reason for this is that these fishes occur in watersheds that have been isolated for long periods of time, sometimes millions of years, and that support other endemic species, including fishes. This is especially true in California (Moyle 2002, Harrison 2013). Except in waters that also support anadromous fishes, Speckled Dace are often the only non-endemic native fish species listed for these watersheds. Smith *et al.* (2002, 2017) explain this phenomenon as the result of the dace's ability to colonize areas through headwater stream capture or similar routes not available to larger, less active fishes. If dace already occupy an invaded watershed, then a hybrid population emerges. Multiple events like this result in 'reticulate evolution' which presumably keeps populations from diverging at the species level. This process is assumed to prevent development of distinctive characteristics in dace populations, especially morphometric characters, even though the populations are currently isolated and may have been so for long periods of time (Smith *et al.* 2017, Bangs *et al.* 2020.

FIGURE 1. Top: Lahontan Speckled Dace (*ca.* 70 mm TL) and cover habitat in Taylor Creek, California, a tributary to Lake Tahoe. The body shape, stripe on head, and speckling are characteristic of live fish in many populations from Mexico to Canada that have been considered to be just one species, Speckled Dace (*Rhinichthys osculus*). Photo by T. L. Taylor, July 17, 1991. Bottom: Preserved specimen of Sacramento Speckled Dace, collected by John Otterbein Snyder from Alameda Creek, California in 1898, showing basic external anatomy. Note the presence of tiny maxillary barbels on head, an example of a distinctive characteristic of some populations. Photo by Jon Fong, California Academy of Sciences, of specimen SU 16172.

Evidence supporting reticulate evolution of Speckled Dace is mainly that morphologically distinct species have not developed in most areas based on the combined fossil record, morphometric and meristic analyses, zoogeography, and mtDNA analyses (Smith *et al.* 2002, 2017). However, this has not prevented many subspecies from being recognized, usually because each subspecies occupies a distinct, often small, geographic region where isolation is assumed to prevent gene flow with other populations under current conditions. The subspecies often show adaptations to habitats in their particular region (*e.g.*, large pectoral fins, narrow caudal peduncles in fast moving streams) which may or may not distinguish them from other subspecies that live in similar habitats.

The ichthyologists who first described the fish fauna of the American West often encountered fish in their samples that reminded them of members of the genus *Rhinichthys*, which are widespread and well-known in the eastern USA. If the biologists were collecting fishes from an unexplored area, they often described 'dace' they encountered as new species although usually not as a *Rhinichthys* species (*e.g.*, Girard 1856, 1858, Cope 1872, Cope and Yarrow 1875, Evermann and Meek 1898). Jordan and Evermann (1896) list 10 species of Speckled Dace-like fish, all placed in the genus *Agosia.* The species were recognized despite having overlapping morphometric and meristic characteristics.

Thus, at least 20 species in the dace complex were described in 1856–1904 (Table 1). Four are still recognized as separate species: *R. umatilla* and *R. falcatus* from the Columbia River, *R. osculus* [*sensu lato]*, and *Agosia chrysogaster* from the Gila River, Arizona. Eight are regarded as invalid (synonymized with other names), and six are now subspecies of *R. osculus.* An additional eight subspecies were described in the period 1937–84, mostly small populations from spring systems.

The fish now known as Speckled Dace was first described by Charles Girard (1856) as *Argyreus osculus*, from the Babocomari River, a tributary to the San Pedro River in Arizona (Table 1). Girard described two other species of *Argyreus* in the same paper including *A. nubilus* from Puget Sound, Washington, which became a default species epithet for dace in the Columbia Basin. Jordan and Evermann (1896) regarded the species of *Argyreus* as belonging to either *Rhinichthys* or *Agosia*. Girard also described *Agosia chryosgaster* which is currently the only valid species of *Agosia* (Page *et al.* 2013). *Agosia oscula* became the scientific name for the widespread 'Speckled Dace' and the species name for all subspecies because it was the first species to be described by Girard (1856). Jordan and Evermann's (1896) description of the genus *Agosia* noted that "This genus differs from *Rhinichthys* only in having the premaxillaries protractile. Even this character shows a disposition to disappear by degrees... (p.308)."

The placement of *Agosia oscula* in the genus *Rhinichthys* was the result of an informal consensus of fish biologists throughout western North America, perhaps because of the high esteem in which ichthyologists Carl Hubbs and Robert Miller were held; they had collected dace from many remote areas. *Rhinichthys* seems to have been first applied to Speckled Dace in California by Murphy (1941) and then by Hubbs and Miller (1948a, b), both without formal analysis. Hubbs and Miller (1948a) do mention in a footnote that "The forms of *Rhinichthys* (subgenus *Apocope*) in the West exhibit so much overlapping in their characters that most of the nominal species are now regarded as comprising a single, wide-ranging species, *R. osculus* (Girard)." This footnote lumping all Speckled Dace taxa was widely accepted, apparently without question. The name then spread to all subsequent citations (Woodman 1992). Hubbs *et al.* (1974:97) confirmed this application of the name, "stating that *Rhinichthys* seems to be the best resting place for this western group, in the present confusion of the generic recognition of American cyprinids that appears to approach potential chaos."

The switch from classifying the different regional dace taxa as full species within *Rhinichthys* to being subspecies seems to have occurred in the same general period, also without formal discussion. Evermann and Clark (1931) listed three species of dace from California, *Apocope robusta*, *A. carringtoni*, and *A. klamathensis.* Murphy (1941) listed only *R. oscula* from the Central Valley. Hubbs and Miller (1948b) used subspecies names under *R. osculus*. The two described subspecies were *R. o. robustus* and *R. o. klamathensis.* Shapovalov and Dill (1959) listed four subspecies for California (*R. o. robustus*, *R. o. klamathensis*, *R. o. nevadensis*, and *R. o. carringtoni*). Hubbs *et al.* (1974) considered all described forms to be subspecies. The 1960 version of the official American Fisheries Society list of common and scientific names of North American fishes recognized only *R. osculus* for all the diverse forms, as did the five subsequent editions. Moyle (1976) and Shapovalov *et al.* (1981) recognized the one species with just three subspecies for California (*R. o. klamathensis*, *R. o. nevadensis*, and *R. o. robustus.)*; they dropped *R. o. carringtoni* from the list because this dace was described from Utah and the name was improperly applied to fish from California. Hubbs *et al.* (1979) in their California fish list, also excluded *R. o. carringtoni* but added the Santa Ana Speckled Dace as an undescribed subspecies. Moyle and Davis (2000) listed the three named subspecies but included four additional subspecies without formal epithets: Sacramento, Santa Ana, Owens Valley, and Long Valley Speckled Dace, an arrangement repeated in Moyle (2002).

TABLE 1. Speckled Dace taxa that have been formally described (1856–1984) and that mostly have some connection to Speckled Dace taxa in California (e.g., shared watershed, shared name) or are important in the current Speckled Dace hierarchy. Not included are most subspecies listed in Smith *et al.* (2017) from Columbia, Colorado, and Bonneville basins, mostly undescribed. The current (2022) status column represents the opinion of the authors and applies to the species or subspecies epithet and not to the genus name. Under Smith *et al.* (2017), all valid taxa are subspecies of *R. osculus,* except *R. umatilla* and *R. falcata* which are full species. J&E stands for Jordan and Evermann (1896) who made the first revision of Speckled Dace taxonomy and invalidated some species by synonymizing them with *A. oscula* or *A. nubilis*.

Name	year	Describer	Location	J&E 1896	Current status[1]
Argyreus osculus	1856	Girard	Gila River	*Apocope oscula*	*Rhinichthys osculus*
Argyreus nubilus	1856	Girard	Puget Sound	*Agosia nubila*	*R.o. nubilus*
Argyreus notabilis	1856	Girard	Sonora, Mexico	invalid	invalid
Agosia chrysogaster	1856	Girard	Sonora, Mexico	full species	*Agosia chrysogaster*[2]
Rhinichthys maxillosus	1864	Cope	Utah	invalid	invalid
Apocope carringtonii	1872	Cope	Utah	*Agosia nubila carringtoni*	invalid for CA
Apocope vulnerata	1872	Cope	Utah	invalid	invalid
Tigoma rhinichthyoides	1872	Cope	Utah	invalid	invalid
Apocope henshavii	1874[3]	Cope	Utah	invalid	invalid
Apocope couseii	1874	Yarrow	Colorado Basin,	*Agosia couseii*	invalid
Certatichthys ventricosa	1874	Cope	Utah	invalid	invalid
Agosia novemradiata	1883	Cope	Utah	invalid	invalid
Agosia yarrowi	1889	J & E	Colorado Basin	*Agosia yarrowi*	*R. o. yarrowi*
Agosia adobe	1889	J & E	Utah	*Agosia adobe*	*R. o. adobe*
Rhinichthys (Apocope) nevadensis	1893	Gilbert	Ash Meadows NV	_	*R. o. nevadensis*
Rhinichthys (Apocope) velifer	1893	Gilbert	Pahranagat Valley NV.	_	*R. o. velifer*
Agosia umatilla	1894	Gilbert & Evermann	Idaho Columbia River	_	*R. umatilla*
Agosia falcata	1893	Eigenmann & Eigenmann	Idaho, Columbia R	_	*R. falcatus*
Agosia klamathensis	1898	Evermann and Meek	Klamath Lakes	_	*R. o. klamathensis*
Agosia falcata	1903	Rutter	Lahontan Basin	--	*R. o. robustus*
Rhinichthys o. thermalis	1937	Hubbs and Kuhne	Wyoming	_	*R. o. thermalis*
R. o. oligoporus	1972	Hubbs & Miller	Clover Valley NV	_	*R. o. oligoporus*
R. o. lethoporus	1972	Hubbs & Miller	Independence Valley NV	_	*R. o. lethoporus*
R. o. reliquus	1972	Hubbs & Miller	Lander Co. NV	_	*R. o. reliquus*
R. o. lariversi	1974	Hubbs *et al.*	Big Smoky Valley NV Lander Co.	_	*R. o. lariversi*
R. o. moapae	1978	Williams	Clark Co. NV	--	*R. o. moapae*
Rhinichthys deaconi	1984	Miller	NV (Las Vegas)	_	Extinct *R. deaconi*

---

[1] As of 2021. Both the switch to *Rhinichthys* as the Speckled Dace genus and the switch to using subspecies, rather than species names, took place in the late 1940s and 1950s. See text for discussion.

[2] See Woodman (1992) for reasons why this species should probably be *Rhinichthys chrysogaster.*

[3] Cope's species were all synonymized into *Agosia nubila carringtoni* by Jordan and Evermann (1896)

La Rivers and Trelease (1952) recognized four subspecies of dace in Nevada, all under *R. nubilis*, including *R. n. robustus* and *R. n. nevadensis*. The reason for using *nubilis* as the specific epithet is not clear but the species was described in the same publication as *A. osculus* by Charles Girard (1856). Deacon and Williams (1984) updated the Nevada list to include 15 subspecies of *R. osculus*, plus one undescribed species (now *R. deaconi*, the extinct Las Vegas dace). The subspecies included six undescribed forms and four named forms that occur mainly in isolated spring systems in the Lahontan Basin. Subspecies with broad distributions were *R. o. carringtoni* (Snake River Speckled Dace), *R. o. robustus* (Lahontan Speckled Dace), *R. o. yarrowi* (Colorado River Speckled Dace), *R. o. velifer* (Pahranagat Speckled Dace) and *R. o. nevadensis* (Amargosa Speckled Dace). Of these five taxa, only Lahontan Speckled Dace and Amargosa Speckled Dace occur in California. Similarly, Sada and Vinyard (2002) listed 16 subspecies for the Great Basin alone, 11of them undescribed.

Smith *et al.* (2017) listed 16 named subspecies of Speckled Dace and four undescribed subspecies from throughout the range of *R. osculus*. Just four (*R. o. robustus*, *R. o. pitensis*, *R. o. klamathensis* and *R. o. nevadensis)* occur in California but *R. o. carringtoni* is mentioned as occurring in northern California as well as in the Snake River and Bonneville basins. An additional six populations, while presumptive subspecies, do not have subspecies status indicated. Smith *et al.* (2017) did not find a relationship between morphology (31 characters analyzed) and mtDNA haplotypes, so they concluded that *Rhinichthys* populations had not diverged sufficiently in isolation to be labelled as species but could still be labelled as subspecies even without a formal description. For further discussion of the taxonomic issues as related to non-California populations see Minckley and Marsh (2009).

Because of the above complexities, most citations in the recent (since ca. 1950) non-taxonomic literature on Speckled Dace biology refer to it only as *Rhinichthys osculus.* In the list of synonymies in the new taxa accounts in this paper, only citations with taxonomic or historical significance are used.

Designation of species and subspecies

For this study we started with the accepted designation of the Speckled Dace as a single species throughout its wide range (Smith *et al.* 2017) but with the expectation that it was in fact a complex array of species and subspecies. We then looked for evidence that there were lineages within the species that might be distinct enough to qualify as separate species, using the Evolutionary Species Concept. This concept says, roughly, that a species is a discrete (separately evolving) lineage with a long evolutionary history that is independent of that of similar species. Essentially, a species consists of interbreeding individuals that do not breed outside the group and consequently maintain a distinct evolutionary identity through time and space. In the Speckled Dace complex, species and subspecies identity is maintained through geographic isolation. It is assumed by Smith *et al.* (2017) that dace from different isolated populations can interbreed if brought together and headwater connections of adjacent stream systems allow such interbreeding to take place. However, evidence of interbreeding is scant. Nevertheless, Freudenstein *et al.* (2017) argue that a flexible approach to taxonomy is needed in a situation in which there are cryptic species, such as those found within the Speckled Dace complex

The utility of subspecies is discussed in Taylor *et al.* (2017:17) who also provide a definition: “A *subspecies* is a population, or collection of populations, that *appears to be* a separately evolving lineage with discontinuities resulting from geography, ecological specialization, or other forces that restrict gene flow to the point that the population or collection of populations is diagnosably distinct. This definition encompasses some of the uncertainty when it comes to separating species from subspecies. Species *are* separately evolving lineages while subspecies *appear to be*.” Importantly, the application of molecular sequence data in the definition of subspecies permits the diagnosis of subspecies (Taylor *et al.* 2017). In this study, we recognize species or subspecies based on a combination of the following inter-related criteria (Moyle and Campbell 2020):

(a) **Taxonomy**. The species/subspecies is already designated as a distinct taxon based on non-genetic taxonomic methods or on distribution. Traditional morphometrics and meristics have had some utility for separating Speckled Dace taxa if based on statistical analyses of populations with large sample sizes that allow small differences to emerge as significant. Unfortunately, such analyses have not been particularly useful for species/subspecies diagnosis, i.e., for assigning individuals from each population to specific taxa (Sada *et al.*1995, Cornelius 1969).

(b) **Zoogeography**. The taxon is confined to a geographically defined area that supports other endemic species of fishes. Endemic fishes tend to occur in clusters of species adapted to a particular set of conditions, in isolation, especially in California (Moyle 2002).

(c) **Geology**. Closely tied to zoogeography, the geology of a taxon's geographic range usually indicates long isolation although periods of connectivity to adjacent watersheds may also be shown. In theory it is possible for subspecies or even similar species to be sympatric, based on ecological differences (*e.g. R. falcatus* and *R. umatilla* in the Columbia River, Peden and Hughes 1988, Wydoski and Whitney 2003). However, subspecies usually occupy distinct segments of a species' range. Overall, Speckled Dace subspecies are not sympatric.

(d) **Genetics/genomics**. Taxonomic distinctness is supported by genomic and other genetic studies. Our assumption is that the evolutionary distances among populations provide support for designation of species and subspecies within the Speckled Dace complex (Su *et al.* 2022). Genetic/genomic studies should indicate if there is evidence for inbreeding with other populations and if such interbreeding has played a role in a dace population's evolution, especially prior to the invasion of Euro-American people into western North America.

Genetics

In recent years, the most widely used genetic approach to the systematics of Speckled Dace has been mitochondrial DNA (mtDNA) analyses (Oakey *et al.* 2004; Smith *et al.* 2017). This approach greatly improved the ability of researchers to look at genetic diversity within the Speckled Dace complex and to improve phylogenetic analyses. Some key studies using mtDNA are as follows.

Oakey *et al.* (2004) examined mtDNA from 59 dace populations scattered across the western USA. They found that Speckled Dace populations could be assigned to the following well-resolved clades (evolutionary lineages): the Colorado Basin clade, Lahontan Basin clade, and Columbia River clade. The Colorado Basin clade is divided into Lower, Middle, and Upper basin clades plus the Los Angeles clade (sister to the Middle Colorado clade), while the Lahontan Basin clade includes Death Valley populations. The Columbia River clade includes a Klamath-Pit River clade as a sister clade to a Columbia Basin clade. Oakey *et al.* (2004) indicated that the phylogeny represented by the clades could generally be explained by the geologic history of each region. Their findings indicate three separate invasions of California by speckled dace (via Klamath-Pit rivers, middle Colorado River, and the Lahontan Basin.

Pfrender *et al.* (2004), using mtDNA, focused on genetic relationships of dace in five river basins in Oregon. They found "deep divergences among major drainage basins [that were] ...on the order of species-level differences noted in other studies of cyprinids...(p. 46)."

Similarily, Billman *et al.* (2010) used mtDNA to examine the phylogeny of 22 populations from three adjacent major watersheds: Snake, Bonneville, and Lahontan. They found that the dace from each major watershed formed a separate clade, demonstrating long independent evolution with little gene flow between basins. Nevertheless, "they concluded that Speckled Dace contain a large amount of genetic variation, characteristic of a widespread species... (p. 44)."

Ardren *et al.* (2010) looked at the genetics of dace populations from the Warner Basin. Their mtDNA analysis indicated that Warner Basin dace populations were different at the species level from dace populations from the nearby Goose Lake basin (which is part of the Sacramento River watershed). In a somewhat broader study, Hoekzema and Sidlauskas (2014) examined dace populations in the Great Basin in Oregon within four watersheds (Goose Lake, Lake Abert, Silver Lake, and Malheur Lake) that surround the Warner Basin. They used mtDNA as well as nuclear DNA (nuclear s7 intron). They found that dace from throughout the Warner Basin formed a lineage that was distinct enough from lineages in the other four basins to merit consideration as a species.

Smith *et al.* (2017) conducted a major study comparing Speckled Dace populations from throughout their known range, using mtDNA, morphology, fossils, and the complex, dynamic geologic record of the region. Their goal was to "discover evolutionary processes that operated to produce this widespread, polytypic fish group in an intermountain landscape of hundreds of small, isolated drainages (Smith *et al* 2017:45)". This study was the latest in a series of papers on the distribution and systematics of fishes of the western North America, but especially the Great Basin (Hubbs and Miller 1948a,b, 1972, Smith *et al.* 2002, 2017, Smith and Dowling 2008). These studies relate fish distribution and endemism to the combination of the repeated filling and draining of Pleistocene waterways in relation to climate and, on a longer scale, to the changes in underlying geology (tectonics) that cause shifts in flow direction of major rivers. While their analyses indicated a number of distinct lineages of Speckled Dace were present, Smith *et al.* (2017) also hypothesized that there was considerable, if sporadic, gene flow among populations that reflected complex geologic events. This gene flow was perceived as preventing the formation of morphologically distinct populations that could be defined as species, resulting in the conclusion that "*Rhinichthys osculus* persists as a series of metapopulations (Smith *et al.* 2017:78)."

Genomic analyses

Mussmann *et al.* (2018, 2020) investigated the relationships of dace populations in the Death Valley system using double digest RAD (ddRAD) methods, which identified 14,355 SNP loci across 10 populations (N = 140). Their purpose was to identify discrete, genetically based management units within Speckled Dace populations; they recognized that such units should be supported by other information on the fish, including morphometrics and ecological and life history differences. Their analysis designated three Evolutionary Significant Units under the subspecies *R. o. nevadensis*: Long Valley, Owens Valley [including Benton Valley], and Ash Meadows Speckled Dace. The Amargosa Canyon Speckled Dace was also recognized as a Distinct Population Segment, although it apparently originated as a recent hybrid between Ash Meadows and Owens Valley Speckled Dace. The Speckled Dace outgroup for comparison was Lahontan Speckled Dace.

To determine evolutionary lineages within California populations, Su *et al.* (2022) collected samples from 38 locations in the western USA, with a focus on California. They used RAD sequencing to extract thousands of SNPs across the genome to identify genetic differences among all the samples. Principal component analysis, admixture analysis, and pairwise Fst calculations were performed to construct molecular phylogenies, which characterized genetic and phylogenetic relationships among the Speckled Dace populations. A range-wide phylogenetic tree was then generated.

The analyses found three major lineages in California: 1) Sacramento River, Central California Coast, Klamath River and Warner Basin; 2) Death Valley and Lahontan Basin; 3) Santa Ana River basin, in southern California. These lineages fit well with the geologic history of California, which has promoted isolation of populations of Speckled Dace and other fishes.

The three lineages coincide with zoogeographic regions that are isolated from one another and other regions; they also contain other endemic fishes (Moyle 2002, Oakey *et al.* 2004). These same lineages are imbedded (as sub-lineages) within the much more complex cladograms of Smith *et al.* (2017): Klamath-Sacramento-Warner, Lahontan- Amargosa, and Los Angeles (Colorado). The Smith *et al* (2017) cladograms are based on mtDNA over the region containing Speckled Dace populations.

While some morphometric and meristic differences exist among the lineages, they reflect adaptations to regional conditions rather than traits that allow species to be designated based on fixed, measurable characters. Smith *et al.* (2017) indicated that the lack of clear differences was the result of hybridization events that allowed gene flow among populations over wide areas. We saw little evidence of hybridization events shaping the genome but instead found isolated lineages that retain their distinctiveness over broad areas despite possible ancient hybridization events (e.g., Billman *et al.*, 2010). We therefore find it appropriate to label lineages with broad genomic differences from other lineages as species and geographically isolated lineages with less genomic differentiation as subspecies or distinct population segments. This is possible in part because the improved genetic techniques used here make no assumptions that species must be morphologically distinct from one another if genetic differences are large (Su *et al.* 2022). In any case, our designations of species and subspecies are not solely based on genomics, but on other criteria as well, as mentioned.

Methods

Meristics and morphometrics. Much of the data for standard counts of meristics and measurements of morphological characteristics were taken from existing reports and publications, including data from original descriptions where available. Major sources were Cornelius (1969), Sada *et al.* (1993), and Smith *et al.* (2017). The availability of large data sets, published and unpublished, from over 2000 dace (including about 1600 from California) meant that collecting additional data was not essential for taxonomic determinations. However, meristic counts were made for all new types and paratypes in this paper (n=40), following Armbruster (2012) and documents from Kevin W. Conway, Texas A&M University. We used a Nikon SMZ800 Stereo Microscope (1x to 6.5x) at the UCD Bohart Museum of Entomology. Specimens were dried along the left side with gentle compressed air before counting and fins were moistened with ethanol or water as needed. One fiber optic light source was positioned so that it cast light parallel to the fish's body from right/tail side towards the head. This greatly helped to accentuate the edges of scales. An insect pin attached to a 2mm wide dowel was used as a pointer.

Genomics. We used information and analyses from Su *et al.* (2022) to examine relationships of Speckled Dace from 38 locations using restriction-site associated DNA (RAD) sequencing. This approach uses thousands of loci in each individual. The results from genomic analysis are repeatable and robust, requiring less interpretation than mtDNA-based analyses. Because of the large quantity of data possible, variation in the sequencing data across the entire genome was analyzed (Su *et al.* 2022). The phylogenetic tree (Figure 2) was generated from all possible SVDQuartets using RAD sequencing data, with 100 bootstrap analyses run on each quartet to assess confidence. The value of the bootstraps was added to each lineage. 421,929 SNPs were available for developing the phylogeny. A high proportion of these SNPs were used in the bootstrap analysis, although each run of 100 bootstraps returned a consistent result. For further discussion of this approach as applied to California fishes, see Baumsteiger *et al.* (2017) and Moyle and Campbell (2022).

Distribution. Distribution of the dace taxa was first mapped using the PISCES database, which shows distribution in HUC12 watersheds statewide (Santos *et al.* 2013). Distribution was refined by examining the published literature, records in the UC Davis Museum of Wildlife and Fish (WFB) and field notes of Moyle, and through personal communications with other fish biologists (see Acknowledgements).

Species/Subspecies Descriptions

In this section of this paper, we describe or redescribe the following taxa of Speckled Dace that occur in California. Holotypes and paratypes of new taxa are deposited in the Museum of Wildlife and Fish Biology, University of California, Davis. Paratypes have also been deposited at the California Academy of Sciences.

Santa Ana Speckled Dace, *Rhinichthys gabrielino* new species
Desert Speckled Dace, *Rhinichthys nevadensis* (Gilbert) new common name
    Lahontan Speckled Dace, *R. nevadensis robustus* (Gilbert) new combination
    Amargosa Speckled Dace, *R. nevadensis nevadensis (*Gilbert) new combination
    Long Valley Speckled Dace, *R. n. caldera* new subspecies
Western Speckled Dace, *R. klamathensis* (Evermann and Meek)
    Klamath Speckled Dace, *R. klamathensis klamathensis* (Evermann and Meek) new combination
    Sacramento Speckled Dace, *R. klamathensis achomawi* new subspecies
    Warner Speckled Dace *R. klamathensis goyatoka* new subspecies

***Rhinichthys gabrielino*, new species, Santa Ana Speckled Dace**

Figs. 3, 4a, 5

Synonymy. *Agosia nubila carringtoni* Jordan and Evermann 1896:312; Culver and Hubbs 1917:82; *Rhinichthys osculus carringtoni* Shapovalov and Dill 1950:386; Shapovalov, Dill, and Cordone 1959; Kimsey and Fisk 1960:469; Cornelius 1969:1; Oakey *et al.* 2004:212; *R. osculus* subsp. widely used in California since the 1950s (for example: Moyle 2002, Moyle *et al.* 2015).

Holotype. WFB 3498 (Fig. 4a), 73 mm SL, East Fork San Gabriel River, South of Upper Monroe Road, Angeles National Forest, Los Angeles County, California, 34 14' 15.85"N 117 49' 14.58"W, USA, 2 July 2021, J. Pareti (California Department of Fish and Wildlife).

Paratypes. WFB 3499–3500, WFB 3501–3507 (n =9). Same data as holotype.

Meristics: holotype (paratypes):

Lengths(mm): standard 73(45–78), fork 82 (54–84), total 89 (57–90)

Lateral line scales: 73(69–75). Lateral line complete on all fish, although there were 1–3 scale rows beyond the end of the lateral line (counted).

Scales above lateral line 13(12–14).

Scales below lateral line (10 (8–11)

Dorsal-fin rays 7(7)

Anal-fin rays 6(6)

Pectoral-fin rays 11 (10–12)

Pelvic 6 (6–7)

Caudal-fin rays 19(19), 10 upper rays, 9 lower rays

Diagnosis. Separated from all other Speckled Dace by the absence of supraorbital bones (vs. present, Smith *et al.* 2017). A cryptic species otherwise not distinguishable from other species/subspecies of the Speckled Dace complex except through genomics and geography. Slightly higher lateral line scale counts (mean 74, mode 76, range 64–82) than Sacramento Speckled Dace (mean 70, mode 72, range 54–82) and Lahontan Speckled Dace (mean 68, mode 72, range 60–77) (Table 2).

Description. A cryptic species, as shown by genomic analyses; endemic to streams of Los Angeles, San Gabriel, and Santa Ana watersheds in southern California. Recognizable by typical stocky morphology of all *Rhinichthys* species; small size (adults 6–11 cm SL), wide caudal peduncle (about 1/3 the body depth), blunt-pointed snout, and subterminal mouth. Meristics overlap all other Speckled Dace taxa (Table 2). Body color variable, but adult fish usually pale yellow/white to dusky olive, often with small black spots. Head stripe and lateral spots/blotches pale or absent. Breeding adults of both sexes with orange to red fins; males also with red snouts and lips (Fig. 5). Lateral line usually complete, although last 1–10 scales may lack pores. High overlap in meristic counts with other California Speckled Dace populations (Table 2, Cornelius 1969).

Morphometrics. Cornelius (1969) compared the body and fin morphology of 491 dace using 23 truss measurements (divided by standard length or head length, with all values converted to natural logarithms). Only small differences were found between Santa Ana Speckled Dace and dace taxa from other areas. His analysis showed that Santa Ana Speckled Dace had slightly longer fins, more anterior dorsal fins, somewhat longer and narrower heads, smaller eyes, and shorter upper jaws than dace from Sacramento, Lahontan, and Colorado river basins. All differences were not statistically different. However, morphometric differences were sufficient to distinguish lineages when combined meristic measurements and measures of jaw structure (below). Thus, Santa Ana Speckled Dace could be distinguished statistically from nearby Sacramento Basin populations and from Speckled Dace from Lake Tahoe (Lahontan Basin), although overlapping morphometrics made it difficult to assign individuals to any one taxon.

Cornelius (1969:26) found that mouth structure provided the strongest separation of the taxa; he used a unique measure of jaw angle: "The lateral angle of the upper jaw formed by the premaxillary and maxillary as measured from photographs of the left side of the head." Presumably a larger jaw angle is a measure of increased gape and size of prey. Cornelius (1969) found that Santa Ana Speckled Dace had a mean jaw angle of 145 degrees (n = 34, range 128–148) while the Sacramento dace had a mean jaw angle of 160 degrees (n=44, range 146–172). He also found that a frenum is fully developed in 54% (n=277) of the Santa Ana Speckled Dace but in only 2% (n =180) of Sacramento dace. Most (8 of 11 fish examined) Colorado Basin fish had a well-developed frenum. It was absent from (n=41) in Lahontan (Lake Tahoe) dace. Maxillary barbels were present on one or both sides of the mouth in all four dace populations compared, but they were variable in number and size so not useful for distinguishing Santa Ana Speckled Dace. Overall, Cornelius (1969) found that jaw angle, combined with other less quantitative features of the jaw, supported his finding that the Santa Ana Speckled Dace was distinct from dace from Lahontan and Sacramento basins. In combination with other features, jaw structure indicated that Santa Ana Speckled Dace had a common ancestry with fishes from the Colorado River watershed (Virgin River) (Cornelius 1969). This conclusion is supported by genetic and genomic studies (Smith *et al.* 2002, 2017, Su *et al.* in 2022).

Genomics/Genetics. Genetic studies (mostly using mtDNA) generally indicate that the Santa Ana Speckled Dace is a sister lineage to Speckled Dace populations in the Colorado River Basin as result of a split in lineages approximately 3.6 million years ago (mya) (Oakey *et al.* 2004, Smith and Dowling 2008). Smith and Dowling (2008), using mtDNA well as morphometrics and meristics, indicate that populations of Speckled Dace in Los Angeles region streams have been isolated long enough (through the Pleistocene) to have diverged from one another and developed some small differences in morphological characters, supporting the findings of Cornelius (1969). The mtDNA analysis by Smith *et al.* (2017:77) showed "extreme molecular divergence" (about 7%) from other

Speckled Dace populations, the highest they encountered. Oakey *et al.* (2004) also determined that Speckled Dace from the Santa Ana and San Gabriel rivers formed a distinct, monophyletic lineage. Su *et al.* (2022), using genomic data, confirmed that the Santa Ana Speckled Dace is a sister lineage to dace in the Colorado River Basin. In short, Santa Ana Speckled Dace are quite different genetically from Speckled Dace of other lineages in California and elsewhere (Smith *et al.* 2017, Su *et al.* 2022), supporting their designation as a full species (Figure 2).

Distribution. Santa Ana Speckled Dace are endemic to three streams, and their tributaries, of the Los Angeles Region in southern California: the Los Angeles, San Gabriel, and Santa Ana rivers. In addition, the San Jacinto River is often treated as a separate river system. However, it historically flowed into the Santa Ana River, a connection severed by dams except in exceptionally wet years. The three river's headwaters are in the Transverse Mountain Ranges, specifically the San Bernadino, San Gabriel, and Santa Ana mountains. The rivers flowed into an alluvial plain, now covered with Orange County development. During wet years, before the present era, this region would have flooded, connecting the Speckled Dace populations of the rivers. Today the scattered populations of Speckled Dace are largely confined to streams in a band of habitat on public lands that is below the high gradient upper regions of the three watersheds and above the developed alluvial plain. Santa Ana Speckled Dace are absent from many parts of their historic range (Moyle *et al.* 2015, O'Brien *et al.* 2011). Each population fragment is increasingly isolated from other populations as the result of dams and other modern infrastructure.

Note: Biogeography. There is debate over exactly how the ancestors of Santa Ana Speckled Dace managed to move from the ancestral Colorado River basin to the Los Angeles region (Minckley *et al.* 1986; Spencer *et al.* 2008, Smith *et al.* 2017). They had to survive in a region with a dynamic geology to do so. To colonize coastal California, the dace would have had to travel several hundred kilometers overland (in the modern landscape) over an extended period of time. Speckled Dace in general are freshwater dispersers (Moyle and Cech 2004) so cannot move though marine environments to colonize new areas (Moyle 2002). The dispersal route also has to accommodate two sympatric freshwater dispersers, Santa Ana Sucker (*Pantosteus santaanae*) and Arroyo Chub (*Gila orcutti*), both which share ancestry with fishes in the Colorado Basin (Unmack *et al.* 2014). Smith *et al.* (2017) argue the fish were able to gradually make their way to California via successive stream captures in a geologically active landscape. This allowed fish to move between headwaters, eventually reaching streams that flowed into the Pacific Ocean from the Coast Range (Santa Monica Mountains). The exact route has been largely erased by the active geology. In contrast, Spencer *et al.* (2008) present evidence that a likely route was through a combination of two dispersal methods: movement of a plate carrying the fishes followed by colonization via headwater capture.

It is likely that dace and other fishes were ultimately moved into the vicinity of the coastal drainages through a combination of the methods proposed by Smith *et al.* (2017) in concert with the periodic shifting of the main channel of the Lower Colorado River. This channel migration was a dynamic process driven by sediment deposition in the Colorado River channels. Fish presumably followed the river into new channels, including those adjacent to the proto-Santa Ana River and other coastal drainages. The channel migrations eventually blocked the Colorado River, diverting its flow into a large Pleistocene/Holocene lake basin (Lake Cahuilla) subsequent to the formation of the Salton Trough (ca. 1.3 mya). This lake, a predecessor of the Salton Sea, was colonized by lower Colorado River fishes. Bones of the larger fish species have been found in middens of fishing villages along Lake Cahuilla (Wilke 1980). Today, the Lower Colorado River and the Salton Trough are separated from the Santa Ana Basin by the 8–km-high San Jacinto and San Gorgonio Ranges. These ranges are parts of the Peninsula Range and were likely formed by complex plate movements associated with the development a bend in the San Andreas Fault System (ca. 1.1–1.5 mya) (Spencer *et al.* 2008, Fattaruso *et al.* 2016).

The geologic movements transformed low-relief upland habitat into the dramatic landscape of today. The uplift of the ranges is associated with their westward tilting, resulting in the progressive capture and redirection of eastward-flowing tributaries at a rate of 20–44 km/my (Dorsey and Roering 2006), presumably with the fish. The rapid vertical motions driving these events were dramatic – sometimes exceeding 10m at one time (McClay and Bonora 2001). The suddenness of this redirection of western Colorado River tributaries into coastal-draining basins likely allowed the transfer of freshwater-dispersing fishes into the basin. These fishes apparently became completely isolated no later than ~1.1 mya (Fattaruso *et al.* 2016, Smith *et al.* 2017) when uplift of the mountains and downfaulting of the trough created an insurmountable barrier to further dispersal. The uplift the in the Peninsula Ranges (about 1.1–1.5 mya, Fattaruso *et al.* 2016) created a formidable barrier to freshwater fish dispersal and can be treated as the last point in time that dace could have colonized coastal waters. It is possible that dace were isolated slightly before the San Andreas fault began to shift, as suggested by previous studies (*i.e.* Spencer *et al.* 2008), but it is highly unlikely that isolation occurred subsequent to onset of the formation of the Salton Sink (*ca.* 1.1–1.3 mya)

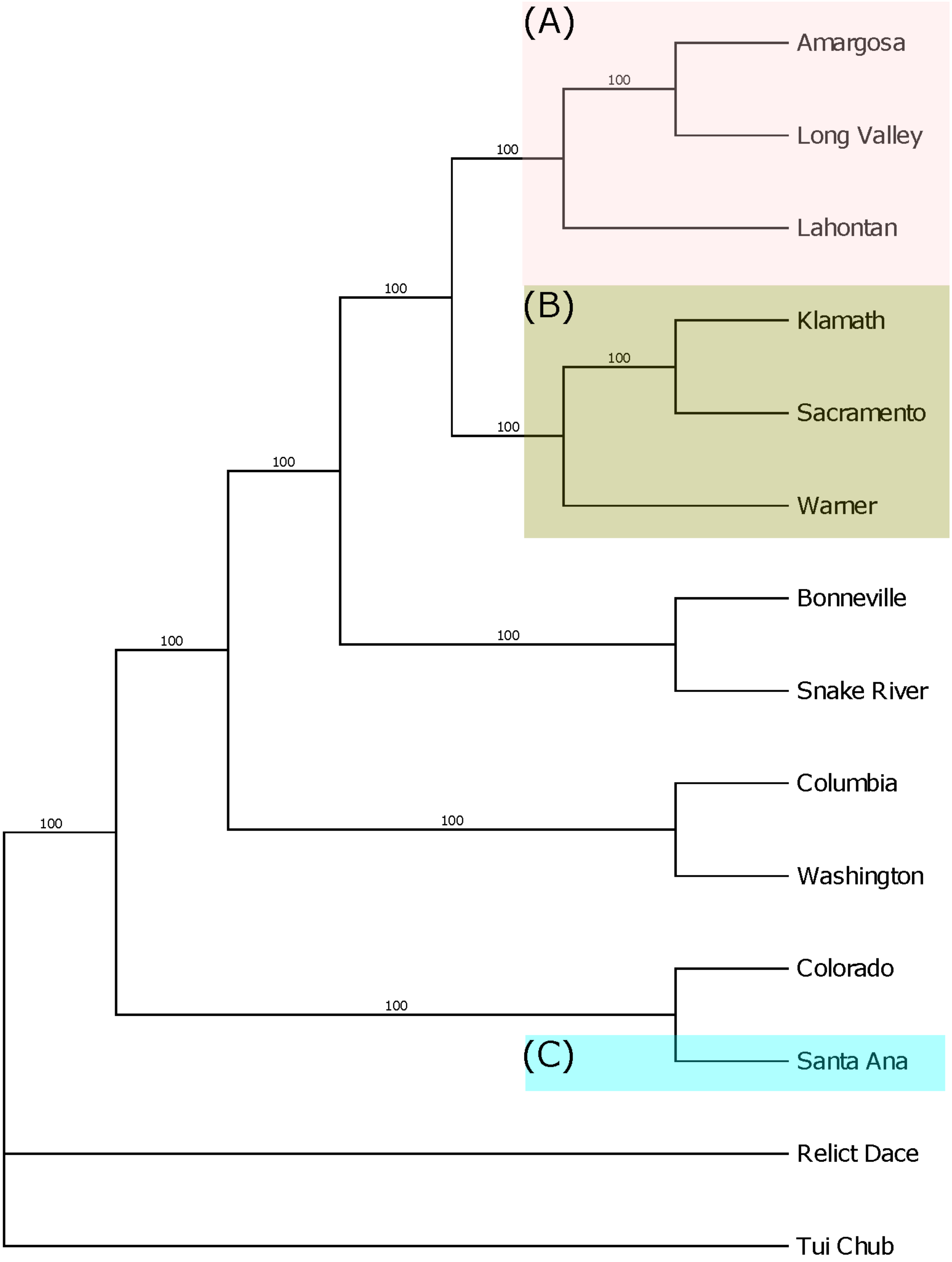

FIGURE 2. Phylogenetic relationships among Speckled Dace populations in this study, modified from Su *et al* (2022). The molecular phylogeny was generated by an ML coalescent model in SVDQuartets with 100 bootstraps, using RAD sequencing data. Numbers on each lineage refer to the percentage of bootstrap runs (out of 100) that produced the same result. Details can be found in Su *et al.* (2022). The lineage names refer to major drainages from which our Speckled Dace samples were collected from California, as well as from major basins outside of California. We did not examine the latter findings in detail; they probably represent multiple undescribed species/subspecies. The capital letters refer to lineages identified as species in this paper. A. Desert Speckled Dace (*R. nevadensis*), B. Western Speckled Dace (*R. klamathensis),* C. Santa Ana Speckled Dace (*R. gabrielino*). Tui Chub (*Siphatales bicolor*) and Relict Dace (*Relictus solitarius*) were outgroups used to root the phylogeny because they are both western cyprinids distantly related to *Rhinichthys* (Schönhuth *et al.* 2012).

TABLE 2. Mean, mode, and range of meristic counts on Santa Ana, Sacramento, Lahontan and Colorado basin populations of Speckled Dace, from Cornelius (1969). The Sacramento fish were from coastal streams just north of the Los Angeles Basin (Santa Maria, San Luis Obispo, Salinas). LL is lateral line.

Character	Number	Mean	Mode	Range
Lateral lines scales				
Santa Ana	156	74.3	76	64–82
Sacramento	123	69.7	72	54–82
Lahontan	17	68.4	72	60–77
Colorado	7	68.7	72	62–74
Scales above LL				
Santa Ana	105	15.9	15	12–20
Sacramento	124	16.4	16	12–20
Lahontan	20	14.1	15	10–21
Colorado	5	15.8	15	15–17
Scales below LL				
Santa Ana	106	12.8	13	11–16
Sacramento	121	14.2	14	10–19
Lahontan	19	12.8	13	11–16
Colorado	7	12.3	13	11–16
Vertebrae				
Santa Ana	111	35.8	36	34–37
Sacramento	99	37.1	36	34–39
Lahontan	17	36.0	36	35–38
Colorado	10	36.5	36/37	35–38
Dorsal-fin rays				
Santa Ana	99	8.0	8	7–9
Sacramento	112	8.1	8	7–9
Lahontan	20	7.9	8	7–8
Colorado	7	8.0	8	8
Anal-fin rays				
Santa Ana	99	7.1	7	5–8
Sacramento	129	7.1	7	5–8
Lahontan	20	7.1	7	7–8
Colorado	7	7.0	7	7
Pectoral-fin rays				
Santa Ana	110	15.1	15	14–16
Sacramento	121	14.4	14	12–16
Lahontan	20	15.0	14	12–15
Colorado	7	13.4	13	12–15
Pelvic-fin-rays				
Santa Ana	110	8.0	8	6–9
Sacramento	126	8.0	8	7–9
Lahontan	18	8.0	8	7–9
Colorado	7	7.8	8	7–8
Caudal-fin rays				
Santa Ana	113	18.8	19	16–20
Sacramento	160	19.0	19	17–20
Lahontan	14	17.5	19	16–20
Colorado	7	18.7	19	18–19

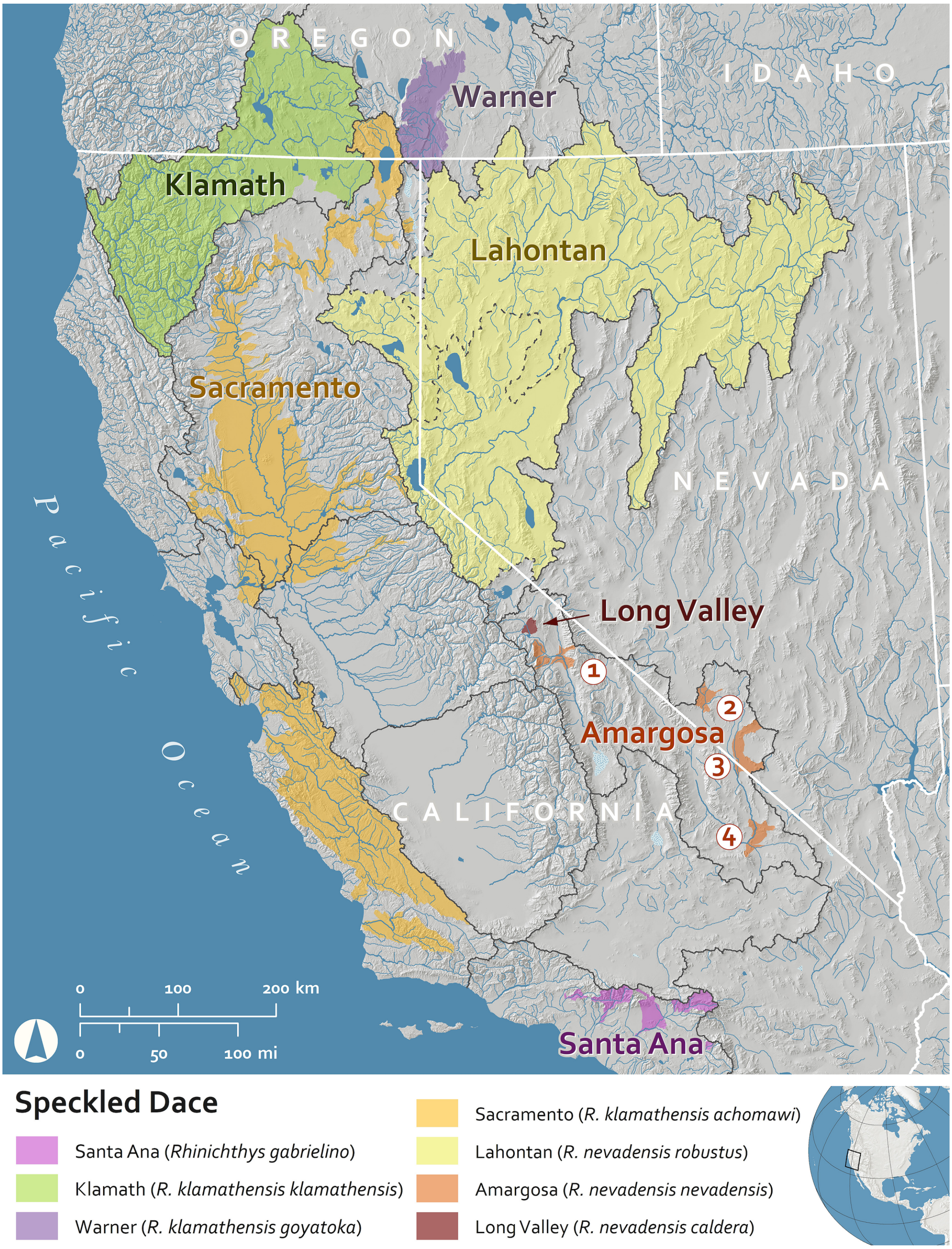

FIGURE 3. Current distribution of *Rhinichthys* in California and adjacent watersheds. The distributions are only approximate but based on occurrence in HUC 12 watersheds. The numbers refer to populations in the Owens Valley and Death Valley that are included in Amargosa Speckled Dace, *R. nevadensis nevadensis* and can be recognized as Distinct Population Segments (1) Owens Speckled Dace, (2) Oasis Valley Speckled Dace, (3) Ash Meadows Speckled Dace, and (4) Amargosa River Speckled Dace. Long Valley Speckled Dace are a distinct subspecies. Dace have been extirpated from the south San Francisco Bay-Santa Clara Valley region. See text for more specific distributional information. Information for this map was gleaned from Gesch *et al.* (2002), Patterson and Kelso (2021), Santos *et al.* (2013), US Census Bureau (2001), USGS (2004, 2013). Speckled Dace are typically present in a limited number of streams, springs and ditches within each mapped region. Map by Amber Manfree.

FIGURE 4. Holotypes of new taxa of *Rhinichthys* described in this paper, A. Santa Ana Speckled Dace (*R. gabrieleno* WFB 3498. B. Long Valley Speckled Dace (*R. nevadensis caldera*) WFB 5000, C. Warner Speckled Dace (*R. klamathensis goyatoka*) WFB 122-10-44, D. Sacramento Speckled Dace (*R. klamathensis achomawi*) WFB 3171.

Note: **Taxonomy**. This study confirms that Santa Ana Speckled Dace is a full species, using the following lines of evidence.

Taxonomy: While lacking formal description until now, the Santa Ana Speckled Dace has long been recognized as distinct (Swift *et al* 1993, Moyle 1976, 2002, Oakey *et al.* 2004). Definitive morphometric and meristic characters are largely absent. However, when combined, they can be used to distinguish Santa Ana Speckled Dace statistically from populations of other Speckled Dace species/subspecies, as well as from Colorado River Speckled Dace, indicating their long isolation (Cornelius 1969). The apparently unique feature of complete absence of supraorbital bones further supports the species status of this dace.

Geology: Improved understanding of the dynamic geology of southern California and of the shifting channels of the Colorado River have resulted in more supportable hypotheses as to how Speckled Dace and other endemic fishes were able to colonize coastal southern California streams.

Zoogeography: The historic distribution of the species in streams of the Los Angeles region shows long separation from their ancestral population and long isolation without access to other populations that could lead to hybridization. Although Smith *et al.* (2017) regard hybridization as the reason *R. osculus* is just one species throughout its enormous range, including the Los Angeles region, hybridization has clearly not been an issue with the Santa Ana Speckled Dace, which has had no opportunities for over 1.3 million years.

Genomics/genetics. Su *et al.* (2022) show that the Santa Ana Speckled Dace is the most distinct genetically of all other dace populations in California, indicating a long history without gene flow from other dace populations.

Etymology. The species epithet honors the Gabrielino-Tongva people, the indigenous inhabitants of the region at the time of the Spanish invasion and who still have a significant presence (https://gabrielinotribe.org/). The original range of the Santa Ana Speckled Dace was in the streams that flowed through the band's homeland. The tribe is also known as San Gabriel Band of Mission Indians. The common name, Santa Ana Speckled Dace, is widely used for this fish (*e.g.* Moyle 2002); it shares its name with the Santa Ana Sucker which also occurs in the Santa Ana River and adjacent watersheds.

Note: nomenclature. The scientific name has long been a source of confusion. Jordan and Evermann (1896:312) list *Agosia nubila carringtoni* as having a wide distribution in the Great Basin but state "To this form we also refer provisionally specimens from Lake Tahoe and elsewhere in the Lahontan basin but also those from various coastwise localities in central and southern California, where it is abundant in clear streams and springs as far south as San Luis Obispo." *Agosia n. carringtoni* consequently was applied by early workers (*e.g*., Snyder 1918) to most dace populations in central and southern California including in the first paper mentioning Speckled Dace in the Los Angeles region (Culver and Hubbs 1917). Cornelius (1969:18) summarized the history of the use of *carringtoni* and quoted a personal communication from Carl Hubbs that there was "no sound basis for continued use of *carringtoni* in reference to Santa Ana Speckled Dace." Despite this comment, Cornelius (1969) concluded that *R. osculus carringtoni* was the only available scientific name. Nevertheless, *carringtoni* reverted, with no real discussion, to being the name for Speckled Dace found in the Bonneville basin of Utah and Idaho (Smith *et al.* 2017) from whence it was originally described (Cope 1872). The Santa Ana Speckled Dace has subsequently been referred to as just *R. osculus* (*e.g.* Swift *et al.* 1993, Moyle 1976, 2002) or *R. osculus subsp.* (e.g., Moyle and Davis 2000, Moyle *et al.* 2015, Smith *et al.* 2017) but has resisted formal description until now.

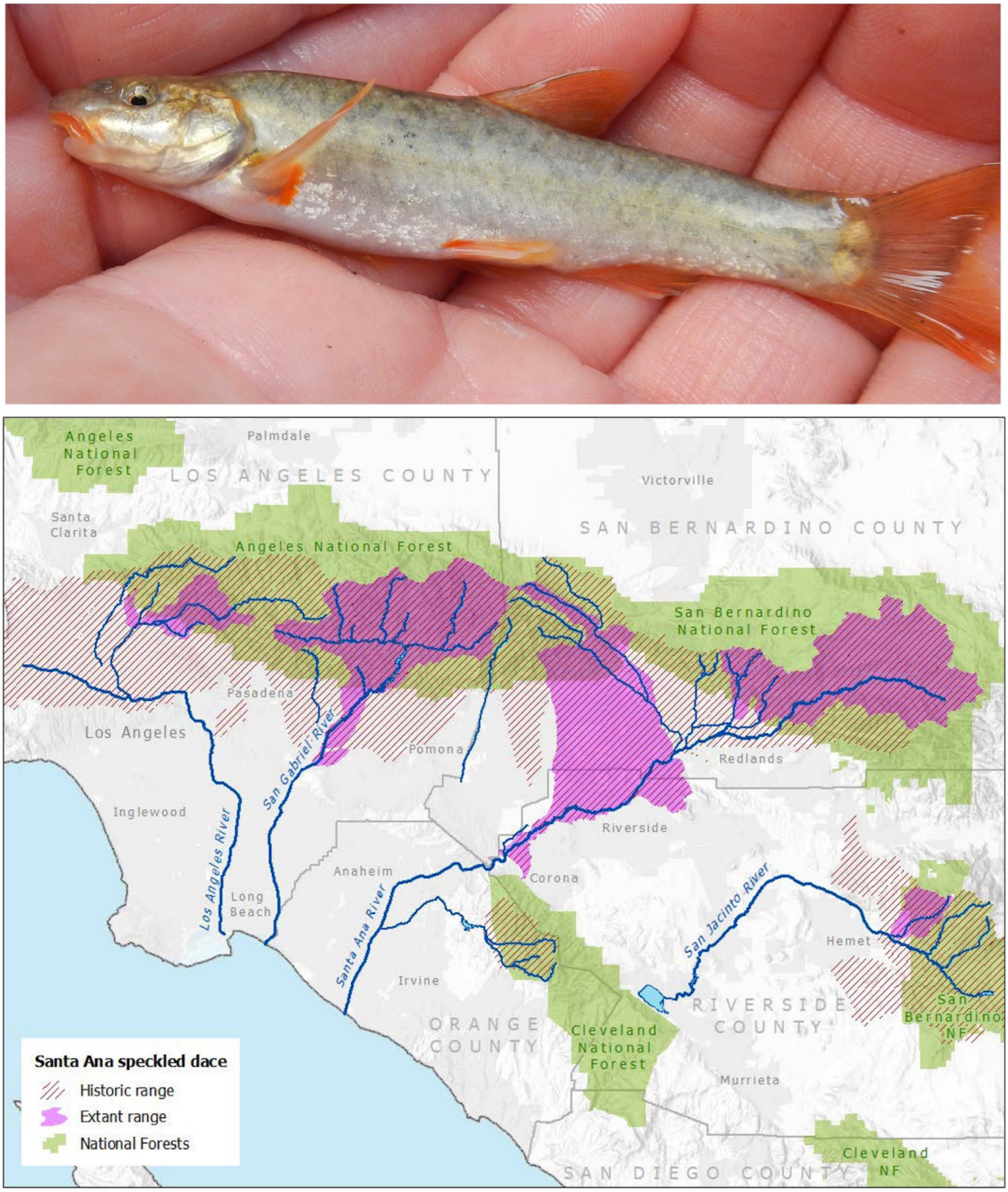

FIGURE 5. Top: Male Santa Ana Speckled Dace in breeding colors. Photo by Jennifer Pareti, CDFW. Bottom: Approximate historic and extant distribution of Santa Ana Speckled Dace (from Center for Biological Diversity, 2020). This figure also shows the importance of public lands (green) for their conservation. Historic range shows areas from which they have been extirpated.

Conservation Status. In California, Santa Ana Speckled Dace historically inhabited streams in the upland areas of the San Jacinto, Santa Ana, San Gabriel and Los Angeles rivers which were interconnected by low-elevation floodplains (Swift *et al.* 1993, Moyle 2002, Moyle *et al.* 2015) (Figure 5). They have since disappeared from much (75%) of their range, including the middle reaches and tributaries of the Santa Ana River, most of the Los Angeles River and San Jacinto River basins (Moyle *et al.* 2015, Center for Biological Diversity 2020). Their current distribution is restricted to headwater streams of the San Jacinto, Santa Ana, and San Gabriel rivers and Big Tujunga Creek (Los Angeles River drainage). In 2005, Speckled Dace were reintroduced into the North Fork of Lytle Creek; a similar introduction was made into the Middle Fork in 2007 (Moyle *et al.* 2015). Both were apparently successful. Attempts to establish populations of Santa Ana Speckled Dace outside their native range were made through introductions into the Santa Clara and Cuyama rivers. Success of these populations is uncertain. An additional introduction into River Springs, Mono County, failed

The third edition of the Fish Species of Special Concern Report of the California Department of Fish and Wildlife (Moyle *et al.* 2015) rates the Santa Ana Speckled Dace as one of the most endangered fish in California. The report notes that the Santa Ana Speckled Dace is a U.S. Forest Service Sensitive Species in the three national forests in which it is found (Angeles, San Bernardino, Cleveland NFs). However, it is likely extirpated from Cleveland National Forest (Santiago Creek). The California Natural Diversity Database ranks Speckled Dace as secure at the global scale (G5) but the Santa Ana subspecies as Imperiled (T1S1; www.natureserve.org). It is listed as Threatened by the American Fisheries Society (Jelks *et al.* 2008). The habitat of this species continues to shrink due to urbanization of the Los Angeles region, resulting in fragmentation and reduction of populations. Intense human use of their streams on public lands for recreation and water supply also contributes to their decline. Extinction seems likely in the next few decades without special protection for all remaining populations (Swift *et al.* 1993, Moyle 2002, Moyle *et al.* 2015).

Listing Santa Ana Speckled Dace as threatened or endangered under state and federal Endangered Species Acts would be a major step towards preventing extinction. It appears that lack of a formal species description has been a barrier to listing, even though recent genetic and phylogenetic studies show it to be distinct from all other Speckled Dace (Oakey *et al.* 2004; Smith and Dowling 2008, Mussmann 2018, Su *et al.* in 2022). It could therefore be listed as a Distinct Population Segment, even without formal description. Our paper resolves whatever taxonomic uncertainty previously confounded action by regulatory authorities.

Rhinichthys nevadensis **Gilbert 1893, new common name, Desert Speckled Dace**

Rhinichthys (*Apocope*) *nevadensis*, Gilbert 1893:230
Agosia nevadensis Jordan and Evermann 1896:310
Agosia nubila carringtoni, Jordan and Evermann 1896:311
Agosia robusta Rutter 1903:148; Snyder 1917:2002
Agosia carringtoni: Snyder 1913:70
Apocope robusta Snyder 1918:33; Evermann and Clark 1931:55
Rhinichthys osculus robustus: Shapovalov and Dill 1950:387; Kimsey and Fisk 1960:46; Hubbs *et al.* 1979:12; Moyle 2002:161.
Rhinichthys osculus nevadensis Shapovalov and Dill 1950: 387; Shapovalov *et al.*1981: 25; Hubbs *et al* 1979:12; Smith *et al*, 2002: 33; Moyle 2002:161; Mussmann *et al.* 2020:10805

Holotype: *Rhinichthys* (*Apocope*) *nevadensis*, USNM 46111, 65 mm SL, Ash Meadows, Nye County, Nevada, Amargosa River watershed, March 4,1891, T.S. Palmer.

Paratypes: USNM 350556, 3(42–51 mm SL), March 4,1891, T.S. Palmer; and USNM 46112, 5, March 3,1891, A.K. Fisher, both from same locality as holotype.

Diagnosis. Desert Speckled Dace are best recognized as small (adult lengths of 5–9 cm) cyprinoid fish that have the typical Speckled Dace phenotypic characters, inhabit Lahontan, Owens Valley and Death Valley drainages and are a distinct genetic lineage that encompasses three sublineages. The mouth is slightly subterminal, often with a frenum. Meristics and morphometrics are in the ranges shown in Table 3 but are not distinctive. Color is variable but there are usually speckles and blotches on the body which join to form a black lateral band on each side. The band is most prominent underneath each eye, sometimes extending to the snout. We recognize three subspecies, based on genomics and distribution: *R. n. nevadensis*, *R. n. caldera*, and *R. n. robustus.* Each has a separate account.

Description. The complete original description of *R. nevadensis* is as follows, from Gilbert (1893: 230) although numerical fractions in the original description have been converted to decimals. All morphometric measurements are standardized by dividing into standard length.

"Differing from other known species in the large head, short deep body, very small eye, and the reduction of the outer ventral ray to a mere rudiment. Head, 3.66 [times into] length (varying from 3.5 to 4.0); depth 3.66 (varying from 3.5 to 4.0); D. [dorsal rays],8; A. [anal rays],7; Lat. l. [Lateral line scales] 65. Ventrals apparently with seven rays, the outer one rudimentary, and often detected with difficulty."

"Body robust, with broad heavy head, the least depth of caudal peduncle less than half the greatest height of body. Greatest depth of head at occiput 5 in length of body. Eye very small, half the interorbital width, which equals distance from tip of snout to middle of eye, and is contained 2.66 times in head."

"Mouth terminal, very oblique, the lower jaw included, the premaxillaries not at all overlapped by the snout. The maxillary reaches the vertical from front of eye and is one-third length of head. Maxillary barbles [sic] well developed."

"Scales very irregularly placed and difficult to enumerate. The lateral line is incomplete in adults and usually does not reach to opposite dorsal fin. In the young it is variously developed, often extending though with many interruptions, to end of dorsal or base of caudal. Pores in lateral line (when complete) 58, about 66."

"Fins small, the pectorals not reaching ventrals, the latter not to vent. Front of dorsal midway between base of caudal and middle of occiput."

"In spirits, the upper half of sides is speckled and marbled with brown and the belly and lower half of sides immaculate or sparsely spotted. A broad dark lateral stripe usually present, becoming more conspicuous posteriorly, and ending in an obscure black spot on base of tail. A dark stripe sometimes present along middle of lower half of sides."

This description is for dace now treated as a population of Amargosa Speckled Dace (*R. nevadensis nevadensis*) from Ash Meadows in Death Valley. It also fits the other two subspecies as well, although *R. n. robustus* is typically more darkly pigmented and *R. n. caldera* is typically pale without much dark pigmentation. Sada *et al.* (1993) compared meristics (Table 3) and morphometrics of dace of all three subspecies and found only small, overlapping differences, which could not be used to distinguish the three groups for identification purposes

Distribution. Desert Speckled Dace are widespread in the southern Lahontan Basin and also inhabit small desert springs and streams in the Owens Valley and Death Valley regions. The common genetic heritage (ancestry) of the three subspecies is the result of late Pleistocene aquatic connections, which allowed the ancestral population(s) to spread throughout the Great Basin and into Death and Owens valleys. During the periods of high rainfall, large inter-connected lakes were formed throughout the Great Basin (Grayson 1993).

One of the largest lakes was Lake Lahontan. Its remnant lakes and tributaries support Lahontan Speckled Dace to this day. Lake Russell (whose remnant is fishless Mono Lake), drained into Lake Lahontan's southern end. About 1.3 million years ago, this connection to Lake Lahontan was blocked by vulcanism and Lake Russell subsequently spilled multiple times directly into the Owens River basin (Reheis *et al.* 2002). The subsequent eruption of the Long Valley caldera (0.76 mya) formed Long Valley Lake in the upper Owens Basin. Long Valley Lake, and adjacent Adobe Lake, drained into the Owens River which flowed into Owens Lake. Owens Lake spilled into Searles Lake, which drained into the Panamint Valley and Lake Manley, the site of present-day Death Valley (Grayson 1993). Lake Manly was the ultimate end for the water. Speckled Dace managed to make it through this chain, leaving populations behind in spring systems when dry desert conditions returned. The reverse movement of fish from Lake Manly to the Owens Basin was apparently geologically improbable, given the large waterfalls in the Owens River gorge and elsewhere (Hildreth & Fierstein 2016). The ancestral dace also colonized the Amargosa River which flowed into Lake Manly from the east by moving upstream from the lake.

The Eastern California Lake Chain, described above, was possible because of the elevational gradient starting at about 2200 m in elevation in the Lake Russell and dropping to sea level in Lake Manly (Orme 2008). The flow, however, was not continuous because connections between lakes were variable through time. Thus, based on estimates of the timing of lake spills, Lahontan fishes were isolated in the Lake Russell Basin about 1.3 million years ago. This basin spilled numerous times. The last spill was as recently as 100,000 years ago (Reheis 2002), when the Owens River carried Lahontan fishes to Owens Lake and allowed Speckled Dace and other fishes to colonize streams flowing into the caldera. The last spill event from Owens Lake seems to have been 10–12,000 years ago (Orme 2008), although the dace had presumably already colonized Lake Manly and the Amargosa River by that time. In the Owens Valley, Long Valley Speckled Dace and the Owens Valley populations of Amargosa Speckled Dace now occupy a few spring systems or artificial refuges. They have been extirpated from most of their historic ranges. Amargosa Desert Speckled Dace apparently were once found throughout the lower elevation reaches of the Owens River and tributaries (Snyder 1917).

Genetics/Genomics. The genomics-based analysis of Su *et al.* (2022) supports treating the Desert Speckled Dace as a widely distributed lineage, with three sub-lineages. The major lineage fits our definition of a species. The three sub-lineages can be regarded as subspecies: *R. n. nevadensis*, *R. n. caldera*, and *R. n. robustus* (described below). The analysis also shows that Speckled Dace from the Death Valley and Owens Valley regions share a recent ancestry (via the Amargosa River) but also show some divergence. They are best treated as Distinct Population Segments of *R. nevadensis nevadensis.*

Notes. This analysis supports the finding that the Desert Speckled Dace is a species with three geographically and genomically defined subspecies. However, most of its distribution is encompassed by *R. n. robustus* in the Lahontan Basin. See subspecies accounts for more details.

Etymology. Desert Speckled Dace is the new common name we propose for the Speckled Dace species which occurs in the Lahontan Basin and in the Owens and Death Valley systems. These regions are all very arid, and include Death Valley, one of the hottest and driest places on Earth. The first description of this species was based on specimens from Ash Meadows, Nevada, hence *nevadensis.* Genomics allows us to recognize three subspecies of Desert Speckled Dace that have been isolated from one another, Lahontan Speckled Dace, Amargosa Speckled Dace, and Long Valley Speckled Dace. Both the Lahontan Speckled Dace and the Amargosa Speckled Dace were originally described as species, *R. robustus* and *R. nevadensis*, respectively. However, they both also have a long history of being treated as subspecies of *R. osculus. R. nevadensis* is used as the species name for Desert Speckled Dace because it was described in 1893, nine years before *R. robustus* was described. The rules of zoological nomenclature declare that the oldest name used in a species description has precedence as the name for the species (International Code of Zoological Nomenclature, 1999, 4th Edition, Chapter 11, Article 50.4. 1999)

Rhinichthys nevadensis robustus **(Rutter 1903), new combination, Lahontan Speckled Dace**

Tables 2, 1g; Figs. 1,6

Agosia nubila carringtoni Jordan and Evermann 1896:311
Agosia robusta Rutter 1903:148; Rutter 1908:139; Snyder 1917:202
Apocope robusta Snyder 1918:33
Apocope robusta Evermann and Clark 1931:55
Rhinichthys osculus robustus Hubbs and Miller 1948 (a, b) and most subsequent publications.
Rhinichthys osculus robustus Hubbs *et al.* 1974:12
See *R. nevadensis* for additional synonyms

Holotype: USNM 50589, collected from Prosser Creek, California, Rutter and Atkinson (Rutter 1903).

Diagnosis. The Lahontan Speckled Dace fits the image of what Speckled Dace are expected to look like (Fig. 1). It is a small (adults usually <8 cm SL) active fish with blotches on the side that can merge to become a stripe leading to a dark band around the eye. The caudal peduncle is thick, about half the body depth, while the body is subcylindrical (robust). The head is bluntly pointed, with a tiny sub-terminal mouth. Fins are small (the dorsal fin usually has 8 rays, the anal 7 rays). Presence of tiny maxillary barbels at the corners of the mouth is variable as is the presence of a frenum. It is distinguished from the other two subspecies of *R. nevadensis* by genomics and by its being endemic to the Lahontan Basin in Nevada, Oregon, and California.

Description. The following is the original description from Rutter (1903:148) for Lahontan Speckled Dace. "Body heavy, highest above insertion of pectorals; the ventral outline curved almost as much as the dorsal. Head 3.8 to 4 in body; snout blunt, but little overlapping the premaxillary and never extending beyond it; mouth oblique, barbels usually absent, present on 10 to 50 per cent of specimens from any one locality. Fins small; D. 8; A. 7; pectoral about equal to head behind nostril variable; caudal moderately forked, middle rays two-thirds length of longest; rudimentary caudal rays forming prominent keels along upper and lower edges of tail; margin of anal slightly rounded, the anterior rays not all produced, not extending beyond posterior rays when fin is depressed. Lateral line nearly always incomplete, but with scattered pores frequently extending to base of caudal; scales 56 to

77, varying about 12 in any one locality. Usually two dusky lateral stripes, the upper extending from snout to caudal, the lower branching off from the upper behind the head and ending along base of anal; cheek abruptly silvery below lateral stripe; tinged with orange about lower jaw, upper end of gill-opening, and at base of lower fins (p. 148).

Note that the coloration described above is based on breeding colors. Hubbs *et al.* (1974) provide descriptions of the variety of pigmentation patterns present in scattered Speckled Dace populations in the Great Basin and elsewhere.

Distribution. Lahontan Speckled Dace are widely distributed in desert basins in northeastern California and northern Nevada (Fig. 3), as described by Hubbs *et al.* (1974). In California, Rutter (1903) collected specimens from Spring Creek, Willow Creek, Susan River, Little Truckee River, and Prosser Creek, all streams on the western edge of the Lahontan basin. It is also common in Eagle Lake and its inflowing streams (Lassen County) and in the watersheds of the Susan, Truckee, Walker and Carson rivers. The Truckee watershed includes Lake Tahoe and Prosser Creek (tributary to the little Truckee River), the type locality. More broadly, the range of this subspecies includes the drainage of pluvial Lake Lahontan, which covered much of northern Nevada and with fringes in California and Oregon (Hubbs *et al.* 1974). This region is mostly Great Basin Desert today and includes Pyramid Lake, Nevada, the largest remnant of Lake Lahontan, and the Humboldt River in Nevada. Wherever there is permanent water in the Lahontan Basin, Speckled Dace are likely to be encountered, including isolated populations in spring systems (Hubbs and Miller 1948a, Hubbs *et al.* 1974, Deacon and Williams 1984). They often co-occur with other Lahontan endemic fishes, such as Tahoe Sucker (*Catostomus tahoensis*), Lahontan Redside (*Richardsonius egregius*), Lahontan Tui Chubs (*Siphatales bicolor subspp.*) and Lahontan Cutthroat Trout (*Oncorhynchus clarki lewisi*) (Moyle 2002). In recent years, Lahontan Speckled Dace have managed to colonize the headwaters of the North Fork Mokelumne River (Central Valley watershed) as the result of a water project. Lahontan Redsides were also transferred by this same route (Garcia and Associates 2000).

Genetics/Genomics. Billman *et al.* (2010) analyzed mtDNA of dace from the Great Basin; they found support for three distinct lineages (clades): Lahontan, northern Bonneville (Snake River), and southern Bonneville. Smith *et al.* (2017), using mtDNA, meristics, morphometrics, and fossils, placed all Speckled Dace into three clades, Lahontan, Pacific Northwest (Columbia) and Colorado. Su *et al.* (2022), using genomics, provide strong support for Lahontan Speckled Dace as a distinct lineage that is a subspecies of Desert Speckled Dace, as are Amargosa Speckled Dace and Long Valley Speckled Dace.

Notes. Rutter (1908) found considerable overlap in morphometrics between Lahontan Speckled Dace and dace from the Sacramento drainage, so treated them together as one species. This move was generally not accepted, presumably because the fish faunas of the two basins are otherwise very different. Comparisons of meristics and other features of Lahontan Speckled Dace with those of other dace species and subspecies (including Amargosa and Long Valley Speckled Dace) reflect that there are no external features to easily distinguish the dace subspecies (Tables 2, 3, Figure 1). Our genomic analysis nevertheless shows that Lahontan Speckled Dace is a valid subspecies that is found throughout the Lahontan basin, wherever there is permanent water. The following lines of evidence support this conclusion.

Taxonomy. The Lahontan Speckled Dace was described by Rutter (1903) and recognized as a full species until ichthyologist Carl Hubbs and others started calling it a subspecies, *Rhinichthys osculus robustus.* This designation was justified by the lack of features easily separating it from other Speckled Dace taxa.

Geography/Geology. The distribution of Lahontan Speckled Dace coincides with the northern part of the region called the Great Basin Desert (Deacon and Williams 1984; Moyle 2002).

Genomics/genetics. Three genetic/genomic studies have shown that Lahontan Speckled Dace belong to a distinct evolutionary lineage as do the two other subspecies of Desert Speckled Dace (Oakey *et al.* 2004; Billman *et al*, 2010; Su *et al.*, 2022). The long isolation of this subspecies in the region is reflected in the lack of genomic evidence for recent hybridization with other dace species/subspecies.

Etymology. The Lahontan Speckled Dace was originally described by Rutter (1903) as *Agosia robusta* without explanation of the species name, although he described the body as heavy, perhaps reflecting the roundness of the body in cross-section, the blunt snout, and thick caudal peduncle. Gilbert (1893) also described the Amargosa Speckled Dace as being robust.

Conservation Status. The Lahontan Speckled Dace is widespread and abundant in many places in the Great Basin Desert and in streams and lakes of the Eastern Sierra Nevada. Because streams are increasingly dammed and diverted for human use, dace populations are increasingly fragmented. Speckled Dace are rare in or absent from most reservoirs. The safe status of Lahontan Speckled Dace should therefore not be taken for granted, especially in the face of climate change.

Rhinichthys nevadensis nevadensis **Gilbert 1893 new combination,**

Amargosa Speckled Dace. Table 3.

Synonymy. See Desert Speckled Dace, *Rhinichthys nevadensis*, account.

Holotype. See Desert Speckled Dace, *Rhinichthys nevadensis*, account.

Diagnosis. The Amargosa Speckled Dace is a cryptic taxon diagnosable with genomics and distribution as the Speckled Dace found in the springs, streams, and ditches of Death Valley, Owens Valley, and the Amargosa River. Individuals are typically small (8–11cm SL) and recognizable as Speckled Dace by their thick caudal peduncle, sub-cylindrical body, small fins, small eyes, and blunt pointed snout. The sides of the body are usually covered with black blotches which merge into a black stripe, which is especially dark below the eye. Gilbert's (1893:230) short diagnosis is: "Differing from other known species [of dace] by the large head, the short deep body, very small eye, and in the reduction of the outer ventral [fin] ray to a mere rudiment." He also noted the presence of an incomplete lateral line, of maxillary barbels, and of a conspicuous lateral stripe. See Table 3 for meristics. However, these characters, except genomics and distribution, do not separate the three *R. nevadensis* subspecies from one another.

Description. The formal description of Amargosa Speckled Dace (as a species) by Gilbert (1893) is thorough (Figure 6) and is included in this paper as the description of Desert Speckled Dace, *R. nevadensis.* Scoppettone *et al.* (2011) measured 1354 dace from the Amargosa River Canyon, which had a mean fork length of 51mm and a maximum FL of 92 mm FL. None of Gilbert's characters separate the regional Speckled Dace populations from one another, demonstrating the cryptic nature of Speckled Dace taxa.

Sada *et al.* (1995) performed a principal component analysis on 20 morphological measurements (truss analysis) and eight meristic characters on 484 Speckled Dace (386 Amargosa Speckled Dace and 98 Lahontan Speckled Dace) from 13 localities (Table 3); they found that "Meristic and proportional mensural characters were all within ranges documented for Speckled Dace…Highly significant differences among all populations for all characters showed the morphology of each population to be unique (Sada *et al.* 1995:352–353)." Essentially, they found evidence of local adaptation and genetic drift, but no features that could readily distinguish individual Amargosa Speckled Dace from individuals in other regional dace populations, including Lahontan and Long Valley Speckled Dace. Lahontan Speckled Dace, however, did have slightly more lateral line scales than the other two subspecies but overlap in scale counts and incomplete lateral lines in many individuals makes this character unreliable for identification (Table 3).

Distribution. Gilbert (1893) reported the distribution of *R. nevadensis* as warm water springs in Ash Meadows, Indian Creek, and Vegas Creek, Nevada. Vegas Creek has been covered up by Las Vegas and its endemic Speckled Dace, *Rhinichthys deaconi*, is extinct (Smith *et al.* 2017). The Amargosa Speckled Dace is endemic to springs, small streams, and rivers in the Death Valley system (which includes the Owens Valley) in California and Nevada (Figure 3). In the Owens Valley, it is assumed they once were found throughout the length of the Owens River (Snyder 1917). For more details of distribution see the Notes section of this account.

Genetics/genomics. Early genetic studies generally concluded that Speckled Dace from the Death Valley region were all one lineage but included branches variously designated as Owens, Ash Meadows, Amargosa River, and Long Valley Speckled Daces. Thus, Sada *et al.* (1993, 1995) used protein electrophoresis to examine relationships among dace from 13 localities in the region and from the once-interconnecting Amargosa River. They found that all populations had some statistically identifiable features and that the regional Speckled Dace populations likely diverged from Lahontan Speckled Dace after vulcanism and drying-up of interconnecting waterways isolated them in the Death/Owens Valley region. Oakey *et al.* (2004), using mt/DNA found that all populations of Speckled Dace in the region formed a clade. The genomic analysis of Mussmann *et al.* (2020) produced similar results. They recommended that the populations be treated as Distinct Population Segments within the Amargosa Speckled Dace lineage because they met three criteria: current geographic isolation, genetic differentiation, and local adaptation.

According to Mussmann *et al.* (2020:13) "the identities of the various lineages is intimately tied to the prehistoric lakes and rivers of the region, with diversifications occurring within modern drainages. This pattern clearly reflects a relictual biodiversity with high endemicity, with patterns driven by Plio-Pleistocene tectonics and hydrology (i.e., dispersal of Speckled Dace from Owens Valley to the Amargosa Basin during fluvial events)…". The analysis of Su *et al* (2022) agrees with this statement and recognizes that the Desert Speckled Dace includes three subspecies-level lineages (Lahontan, Amargosa, and Long Valley) with the Lahontan lineage likely being the most immediate ancestral population.

Notes: Subspecies. The Amargosa Speckled Dace is here designated as a subspecies of Desert Speckled Dace (*Rhinichthys nevadensis)*, going back to Gilbert's original description and name, based on the following lines of evidence:

Taxonomy. The Amargosa Speckled Dace has been a stable taxon since it was described, although it was mysteriously switched from being a species to a subspecies of *Rhinichthys osculus* in the 1940s, following the Great Basin studies of Hubbs and Miller (1948) and Miller (1946). Gilbert's original description only encompassed dace in Ash Meadows, leaving as undescribed other dace populations in the Amargosa River, Oasis Valley, and Owens Valley. The undescribed forms have been variously lumped with Amargosa (Moyle 1976) or Lahontan Speckled Dace (Snyder 1917, 1918) or treated as undescribed subspecies of *R. osculus* (Miller 1973). Moyle *et al.* (2015) divide the Death/Owens Valley daces into Long Valley, Owens, and Amargosa populations. Su *et al.* (2022), however, show that the Owens Valley populations are best treated a part of the Amargosa subspecies, *R. nevadensis nevadensis.*

Zoogeography. During pluvial periods of the Pleistocene, the Death Valley and Lahontan regions supported many interconnected large lakes, with abundant fishes (Hubbs and Miller 1948). When the climate changed and frequent precipitation stopped, the lakes and rivers dried up or became small, disconnected remnants of what they once were. As a result, the Death Valley region became an endemism hot spot with numerous endemic plants and animals in springs and wetlands (Sada *et al.* 1995). The fish that survived became restricted to relatively small areas where permanent stream flows were created by springs, which is where we find them today. For Speckled Dace, this process resulted in numerous isolated populations with little opportunity for genetic exchange in the present landscape. In Death Valley proper, including Ash Meadows, the Speckled Dace shares spring systems with four species and eight subspecies of pupfish (*Cyprinodon* spp.). In the Owens Valley, other endemic fishes are Owens Tui Chub (*Siphatales bicolor snyderi*), the undescribed Toikona Tui Chub (Chen *et al.* 2007), Owens Sucker (*Catostomus fumeiventris*) and Owens Pupfish (*Cyprinodon radiosus*).

Genomics. Su *et al.* (2022) support Amargosa Speckled Dace as a distinct lineage within Desert Speckled Dace.

Note: Distinct Population Segments. The Federal Endangered Species Act of 1973 defines species fairly broadly for fishes and other vertebrates. The act recognizes that populations that are distinct and important segments (usually defined by genetics and distribution) of a species total population can be listed as Threatened or Endangered, even if the species is not so listed. To be recognized, Distinct Population Segments (DPSs) do not go through a formal taxonomic description process.

Thus, Mussmann *et al.* (2020) used genomics to determine that the populations of Desert Speckled Dace could be divided into three DPSs: Long Valley, Owens River, and Oasis Valley. "Ash Meadows and Amargosa River populations are included within the Oasis Valley DPS. In addition, they recognized that dace in Amargosa Canyon are of hybrid origin (Amargosa X Ash Meadows). We treat this fish as a population of Amargosa Speckled Dace. Our analysis agrees with Mussmann *et al.*, (2020) that the Long Valley Speckled Dace are sufficiently different to be recognized as a subspecies. However, our analysis also recognizes Ash Meadows and Owens Valley Speckled Dace as two DPS's within Amargosa Speckled Dace.

The Ash Meadows Speckled Dace was first described from springs and their outflows in Ash Meadows. Genetically similar fish occupy similar habitat in the Oasis Valley, Nevada. In some years, the water from both areas ultimately flows into the Amargosa River and down into Amargosa Canyon. Therefore, this DPS includes daces from Ash Meadows, Oasis Valley, and Amargosa Canyon, including Willow Creek (Mussmann *et al.* 2020).

The Owens Valley Speckled Dace is found only in streams, springs and ditches of the Owens Valley, California. It was considered by La Rivers and Trelease (1962) and Moyle (1976) to be a population of Amargosa Speckled Dace (*R. osculus nevadensis)*. Sada (1989) and Sada *et al.* (1993, 1995) showed it was genetically and morphometrically separable from populations in Ash Meadows, Amargosa River, and Long Valley. Moyle (2002) and Moyle *et al.* (2015) recognized it as an undescribed subspecies related to Amargosa Speckled Dace. Otherwise, synonymies are as for the species (*R. nevadensis*) and subspecies (*R. n. nevadensis*, *R. n. caldera*).

Etymology. This subspecies, as the species *Rhinichthys (Apocope) nevadensis*, was described by Gilbert

(1893:230) from “Ash Meadows, Amargosa Desert, on boundary between California and Nevada” hence the common and scientific names. The springs in Ash Meadows ultimately drain into the Amargosa River, which flows into Death Valley. Amargosa is derived from a Spanish word meaning bitter and refers to the unpalatability of the water. Jordan and Evermann subsequently (1896) placed the species in *Agosia.* The members of this genus were returned to *Rhinichthys* in the 1940s and the species simultaneously became a subspecies of *R. osculus*, both without a formal process.

Conservation Status. All populations of *R. n. nevadensis* are threatened with extinction to a greater or lesser degree. In 1984, the Ash Meadows population was listed as endangered under the federal Endangered Species Act of 1973. The Center for Biological Diversity (2020) has petitioned to have all Speckled Dace in the Death Valley and Owens Valley region be included under that listing, albeit with a separate listing for Long Valley Speckled Dace. The main populations of Speckled Dace in the Owens Valley are in highly modified habitats in North Fork Bishop Creek and Lower Horton, Pine, and Rock creeks, and associated ditches near Bishop (N. Buckmaster, unpublished observations). Their need for special protection is illustrated by recent disappearance of the isolated Benton Valley population of Owens Speckled Dace (N. Buckmaster unpublished observation, 2022). While captive populations are maintained by the California Department of Fish and Wildlife (CDFW), it is a tenuous situation for the long-term survival of these dace. Long Valley, Amargosa River, and Owens Valley Speckled Dace are all listed as Species of Special Concern by CDFW (Moyle *et al.* 2015). The causes of endangerment of dace are documented in Moyle *et al.* (2015) and in Center for Biological Diversity (CBD 2020).

***Rhinichthys nevadensis caldera*, new subspecies, Long Valley Speckled Dace**

Table 3, Fig. 4.

Synonymy: Rhinichthys *osculus subsp.* Sada *et al.* 1995:356; Moyle 2002:161.
Otherwise see synonyms for Desert Speckled Dace, *Rhinichthys nevadensis.*

Holotype: WFB 5000 (Fig. 4). Standard length 60 mm, fork length 70 mm; White Mountain Research Center, Northeast Pond 37.360618°N 118.329370°W. Inyo County, California, July 29, 2021. Nicolas Buckmaster, Rosa Cox, California Department of Fish and Wildlife

Paratypes: WFB 5001-5009 (n=9). Same as holotype.

Meristics: holotype (paratypes)

Lateral line scales: 64 (59–80). Lateral line incomplete.

Scales above lateral line: 10 (9–12), scales difficult to discern.

*Scales below lateral line:*9 (6–10), scales hard to discern

Dorsal-fin rays: 8(7–8), counts include single unbranched ray.

Anal-fin rays: 7 (6–7), counts include single unbranched ray.

Pectoral-fin rays 13 (11–12), counts include anterior and posterior single unbranched rays.

Pelvic 7 (6–8), counts include single unbranched ray.

Caudal-fin rays 19 (19).

Diagnosis. The Long Valley Speckled Dace is a cryptic taxon, very similar in its meristics to the Amargosa Speckled Dace (Table 3). They are distinguished from other Speckled Dace by their being endemic to the Long Valley region and having a distinct evolutionary lineage, as revealed by genomics (Su *et al.* 2022). Adults are small (rarely more than 75 mm SL) and recognizable as Speckled Dace by their thick caudal peduncle, sub-cylindrical body, small fins, small eyes (relative to head), and blunt, pointed snout. In life, they are a bronzy color with light speckling (Fig. 6). Striping is largely absent. Maxillary barbels and a frenum are usually absent. They can be distinguished statistically from similar Amargosa Speckled Dace by slightly higher average numbers of pectoral and pelvic, higher lateral line scale count, lower lateral line pore scale count, and absence of maxillary barbels (Sada *et al.* 1989, 1995). The following mean counts (standard error) are from Long Valley Speckled Dace collected in Whitmore Hot Springs and at an unnamed spring at Little Alkali Lake (Sada 1989, Table 3): lateral line scales 61.7 (1.4); lateral line scales with pores 19.0 (5.0); dorsal-fin rays 8.0 (0.0); anal-fin rays 7.0 (0.0); pectoral-fin rays 13.0 (0.4); pelvic 7.4 (0.2).

Description. Long Valley Speckled Dace are small, active fish with the typical Speckled Dace morphology, as described for the species.

Genetics/Genomics. Sada *et al.* (1989, 1995), using isozymes and morphometrics, were the first to recognize Long Valley Speckled Dace as different from other dace populations in the region. Oakey *et al.* (2004), Mussmann *et al* (2020) and Su *et al* (2022) all found genetic differences that separated Long Valley Speckled Dace from Amargosa and Lahontan Speckled Dace.

Distribution. The historic range of this dace was in the outlets of hot springs and associated marshes in the remains of the Long Valley volcanic caldera, just east of Mammoth Lakes, Mono County, as well as in Hot Creek. It quite likely had its origins when Speckled Dace colonized the upper Owens Valley region from the Mono Lake Basin via Adobe Valley, during a late Pleistocene pluvial period. During this time, Mono Lake levels were high enough so that it periodically spilled into Adobe Valley, which drained into the Owens River, from which fish presumably moved upstream into Long Valley. Subsequent down-faulting of the Owens River and formation of steep waterfalls in the Owens River gorge likely isolated Long Valley from the Owens Valley around 100,000 years ago (Hildreth and Fierstein 2016).

Note. Long Valley Speckled Dace were considered to be one of the scattered populations of Owens Valley Speckled Dace until Sada *et al.* (1993, 1995) showed it was genetically and morphometrically distinct and that it was closely related to dace populations in Ash Meadows, Amargosa River, and elsewhere in Owens Valley and Death Valley. Moyle (2002) and Moyle *et al.* (2015) recognized it as an undescribed subspecies. Our analysis shows that the Long Valley Speckled Dace is a distinct lineage confined to a small part of the Owens Valley region. It merits subspecies designation based on the following lines of evidence.

Taxonomy. Multiple analyses indicate that Long Valley dace is a distinct lineage (subspecies) within Desert Speckled Dace, *R. nevadensis* (Oakey *et al* 2004, Mussmann *et al.* 2020, Sada *et al.*1995, Moyle 2002, Moyle *et al.* 2015 and Su *et al.*, 2022).

Geography/geology. During pluvial periods of the Pleistocene, the Death Valley region was a series of interconnected large lakes, with abundant fishes (Hubbs and Miller 1948). When the climate changed and heavy precipitation stopped falling, the lakes and rivers dried up or became small remnants of what they once were. This process resulted in numerous isolated Speckled Dace populations with little, or at least very infrequent, opportunity for genetic exchange. See Desert Speckled Dace account for more details.

Long Valley is part of the Death Valley regional endemism hotspot with numerous endemic plants and animals, including fishes (Sada *et al.* 1995). Long Valley Speckled Dace can be regarded as another organism endemic to the isolated Owens Valley region.

Genetics/genomics. Sada *et al.* (1993, 1995) were first to recognize that Long Valley Speckled Dace were genetically distinct from other dace, a finding confirmed by other studies (Mussmann *et al.* 2020, Su *et al.* 2022). See Amargosa Speckled Dace (*R. nevadensis nevadensis*) description for more details.

Etymology. The Long Valley Speckled Dace was historically known only from small streams flowing into the Long Valley Caldera, the remnants of a gigantic volcano that last erupted 0.7 million years ago (Hildreth and Fierstein 2016). They colonized the remnants of the caldera during the late Pleistocene, hence *caldera*.

Conservation Status. Long Valley Speckled Dace have been extirpated from all but one of their historic collection sites, including Hot Creek. The only population left in its native range (as of 2021) is in Whitmore Marsh and its inlet stream in Long Valley (Moyle *et al.* 2015). Unfortunately, this marsh is now maintained by the outflows of a hot spring system that has been developed as a public swimming pool by the Town of Mammoth Lakes. Discharge is approximately 2 cfs and is lightly chlorinated. The outlet stream feeds an alkaline marsh of roughly 1 acre. In 1989, dace occupied 250 meters of stream and two large shallow ponds less than a half meter deep (Moyle *et al* 2015). Surveys in 2002 and 2009 by CDFW found this population to be relatively stable (S. Parmenter, CDFW, pers. comm. 2009). In 2018, 2019, and 2020, they were not found in these habitats (S. Parmenter, CDFW, in Center for Biological Diversity, 2020). However, in 2021 and 2022, trapping produced a few fish (R. Black, CDFW, pers. comm, 2021). The only other population is in a single artificial pond into which they were introduced at the White Mountain Research Center, outside their native range; the status of this dace population is checked by CDFW on a routine basis (R. Black, CDFW, pers. comm.).

The multiple causes of decline are discussed in Moyle *et al.* (2015) and Center for Biological Diversity (2020). The CBD (2020) has petitioned to have this dace listed as endangered under the federal ESA or else have all Speckled Dace in the Death Valley region included under the 1984 listing of Ash Meadows Speckled Dace as endangered. It is listed as a Species of Special Concern (critical concern) by CDFW.

Rhinichthys klamathensis **(Evermann and Meek 1898), Western Speckled Dace**

Fig. 6.

Agosia klamathensis Evermann and Meek 1898:74; Snyder 1908:98
Apocope klamathensis Evermann and Clark 1931:55
Rhinichthys osculus klamathensis Shapovalov and Dill 1950:386; Hubbs *et al.* 1979:12; Shapovalov *et al.* 1981:25; Moyle 2002:161; Markle 2016:50

Holotype: USNM 48225 (64 mm SL) as *Agosia klamathensis* Evermann and Meek 1898. November 3, 1896, mouth of small creek flowing into Pelican Bay, Upper Klamath Lake, Oregon, USA, Seth Meek and A.R. Alexander.

Paratypes. USNM 48231 (39 specimens) and 125012 (38 specimens). Same date and place as holotype.

Diagnosis. A cryptic species readily recognized as Speckled Dace by small adult size (6–11 cm SL) and distinctive body shape. Dark blotches on sides merge into a line of dark pigmentation below eye, to snout. Meristics are in Table 3. The best way to characterize this abundant fish is as a distinct Speckled Dace lineage found throughout the Klamath, Sacramento, and Warner watersheds with three sub-lineages that cannot be readily distinguished from one another.

Description. According to Evermann and Meek (1898:74-75, Fig. 6) *"*the fish from [Upper Klamath Lake]… possess certain characters which serve to distinguish it from *A. nubila*. While the differences are slight, they are plainly evident and must be recognized, and we therefore describe it as a new species (p. 74). Head 4 [times into standard length]; depth 4.5; eye 4.5 in head; D[orsal rays]i.8; A [anal rays] i,7; [lateral line] scales about 14–78–10 (average, 73 in 49 specimens)."

Body robust, subcylindrical, back somewhat elevated; snout rather long, mouth inferior, little oblique, the lower jaw included; maxillary not reaching front of orbit; upper lip without frenum; barbels present but small. Lateral line incomplete, interrupted in many places, about 30 pores developed. Origin of dorsal fin midway between front of pupil and base of caudal fin; pectorals rather short, reaching about three-fourth the distance to ventrals; ventrals reaching vent; anal[fin] large, its longest ray 1.5 in head.

Color in alcohol, olivaceous, mottled and blotched with darker on back and sides; under parts pale; an obscure pale streak from eye to base of caudal fin, below which is a broad dark band; dorsals, pectorals, caudal dusky; other fins plain; a black blotch at base of caudal. This form is distinguished from *Agosia nubila* chiefly by the smaller size of the scales. *A. nubila* has 49–66 lateral line scales (mean 57, n=73), while *A. klamathensis* has 68–78 *(mean 73*, *n =49)*.

Overall, there are only minor (statistical) differences among the three subspecies from this basic description. However, Markle (2016) used lateral line scale number as the principal character to separate Western Speckled Dace from other dace taxa in Oregon. In contrast, Smith *et al.* (2017) could not readily distinguish lineages despite multivariate analyses of combined meristic, morphological, mtDNA, and fossil data from the entire region in which Speckled Dace *sensu lato* occur.

Distribution. The Western Speckled Dace is found throughout the Klamath and Sacramento watersheds, including streams as far south as the Santa Maria River in southern California. Its distribution in the Warner basin is mostly in springs and small cool-water streams. Only the headwaters of Twelvemile Creek are in California (Modoc County). Before the introduction of non-native game fishes, it probably had a wider distribution within the basin. See the subspecies accounts for more detailed distributional information.

Note: Geology. The Klamath River has not been connected to the ancestral Sacramento River system since the end of the Pliocene (*ca.* three mya); however, extensive deformation (*e.g.* down-faulting of the Klamath Graben) and vulcanism (both from the Cascade-arc and Medicine Lake volcanic fields) occurred almost continuously in the northern Sacramento and southern Klamath Basins (Colman *et al.* 2004). It is probable that this activity led to repeated drainage captures of between the two basins and allowed for intermittent gene flow among dace populations. Inter-basin connectivity presumably was less frequent between Klamath/Sacramento streams and those in the Warner Basin. The development of the Great Basin faulting and extension belt of down-faulting resulted in creation of the Warner Range (*ca.* 3 mya) which resulted in a permanent topographic separation of the basins sometime in the late-Pleistocene (1.0–0.1 mya) (Egger *et al.* 2011).

As the result of these active geologic processes, each of the three major subspecies of *R. klamathensis*, as discussed here, is endemic to a single large watershed, plus some coastal watersheds in the case of Sacramento Speckled Dace. They share these waters with other endemic fishes. Dace ultimately colonized these three watersheds from the ancient Columbia River Basin during a series of volcanic and other geologic events that caused the predecessor of the upper Snake River to flow into the Pacific Ocean via the Klamath-Sacramento region, apparently during the Pliocene period. Fish fossils from ancient deposits in the Idaho region, that predate the rise of the Sierra Nevada and coastal mountain ranges, indicate a source of the predecessors of the highly distinctive endemic fish fauna of the lower Sacramento-San Joaquin Watershed (Minckley *et al.* 1986). It is likely that the Speckled Dace was not part of those early colonization events but arrived later, during a period when volcanic activity caused the upper Pit River to switch from flowing into the Sacramento River to flowing into the Klamath instead, which had its own endemic fish fauna. Some Klamath fishes (*e.g. Cottus* spp., *Siphatales bicolor*) were able to colonize the upper Pit watershed as a result. The ancestral Pit River then broke through the volcanic dike barrier and rejoined the Sacramento River system, bringing in its water members of the Klamath fish fauna. Alternately, Smith *et al.* (2017) suggest colonization of the Sacramento system could have come from a pass through the southern Sierra Nevada that apparently was open 3.2 million years ago or earlier. However, the genomic similarities between Sacramento and Klamath daces and between them and Warner Speckled Dace are presumably the result of their ancestors colonizing the region during a long geologically active period in the Klamath-Pit region. The genomic study of Su *et al.* (2022) supports this view (Figure 2) and that the Western Speckled Dace merits full species status.

Note: History. The three lineages that make up this species have different taxonomic histories (Evermann and Clark 1931, Moyle 2002). The Klamath Speckled Dace was recognized in 1898 as a species, and it retained its identity even when subsumed as a subspecies under *R. osculus.* The Sacramento Speckled Dace was largely ignored as a taxon despite its abundance and wide distribution. Presumably early workers such as Cloudsley Rutter, Charles Gilbert, and John Otterbein Snyder saw that it could not be readily distinguished from other Speckled Dace and accepted by default the use of an improper name (some variant of *Agosia carringtoni*) or else treated it as Lahontan Speckled Dace. The Warner Speckled Dace came to our attention because of controversy over the status of the population in remote Foskett Spring, which modern genetic analysis showed to be part of the Warner Speckled Dace lineage described in this paper. Su *et al.* (2022) show that, based on genomics, the three lineages are similar enough so that together they can be treated as a single species, *Rhinichthys klamathensis.*

Nevertheless, all three populations are isolated from one another, with long independent histories. The early history of each basin includes one or more periods of ancient interconnectedness which allowed Speckled Dace to colonize all three basins. The three lineages co-occur with other endemic fishes in their respective basins. The endemic fishes in each basin have close relatives in the other basins (*e.g. Siphatales bicolor subspp.*), as well as species unique to each basin.

Etymology. The name 'Western Speckled Dace' (Markle 2016, Smith *et al.* 2017) covers three lineages: Klamath Speckled Dace (*R. k. klamathensis*), Sacramento Speckled Dace (*R. k. achomawi*) and Warner Speckled Dace (*R. k. goyatoka*). Only the Klamath Speckled Dace has been previously named, so *R. klamathensis* becomes the species epithet for three subspecies. Klamath is an anglicized version of a name for the native peoples inhabiting the upper Klamath Lake region in Oregon (Gudde and Bright 1998). See subspecies accounts for further explanations.

Conservation Status. Sacramento and Klamath Speckled Dace are wide-spread and abundant in the large basins they inhabit. Warner Speckled Dace, including the population in Foskett Spring, are limited by the low availability of water in the desert Warner Basin. Their populations for now seem reasonably secure, although the basin has been invaded by non-native species. The Foskett Spring population was listed in 1985 as a Threatened species under the federal Endangered Species Act but it was delisted in 2019, following implementation of the recovery plan.

***Rhinichthys klamathensis klamathensis*, new combination, Klamath Speckled Dace,**
Fig. 6

Synonymy. Same as for Western Speckled Dace, *R. klamathensis*.

Holotype and paratypes are the same as for Western Speckled Dace, *R. klamathensis*.

Diagnosis. Same as Western Speckled Dace, *R. klamathensis*; the Speckled Dace lineage that is abundant in the streams, lakes, and other aquatic habitats in the Klamath River Basin in Oregon and California, including the Trinity River in California. Distinguished statistically by having somewhat smaller scales (scales in lateral line, 68–78; mean 73, n =49) than the other two subspecies (Sacramento, 54–83, mean 70, n=123; Warner, 68–71, mean 69, n=58). Otherwise, it is not distinguishable from other Speckled Dace except by genomics and distribution.

Description. Evermann and Meek (1898) described this cryptic subspecies as *Agosia klamathensis*. Therefore, the description quoted in the Western Speckled Dace account is also for this subspecies, and it applies to the other two subspecies as well.

FIGURE 6. Top. Holotype, Lahontan Speckled Dace, from Rutter (1903). Middle, Long Valley Speckled Dace from Whitmore Marsh, 2014, showing life colors. Photo by Jacob Katz. Bottom: Western Speckled Dace, type specimen, from Evermann and Meek (1898).

Distribution. The Klamath Speckled Dace is found throughout the Klamath Basin in Oregon and California, including the Klamath and Trinity rivers and tributaries, as well as in the Rogue River to the north (Wiesenfeld *et al.* 2017). It is also widespread in the upper Klamath Basin, including Upper Klamath Lake. The Speckled Dace in the Eel River, to the south of the Klamath Basin, is an introduced population of *R. k. klamathensis* (Kinziger *et al.* 2011).

Geology/zoogeography. The geologic history of the Klamath region is complex. The Snake River, now a tributary to the Columbia River, was once a major river that originated in the Idaho region and flowed to the ocean via the ancestral Klamath River during the Pliocene (Minckley *et al.* 1986, Smith *et al* 2017). When the Snake broke through to the Klamath, it carried with it the lake fauna of the Great Basin, which gave rise to the present-day endemic, freshwater-dispersing fish fauna (12 species) of the upper Klamath basin (Moyle 2002), presumably including Speckled Dace. Pfrender *et al.* (2004:498), using a molecular clock based on mtDNA from Speckled Dace from the major river basins of Oregon, speculated that "…the levels of sequence divergence in *R. osculus* among these major basins are more consistent with a Pliocene or Miocene sundering of gene flow between major basins. Miocene isolation of these river systems is substantially earlier than has previously been suggested." They thought such ancient divergence could explain the genetic diversity found in dace within the Klamath basin, a diversity that was also documented by Wiesenfeld *et al.* (2017). See also the geology discussion under Western Speckled Dace.

Geographically, Klamath Speckled Dace co-occur with other fish species endemic to the Klamath watershed. However, the endemic fishes in the upper watershed (above Klamath Falls) are different from those in the lower river and it appears that dace from the two regions diverge as well, a situation noted also for Marbled Sculpin, *Cottus klamathensis* (Daniels and Moyle 1984).

Genetics/genomics. The genomic study of Su *et al.* (2022) unveiled the three lineages within *R. klamathensis*, as discussed. Within the Klamath drainage, Wiesenfeld *et al.* (2017:8), using analyses of microsatellites and mtDNA, found that The Klamath–Trinity Basin Speckled Dace were resolved as nearly monophyletic [bootstrap (BS) 77], and exhibited a sister group relationship with nearby basins in California and Oregon (Sacramento, Pit River, and Goose Lake). The Klamath River and Trinity River populations, however, were found to be sufficiently distinct to suggest the two rivers were once isolated from one another, with their connection being fairly recent. The presence of apparent hybrids in the region where the two rivers meet today also supports this conclusion (Wiesenfeld *et al.* 2017). A genetically distinct population is also found in Jenny Creek, a tributary to the Klamath River that is largely in Oregon (Wiesenfeld *et al.* 2017).

Pfrender *et al* (2004) used mtDNA to compare dace from the upper Klamath and Rogue rivers with those from two tributaries to the Columbia River in Oregon. They found species-level differences between dace in the two great watersheds, with estimated divergence times of 3.9 to 9.6 million years ago. Within the upper Klamath basin, Pferender *et al.* (2004) found considerable genetic structure but of more recent origin (< 1 million years), including Jenny Creek as a distinct population.

Overall, analysis of mtDNA data of dace from their entire range showed that dace from the Klamath, Sacramento, and Warner basins share much of the same lineage; together they form a separate lineage within the Northwest clade of Smith *et al.* (2017).

Note. The Klamath Speckled Dace was originally described as a species that differed from other Speckled Dace by having finer scales (Evermann and Meek 1898). Subsequently, it retained its identity as a subspecies, *R. osculus klamathensis.* This is not surprising given that the Klamath Basin has long been recognized as an isolated basin which supports high endemism in its fishes (Moyle 2002). The Klamath Speckled Dace has retained its identity through the region's complex geologic history, enduring the rise of mountain ranges, high levels of vulcanism, and invading interior rivers (Minckley *et al.* 1986). This complex geologic history has kept the Klamath fish fauna isolated and distinct. In the upper Klamath basin, Speckled Dace live with other endemic fishes that had their ancestors in the Great Basin. Even in the lower Klamath River, which is too swift for the lake-adapted fishes of the upper basin, it co-occurs with the endemic Klamath Smallscale Sucker, *Catostomus rimiculus* (Moyle 2002). Given the genetic structure that Wiesenfeld *et al.* (2017) found in the basin, it is possible that dace populations from the upper and lower river should be treated as separate subspecies. Su *et al.* (2022) confirmed results from other genetic methods that the Klamath Speckled Dace is a distinct evolutionary lineage.

Etymology. The Klamath Speckled Dace is named for the river system to which it is endemic. The river is named for the native peoples who lived (and still do) in the upper Klamath Basin.

Conservation Status. The Klamath Speckled Dace is widespread and abundant in streams and natural lakes in the Klamath Basin, including the Trinity River. The main concern is that some distinct populations, such as in Jenny Creek, may be lost as the waters are dammed and diverted. The genetic diversity of Speckled Dace populations within the river system is just beginning to be appreciated (Pfrender *et al.* 2004; Wiesenfeld *et al.* 2017).

***Rhinichthys klamathensis achomawi*, new subspecies. Sacramento Speckled Dace.**
Figs. 1, 4D,

Synonymy. See *R. klamathensis* account for subspecies synonymies.

Holotype: WFB-3171 (Figure 1), 70 mm SL. Bear Creek at Pondosa Bridge,1.6 km SW of Pondosa, Siskiyou County, California. 41.1884°N -121.700667°W._July 20, 2015. Jason Baumsteiger, Mollie Ogaz, Christopher R. Jasper, Tyler R. Goodearly, and Matthew J. Young

Paratypes WFB-3171a-3171i (n=9) . data the same as holotype.

Meristics: holotype (paratypes)

Standard length: 70 (41–56 mm)

Lateral line scales: 74 (63–73). Lateral line incomplete in most; counts include 2–3 scales beyond lateral line.

Scales above lateral line: 13 (11–14)

Scales below lateral line: 9 (8–10)

Dorsal-fin rays: 8(8), *counts include single unbranched ray.*

Anal-fin rays: 7 (7), *counts include single unbranched ray.*

Pectoral-fin rays 15 (12–15), *counts include unbranched rays.*

Pelvic 7 (8–9), *counts include unbranched rays.*

Caudal-fin rays 19 (19).

Basic morphology is described below. Barbels and frenum are usually present.

Diagnosis. Same as for Western Speckled Dace, *R. klamathensis*. Distinguished by distribution and genomics as the Speckled Dace endemic to aquatic habitats in Sacramento River drainage basin and associated coastal drainages.

Description. Sacramento Speckled dace are identical to Klamath, Warner, and Lahontan Speckled Dace based on meristics and morphometrics. This is presumably the reason they have been undescribed for so long. The general description of Speckled Dace in Moyle (2002:161) was based on Sacramento dace, so fits the subspecies well:

The Speckled Dace is a small (usually <8 cm SL, occasionally to 11 cm SL), highly variable species distinguished by a thick caudal peduncle, a small subterminal mouth, a pointed snout, and small scales (47–89 in lateral line). The origin of the dorsal fin (6–9 rays, usually 8) is well behind that of the pelvic fins. The anal fin normally has 7 rays (6–8). The pharyngeal teeth (1,4-4,1 or 2,4-4,2) are strongly hooked and have only a slight grinding surface Color is highly variable but most fish over 3 cm SL have dark speckles on the sides and back, dark blotches on the sides that often coalesce to resemble a dark lateral band, and a stripe on the head that runs through the snout. The background color on the back and sides is dusky yellow to dark olive, with the belly yellowish to whitish. The bases of the fins of both sexes turn orange to red during breeding and males often have red snouts and lips as well. Presence of maxillary barbels and a frenum is variable.

Rutter (1908:140) noted that Sacramento dace were quite variable in their characteristics and found that Sacramento dace from 12 localities (n=94) had 49–77 scales in the lateral line, 7–9 dorsal rays, and 6–8 anal rays. Cornelius (1969) using data from six localities, counted 54–82 scales on the lateral line (mean 70, n = 123); other counts: scale rows above the lateral line (12–20, mean 16, N = 124) scale rows below lateral line (10–19, mean 14, n = 121), vertebrae (34–39, mean 37, n=99), dorsal-fin rays (7–9, mean 8, n=131), anal-fin rays (5–8, mean 7, n =129). See also Table 3.

Distribution. The Sacramento Speckled Dace is found in streams and lakes in the Goose Lake (Oregon and California) and Pit River watersheds, the Sacramento River and its tributaries, the Salinas basin, and, in the far south, San Luis Obispo Creek, Arroyo Grande, and the Santa Maria River (Figure 3). It is conspicuous by its absence from the San Joaquin River watershed, although Rutter (1908) collected two small dace from the Kings River at Centerville. Collections made on Los Gatos Creek, an east-side tributary to the San Joaquin River, in 1941 contained Speckled Dace but there are no records of them since then (R. Leidy, pers. comm., 2021).

Sacramento Speckled Dace are absent naturally from the Russian River watershed and from all other coastal watersheds, except the San Lorenzo River, Salinas River, San Luis Obispo Creek and the Santa Maria River in southern California. They are also absent from Clear Lake (Lake County) and its tributaries. However, they are present in Cache Creek which flows out of Clear Lake (Moyle 2002, unpublished data).

TABLE 3. Mean values of meristics of Amargosa Speckled Dace (from Amargosa River, Ash Meadows, and Owens Valley) compared to Long Valley and Lahontan Speckled Dace, from Sada *et al.* (1993). LLS, lateral line scales; LLP, lateral line scales with pores, PFR, pectoral-fin rays; PEFR, pelvic; Vert, vertebrae; Barbels, percent with maxillary barbels; STB canal, percent with a complete supratemporal canal; Frenum, percent with complete frenum. All counts are mean numbers.

Locality	N	LLS	LLP	PFR	PEFR	Vert	Barbels (% with)	ST canal (%)	Frenum (% present)
Amargosa River									
Tecopa	34	54	27	13	7	37	90	100	0
Beatty NV	54	56	51	13	7	37	100	100	0
Ash Meadows									
Bradford Spring, NV	10	48	32	13	7	37	100	100	0
Tubbs Ranch NV	10	48	40	14	7	37	40	100	0
Owens Valley									
A1 Drain	30	62	42	13	7	37	100	100	0
Pine Creek	31	63	45	13	7	37	80	100	0
Little Lake	49	65	62	13	7	37	100	100	0
Canal, S Bishop	30	62	42	13	7	38	90	100	0
Marble Creek	35	55	13	13	7	37	100	100	0
Long Valley									
Whitmore Marsh	59	62	26	14	7	36	0	100	0
Hot Creek	29	60	20	14	8	37	0	90	0
Lahontan Basin									
Huntington Cr	39	63	50	13	8	37	80	80	0
Reese River NV	59	68	66	14	8	39	100	50	100

Zoogeography. The Sacramento basin is a large, well-defined region, isolated by the Sierra Nevada Range on the east, the Coast Range on the west, and the Cascade Range in the north. The ancestors of this highly endemic freshwater dispersant fish fauna have ancient roots in ancient lakes and rivers of the region to the east, now drained mostly by tributaries to the Snake River (Minckley *et al* 1986; Moyle 2002). Speckled Dace presumably entered the region by first colonizing the Klamath Basin with other Great Basin fishes and then by expanding their population to the Sacramento-San Joaquin basin when Klamath River headwaters connected to the region via the Pit River. Dace then found it possible to colonize most of the entire basin (except where noted), reaching as far south as the Santa Maria River (via the Pajaro-Salinas River system). The Sacramento Speckled Dace thus became a member of one of the most highly endemic assemblages of freshwater dispersing fishes in the western USA. The Sacramento Speckled Dace, however, may have been a rather late addition to this fauna, which would explain its close genetic relationship with Klamath Speckled Dace.

Genetics/genomics. The Sacramento Speckled Dace is one of three lineages, defined by genomics, that make up the Western Speckled Dace, *Rhinichthys klamathensis* (Smith *et al.* 2017; Su *et al.* 2022). The three lineages are also supported by Wiesenfeld *et al.* (2017) and Smith *et al.* (2017) using mtDNA and microsatellites.

Etymology. The species name honors the Achomawi people ("river people") whose historic homelands were along the Pit River and tributaries in northeastern California, from Goose Lake to Pit River Falls, and beyond (Dixon 1908). The Pit River is a branch of the Sacramento River that drains much of northeastern California. This region includes the Fall River system and Achjumawi Lava Springs State Park. The Speckled Dace is one of the most abundant native fishes in streams flowing through Achomawi lands. Alternate spellings include Achjumawi and Achumawi (Dixon 1908).

The scientific names have a confusing history, starting with Jordan and Evermann (1896), who did not mention by name Speckled Dace in the Sacramento or Klamath rivers. They did include Sacramento Speckled Dace, vaguely from California, within *Agosia nubila carringtoni.* This taxon was first described in 1876 as *Apocope carringtoni* from Utah. Jordan and Evermann (1896) basically used this taxon to include miscellaneous Great Basin populations, and provisionally fish from the Lahontan Basin, as well as from various localities in southern and central California. “These California and Nevada forms may be distinct species, but if so, we are unable to define them (Jordan and Evermann 1896:312).” Snyder (1908) followed Jordan and Evermann (1896) in using *A. n. carringtoni* for a grab-bag of Speckled Dace from Oregon and California. By default, *carringtoni* became the species epithet for Sacramento Speckled Dace as *Agosia carringtoni* (Snyder 1913, 1917) and *Rhinichthys osculus carringtoni* (Shapovalov and Dill 1950, Kimsey and Fisk 1960). Moyle (1976, 2002) did not provide a name for Sacramento populations. See Table 1 for other synonyms.

Conservation Status. The Sacramento Speckled Dace is widespread and abundant in the Sacramento River and tributaries, the Pit River system, Pajaro-Salinas watershed, San Luis Obispo Creek, and the Santa Maria River. It seems to have been extirpated from the San Joaquin River and tributaries although old records are scarce. The Speckled Dace is also absent from streams tributary to the San Francisco Estuary, including the Guadalupe River and tributaries, Coyote Creek, and Alameda Creek, for which there are historic records (Leidy 2007, R.L. Leidy, pers. comm. 2021). The dace was extirpated from Coyote Creek in the 1970s (Scoppettone and Smith 1976; J.J. Smith, pers. comm. 2021) and from Alameda Creek in the early 1900s (R. Leidy, pers. com. 2021). It has been extirpated from the Pajaro River, which flows into Monterey Bay, although it is still found in the upper and middle reaches of the San Benito River, a tributary to the Pajaro (J. J. Smith, pers. comm. 2021). The historic records, though few, indicate that the Speckled Dace was extirpated from these watersheds as the result of dams, habitat change, and diversions of water, coupled with severe drought.

***Rhinichthys klamathensis goyatoka*, new subspecies. Warner Speckled Dace**

Fig. 4C

Agosia nubila carringtoni Snyder 1908:98
Agosia robusta Rutter 1908: 139
Apocope carringtoni Evermann and Clark 1931:55
Rhinichthys osculus subsp. Williams *et al.* 1990:243
Rhinichthys osculus klamathensis Markle 2016:50

Holotype: WFB-122-10-44 (Figure 1). 59 mm SL. Twelve Mile Creek, Lake County, Oregon. Jack E. Williams. November 2, 1988.

Paratypes: WFB-122-10-42a—122-10-42j (n = 10**).** Same location and collector

Meristics: Holotype (paratypes)

Length (mm): standard 59; fork 67; total 71

Lateral line scales: 76 (61–84). Lateral line incomplete in most individuals; counts include 2–3 scales beyond end of lateral line.

Scales above lateral line: 13 (11–14)

Scales below lateral line: 11 (9–13)

Dorsal-fin rays: 8(8), counts include single unbranched ray.

Anal-fin rays: 7 (7), counts include single unbranched ray.

Pectoral-fin rays 12 (10–13), counts include unbranched rays.

Pelvic 7 (7–9), counts include unbranched rays.

Caudal-fin rays 19 (19–20).

Diagnosis. Genetically distinct Speckled Dace endemic to the isolated Warner Basin in Oregon and California. Relatively small adult size (<10 cm SL); classic Speckled Dace body shape: thick caudal peduncle, robust (subcylindrical) body, small fins, and bluntly pointed snout with subterminal mouth. Maxillary barbels and frenum usually present.

Description. The description is the same as Sacramento Speckled Dace. Snyder (1908) examined Speckled Dace from throughout the arid basins of southeastern Oregon and could find no distinguishing morphological or meristic features to separate Warner Speckled Dace from dace in other basins, not even lateral line scale numbers (which partially define Klamath Speckled Dace). For lateral line scales, Snyder’s counts were: Warner Basin 68–71(N=58), Sacramento, 61–74 (N=143), and Klamath 68–78 (n=18). He also noted that in Warner Speckled Dace, maxillary barbels were usually present (45 out of 53 fish examined). For comparison, they were present on 43/48 Klamath basin dace but only 9/68 for Sacramento basin dace. A frenum is usually present.

Distribution. In a survey of fishes of the Warner Basin, Williams *et al.* (1990) found Speckled Dace in Twelvemile Creek, Twentymile Creek, Deep Creek, and upper Honey Creek, plus the isolated Foskett Spring. Only Twelvemile Creek has headwaters (and Speckled Dace) in California. Foskett Spring is on the edge of Coleman Lake, on the southeast corner of the basin; the lake is dry most of the time. The mtDNA study by Smith *et al.* (2017) indicates Speckled Dace in the Warner Basin share a recent ancestry with those from the Chewaucan River to the north (which flows into Lake Abert, Oregon) and with those in Wall Canyon Creek (Nevada) to the southeast. Further genomic studies may show these populations could be included within Warner Speckled Dace.

Geology. The Warner Valley is one of a number of isolated watersheds within the northern Great Basin, which have a long complex history of occasional connectivity to big river systems, such as the Snake and the Klamath (Smith *et al.* 2002). The onset of Great Basin faulting and uplift of the Warner Range (*ca.* 3 mya) likely resulted in a permanent separation and isolation of the Warner Basin from the Sacramento and Klamath basins, sometime in the late-Pleistocene (~1.0 mya) (Eggar *et al.* 2011). This isolation is reflected in other endemic fishes which co-occur with Warner Speckled Dace: Warner Sucker (*Catostomus warnerensis*), Great Basin Redband Trout (*Oncorhynchus mykiss* subsp.) and Tui Chub (*Siphatales bicolor* subsp.) (Williams *et al.* 1990; Markle 2016). In fact, the Warner Valley is one of a number of isolated watersheds within the northern Great Basin that support endemic aquatic species (Hubbs *et al.* 1978), so it is likely that Speckled Dace are endemic to other watersheds as well.

Genetics/genomics. Ardren *et al.* (2010), using mtDNA, suggested that Speckled Dace in the Warner Basin are different at the species level from dace in the neighboring Goose Lake Basin (Sacramento drainage). Hoekzema and Sidlauskas (2014) examined mtDNA from dace populations in the Warner Basin and in surrounding basins in Oregon. They found a high level of genetic divergence in dace from the basins, dating to the Pliocene or early Pleistocene, which "…should likely be elevated to species-status once their full geographic extent is discovered, and their morphological diversity described (Hoekzema and Sidlauskas 2014:245). Distinct lineages included fishes from Goose Lake, Silver Lake, Lake Abert, and the Warner basin, including Foskett Spring. The mtDNA study of Smith *et al.* (2017) and the genomic study of Su *et al.* (2022) both indicate that Warner Basin Speckled Dace are a distinct lineage, divergent from the Sacramento and Klamath lineages, at the subspecies or species level.

Etymology. The name honors the Goyatöka people who, before the invasion of their homeland by Euro-Americans, lived on lands in the Warner Basin where Speckled Dace occupied the streams, lakes, and springs (Dixon 1908, Stewart 1939). The common name indicates the geographic location of the dace populations. The basin is named for William Warner, an army officer who died while mapping the region.

Notes. Our study supports the finding that the Warner Speckled Dace is a distinct lineage (subspecies) allied with Klamath and Sacramento Speckled Dace. Ardren *et al.* (2010) and Su *et al.* (2022) show that Warner Speckled Dace have evolutionary ties to the daces in the Klamath and Sacramento Basins. These Speckled Dace became a species of interest when dace in Foskett Spring, in an isolated part of the Warner Basin, were listed as a threatened species without any special taxonomic designation. Subsequent genetic analyses revealed Foskett Spring Speckled Dace could at best be considered a Distinct Population Segment of Warner Speckled Dace; these same analyses suggested that Speckled Dace throughout the Warner Basin constituted a distinct taxon (Ardren *et al.* 2010).

Conservation Status. Most of what is known about the Warner Speckled Dace and other fishes of the basin comes from surveys for (a) Warner Sucker, which was listed as threatened in 1985, (b) Foskett Spring Speckled Dace, which was also listed as a threatened species in 1985 (USFWS 2019, https://ecos.fws.gov/ecp/species/651), and (c) Great Basin Redband Trout. The Foskett Spring Speckled Dace was delisted in 2019 as the result of extensive habitat improvement, although it remains a conservation dependent species (USFWS 2019). Most of the permanent water in the basin inhabited by the Warner Sucker is dominated by non-native fishes, but a population of native Tui Chub is also present (Williams *et al.* 1990). The remaining Warner Speckled Dace populations (and those of Warner Sucker and Tui Chub) probably qualify for listing as Threatened under the federal ESA. Their decline is due to the combined problems of non-native predatory fishes occupying much of the aquatic habitat, inadequate management of grazing and diversions, and climate change/drought reducing flows and increasing temperatures in streams (Williams *et al.* 1990).

Discussion

This study shows that Speckled Dace in California (including watersheds shared with neighboring states), can be recognized as three species with six subspecies:

Santa Ana Speckled Dace*, Rhinichthys gabrielino* new species
Desert Speckled Dace, *Rhinichthys nevadensis* (Gilbert) new common name
    Lahontan Speckled Dace, *R. nevadensis robustus (*Gilbert) new combination
    Amargosa Speckled Dace, *Rhinichthys nevadensis nevadensis (*Gilbert) new combination
    Long Valley Speckled Dace, *R. nevadensis caldera* new subspecies
Western Speckled Dace, *R. klamathensis* (Evermann and Meek)
    Klamath Speckled Dace, *R. klamathensis klamathensis* (Evermann and Meek), new combination
    Sacramento Speckled Dace, *R. klamathensis achomawi* new subspecies
    Warner Speckled Dace, *R. klamathensis goyatoka* new subspecies

Our findings and those of Su *et al.* (2022) are consistent with the long isolation of California from other zoogeographic regions as well as the isolation of many basins within California, resulting in exceptionally high endemism (ca. 80%) in California fish species (Moyle 2002, Leidy and Moyle 2021). This endemism now includes species and subspecies of Speckled Dace even though Speckled Dace *sensu lato* seem to have exceptional abilities to overcome zoogeographic barriers, allowing them to spread widely within basins. For example, Sacramento Speckled Dace have managed to colonize most basins within central California; they made their way through the Pit and Sacramento River systems, and then via the Salinas/Pajaro River system, to coastal streams as far south as the Santa Maria River, Santa Barbara County. Genomic analyses show that Speckled Dace diversification tracks that of endemism in other species complexes. While Speckled Dace show an ability to adapt to diverse habitats, producing distinctive morphs, the distinctiveness tends to be found in local populations and with features that have evolved repeatedly in response to stream flow or lake-like environmental conditions (Minckley and Marsh 2009, Smith *et al.* 2017). This means that forms designated as belonging to distinct lineages by genomics can be highly variable in morphometrics, meristics, and other features, making it difficult to define those lineages as distinct species or subspecies using conventional taxonomic techniques.

Smith *et al.* (2017) contend that the morphological similarity of dace from diverse watersheds is due to 'reticulate evolution' whereby repeated hybridization events keep dace in neighboring basins from diverging from one another, even if the basins support other endemic fishes (Bangs *et al.* 2020). In contrast, genomic analyses, using thousands of SNPs, generally reflect the patterns of endemism shown by other sympatric fishes. This indicates genomic evolution can take place while morphological and other features are conserved. The result is a cluster of cryptic species, adapted to local conditions in ways not reflected in conventional features. But in the long history of Speckled Dace (*sensu lato*) evolution, such hybridization seems to have been rare.

While we have only limited genomic data from populations of Speckled Dace outside California, the literature suggests species-level lineages exist in the Colorado River basin and in the Columbia River (and related) basins. We recommend, following Minckley and Marsh (2009), that *R. osculus* be applied only to dace in the Gila River basin, given that the first description of this species was of fish from the San Pedro River in Arizona, a tributary to the Gila River. The Gila River flows into the lower Colorado River. For Columbia River Speckled Dace, the name *R. nubila* could be applied because the name has been widely used for dace in this basin in the past. Of course, further genomic analyses of populations in these two huge basins may uncover other cryptic species, as it has in California.

We conclude that many discrete evolutionary lineages exist within the Speckled Dace complex which can be described as species or subspecies. Most of these taxa have meristic and morphometric characteristics that broadly overlap within those of other dace taxa. Genomic studies define these taxa as cryptic species or subspecies (Hoekzema and Sidlauskas 2014). Such cryptic taxa are being increasingly recognized in fishes worldwide (Bickford *et al.* 2007), as well as in California (Baumsteiger and Moyle 2019, Su *et al.* 2022). While they are best defined initially by genetic approaches, following Baumsteiger *et al.* (2017) and Su *et al.* (2022), taxon designations should also be supported by zoogeographic and geologic information, and, where possible, by conventional taxonomic approaches.

Finally, we emphasize the need to conserve the diversity of forms and taxa in this fascinating group of fishes, protecting the many isolated populations and their habitats before they disappear. It is therefore important to assign names to the diverse lineages. As Minckley and Marsh (2009:170) state in relation to ‘Speckled Dace’, there is a “human tendency to allow the unexplored to vanish.” Even recognizing Distinct Population Segments of dace, as recommended by Mussmann *et al.* (2020), can offer some protection under state and federal endangered species acts. We can only hope, given the rapid changes taking place on this planet today, that some of this Speckled Dace diversity will survive and with it the diversity of other species, fish and non-fish, that live with them (Grantham *et al.* 2017, Leidy and Moyle 2021).

Acknowledgements

Cathryn Lawrence and Jay Lund made space and funds available at the Center for Watershed Sciences to allow this study to be conducted. Special thanks to Irene Engilis, Collection Manager for the UC Davis Museum of Wildlife and Fish Biology, who provided specimens from the collection and conducted the tedious counts and measurements on types and paratypes, assisted by Rachel Alsheikh. Kevin W. Conway (Curator of Ichthyology, Biodiversity Research and Teaching Collections, Texas A& M University) made helpful suggestions for measuring taxonomic characteristics. Jason Baumsteiger, Michael Miller, and Matt Campbell provided assistance and information on genomic aspects of the project and their interpretation. Information, specimens and photos were provided by Jerry J. Smith, Jason Baumsteiger, and Steve Parmenter. The following people provided fish samples for us: Scot Lucas (Klamath River), Mollie Ogaz (Sacramento River system), Steve Parmenter and Rosa Cox (Owens Valley, Lahontan Basin), Kevin Guadalupe and Gregory Munson (Virgin River, Oasis Valley, Amargosa River), Hal Fairfield (Death Valley region), Jennifer Pareti (Santa Ana River), and Claire Ingel (Southern California). Amber Manfree created the distribution map. The map of Santa Ana Speckled Dace distribution is from the Center for Biological Diversity, via Jeff Miller. We benefited from discussions with Steve Parmenter, Andrew Engilis, Robert Leidy and Jerry J. Smith. The editorial advice of Jonathan Armbruster (Auburn University) greatly improved the paper and the taxonomy therein.

References

Ardren, W.R., Baumsteiger, J. & Allen, C.S. (2010) Genetic analysis and uncertain taxonomic status of threatened Foskett Spring Speckled Dace. *Conservation Genetics*, 11 (4), 1299–1315.
https://doi.org/10.1007/s10592-009-9959-0

Armbruster, J.W. (2012) Standardized measurements, landmarks, and meristic counts for cypriniform fishes. *Zootaxa*, 3586 (1), 8–16.
https://doi.org/10.11646/zootaxa.3586.1.3

Bangs, M.R., Douglas, M.R. Brunner, P.C. & Douglas, M.E. (2020) Reticulate evolution as a management challenge: patterns of admixture with phylogenetic distance in endemic fishes of western North America. *Evolutionary Applications*, 13 (6), 1400–1419.
https://doi.org/10.1111/eva.13042

Baumsteiger, J. & Moyle, P.B. (2019) A reappraisal of the California Roach/Hitch (Cypriniformes, Cyprinidae, *Hesperoleucus/ Lavinia*) species complex**.** *Zootaxa*, 4543 (2), 2221–2240.
https://doi.org/10.11646/zootaxa.4543.2.3

Baumsteiger, J., Moyle, P.B., Aguilar, A., O’Rourke, S.M. & Miller, M.R. (2017) Genomics clarifies taxonomic boundaries in a difficult species complex. *PLoS ONE*, 12 (12), e0189417.
https://doi.org/10.1371/journal.pone.0189417

Bickford, D., Lohman, D.J., Sodhi, N.S., Ng, P.K., Meier, R., Winker, K., Ingram, K.K. & Das, I. (2007) Cryptic species as a window on diversity and conservation. *Trends in Ecology & Evolution*, 22 (3), 148–155.
https://doi.org/10.1016/j.tree.2006.11.004

Billman, E.J., Lee, J.B., Young, D.O., McKell, M.D., Evans, R.P. & Shiozawa, D.K. (2010) Phylogenetic divergence in a desert fish: differentiation of Speckled Dace within the Bonneville, Lahontan, and upper Snake River basins. *Western North American Naturalist*, 70 (1), 39–48.
https://doi.org/10.3398/064.070.0105

Center for Biological Diversity (2020) Petition to List Three Populations of Speckled Dace (Rhinichthys osculus) in the Death Valley Region under the Endangered Species Act: Amargosa Canyon Speckled Dace, Long Valley Speckled Dace, Owens

Speckled Dace. *Submitted to US Fish and Wildlife Service*, 8 June 2020, 1–48.

Chen, Y., Parmenter, S. & May, B. (2007) Introgression between Lahontan and endangered Owens Tui Chubs, and apparent discovery of a new Tui Chub in the Owens Valley, California. *Conservation Genetics*, 8 (1), 221–238. https://doi.org/10.1007/s10592-006-9164-3

Colman, S.M., Platt Bradbury, J. & Rosenbaum, J.G. (2004) Paleolimnology and paleoclimate studies in Upper Klamath Lake, Oregon. *Journal of Paleolimnology*, 31 (2), 129–138. https://doi.org/10.1023/B:JOPL.0000019235.72107.92

Cope, E.D. (1872) Report on the recent reptiles and fishes of the survey, collected by Campbell Carrington and C. M. Dawes. *In*: *Part IV: Zoology and Botany of Preliminary Report of the U. S. Geological Survey of Montana and Adjacent Territories. Annual Report of Progress*, 5, pp. 467–476.

Cope, E.D. (1883) On the fishes of the recent and Pliocene lakes of the western part of the Great Basin and of Idaho Pliocene Lake. *Academy of Natural Sciences, Philadelphia, Proceedings*, 35, 134–166.

Cope, E.D. & Yarrow, H.C. (1875) Report upon the collection of fishes made in portions of Nevada, Utah, California, New Mexico, and Arizona during the years 1871, 1872, 1873, and 1874. *Report on Geographical and Geological Explorations and Surveys, W100th Meridian (Wheeler Survey)*, Chapter VI, 637–703.

Cornelius, R.H. (1969) *The Systematics and Zoogeography of Rhinichthys osculus (Girard) in Southern California*. M.A. Thesis, California State University, Fullerton, California, 195 pp.

Culver, G.B. & Hubbs, C.L. (1917) The fishes of the Santa Ana system of streams in southern California, *Lorquinia*, 1 (11), 82–83.

Daniels, R.A. & Moyle, P.B. (1984) Geographic variation and a taxonomic reappraisal of the Marbled Sculpin, *Cottus klamathensis*. *Copeia*, 1984, 949–959. https://doi.org/10.2307/1445339

Deacon, J.E. & Williams, J.E. (1984) Annotated list of the fishes of Nevada. *Proceedings of the Biological Society of Washington*, 97 (1), 113–118.

Dixon, R.B. (1908) Notes on the Achomawi and Atsugewii Indians of northern California. *American Anthropologist*, 10 (2), 208–220. https://doi.org/10.1525/aa.1908.10.2.02a00030

Dorsey, R.J. & Roering, J.J. (2006) Quaternary landscape evolution in the San Jacinto fault zone, Peninsular ranges of Southern California: transient response to strike-slip fault initiation. *Geomorphology*, 73 (1–2), 16–32. https://doi.org/10.1016/j.geomorph.2005.06.013

Egger, A.E. & Miller, E.L. (2011) Evolution of the northwestern margin of the Basin and Range: The geology and extensional history of the Warner Range and environs, northeastern California. *Geosphere*, 7 (3), 756–773. https://doi.org/10.1130/GES00620.1

Evermann, B.W. & Meek, S.B. (1898) A report upon salmon investigations in the Columbia River and elsewhere on the Pacific Coast in 1896. *Bulletin of the U.S. Fish Commission*, 17, 15–84. https://doi.org/10.5962/bhl.title.35601

Evermann, B.W. & Clark, H.W. (1931) A distributional list of freshwater fishes known to occur in California. *Division of Fish and Game, Fish Bulletin*, 35, 1–67.

Fattaruso, L.A., Cooke, M.L., Dorsey, R.J. & Housen, B.A. (2016) Response of deformation patterns to reorganization of the southern San Andreas fault system since ca. 1.5 Ma. *Tectonophysics*, 693, 474–488. https://doi.org/10.1016/j.tecto.2016.05.035

Freudenstein, J.C., Broe, M.B., Folk, R.A. & Sinn, B.T. (2017) Biodiversity and the species concept -lineages are not enough. *Systematic Zoology*, 66, 644–656. https://doi.org/10.1093/sysbio/syw098

Garcia & Associates (2000) *The Distribution and Abundance of the Benthic Macroinvertebrate Fauna and Fish Populations in Tributaries Leading into and including the North Fork Mokelumne and Mainstem Mokelumne Rivers. Final Report Volume 3*. Prepared for Pacific Gas and Electric Company by Garcia and Associates, San Anselmo, California. [unknown pagination]

Gesch, D., Oimoen, M., Greenlee, S., Nelson, C. Steuck, M. & Tyler, D. (2002) The National Elevation Dataset. *Photogrammetric Engineering and Remote Sensing*, 68 (1), 5–11.

Gilbert, C.H. (1893) Report on the fishes of the Death Valley expedition collected in southern California and Nevada in 1891 with descriptions of new species. *U.S. Department of Agriculture*, *North American Fauna*, 7, 229–234. https://doi.org/10.3996/nafa.7.0003

Gilbert, C.H. & Evermann, B.W. (1894) A report upon investigations in the Columbia River basin, with descriptions of four new species of fishes. *Bulletin of the U. S. Fish Commission*, 14, 169–207.

Girard, C.F. (1856) Researches upon the cyprinoid fishes inhabiting the fresh waters of the United States, west of the Mississippi Valley, from specimens in the museum of the Smithsonian Institution. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 8, 165–213.

Girard, C.F. (1858) Report upon fishes collected on the survey. *In*: *U.S. War Department, Reports of Explorations and Surveys, to Ascertain the most Practicable and Economical Route for a Railroad from the Mississippi River to the Pacific Ocean 10*. U.S. Government Printing Office, Washington, D.C., pp. 83–91.

Grantham, T.E., Fesenmyer, K.A., Peek, R., Holmes, E., Quiñones, R.M., Bell, A., Santos, N., Howard, J.K., Viers, J.H. & Moyle, P.B. (2017) Missing the boat on freshwater fish conservation in California. *Conservation Letters*, 10, 1077–1085. https://doi.org/10.1111/conl.12249

Grayson, D.K. (1993) *The Desert's Past: A Natural Prehistory of the Great Basin*. Smithsonian Institution Press, Washington, xx + 356 pp.

Gudde, E.G. & Bright, W. (1998) *California Place Names*. University of California Press, Berkeley, California, xxviii + 467 pp. https://doi.org/10.1525/9780520920545

Harrison, S.P. (2013) *Plant and Animal Endemism in California*. University of California Press, Berkeley, California, ix + 189 pp. https://doi.org/10.1525/california/9780520275546.001.0001

Hildreth, W. & Fierstein, J. (2016) Long Valley Caldera Lake and Reincision of Owens River Gorge. *U.S. Geological Survey Scientific Investigations Report*, 5120, 1–63. https://doi.org/10.3133/sir20165120

Hoekzema, K. & Sidlauskas, B.L. (2014) Molecular phylogenetics and microsatellite analysis reveal cryptic species of Speckled Dace (Cyprinidae: *Rhinichthys osculus*) in Oregon's Great Basin. *Molecular Phylogenetics and Evolution*, 77, 238–250. https://doi.org/10.1016/j.ympev.2014.04.027

Hubbs, C.L., Follett, W.I. & Dempster, L.J. (1979) List of the fishes of California. *Occasional Papers of the California Academy of Sciences*, 133, 1–54.

Hubbs, C.L. & Kuhne, E.R. (1937) A new fish of the genus *Apocop*e from a Wyoming warm spring. *Occasional Papers of the Museum of Zoology, University of Michigan*, 343, 1–21.

Hubbs, C.L. & Miller, R.R. (1948a) The Great Basin, with emphasis on glacial and postglacial time. The zoological evidence: correlation between fish distribution and hydrographic history in the desert basins of western United States. *University of Utah Bulletin*, 38 (20), 17–166.

Hubbs, C.L. & Miller, R.R. (1948b) Two new relict genera of fishes from Nevada. *Occasional Papers of the Museum of Zoology, University of Michigan*, 507, 1–31.

Hubbs, C.L. & Miller, R.R. (1972) Diagnoses of new cyprinid fishes of isolated waters in the Great Basin of western North America. *Transactions, San Diego Natural History Society* 17, 101–106.

Hubbs, C.L., Miller, R.R. & Hubbs, L.C. (1974) Hydrographic history and relict fishes of the North-central Great Basin. San Francisco: *California Academy of Sciences Memoir*, 7, 1–259.

Jelks, H.L., Walsh, S.J., Burkhead, N.M., Contreras-Balderas, S., Diaz-Pardo, E., Hendrickson, D.A., Lyons, J., Mandrak, N.E., McCormick, F., Nelson, J.S. & Platania, S.P. (2008) Conservation status of imperiled North American freshwater and diadromous fishes. *Fisheries*, 33 (8), 372–407. https://doi.org/10.1577/1548-8446-33.8.372

Jordan, D.S. (1885) Identification of the species of Cyprinidae and Catostomidae, described by Dr. Charles Girard in Proceedings Academy of Natural Sciences of Philadelphia for 1856. *Proceedings, US National Museum*, 8, 118–127. https://doi.org/10.5479/si.00963801.8-500.118

Jordan, D.S. & Evermann, B.W. (1896) The Fishes of North and Middle America. *Bulletin, US National Museum*, 47, Part 1, 1–1240.

Kimsey, J.B. & Fisk, L.O. (1960) Keys to the freshwater and anadromous fishes of California. *California Fish and Game*, 46, 453–479.

Kinziger, A.P., Nakamoto, R.J., Anderson, E.C. & Harvey, B.C. (2011) Small founding number and low genetic diversity in an introduced species exhibiting limited invasion success (Speckled Dace, *Rhinichthys osculus*). *Ecology and Evolution*, 1 (1), 73–84. https://doi.org/10.1002/ece3.8

La Rivers, I. & Trelease, T.J. (1952) An annotated checklist of the fishes of Nevada. *California Fish and Game*, 38, 113–123.

Leidy, R.A. (2007) Ecology, *Assemblage Structure, Distribution, and Status of Fishes in Streams Tributary to the San Francisco Estuary*. San Francisco Estuary Institute Contribution, 530 pp.

Leidy, R.A. & Moyle, P.B. (2021) Keeping up with the status of freshwater fishes: a California (USA) perspective. *Conservation Science and Practice*, 3 (8), e474. https://doi.org/10.1111/csp2.474

Markle, D.F. (2016) *A Guide to the Freshwater Fishes of Oregon*. Oregon State University Press, Corvallis, Oregon, 140 pp.

McClay, K. & Bonora, M. (2001) Analog models of restraining stepovers in strike-slip fault systems. *American Association of Petroleum Geologists Bulletin*, 85, 233–260. https://doi.org/10.1306/8626C7AD-173B-11D7-8645000102C1865D

Miller, R.R. (1973) Two new fishes, *Gila bicolor snyderi* and *Catostomus fumeiventris* from the Owens River Basin California. *Occasional Papers of the Museum of Zoology, University of Michigan*, 667, 1–19.

Miller, R.R. (1984) *Rhinichthys deaconi*, a new species of dace (Pisces: Cyprinidae) from southern Nevada. *Occasional Papers of the Museum of Zoology, University of Michigan*, 707, 1–21.

Minckley, W.L., Hendrickson, D.A. & Bond, C.E. (1986) Geography of western North America freshwater fishes: Description and relationship to intercontinental tectonism. *In*: Hocutt, C.H. & Wiley, E.O. (Eds.), *The Zoogeography of North American*

Freshwater Fishes. New York, John Wiley and Sons, pp. 519–614.

Minckley, W.L. & Marsh, P.C. (2009) *Inland Fishes of the Greater Southwest: Chronicle of a Vanishing Biota.* University of Arizona Press, Tucson, Arizona, 576 pp.

Moyle, P.B. (1976) *Inland Fishes of California.* University of California Press, Berkeley, California, 405 pp.

Moyle, P.B. (2002) *Inland Fishes of California, Revised and Expanded*. University of California Press, Berkeley, California, 504 pp.

Moyle, P.B., Katz, J.V.E. & Quiñones, R.M. (2011) Rapid decline of California's native inland fishes: a status assessment. *Biological Conservation*, 144, 2414–2423. https://doi.org/10.1016/j.biocon.2011.06.002

Moyle, P.B. & Campbell, M.A. (2022) Cryptic species of freshwater sculpin (Cottidae: *Cottus*) in California. *Zootaxa*, 5154 (5), 501–507.
https://doi.org/10.11646/zootaxa.5154.5.1

Moyle, P.B. & Cech, J.J. (2004) *Fishes: An Introduction to Ichthyology***.** *5th Edition***.** Prentice-Hall, Upper Saddle River, New Jersey, xvi + 726 pp.

Moyle, P.B. & Davis, L.H. (2000) A list of freshwater, anadromous, and euryhaline fishes of California. *California Fish and Game*, 86, 244–258.

Moyle, P.B., Quiñones, R.M., Katz, J.V.E, & Weaver, J. (2015) *Fish Species of Special Concern in California*. *3rd Edition*. Sacramento, California Department of Fish and Wildlife. Available from: https://wildlife.ca.gov/Conservation/SSC/Fishes (accessed 8 February 2023)

Murphy, G.L. (1941) A key to the fishes of the Sacramento-San Joaquin Basin. *California Fish and Game*, 27, 165–171.

Mussmann, S.M. (2018) *Diversification Across a Dynamic Landscape: Phylogeography and Riverscape Genetics of Speckled Dace (Rhinichthys osculus) in Western North America* Ph.D. Dissertation, University of Arkansas, Fayetteville, Arkansas, 166 pp.

Mussmann, S.M., Douglas, M.R., Oakey, D.D. & Douglas, M.E. (2020) Defining relictual biodiversity: conservation units in Speckled Dace (Leuciscidae: *Rhinichthys osculus*) of the Greater Death Valley Ecosystem. *Ecology and Evolution*, 10, 10798–10817.
https://doi.org/10.1002/ece3.6736

Oakey, D.D., Douglas, M.E. & Douglas, M.R. (2004) Small fish in a large landscape: diversification of *Rhinichthys osculus* (Cyprinidae) in western North America, *Copeia*, 2004 (2), 207–221.
https://doi.org/10.1643/CG-02-264R1

O'Brien, J.W., Hansen, H.K. & Stephens, M.E. (2011) Status of fishes in the Upper San Gabriel River Basin, Los Angeles County, California. *California Fish and Game*, 97, 149–163.

Orme, A.R. (2008) Pleistocene pluvial lakes of the American West: a short history of research. *Geological Society, London, Special Publications*, 301 (1), 51–78.
https://doi.org/10.1144/SP301.4

Page, L.M. & Burr, B.M. (2011) *Peterson Guide to Freshwater Fishes of North American North of Mexico. 2nd Edition*. Houghten Mifflin Harcourt, Boston, Massachusetts, 663 pp.

Page, L.M., Espinoza-Perez, H., Findley, L.T., Gilbert, C.R., Lea, R.N, Mandrake, N.E., Mayden, R.L. & Nelson, J.S. (2013) *Common and Scientific Names of Fishes from the United States, Canada, and Mexico. 7th Edition*. *American Fisheries Society Special Publication 34*. American Fisheries Society, Bethesda, Maryland, 243 pp.

Patterson, T. &. Kelso, N.V. (2021) Natural Earth Data. https://www.naturalearthdata.com/ (accessed 30 December 2022)

Peden, A.E. & Hughes, G.W. (1988) Sympatry in four species of *Rhinichthys* (Pisces), including the first documented occurrences of *R. umatilla* in the Canadian drainages of the Columbia River. *Canadian Journal of Zoology*, 66 (8), 1846–1856.
https://doi.org/10.1139/z88-267

Pfrender, M.E., Hicks, J. & Lynch, M. (2004) Biogeographic patterns and current distribution of molecular-genetic variation among populations of Speckled Dace, *Rhinichthys osculus* (Girard). *Molecular Phylogenetics and Evolution*, 30 (3), 490–502.
https://doi.org/10.1016/S1055-7903(03)00242-2

Reheis, M.C., Stine, S. & Sarna-Wojcicki, A.M. (2002) Drainage reversals in Mono Basin during the late Pliocene and Pleistocene. *Geological Society of America Bulletin*, 114 (8), 991–1006.
https://doi.org/10.1130/0016-7606(2002)114%3C0991:DRIMBD%3E2.0.CO;2

Rutter, C. (1903) Notes on fishes from streams and lakes of northeastern California not tributary to the Sacramento basin. *United States Fish Commission Bulletin*, 22, 145–148. [1902]

Rutter, C. (1908) The fishes of the Sacramento-San Joaquin basin, with a study of their distribution and variation. *United States Bureau of Fisheries Bulletin*, 27, 105–152. [1907]

Sada, D.W. (1989) *Status, distribution, and morphological variation of Speckled Dace in the Owens River system. Final Report*. California Department of Fish and Game, Sacramento, California, 37 pp.

Sada, D.W., Britten, H.B. & Brussard, P.F. (1993) Morphometric and genetic differentiation among Death Valley System *Rhinichthys osculus. CDFG Inland Fisheries Repor*t, *Contract*, FG0524, 1–52.

Sada, D.W., Britten, H.B. & Brussard, P.F. (1995) Desert aquatic ecosystems and the genetic and morphological diversity of Death Valley system Speckled Dace. *In*: Nielsen, J.L. (Ed.), *Evolution and the Aquatic System. American Fisheries Society Symposium*, 17, pp. 350–359.

Sada, D.W. & Vinyard, G.L. (2002) Anthropogenic changes in biogeography of Great Basin biota. *In*: Hershler, R., Madsen, D.B. & Curry, D.R. (Eds.), Great Basin Aquatic Systems History. *Smithsonian Contributions to the Earth Sciences*, 33, pp. 277–293.

Santos, N.R., Katz, J.V.E., Moyle, P.B. & Viers, J.H. (2013) A programmable information system for management and analysis of aquatic species range data in California. *Environmental Modeling & Software*, 53, 13–26. https://doi.org/10.1016/j.envsoft.2013.10.024

Schönhuth, S., Shiozawa, D.K., Dowling, T.E. & Mayden, R.L. (2012) Molecular systematics of western North American cyprinids (Cypriniformes: Cyprinidae), *Zootaxa*, 3586 (1), 281–303. https://doi.org/10.11646/zootaxa.3586.1.27

Schönhuth, S., Vukić, J., Šanda, R., Yang, L. & Mayden, R.L. (2018) Phylogenetic relationships and classification of the Holarctic family Leuciscidae (Cypriniformes: Cyprinoidei). *Molecular Phylogenetics and Evolution*, 127, 781–799. https://doi.org/10.11646/zootaxa.3586.1.27

Scoppettone, G.G., Hereford, M.E., Rissler, P.H., Johnson, D.M. & Salgado, J.A. (2011) *Relative Abundance and Distribution of Fishes within an Established Area of Critical Environmental Concern, Inyo and San Bernardino Counties, California. Open-File Report 2011-1161.* U.S. Department of the Interior, U.S. Geological Survey, Reston,Virginia. [unknown pagination] https://doi.org/10.3133/ofr20111161

Scoppettone, G.G. & Smith, J.J. (1978) Additional records on the distribution and status of native fishes in Alameda and Coyote Creeks, California. *California Fish and Game*, 64, 62-65.

Shapovalov, L. & Dill, W.A. (1950) A check list of the fresh-water and anadromous fishes of California. *California Fish and Game*, 36, 382–391

Shapovalov, L., Dill, W.A. & Cordone, A.J (1959) A revised check list of the freshwater and anadromous fishes of California. *California Fish and Game*, 45, 159–180.

Shapovalov, L., Cordone, A.J. & Dill, W.A. (1981) A list of the freshwater and anadromous fishes of California. *California Fish and Game*, 67, 4–38.

Smith, G.R., Chow, J., Unmack, P.J., Markle, D.F. & Dowling, T.E. (2017) Evolution of the *Rhinichthys osculus* complex (Teleostei: Cyprinidae) in Western North America. *Miscellaneous Publications Museum of Zoology University of Michigan*, 204 (2), 1–83

Smith, G.R., Dowling, T.E., Gobalet, K.T., Lugaski, T., Shiozawa, D. & Evans, P. (2002) Biogeography and timing rates of evolutionary events among Great Basin fishes. *In*: Hershler, R., Madsen, D.B. & Curry, D.R. (Eds.), Great Basin Aquatic Systems History, *Smithsonian Contributions to the Earth Sciences*, 33, pp. 175–233.

Smith, G.R. & Dowling, T.E. (2008) Correlating hydrographic events and divergence times of Speckled Dace (*Rhinichthys*: Teleostei, Cyprinidae), in the Colorado River drainage. *In*: Reheis, M., Hershler, R. & Miller, D. (Eds.), Late Cenozoic drainage history of the Southwestern Great Basin and Lower Colorado River region: geologic and biotic perspectives. *Geological Society of America Special Publication*, 439, pp. 301–317. https://doi.org/10.1130/2008.2439(13)

Snyder, J.O. (1908) Relationships of the fish fauna of the lakes of Southeastern Oregon. *U.S. Bureau of Fisheries Bulletin*, 27, 69–102.

Snyder, J.O. (1913) The fishes of the streams tributary to San Francisco Bay. *Bulletin of the United States Bureau of Fisheries*, 32, 49–72.

Snyder, J.O. (1917) An account of some fishes from Owens River, California. *Proceedings, United States National Museum*, 54, 201–205. https://doi.org/10.5479/si.00963801.2233.201

Snyder, J.O. (1918) The fishes of the Lahontan system of Nevada and northeastern California. *United States Bureau of Fisheries Bulletin*, 35, 33–86.

Spencer, J.E., Smith, G.R. & Dowling, T.E. (2008) Middle to late Cenozoic geology, hydrography, and fish evolution in the American Southwest. *In*: Reheis, M.C., Hershler, R. & Miller, D. (Eds.), Late Cenozoic Drainage History of the Southwestern Great Basin and Lower Colorado River Region: Geologic and Biotic Perspectives. *Geological Society of America Special Paper*, 439, pp. 279–299. https://doi.org/10.1130/2008.2439(12)

Stewart, O.C. (1939) The Northern Paiute Bands. *Anthropological Records*, 2 (3), 127–149.

Stout, C.C., Tan, M., Lemmon, A.R., Lemmon, E.M. & Armbruster, J.W. (2016) Resolving Cypriniformes relationships using an anchored enrichment approach. *BMC Evolutionary Biology*, 16 (1), 1–3. https://doi.org/10.1186/s12862-016-0819-5

Su, Y., Moyle, P.B., Campbell, M.A., Finger, A.J., O'Rourke, S., Baumsteiger, J. & Miller, M.R. (2022) Population genomic analysis of the Speckled Dace species complex identifies three distinct lineages in California. *Transactions of American Fisheries Society*, 151, 695–710. https://doi.org/10.1002/tafs.10388

Swift, C.C., Haglund, T.R., Ruiz, M. & Fisher, R.N. (1993) The status and distribution of the freshwater fishes of southern California. *Bulletin, Southern California Academy Sciences*, 92, 101–167.

Tan, M. & Armbuster, J.W. (2018) Phylogenetic classification of extant genera of fishes of the order Cypriniformes (Teleostei: Ostariophysi). *Zootaxa*, 4476 (1), 6–39.

https://doi.org/10.11646/zootaxa.4476.1.4

Taylor, B.L., Perrin, W.F., Reeves, R.R., Rosel, P.E., Wang, J.Y., Cipriano, F., Scott Baker, C. & Brownell Jr., R.L. (2017) Why we should develop guidelines and quantitative standards for using genetic data to delimit subspecies for data-poor organisms like cetaceans. *Marine Mammal Science*, 33 (S1), 12–26.
https://doi.org/10.1111/mms.12413

Unmack, P.J., Dowling, T.E., Laitinen, N.J., Secor, C.L., Mayden, R.L., Shiozawa, D.K. & Smith, G.R. (2014) Influence of introgression and geological processes on phylogenetic relationships of western North American mountain suckers (*Pantosteus*). *PLoS One*, 9 (3), e90061. [11 March]
https://doi.org/10.1371/journal.pone.0090061

U.S. Census Bureau, Department of Commerce (2001) Cartographic Boundary File (U.S. States). Available from: https://www.census.gov/geographies/mapping-files/time-series/geo/carto-boundary-file.html. (accessed 30 December 2007)

U.S. Fish and Wildlife Service (2019) Removing the Foskett Speckled Dace from the list of Endangered and Threatened Wildlife, 84 FR 48290, 48290–48308. Docket No. FWS-R1-ES-2017–0051. Available from: http://www.regulations.gov (accessed 8 February 2023)

U.S. Geological Survey (2004) National Hydrography Dataset. U.S. Department of the Interior, Reston, Virginia. Available from: https://www.usgs.gov/national-hydrography (accessed 30 December 2022)

U.S. Geological Survey and U.S. Department of Agriculture, Natural Resources Conservation Service (2013) National Watershed Boundary Dataset (WBD). 4th Edition. Available from: https://www.usgs.gov/national-hydrography/watershed-boundary-dataset (accessed 30 December 2022)

Wiesenfeld, J.C., Goodman, D.H. & Kinziger, A.P. (2018) Riverscape genetics identifies Speckled Dace (*Rhinichthys osculus*) cryptic diversity in the Klamath–Trinity Basin. *Conservation Genetics*, 19 (1), 111–127.
https://doi.org/10.1007/s10592-017-1027-6

Wilke, P.J. (1980) Prehistoric weir fishing on recessional shorelines of Lake Cahuilla. *Proceedings of the Desert Fishes Council*, XI, 101–103.

Williams, J.E., Stern, M.A., Munhall, A.V. &. Anderson, G.A. (1990) Conservation status of threatened fishes in the Warner Basin, Oregon. *Great Basin Naturalist*, 50 (3), 243–248. [http://www.jstor.org/stable/41712597]

Woodman, D.A. (1992) Systematic relationships within the cyprinid genus *Rhinichthys. In*: Mayden, R.L. (Ed.), *Systematics, Historical Ecology and North American Freshwater Fishes*. Stanford University Press, Stanford, California, pp. 374–391.

Wydoski, R.S. & Whitney, R.R. (2003) *Inland Fishes of Washington*. *2nd Edition*. University of Washington Press, Seattle, Washington, 547 pp.

Yang, L., Sado, T., Hirt, M.V., Pasco-Viel, E., Arunachalam, M., Li, J., Wang, X., Freyhof, J., Saitoh, K., Simons, A.M. & Miya, M. (2015) Phylogeny and polyploidy: resolving the classification of cyprinine fishes (Teleostei: Cypriniformes). *Molecular Phylogenetics and Evolution*, 85, 97–116.
https://doi.org/10.1016/j.ympev.2015.01.014