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Native Trout of Mexico: Treasures of the Sierra Madre

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Introduction

American theatergoers are familiar with director John Huston’s classic movie of 1948, The Treasure of the Sierra Madre, based on a novel written by B. Traven and starring Humphrey Bogart as Fred C. Dobbs. At least north of the border, Traven’s tale of loco gringos prospecting for gold made Mexico’s rugged mountains famous, and many cinephiles still recognize the famous quote by Gold Hat the bandito: “Badges! We ain’t got no badges. We don’t need no badges! I don’t have to show you any stinking badges.” Huston filmed most of his mountain scenes on location in Mexico, and some 50 years later, we found ourselves in the Sierra Madre Occidental (henceforth, SMO) of northwest Mexico with our own saga of prospecting for “gold” beginning to unfold. Always without badges but often stinking after days of back-country camping and hiking, our binational and otherwise diverse cast of academic, government, and nonprofit biologists and fly fishers came to call itself Truchas Mexicanas (Mexican trout), after the different, but also gilded, treasure we were chasing.

Many members of Truchas Mexicanas, besides being film fans, had, as professional biologists working in the American Southwest’s deserts, long been familiar with the rich biodiversity of the Sierra Madre, and the Sky Island conferences (DeBano et al. 1995; Gottf ried et al. 2005, 2013) had started convening botanists, entomologists, mammologists, ornithologists, herpetologists, and the occasional fish biologist, as well as paleo- and modern ecologists and the occasional archaeologists and anthropologists. These conferences were started to celebrate, document, and collaborate to call attention to, and help conserve, the remarkably diverse fauna and

flora of the many high-elevation mountains, islands in a sea of desert, of southern Arizona and New Mexico, Sonora and Chihuahua. The work in those volumes helped set our stage, and many active in that group provided valuable pointers. We knew that the fishes of the area had been comparatively less studied than had been those north of the border, especially when it came to trout, and so we set off to focus on them. But thanks to that diverse background info, we did so with our eyes always wide open to all the other biological treasures of the region.

Our many delightful expeditions to this biologically and culturally diverse region slowly but surely revealed an amazing wealth of eye-catching, rare, endangered, and endemic Mexican trout species. We reported preliminary results in an overview of our Truchas Mexicanas group project (Hendrickson et al. 2002) that we here update with insights from many subsequent expeditions. What follows reflects our own views, but they have been strongly influenced and informed by countless discussions with other Truchas Mexicanas participants to whom we are deeply indebted. As did the actors in that acclaimed movie, we followed footsteps of earlier explorers, most of them driven by the potential wealth of the region's minerals and timber, so we spent a lot of time researching obscure archives of their records. By the time our research began in 1997, the mining and lumber industries had opened many backroads into this vast wilderness, facilitating our exploration of many otherwise inaccessible locations, but it was obvious that the increased accessibility had brought diverse, broad-scale, and often adverse impacts to the fish populations we sought. We quickly realized that acquiring knowledge about the conservation status of Mexico's trout was as, if not more, important than learning about their evolutionary history and giving them scientific names.

One of the most intriguing narratives we investigated began in 1884, when Professor Nathaniel Thomas Lupton embarked on a horseback journey over the SMO of Chihuahua. Though he was primarily focused on mining, Lupton stopped to collect two specimens of trout that found their way to Professor E. D. Cope, who published a one-paragraph note in American Naturalist (Cope 1886) about these first Mexican trout known to science. Lupton evidently did not record his exact location or know which drainage he was in, as Cope stated only, "two specimens of black- spotted trout from streams of the Sierra Madre at an elevation of between 7,000 and 8,000 ft in the southern part of the state of Chihuahua near the boundaries of Durango and

Sinaloa." His mention of "black-spotted trout" and his observation of "teeth on the basihyal bones as in *Salmo purpuratus*" indicated quite unambiguously that Lupton's specimens were Cutthroat Trout *Oncorhynchus clarkii*. His description of the location includes headwaters of several major drainages along the continental divide, including the Río Conchos drainage, a tributary to the Rio Grande. If Lupton's specimens came from there, a Cutthroat Trout would not be too surprising since that major river basin harbors an endemic Cutthroat Trout (Rio Grande Cutthroat Trout *O. c. virginalis*) in its U.S. headwaters in New Mexico and Colorado.

Unfortunately, the Lupton–Cope specimens disappeared, evidently before anyone else examined them, but Cope knew trout well and his report motivated others to look further for trout in Mexico. By the 1950s, trout were known to be in most major Pacific drainages of the SMO, ranging from a couple hundred kilometers south of the U.S. border of Arizona and New Mexico in the Río Yaqui basin southeastward to headwaters of rivers entering the Sea of Cortez near Mazatlán, Sinaloa, at about the latitude of the tip of Baja California (Needham 1955, 1959). Except for the Mexican Golden Trout *O. chrysogaster* that was formally described in the 1960s (Needham and Gard 1964), when we started our sampling, there was no consensus regarding the taxonomy or evolutionary relationships of the other Mexican trout to the well-studied species in the United States. The work of our binational Truchas Mexicanas group in the 1990s and early 2000s took us to all major river basins draining the long, high divide of the SMO, but none of the many native trout we sampled was anything like the Cutthroat Trout Cope had briefly described. Accordingly, Truchas Mexicanas started focusing more of our efforts on remote Río Conchos headwaters, eventually sampling 30 high-elevation potential trout habitats in that watershed and discovering at several locations two undescribed and extremely rare species of trout. However, all characters, including their DNA, tell us clearly that they are not Cutthroat Trout, but instead, close relatives of the trout we had been finding at many places on the Pacific side of the SMO divide. While we cannot rule out that a Cutthroat Trout may still be hiding in the most remote parts of the SMO, we can state confidently that though still relatively poorly studied compared to the salmonids north of Mexico, all currently known Mexican native trout of the SMO comprise a genetically diverse assemblage of species sharing a common ancestor with the Rainbow Trout *O. mykiss* native to Pacific drainages of northern Baja California and the western coasts of the United States and Canada.

Study Area

Drainage divides are natural barriers to all freshwater fishes and thus major factors in their evolution. Habitat impacts are similarly constrained by drainages, with events in headwaters always affecting downstream reaches in some way. We therefore start the description of our study area by describing its major hydrographic subdivisions (Figure 1). The major Pacific drainages harboring native trout in their headwaters are (listed from north to south): Río Santo Domingo in northern Baja California, Río Yaqui (a portion of which heads in far southeastern Arizona), Río Mayo, Río Fuerte (comprised of the Oteros, Urique, and Verde rivers), Río Sinaloa, Río Culiacán, Río San Lorenzo, Río Piaxtla, Río del Presidio, Río Baluarte, and Río Acaponeta (though populations in this last may be of hatchery origin). As mentioned earlier, on the eastern flank of the SMO in Chihuahua and northernmost Durango is the large Río Conchos watershed, draining most of the eastern two-thirds of the state of Chihuahua into the Rio Grande, supplying most of the flow through that river's famous Big Bend area and further downstream to the Gulf of Mexico. North and west of the Conchos, between it and the Yaqui, are some enclosed basins without outlets, known collectively as the Guzmán drainage complex.

These river systems all drain the strikingly beautiful and rugged topography of the SMO of the western third of the state of Chihuahua, easternmost Sonora, western Durango, and the adjacent high country of easternmost Sinaloa. This part of the SMO has often been described as part of the western North American Cordillera and a southern extension of the Sierra Nevada of California. Largely comprised of tuffs and pumice deposited by ancient volcanic eruptions (Montgomery and López- Blanco 2003), its highest points are relatively lower than those of the more northern ranges, with less-prominent, low, rounded peaks or cerros (hills) being far more common than are more precipitous peaks (picachos) typical of western U.S. ranges. The two highest in our study area are Cerro Mohinora in southern Chihuahua and Cerro Barajas in northern Durango, both of which approach and elevation of 3,300 m. However, many peaks in Chihuahua and Durango range from 2,500 to 3,000 m, and so permanent streamflow capable of supporting trout usually is less than 2,750 m above sea level, often flowing through world-class, scenic canyons that rival the Grand Canyon of Arizona, such as the famous Barranca del Cobre (Copper Canyon) and Sinforosa, both exceeding 1,650 m in depth. Not surprisingly, many of the area's

high-gradient streams have impressive waterfalls, the most famous, Cascada de Basaseachi, more than 240 m tall.

Extreme topography influences weather, and so it comes as no surprise that precipitation in the Sierra varies widely, and that impacts the distribution of trout habitat. High altitudes are generally wetter and most of the precipitation is borne from the Pacific Ocean, so rainfall decreases from west to east due to the SMO's rain shadow effect. For example, on the Pacific side of the divide, Guadalupe y Calvo (2,279 m) in extreme southwestern Chihuahua has average annual precipitation of 116 cm (45.6 in), about half falling during the summer monsoon, June–August. The city of Creel (2,321 m), on the Atlantic side in the Conchos basin, averages 74.6 cm (29.4 in) annually, and downstream at Nonoava, about 100 km SSE of Creel (at 1,640 m, several hundred meters below typical trout habitat in Chihuahua), the annual total is 46.5 cm (18.3 in).

Vegetation also responds to elevation, topography, and rainfall, so our study area is botanically diverse (Ramamoorthy et al. 1993). Most mid- to high elevations in our study area are blanketed by Madrean Pine-Oak Woodland forest dominated by Chihuahua pine *Pinus leiophylla*, pino triste or sad pine *P. lumholtzii*, Arizona pine *P. arizonica*, madrone *Arbutus* sp., and any of more than 20 species of scrub oaks including Emory oak *Quercus emoryi* and Gambel's oak *Q. gambellii*. The lower elevations (below 1,800 m, and typically below trout) tend to be covered mostly by scrub oaks *Quercus* spp., Mexican pinyon *P. cembroides*, and juniper *Juniperus* sp., grading into thorn-scrub in the lower valleys far below trout habitat. Mixed conifer forest is common above 2,100 m, predominating on the upper Pacific slopes but also occurring in shady canyons and wetter north-facing slopes in the generally drier Conchos basin. Mexican Douglas-fir *Pseudotsuga lindleyana*, Durango pine *Pinus durangensis*, Mexican cypress *Cupressus lusitanica*, and Durango fir *Abies durangensis* are the usual species, but most of the conifer stands of the SMO have been selectively logged and only a few virgin stands survive in the most remote and steep barrancas. One can also occasionally find pure groves of quaking aspen *Populus tremuloides* in northern Chihuahua in more sheltered pockets above about 2,000 m.

Trout Habitats and Human Impacts

Figures 2–5 exemplify the topography described above and document the range of

trout habitat diversity and some of the anthropogenic habitats that we now describe here. Typically, habitats used by Mexican trout are above 1,900 m elevation, and trout are generally more abundant in shaded arroyos, especially in those that flow to the north and/or east. Trout will occasionally be found in larger streams below these altitudes, and we believe that in some watersheds, deep, cold pools provide seasonal refuges for them downstream of the primary habitat. Local residents have mentioned that in some mountain streams, “the big trouts” appear during the rainy season (June–September), indicating perhaps seasonal upstream movements from lower and warmer reaches during high summer flows. Difficult logistics confronting both access and sampling during the wetter months have limited our ability to study such hypothesized movements.

Europeans arrived in Mexico as early as several thousand years BCE (Hard and Merrill 1992; MacWilliams et al. 2008; Hard et al. 2015), in fact, the SMO in Chihuahua was home to indigenous peoples, including the Rarámuri, also known as Tarahumara. The large area they still occupy is often called the Sierra Tarahumara, where they live in scattered communities of nuclear families, often with 20 dwellings or less. They are subsistence farmers, seasonally moving over large elevation gradients to grow corn, beans, and livestock in shallow, volcanically derived soils on mostly unmechanized small hillside farms. The Rarámuri have a deep knowledge of the local fauna and flora (Lumholtz 1902; Pennington 1996; Merrill and Lopez- Gonzalez 2007). They know the native trout well and call them generically aparique.

The earliest scientific interest in the conservation of the area stems from visits in the 1930s by the noted conservationist Aldo Leopold and his son A. Starker Leopold to the Río Gavilán in the Río Yaqui watershed in northwest Chihuahua. They made multiple trips to the area and knew it very well, but unfortunately, they also witnessed the onset and results of large-scale human disturbance (Forbes 2004). A well-known essay about the values of the area and its demise resulted (Leopold 1940), relating that what had been a narrow channel winding through grassy banks was now a wide, scoured trough of cobblestones left by summer floods. The banks were undercut, and piles of debris marked the high water of recent years. Sand bars in sheltered coves of the channel were mixed with coarse pine sawdust from the mills upstream…the Gavilan was experiencing flash floods—the inevitable result of watershed abuse.”

The Río Gavilán is far from alone in having experienced adverse anthropogenic impacts related to overgrazing, logging, and road building, but we and others (e.g., Forbes 2004) believe that destruction of the "watershed sponge" from overgrazing by cattle, sheep, and horses significantly increases flashiness of discharge, peak flows, sedimentation, and turbidity (Hendrickson and Minckley 1985; Turner et al. 2003). Pastures throughout the SMO generally appear to be overstocked and hence overgrazed and abused, undoubtedly contributing to poorer quality, increased quantity, of runoff, and increased flow variability. Many streams have little shading, with most trees distant from banks as a result of frequent scouring floods. We conclude that out-of-bank flows occur over most of the Sierra watersheds on a regular basis, and they are clearly initiated by rainfall since snowfall rarely accumulates to the point of adding significant volumes to streamflow. To suggest, however, that all erosion is caused by human activities is folly. It is probable that some of the peak flows and accompanying erosion that we have observed in the Sierra are the natural product of steep topography, thin soils, general aridity, and "canyon building" (Chambers and Miller 2004). Whatever the cause, SMO arroyos are dynamic and show the cumulative effects of many years of high flows, with fantastic shapes eroded into large boulders that clutter streambeds and adjacent slopes, and those in stream are often sitting directly on bedrock.

While we have seen very little clear-cutting of SMO forests, selective and sustained forest harvest appears common throughout the region, and water quality is decreased by many small sawmills that have produced massive sawdust piles that wash into streams (Meehan 1991). Mining clearly also has some impact. Most that we have seen is below trout habitat, but we have noted new, large-scale mines growing rapidly in recent years, especially in the Mayo and Yaqui basins. Other anthropogenic impacts on trout habitats that we have observed are forest fires, detergents used instream to wash clothing, and untreated (or minimally treated) effluents from towns and rural communities.

Clarity of Mexico's trout streams varies widely. Much of the woodlands in the Sierra highlands are scarred by dusty, rocky, and poorly designed and maintained logging roads. Especially in the Conchos basin, the volcanic rock in many of these has been ground to a fine dust and the resultant runoff during the rainy season can affect stream clarity, with suspended particles limiting visibility to less than a meter, even

during times of low flow, and imparting a bluish-aqua coloration to the water. In contrast, spring-fed tributaries, in particular those of the Yaqui, Mayo, and Piaxtla, can be very clear, with visibility of 3 m or more. Finally, the picture is perhaps not as grim as the above might lead readers to believe. The famous Gavilán has been shown to be recovering (Fleming and Forbes 2006) and is not alone in that regard. The federal government now offers various incentives to local landowners (often large government-organized cooperatives or ejidos) to conserve and better manage their forests, and many new federal, state and private reserves, including some with trout habitat, have been, or are in the process of being, declared in recent years (Comisión Nacional de Áreas Naturales Protegidas, http://sig.conanp.gob.mx/website/pagsig/datos_anp.htm).

Obviously, the human population of the SMO continues to grow and diversify with ever-increasing impacts on its natural resources, and as is true globally, trout are economically and nutritionally important. Not only are there now many Rainbow Trout hatcheries and grow-out facilities (Espinosa Pérez et al. 2016) raising trout for sale, most streams that harbor native Mexican trout receive at least some fishing pressure, especially near settlements, both by those looking to sell their catch and by subsistence fishers who consume their catch locally. Robert Smith, author of Native Trout of North America, wrote to Dr. Robert Behnke in 1983 (Pennington 1958) and reported that “The fishing pressure by locals is constant (12 months a year) mostly by kids who fish with bait and keep everything they catch no matter how small.” However, while we have witnessed angling by local residents in many parts of the SMO, we have also seen that the Rarámuri are adept at capturing trout and other fishes by hand fishing and we have seen weirs fabricated by the Rarámuri in the streambed using local rock. They clearly take good numbers of trout with those have much greater impacts. Daniel Carleton Gajdusek (1954), Nobel Prize winner, listed seven different plants used by the Rarámuri as piscicides or fish stupefying agents (Meek 1902; Pennington 1958), and one of our Rarámuri guides, Alvaro Fierro, showed us one unidentified root that was used locally to capture trout. Use of native piscicides is clearly common and widespread, and the substances used extend beyond those that are native to include liming and the use of liquid bleach. All such piscicides used in running waters have the potential to cause mortality far downstream of application points, and many impact food chains that support fish communities. Many authors also mention use of dynamite in Mexico to procure fish,

including in the SMO (Stilwell 1948; Needham and Gard 1959). Some streams, especially in segments near road crossings, have particularly heavy harvests of trout and other fishes just prior to Easter for traditional fish dinners at the culmination of Lent. We have consistently found no trout (and sometimes no fishes at all) at road crossings and have sometimes hiked 1–2 km upstream before finding trout.

The threat of hybridization with nonnative Rainbow Trout, well documented in other native trout further north (Behnke and Tomelleri 2002; Young et al. 2016) but not without some controversy (Kovach et al. 2017), is also a significant concern. Introductions of hatchery Rainbow Trout into Mexico began more than a century ago, and there have now been many introductions of hatchery stocks from U.S. hatcheries to widely scattered locations throughout much of the SMO (Espinosa Pérez et al. 2016). Our first-hand observations of Rainbow Trout grow-out facilities in the Yaqui, Fuerte, Mayo, San Lorenzo, Río del Presidio, and Conchos watersheds found none secure against escape of the introduced Rainbow Trout to adjacent streams, and at some, it seemed miraculous that the minimal and poorly constructed structures retained any of the introduced fish at all. Though Mexican native trout are genetically distinct from hatchery Rainbow Trout, and clearly valid species, that does not seem to have endowed them with distinctive behavior or habitat requirements or other attributes that might make them immune to hybridization. There is now DNA evidence from many of Mexico's Pacific watersheds of hybridization of natives with hatchery Rainbow Trout (Escalante et al. 2014, 2016), and even in the Río Conchos drainage where the most highly imperiled forms live, hatchery Rainbow Trout have now been taken on at least three occasions.

For millions of years, Mexico's native trout have been diverging from their shared ancestral stock (Abadía-Cardoso et al. 2015) via isolation of populations widely scattered across this rugged and complex terrain to produce the remarkable diversity of species we find today. Throughout that evolution, they have adapted to what most U.S. trout aficionados would clearly consider marginal trout habitats and they have survived centuries of human impacts. Though now clearly critically endangered by all of the threats mentioned above, as well as climate change, as are also most of their more northern cousins (Penaluna et al. 2016), fortunately much of their genetic diversity still persists, clinging on despite those threats in isolated habitats at the uppermost limits of what appear to be dwindling permanent waters. So, there is still

hope, and even better, there are now serious conservation actions for native trout in progress. As mentioned above, some new reserves that protect trout habitat are being established. Captive breeding is also being explored (Abadía-Cardoso et al. 2016; Barriga Sosa et al. 2016) to not only perhaps allow for reintroductions in case of future extirpations in the wild, but also with an eye toward possible use of native species as replacements for domesticated Rainbow Trout in the growing regional trout aquaculture economy. There have also been recent analyses of some of the human economic and social factors that are likely to impede at least some conservation actions (Cassio Madrazo et al. 2016; Penaluna 2016; Sánchez Ortiz et al. 2016).

So while still clearly imperiled, the future for native Mexican trout is not totally dark, and we now turn our attention to describing the species.

The Native Trout of Mexico

Herein, we give cursory descriptions of the external phenotypes of all the known forms of native Mexican trout. We do not cover all characters we have discovered that differentiate species, considering, for example, details such as vertebral and scale counts, or DNA, to be outside of the scope of this summary. We also omit globally redundant and obvious characters, such as the fact that virtually all native Mexican trout have the anal, pelvic, and dorsal fins tipped with opaque white coloration. Where we have observed deviations, such as the fact that some may have orange or salmon-colored dorsal fin tips, we state that. As revealed in Figure 6, these species differ principally in coloration of the body, disposition/color of the lateral stripe, arrangement/size/shape of the black spotting, number of parr marks, and the number/shape/size of auxiliary parr marks. Illustrations are of what we believe to be pure native specimens, but we mention hybridization and its phenotypic effects for those places where we have documented it. Unless otherwise indicated here, all species remain scientifically undescribed beyond genus (so should be referred to as *Oncorhynchus* sp.)

Río Yaqui trout

Our collections indicate at least four genetically unique lineages of native trout in this basin, the most northern in many tributaries of the Río Bavispe subbasin (Gavilán,

Nutria, and upper Aros rivers, among others), and in the complex southern subbasin (the Sirupa, lower Aros, and Tomochi rivers), we find different lineages in tributaries like the Arroyo Tutuaca, Arroyo Bandarella, and Arroyo El Salto. Yaqui trout from the Bavispe subbasin have strong golden hues on the sides and many prominent black spots above and between parr marks. The reddish-pink lateral "band" is often discontinuous (unlike typical Rainbow Trout) and broken into a series of spots—there being no reddish pigment within the parr marks. This condition persists even once the parr marks have faded on large individuals. All Yaqui trout typically have an orange cutthroat mark under the dentary bone. The pelvic, anal, and pectoral fins are mostly bright orange, and the dorsal fin is sometimes tipped with orange. A similar trout exists in the adjacent and endorheic (without outlet) Guzmán (or Casas Grandes) basin, but it is known to have been stocked there in the early 1900s by Mormon colonists using specimens taken from the Bavispe watershed. Adult trout from the Río Tomochi tributaries (Sirupa basin) are a soft lemon-yellow on the sides, as opposed to gold, have a row of bright pinkish spots along the lateral "band," and have black spots mostly restricted to above the lateral line, many of the spots shaped like an "x" instead of being oval or round.

The Yaqui watershed, on the whole, is sparsely inhabited by humans, is relatively undisturbed, and has probably more high-quality native trout habitat than does any of the other major river basins to the south. Some watersheds that experienced heavy logging impacts 70 or more years ago, such as the famous Gavilán, have since recovered substantially (Forbes 2004; Fleming and Forbes 2006). However, this basin is also relatively more easily accessed, and our perception of its overall condition relative to others might be biased to some extent by us having sampled somewhat more there than in some of the other basins.

Río Mayo trout

These are similar to the Tomochi/Sirupa trout, with males strongly suffused with bright pink and lavender on the cheeks and with the typical lateral reddish band of most other trout broken into a series of bright pink or reddish spots. They also have "x"-shaped spots seen in Tomochi trout. The pelvic fins are orange or pinkish orange, and the anal is usually bicolored, pinkish-orange anteriorly and golden- yellow posteriorly. The Mayo is a relatively small watershed and has active surface and

subsurface mining high in the watershed that is adversely affecting populations in Arroyo El Concheño and other streams. Trout are rare and difficult to come by in this system. We have collected them from only four locations, including three above Basaseachi falls, and in the Río Candameña below the falls.

Mexican Golden Trout

This is the only native Mexican trout with a formal scientific name. The species was described in 1964 (Needham and Gard 1964) based on a handful of collections, and the name applied to specimens spanning three vast Pacific watersheds: Río Fuerte to the north, the Río Sinaloa, and the Río Culiacán to the south. This complex is now clearly the most studied of all native Mexican trout lineages, following publication of a 14-chapter book focusing on it (Ruiz-Luna and Garcia De León 2016). Morphological studies by Gorgonio Ruiz Campos (Ruiz Campos et al. 2016) suggest that at least two species may be masquerading under this name, and Escalante (2010) reports probably at least three unique evolutionary lineages within what we are now calling the Mexican Golden Trout complex. Observations of trout phenotypes across this range reveal distinctive types in both Río Verde and Arroyo Las Truchas in the Fuerte drainage, as well as in both the Río Sinaloa and Río Culiacán basins. In addition, several populations from the Río Culiacán watershed are meristically and morphologically distinct from each other. In contrast to the Yaqui and Mayo trout, Mexican Golden Trout from the Río Verde have a continuous brick-red lateral band. Females and young are typically silvery with conspicuous charcoal-blue parr marks, and they sometimes have an almost blue-black lateral stripe through the parr marks. Spawning males are bright golden-yellow on the sides and upper belly, with a bright-orange lower belly. Anal, pelvic, and pectoral fins are bright orange in males. The black spots are numerous but small and are mostly restricted to the back and upper sides.

Río San Lorenzo trout

The distribution of trout within the San Lorenzo watershed is poorly known, with its largest subbasin (San Gregorio) still completely unsampled, though it surely has trout habitat. Specimens from elsewhere, however, are silvery with bright blue and purple reflections, often with only a faint pink coloration on the opercle and lateral band. Faint yellow or cream coloration is sometimes developed on the lower sides of these

trout, but is often lacking. The ventral fins are light pinkish-gray to light orange. Black spots are almost wholly restricted to above the lateral line, where they are well developed, oval, and angled anteriorly. San Lorenzo trout typically have 12–16 oval parr marks, in contrast to most other North American trout, which usually have 8–11. The body is heavily marked below the lateral line with auxiliary parr marks that are the same dark slate-gray as the principal parr marks.

In November of 1956, more than 700 of these trout, from the Río Truchas, were captured alive and taken to three U.S. hatcheries. The intent was to introduce a new species, likely tolerant of higher temperatures (Needham 1955; Needham and Gard 1959), that would thrive in heavily logged U.S. streams with elevated temperatures that eliminated other trout. Though some females produced eggs, the males were infertile and the trout proved to be very wild and difficult to feed, making the project altogether unsuccessful. Several publications refer to these fish erroneously as Mexican Golden Trout.

We, as part of the Truchas Mexicanas binational group, made several collections in Arroyo La Sidra above and below a relatively large hatchery. Most specimens from below the hatchery show signs of hybridization with hatchery Rainbow Trout; however, samples from above the waterfall almost immediately upstream of the hatchery indicate a native form with distinctive markings that differentiate it from other populations in the San Lorenzo watershed.

Río Piaxtla trout

Trout of the Río Piaxtla watershed are genetically similar to those of the San Lorenzo, but, at least in our samples, they are more brightly colored with orange, red, and gold. Specimens from Arroyo El Granizo have a continuous bright orange lateral band, and those from the Arroyo Santa Barbara have a muted brick-red/orange band. Piaxtla trout have, on average, more parr marks (intersecting the lateral line) than any other known trout, typically with 13 or 14, and up to 18 in some. The number of auxiliary parr marks (below the lateral line) usually number more than 100. The anal, pelvic, and pectoral fins range from bright orange to brick-orange. The dorsal and anal fins are more broadly tipped with white than seen in other species of Mexican trout. The distribution of Piaxtla trout is poorly known because of its remote and rugged terrain and difficult stream access. Residents of Puentecillas told us that they

had made intrabasin transfers of trout from Arroyo El Granizo but had never stocked any exotic trout.

Río del Presidio trout

The origins of trout in the Río del Presidio watershed has been debated for many years. Robert Rush Miller, noted ichthyologist and author of the authoritative Freshwater Fishes of México (Miller et al. 2005), based on decades of collecting in the country starting in the 1960s, believed them to have been stocked from railroads in the late 19th or early 20th century. Early specimens from the area that might have resolved the debate were unfortunately lost. Edward William Nelson at the Smithsonian Institute saw trout in the Presidio headwaters near El Salto in August of 1898 while on an ornithological expedition with Alphonso Goldman and reported this sighting to Barton Warren Evermann in 1906. In 1907, Walter Bishop I, then American vice-consul to the state of Durango, caught five trout from the Presidio headwaters and shipped them to Evermann, who examined them and proclaimed that they were "very distinct from the San Pedro Mártir trout. They will be described in a later paper." The specimens never received a treatment, they were apparently never examined by anyone else, and their whereabouts remains unknown (Needham and Gard 1959).

In March of 2004 we had a lengthy discussion in Ciudad Durango with Mr. Walter Bishop II of that city, who related how his father (Walter Bishop I) had caught trout in the then largely undisturbed and remote wilderness along the Durango/Mazatlán trail in the early 1900s. Mr. Bishop II served as manager of the El Salto Lumber Company from 1937 to 1952 and was an avid fisherman, so both his job and hobby brought him to know the area, trout, and surrounding mountains very well. He related how the railroad from Ciudad Durango arrived at the Presidio headwaters (some 110 km from Ciudad Durango) in 1919, along with the lumber companies and settlers, and he was convinced that stocking Rainbow Trout in tributaries of the Presidio basin before then would have been difficult, if not impossible, even though Rainbow Trout were, by then, in the country but distant in Mexico City (the U.S. Fish Commission first sent Rainbow Trout to Mexico in 1888 to Estéban Cházari in Mexico City [Secretaría de Fomento 1892]). In 1946, Walter Bishop II guided Ralph G. Miller (father of Robert Rush Miller) to native trout in the Presidio basin, resulting in collections still held at

the University of Michigan that are the earliest extant samples of native trout from Durango. Correspondence between Walter Bishop II and J. R. Tomelleri in 2002 relates, “When Ralph Miller was in El Salto the general consensus was that the trout were native. No one had ever heard of trout having been planted.”

Our collections of Presidio trout show considerable phenotypic variability. Individuals from Arroyo Nogales show bright orange-red fins and lateral stripes, but those collected in Quebrada de Vega in 2004 are less brightly colored and more sparsely spotted. At Walter Bishop’s suggestion, we also collected trout in Arroyo la Rosilla, which Mr. Bishop implied to us were different from the native trout below the waterfall at El Salto. Since then, DNA of specimens from the Presidio indicates that they are indeed hybridized with hatchery Rainbow Trout (Escalante et al. 2014).

Río Baluarte trout

Prior to our original collection in October 2000, the Baluarte trout were unknown to science. Subsequent collections were made by our group in February 2004 from Arroyo Santa Barbara, a barranca southwest of El Salto, Durango. Baluarte trout are spectacular for their lemon-gold coloration, their orange bellies, and their bright red spots in lieu of a lateral band. Many specimens also exhibit a unique greenish hue on their anterior parr marks. The anal, pelvic, and pectoral fins are bright yellow-orange. Our guides insisted that there are two forms of trout in the Río Baluarte. Our collections were intriguing, consisting almost entirely of male trout, a sparsely spotted variety, and another form that was more densely spotted. It is possible that some of this variation could be due to hybridization with Rainbow Trout, but further study is needed.

Río Acaponeta trout

Acaponeta trout that we collected from four arroyos in 2001 and 2004 are unusual in having large, round auxiliary parr marks. Unlike trout of the adjacent Baluarte system, though, they are typically silvery and lack strong yellow, gold, and red coloration. Specimens from Arroyo las Moras had an unusual green coloration in the back and few black spots, clustered principally on the peduncle. Some of the larger adults that we collected showed the same pattern of red spots along the sides, as seen in Río Baluarte trout (and in trout from the Conchos, Yaqui, and Mayo rivers). The ventral

fins of Acaponeta trout are a light pinkish-gray or light creamy orange. Studies by Camarena-Rosales et al. (2008) and Escalante et al. (2014) suggest that Acaponeta trout may be of hatchery origin.

Río Conchos trout

The first scientific collections of Conchos trout were made by us in February 2005 (Camarena-Rosales et al. 2006), and another collection was made from a tributary of the Río Hojasichi in 2006. This trout (like the Mayo, Yaqui, Baluarte, and Acaponeta trout) has a distinct series of red spots along its lateral line (in lieu of the typical red band found in Rainbow Trout) and has a strong lemon/gold coloration on its side and upper belly. The pelvic, anal, and pectoral fins are orange. These northern Conchos trout have a lemon-yellow to orange cutthroat mark on the dentary bone and appear most closely allied to Yaqui trout from the Tomochi watershed. They have no basihyal (=basibranchial) teeth or genetic affinity to Cutthroat Trout, so we doubt that they could be the same trout that Cope described as similar to "Salmo purpuratus" (Cutthroat Trout). In 2006, we collected individuals up to 30 cm in total length with densely spotted back and upper sides, including "x"-shaped spots on the lower sides and peduncle. Adults of this species have a series of 7–9 black spots on the edge of the snout.

In 2007, we discovered a second native trout in the Río Porvenir subbasin of the Conchos, north of El Vergel in southern Chihuahua. This southern Conchos trout is known only from one stream and its tributary and is most closely aligned genetically and phenotypically with the Mexican Golden Trout of the Río Fuerte.

The Río Conchos basin lies within the rain shadow of the SMO and is considerably drier than the Pacific drainages. Trout habitat as a result appears restricted to north-flowing streams and/or deep, shaded canyons. Even the best trout habitats in the Conchos would certainly appear marginal at best to most U.S.-trained trout biologists and anglers. Both forms of Conchos trout are highly susceptible to fishing pressure by the local Rarámuri and further perturbations from grazing, logging, and other human activities.

San Pedro Martir Trout

In Baja California, about 100 km south of Ensenada, the Río Santo Domingo (Río San

Ramón in older literature) and Arroyo San Rafael are both inhabited by the San Pedro Martir Trout, sometimes referred to as Baja Trout or Nelson's Trout (for Edward W. Nelson who collected specimens for Evermann in 1906). These have been extensively studied by Truchas Mexicanas colleague Gorgonio Ruiz Campos (Ruiz- Campos and Pister 1995; Ruiz Campos 2017) and his students and colleagues, who followed in the footsteps of other ichthyologists. Trout from the Río Santo Domingo have been collected from a much lower altitude than any other Mexican trout (540 m), no doubt related to the Mediterranean climate and cold marine currents along the nearby Pacific coast. From 1936 to 1938, Dr. Paul Needham of the University of California, Berkeley led three forays into the Río Santo Domingo basin to survey and later collect trout to raise in U.S. hatcheries. Needham believed that these native southern trout might be more tolerant of high water temperatures and prove to be less migratory than U.S. strains of Rainbow Trout with "less strong hereditary tendencies to move downstream after their planting." Needham's San Pedro Mártir hatchery stocks met with unfortunate and unavoidable accidents and by 1940 had been completely wiped out in the United States. Populations of this trout in Mexico, however, are considered stable (Ruiz-Campos and Pister 1995; Ruiz Campos 2017), and their range on the relatively small but well-watered and cool Sierra San Pedro Mártir was expanded by humans. The San Rafael was stocked with trout from the Santo Domingo drainage in 1938 and 1939 by a Charles Edward Utt (no date).

Angling for native Mexican trout

Good fishing has been enjoyed for many years by fishermen willing to travel off the beaten path in Baja California, where trout streams are easily accessible within a day's drive from San Diego and Tijuana, both with major commercial airports. The Sierra San Pedro Martir Trout (Nelson's Trout) is thus well known to anglers via a long history of pursuit by fishermen, starting with Seth Meek (1904) reporting that "Mr. E. Heller" caught and kept four specimens at San Antonio on the Río Santo Domingo in 1902. Subsequently, at the behest of Evermann, Edward W. Nelson (1906) collected nine trout from the "San Ramon River" (Río Santo Domingo) and sent them to Evermann. The trout also occur in a number of Santo Domingo tributaries and were transplanted to nearby Arroyo San Rafael. At least one fly-fishing club in California, San Diego Trout, has made occasional excursions to the Baja peninsula in search of Nelson's Trout. Several guides have operated in the area over the years, including

Mike's Sky Ranch in the Arroyo San Rafael and, until recently, Enrique Meling of the Meling Rancho Family Ranch near San Telmo operating in Río Santo Domingo (arroyos San Antonio de Murillos and La Grulla).

Angling for native trout in the mainland rivers of Mexico is not quite as easy but has a longer history, dating back to at least the 1880s, when Professor Lupton shipped his two specimens of trout he had caught near the Chihuahua–Durango border to Cope. Not much later, a letter to a magazine editor from "J.V.B." reported that he had fished many streams in Chihuahua and Durango but had never caught a trout (Anonymous 1890), but as mentioned earlier, Walter C. Bishop I, a U.S. vice consul living in Ciudad Durango and his son were both avid anglers in Durango who caught trout there starting in the early 1900s. John Hatch of Colonia Juárez, Chihuahua, one of our colleagues and guide for Truchas Mexicanas, has fished extensively in the Guzmán and Yaqui watersheds since the 1950s. His grandfather, Clarence Lunt, guided Aldo Leopold on hunting expeditions in the Yaqui in the late 1930s. Lunt is in a photograph that shows off 19 Yaqui trout caught during one of these trips. In l948, Dr. A. Starker Leopold caught several trout from Río Gavilán in the upper Yaqui (Bavispe subbasin) drainage that he preserved and they are still in the University of Michigan fish collection. Johnson (1997) related how high water had foiled attempts by his 1952 expedition's crew to obtain specimens until "Señor Nuñez's three stalwart young sons volunteered to fish for us and secured six more specimens, much larger—9–13 in."

More recently, Robert Smith caught and photographed Mexican trout in the Yaqui, Fuerte, San Lorenzo, and Presidio River basins. Smith thought Mexican trout peculiar for their habit of taking fishing flies in an unconventional manner, taking not on the retrieve but rather when the fly is left to hang motionless in the current (Smith 1983). We had success with the same technique in l997 in a tributary of the Río Chuhuichupa (Yaqui/Bavispe watershed). Rex Johnson Jr. of Silver City, New Mexico has made several fly-fishing excursions into the SMO in pursuit of trout, catching them in the Yaqui and Fuerte (Verde subbasin) drainages (Johnson 1997). Michael Graybrook (Pittsburgh, Pennsylvania, personal communication) of Pennsylvania accompanied Johnson on a trip to the Río Verde in 1998 and photographed some of the Mexican Golden Trout they caught from Arroyo Zuppe Chico (Fuerte drainage) and other tributaries. Arny Stonkus of Seattle, Washington has been on many of our trout

expeditions to Mexico and has caught trout by fly-fishing in the Yaqui and Fuerte watersheds. He also traveled to Basaseachi in Chihuahua in 2000 and fished the Río Candameña (Río Mayo drainage) below the falls, but caught no trout. Many other members of Truchas Mexicanas have also caught trout by fly-fishing and spin-casting in the Guzmán (Casas Grandes), Conchos, Yaqui, Verde (Fuerte) (Figure 7), Presidio, Baluarte, San Lorenzo, and Mayo watersheds.

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Figure Legends

Figure 1. Map of the major river basins of the study area: Pacific tributaries—Río Santo Domingo, Río Yaqui, Río Mayo, Río Fuerte, Río Sinaloa, Río Culiacán, Río San Lorenzo, Río Piaxtla, Río del Presidio, Río Baluarte, Río Acaponeta; Gulf of Mexico tributary—Río Conchos (tributary of the Rio Grande); endorheic—Guzmán drainage complex.

Figure 2. Cascada de Basaseachi, Río Mayo.

Figure 3. Río Rituchi, Río Conchos.

Figure 4. Arroyo San Antonio, Río Yaqui (Bavispe subbasin).

Figure 5. Overgrazed pasture, near continental divide of the Río Conchos and Río Fuerte.

Figure 6. Illustrations of Mexican trout: (A) Río Yaqui trout (Bavispe subbasin), (B) Río Mayo trout (Río Candameña), (C) Mexican Golden Trout (Los Loera subbasin of Río Fuerte, Arroyo las Truchas), (D) Mexican Golden Trout (Río Sinaloa basin, Arroyo Ran- cho en Medio), (E) Mexican Golden Trout (Río Culiacán basin, Arroyo Santa Rosa), (F) Río San Lorenzo trout (Arroyo la Sidra, above the falls), (G) Río Piaxtla trout (Arroyo el Granizo), (H) Río del Presidio trout (Arroyo Nogales), (I) Río Baluarte trout (Arroyo Santa Barbara), (J) Río Acaponeta Trout (Arroyo las Cebollas), (K) northern Río Conchos trout (Arroyo Ureyna), (l) southern Río Conchos trout (Arroyo del Molino), and (M) San Pedro Mártir Trout Oncorhynchus mykiss nelsoni (Río San Antonio).

Figure 7. A Mexican Golden Trout caught in the Río Verde, a Río Fuerte basin tributary.

Figures

Figure 1

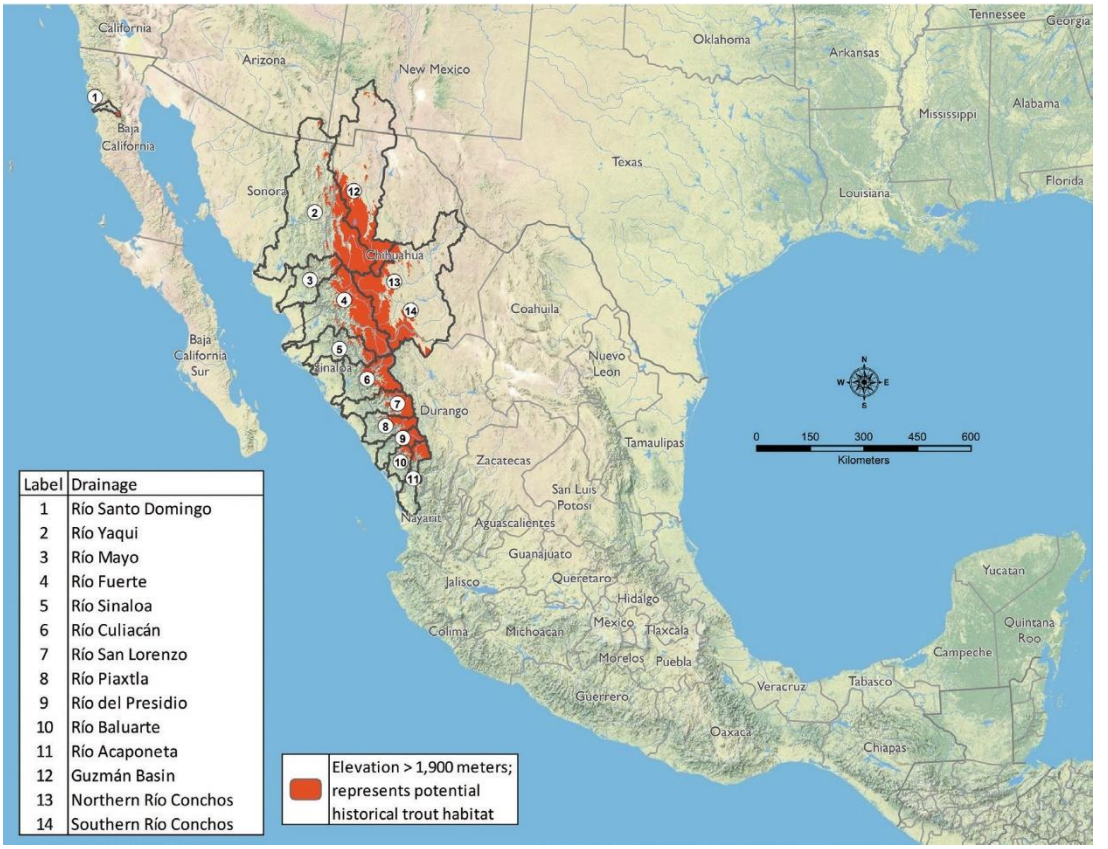

Figure 2

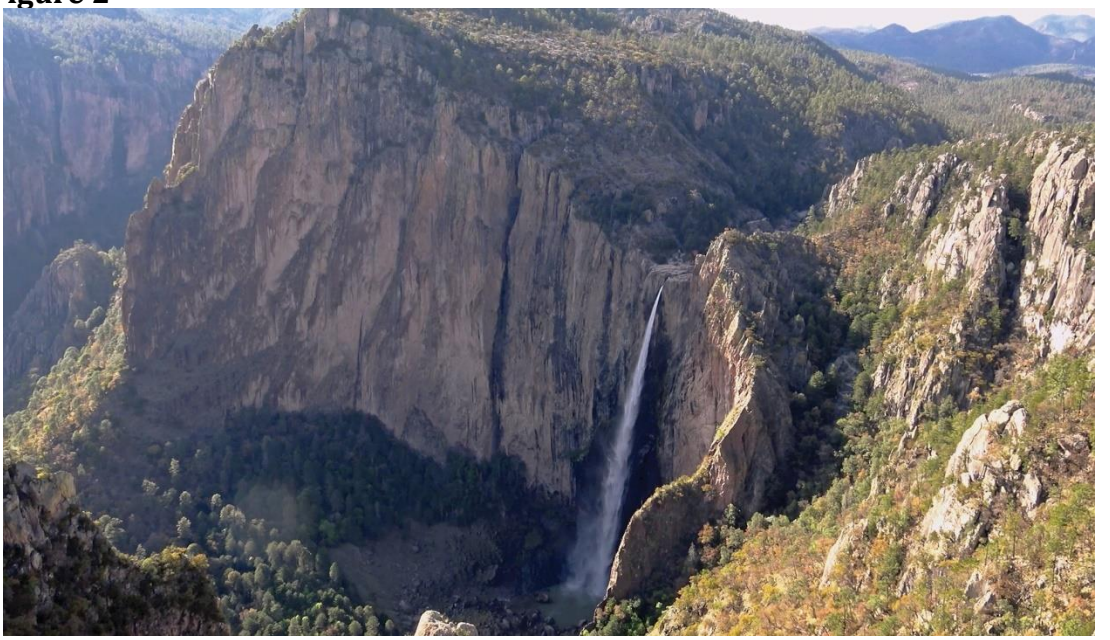

Figure 3

Figure 4

Figure 5

Figure 6

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Figure 7