First record sheds light on the distribution of the cyprinodontiform genus *Jenynsia* (Günther, 1866) in the High Andean Plateau

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Abstract

This is the first record of the genus *Jenynsia* in the High Andean Plateau (HAP). It has been found at elevations between 3,400 to 3,900 m in three endorreheic systems: Salar Antofalla, Antofagasta de la Sierra, and El Peñón, Northwestern of Argentina, South America. This finding increases the number of known HAP fish genera to five. Furthermore, in contrast to the old andean species-rich genus *Orestias*, the presence of *Jenynsia obscura* populations in young high altitude non-marine saline wetlands reported here supports a recent dispersal into the HAP.

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The Andean Plateau is the largest continental-scale high plain on the Earth associated with abundant magmatism located above a 3 km elevation contour extended from 13º S to 27ºS. This wide South American topographic feature was originated in lower Miocene (~25 Ma) through a vicariant multi-stage uplift that, in the southernmost part called Puna, lasted until 1-2 Ma (Allmendinger et al. 1997). The HAP is characterized by extensive evaporitic bodies acting as collectors of a closed drainage network subject to an arid climate and a wide daily thermal amplitude (Risacher et al. 2003). This landscape is dominated by nonmarine brines accumulated in sedimentary basins during Neogene, where ecological heterogeneity is expressed by an array of aquatic ecosystems that include numerous extensive salars and lagoons —such as Antofalla and Laguna Colorada— as well as geothermal springs and other high altitude wetlands (Alonso et al. 1991, Benzaquen et al. 2017). Within the entire HAP, that stretches along 1800 km from southern Perú Altiplano plain to Northwestern Argentina Puna, only four native fish genera were recorded above 3 km: *Astroblepus* (climbing catfish), *Orestias* and *Pseudorestias* (pupfish), and *Trichomycterus* (pencil catfish) (Arraya et al. 2009, Barra et al. 2009, Schaefer 2011, Cruz-Jofré et al. 2014, Arratia et al. 2017, Fernandez & Andreoli Bize 2017, 2018). The Orestiini (sensu Arratia et al. 2017) is recognized as the sole cyprinodontiform clade found in the

HAP. By comparison, the complementary distribution of Anablepidae is considered the outcome of a Neogene diversification in South American coastal marine habitats (Nelson et al. 2016, Amorim & Costa 2018). This family has a quite dissimilar richness. Whereas two of its genera comprise few coastal species from Central America and Northern South America, most of the species-rich genus *Jenynsia* is known to be distributed in several small freshwater wetlands across southern South America, from the Central Andes foothills to Atlantic basins and coastal environments (Ghedotti 2003, Frota et al. 2019). *Jenynsia obscura* (Weyenbergh 1877) (= *J. pygogramma* Boulenger 1902) is one of the species from the Central Andean foothills (Ringuelet et al. 1967, Aguilera et al. 2013).

We hereby report the first record of *Jenynsia obscura* in the Puna, between 3,400 to 3,900 masl. Twelve specimens of *Jenynsia obscura* were recognized by the following combination of characters: 22-23 scales in the predorsal series; 35-36 scales in the lateral line series; very fine line of pigments along the lateral series in the middle of the flank and some vertical spots close to the mid-dorsal line (Koerber & Azpelicueta 2009) (Fig. 1). These fishes were captured at elevations above the limit of the Puna: Salar Antofalla 3,950 m, El Peñón and Antofagasta de la Sierra at 3,400 m in Catamarca province, Argentina (Fig. 2). The specimens were kept alive, later anesthetized with benzocaine and killed by immersion in cold water (0°C) *in situ* (Metcalfe & Craig 2011). Then were fixed in 10% formalin and preserved in 75% ethanol in the Ichthyological Collection of the Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Catamarca, Argentina (FACEN). Extensive ichthyological surveys in the Puna indicate that *Jenynsia* is absent in many

suitable wetlands (LF pers. obs.) but *J. obscura* populations are well established among the small rocky bottom vegetated creeks and ponds reported here (Fig. 1, Suppl. Video).

The distribution of most *Jenynsia* species is uneven across wetlands located below the HAP from 2,300 m to seashore. While *J. luxata*, *J. tucumana* and *J. sulfurica* are reported to occur in few localities of northwestern Argentina, *J. maculata*, *J. alternimaculata* and *J. obscura*, exhibit a more extended regional coverage in what appears to show some degree of endemism; in contrast, *J. lineata* is widely distributed in the vast plains of central Argentina, from Atlantic coastal environments to Andean foothills (Buti & Miquelarena 1995, Ghedotti 2003, Menni et al. 2005, Aguilera et al. 2013, Amorim 2018; Frota et al. 2019 and references therein). The distribution of *J. obscura* encompasses many endorrheic riverine wetlands associated with the easternmost Sierras Pampeanas ranges at Cruz del Eje river (type locality, 470 m) and Conlara river (675 m) to the south. Both basins have their base level (180 m) in Salinas Grandes salt flat. In addition to our records, this species is also present to the west well beyond Salinas Grandes in Andean foothills up to 2,000 m, thus exhibiting a continuous distribution (Ringuelet et al. 1967).

The finding of *J. obscura* in such an unusual location for the Anablepidae like high altitude evaporitic volcanic environments of the Puna shown here, pose some interesting issues in the midst of a current discussion on the adaptive radiation of the genus. The debate focuses on the events that led a cyprinodontiform clade to the invasion of inland wetlands, and the role of the marine-freshwater transitions during marine incursions recorded in Neogene times (Amorim & Costa 2018). In this regard, Amorim & Costa

(2019) have recently proposed that a transition across osmotic barriers towards sea coastal environments evolved during Pleistocene in the clade embracing *J. lineata* and *J. darwini*. Ichthyologists have long considered *J. lineata* highly tolerant to salinity levels and have recently been recorded to occur in the Rio de la Plata estuary under influence of marine water for the first time (Ringuelet et al. 1967, Menni et al. 1996, Guerrero et al. 1997, Menni 2004, Calviño & Alonso, 2016). Moreover, its presence in strictly marine environments was followed by the ichthyology staff of the Museo Argentino de Ciencias Naturales (MACN) since 1947 through 1961 in Mar del Plata sea shore and have also been found in San Blas tidal flat of South Atlantic Ocean. Indeed this species has even been reported in the hypersaline Epecuén lagoon (37°07'52,27"S 62°52'44,65"W) when salinity was near twice marine levels (López et al. 1993). Likewise, among west Andean species, *cox1* gene divergence suggests a recent origin for tolerant microendemic *J. sulfurica* (Aguilera et al. 2019). Physiological issues apart, Miocene diversity of Anablepidae was higher than present as revealed by paleoicthyological studies. Extinct taxa from northwestern Argentina found in ancient coastal facies supports an earlier hypothesis about the strong influence of the middle Miocene marine transgressive phase on the distribution of *Jenynsia* (Aguilera & Mirande 2005, Sferco et al. 2017). Furthermore, late Miocene deposits of "Puchuzum" ephemeral lacustrine environments yielded additional evidence to support an anablepid ongoing adaptive radiation (Bogan et al. 2018). Interestingly, these conditions are analogous to those of Salinas Grandes-Ambargasta system around which *J. obscura* and *J. lineata* co-occur. This arid tectonic depression once harboured a huge

endorrheic lacustrine system (Laguna Grande-Laguna de Ambargasta) that may have lasted from upper Pleistocene to middle Holocene, and was fed in various stages through the Salí river Andean drainage whose channels diverted as a result of Sierras Pampeanas basement uplift since the middle of the Pliocene (Gutiérrez et al. 2017). Since then until Pleistocene extensive tectonic activity took place in the Puna, and also at the eastern edge of the Salar de Antofalla. Here, faulting and thrusting reduced the saltpan basin to its present elongated shape until the end of Middle Pleistocene, (Kraemer et al. 1999). Nevertheless, just as much as Quaternary seismic activity diminished, large amounts of modern alluvial fan deposits like Vega El Colorado were shed (Hongn & Seggiaro 2001, Seggiaro et al. 2007). Hence, the finding of *J. obscura* populations amidst young non–marine evaporitic wetland environments strongly suggests that the late geophysical stability of the Puna allowed a recent dispersal. Finally, this finding contributes to the long needed historical biogeographic assessment of HAP fish diversity (Parenti 1984).

Material Examined

J. obscura: FACEN 31, 3 specimens, Los Nacimientos, 27°9’52.84”S 66°44´41.33”W, 2,019 m, 9 July 2016; FACEN 122, 5 specimens, El Peñón, Antofagasta de la Sierra, 26°28’49.19”S 67°15´14.78”W, 3,440 m, 12 October 2018; FACEN 124, 2 specimens, Villa Vil, 27°5’58.72”S 66°49’38.90”W, 2,186 m, 13 October 2018; FACEN 143, 4 specimens, Laguna Colorada, Antofagasta de la Sierra, 26°1’57.00”S 67°26’54.67”W, 3,400 m, 12 October 2018; FACEN 158, 8 specimens, Laguna Colorada, Antofagasta de la

Sierra, 26°1'57.00"S 67°26'54.67"W, 3,400 m, 11 December 2019, FACEN 123, 3 specimens, Salar Antofalla, Antofagasta de la Sierra, 25°35'39.64"S 67°30'49.38"W, 3,950 m, 12 October 2018; FACEN 145, 4 specimens, Saujil, Fiambalá, 27°34'05.40"S 67°37'14.43"W, 1,615 m, 14 April 2019; MACN-Ict 5306, 15 specimens, Río Salado, cerca de Bazán, 29°6'23.17"S 66°40'33.00"W, 521 m, 14 October 1949, Col. Sr. Rossi

J. lineata: All located at sea level. MACN-Ict 4274, 5 specimens, Laguna El Ostral, Puerto de Mar del Plata, Col. López, 13 April 1954; MACN-Ict 4121, 10 specimens, Mar del Plata, Col. López, 8 March 1947; MACN-Ict 6583, 78 specimens, Mouth of Punta Mogotes stream, Mar del Plata, 29 April 1961; MACN-Ict 4271, 1 specimen, Ría de San Blas, San Blas Bay, 25 January 1952, Col. Siccardi.

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Figure 1. Specimens and habitats of *Jenynsia obscura*. **Top.** Left, FACEN 143, male specimen, 26.2 mm SL; right FACEN 122, female specimen, 38.0 mm SL. **Center.** Left: El Peñon, 3,400 m. Right: Antofagasta de la Sierra, 3,400 m. **Bottom.** Left: Subaquatic view at El Peñon, note shoal at the center of the picture. Right: Vega El Colorado, eastern edge of Salar de Antofalla, 3,950 m.

Figure 2. Map of *Jenynsia obscura* records in Catamarca, Argentina (green dot). High Andean Plateau is depicted in greyscale, and dark green for lands below 3,000 m, (Source map: GTOPO30-DEM, USGS-EROS). Inset: High Andean Plateau is indicated; light green frame show magnification of the view on the left.

Supporting information video. Underwater video of *Jenynsia obscura* in its habitat at El Peñón, Puna plains in Catamarca, Argentina.