Redescription and diagnoses of the genera *Profundulus* and *Tlaloc* (Cyprinodontiformes: Profundulidae), Mesoamerican endemic fishes

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Until recently, the genus *Profundulus* was classified in two subgenera, *Profundulus* and *Tlaloc*, the sole members of the family Profundulidae. Newly discovered molecular data have been used to justify the elevation of these subgenera to genera. Yet morphological analyses to diagnose the two genera are lacking. The aim of this study is to provide a generic diagnosis and a taxonomic key to the species within the family Profundulidae based on morphology. The genus *Tlaloc* is diagnosed on the basis of five unique characters, among which are the prominent and oval-shaped mesethmoid, exceeding the posterior margins of the vomer; the anterior portion of the parasphenoid making contact with the mesethmoid and extend beyond the center of the mesethmoid; and a reduced autopterotic fossa. *Profundulus* is diagnosed here based on the following characters: the mesethmoid is small, crescent-shaped, and does not extend beyond the margins of the vomer; the anterior portion of the parasphenoid just contacting the mesethmoid and not extending beyond the center of the mesethmoid; a large autopterotic fossa. For each genus, description and distribution ranges are provided as well as a key for identification of the species.

Keywords: Distribution, Identification key, Morphological characters, Profundulids, Taxonomy.

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Hasta recientemente, el género *Profundulus* estuvo integrado por dos subgéneros, *Profundulus* y *Tlaloc*, los únicos miembros de la familia Profundulidae. Análisis moleculares recientes se han utilizado como justificación para erigir estos subgéneros a géneros; sin embargo se carecen de los análisis morfológicos que diagnostiquen a ambos géneros. El objetivo de este estudio es proporcionar las diagnosis de los géneros y una clave taxonómica para la identificación de las especies de la familia Profundulidae, basada en la morfología. El género *Tlaloc* se diagnostica con base en cinco caracteres morfológicos únicos, entre ellos, el mesetmoides prominente y de forma oval, sus bordes exceden el margen posterior del vómer; la porción anterior del parasfenoides está en contacto con el mesetmoides y sobrepasa la parte media de este; la fosa autopterótica es reducida. *Profundulus* es diagnosticado con base en seis caracteres morfológicos únicos, entre ellos el mesetmoides pequeño, en forma de media luna, y no excede los márgenes del vómer; la porción anterior del parasfenoides, justo en contacto con el mesetmoides y no va más allá de la parte medial de este último hueso; la fosa autopterótica grande. La descripción y los rangos de distribución para cada género, así como una clave para la identificación de las especies, son provistas.

Palabras clave: Caracteres morfológicos, Clave de identificación, Distribución, Profundúlidos, Taxonomía.

INTRODUCTION

The family Profundulidae Hoedeman & Bronner, 1951 is a group of freshwater fishes with a restricted geographical distribution, extending from southern Mexico to Central America (Miller, 1955; Matamoros *et al*., 2012). It is one of the characteristic elements of the endemic fauna of Central America and the southern Mexico highlands (Miller, 1955), with most of the included species having a restricted distribution range and occurring only in a few adjacent river systems (Matamoros *et al*., 2012). The Profundulidae is one of the least speciose within the order Cyprinodontiformes (killifishes, pupfishes, and relatives), with only thirteen described species, compared to, for example, approximately 59 nominal species in the family Goodeidae, its sister-group (Nelson *et al*., 2016; Piller *et al*., 2022). The profundulids or Middle American killifishes are commonly known as escamudos (Lozano-Vilano, De La Maza-Benignos, 2016).

Until recently, the genus *Profundulus* was classified in two subgenera, *Profundulus* and *Tlaloc*, the sole members of the family Profundulidae (Miller, 1955, 2009; Parenti, 1981). Newly discovered molecular data have been used to justify the elevation of these subgenera to genera by Morcillo *et al*. (2016). In the absence of a diagnosis, the new clades were supported based on previously documented differences in both subgenera: presence or absence of a humeral spot at the base of the pectoral fin and the number of scales in the preorbital region and base of the caudal fin (Miller, 1955, 2009), as well as by a series of osteological characters of the axial and appendicular skeleton (González-Díaz *et al*., 2014). These morphological-osteological differences were based on a review of only six species. Our knowledge of the Profundulidae is growing rapidly, and the number of valid species has more than doubled since Miller's comprehensive revision of *Profundulus* in 1955. Five new species were described within the genus *Profundulus* and one in the genus *Tlaloc*. Additionally, *Profundulus balsanus* Ahl, 1935 was redescribed and recognized as a valid species (Jamangapé *et al*., 2016).

External morphological traits (meristic and morphometric) were once the primary sources of characters to distinguish the subgenera and species and to classify profundulid fishes (Miller, 1955, 2009). Different types of morphological characters were gradually introduced to killifish systematics (Parenti, 1981; Costa, 2006) and the morphological analysis of bones has been an important source of morphological characters for hypothesizing relationships among profundulids and cyprinodontoid sister families (Parenti, 1981; Costa, 1998; Ghedotti, Davis, 2013) and between the subgenera and some species of the Profundulidae (*e.g*., Uyeno, Miller, 1962; González-Díaz *et al*., 2014).

Profundulids are among the least studied Cyprinodontiformes, and the systematics of the family is still in its early stages, with genera and some species poorly defined, and few descriptions of their osteology (Lozano-Vilano, De La Maza-Benignos, 2016; Morcillo *et al*., 2016). Several recent molecular studies provide hypotheses on the relationship of profundulid taxa and confirm the monophyly of two previously proposed genera (or subgenera) (*e.g*., Doadrio *et al*., 1999; Morcillo *et al*., 2016; Calixto-Rojas *et al*., 2021). Molecular data support profundulid clades (genera) which have been scarcely described by morphological characters, highlighting the need to improve the osteological-morphological database for this group. Therefore, the aim of this study is to provide accurate descriptions of morphological characters, including external morphology of body, osteology, neuromasts (cephalic pores), and contact organs in *Profundulus* and *Tlaloc*, and to discover additional informative characters to diagnose and characterize both genera. A dichotomous key for the identification of the species of the family Profundulidae is presented.

MATERIAL AND METHODS

The examined material is deposited in the fish collection of the Centro Interdiciplinario de Investigación para el Desarrollo Integral Regional, Oaxaca (CIDOAX); Colección Nacional de Peces, Universidad Nacional Autónoma de México, Mexico (CNPE-IBUNAM); Field Museum of Natural History, Chicago (FMNH); Louisiana Museum of Natural Science, Louisiana (LSUMZ or LSU MNS); Universidad de Ciencias y Artes de Chiapas, Mexico (MZ-UNICACH). The list of the examined material includes the acronym of the collection and the catalog number, followed by the number of specimens, in parentheses the specimens cleared and stained (c&s), and by their standard-length range.

Measurements and counts follow Miller (1955) and are presented as percentages of standard length (SL), except for those relative to head morphology, which are expressed as percentages of head length (HL). Seventeen morphometric measurements (in mm) and nine meristic variables were recorded from species of the genera *Tlaloc* and *Profundulus*.

Morphometric (Fig. 1): 1, standard length (SL); 2, head length (HL); 3, predorsal length (PL); 4, prepelvic length (PPL); 5, anal origin to caudal base (AOCB); 6, body, greatest depth (BGD); 7, body, greatest width (BGW); 8, caudal peduncle, length (CPL); 9, caudal peduncle, least depth (CPLD); 10, dorsal fin, basal length (DFBL); 11, anal fin, basal length (AFBL); 12, head depth (HD); 13, head width (HW); 14, interorbital, least bony width (IOLBW); 15, orbit length (OL); 16, snout length (SNL); 17, upper jaw length (UJL).

Meristic: 1, dorsal-fin rays; 2, anal-fin rays; 3, caudal-fin rays; 4, pectoral-fin rays; 5, pelvic-fin rays; 6, scales in lateral series; 7, predorsal scales; 8, scales count around the body; 9, scales count around peduncle. The number, morphology, and arrangement of sensorial pores in the cephalic region were studied and named following the methods and terminology of Gosline (1949) and Miller (1955).

Osteological characters were obtained from specimens of the 13 profundulid species, cleared and double stained (bone alizarin and cartilage counter-stained with alcian blue), according to the technique described by Taylor (1967), with some modifications proposed by Taylor, Van Dyke (1985). The identification of bone elements was based on the bone nomenclature proposed by Gosline (1961), Parenti (1981), and Costa (1998). The terminology of fin rays and the count of vertebrae follows Arratia (2008) and Schultze, Arratia (2013). Based on the variation in meristic, morphometric, and osteological characters as well as the distribution of the species, a dichotomous key for the identification of the species of the family Profundulidae was established.

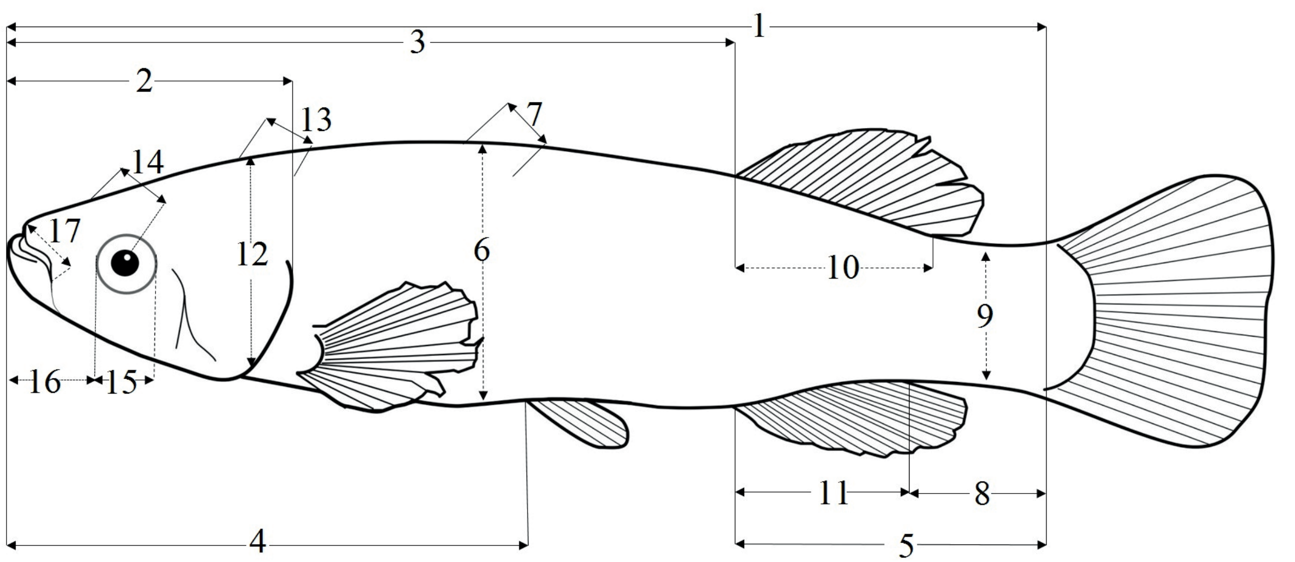

FIGURE 1 | Morphometric characters, based on sketches of *Profundulus* in lateral view. Morphometric measurements in the Material and Methods section.

RESULTS

Four species are recognized in the genus *Tlaloc* (Morcillo *et al*., 2016; Lozano-Vilano, De La Maza-Benignos, 2016): *T. labialis* (Günther, 1866), *T. candalarius* (Hubbs, 1924), *T. hildebrandi* (Miller, 1950), and *T. portillorum* (Matamoros & Schaefer, 2010).

Tlaloc Álvarez & Carranza, 1951

Tlaloc Álvarez, Carranza, 1951:40 (type species *Fundulus labialis* Günther, 1866, by monotype).

Diagnosis. *Tlaloc*, one of the two genera of the family Profundulidae, is diagnosed here by the following combination of characters: The mesethmoid is prominent and oval in shape, extending beyond the posterior margins of the vomer, encompassing the posterior medial extension and touching the lateral ethmoids (Fig. 2B). The anterior portion of the parasphenoid making contact with the mesethmoid and extend beyond the center of the mesethmoid. The autopterotic fossa is reduced (Fig. 2A). The dorsal margin of the interoperculum, with a long extension, is exceeding the edge of the bone (Fig. 3A). The ventral margin of the lacrimal is straight (Figs. 4A–B). *Tlaloc* is further distinguished from *Profundulus* by having less than the basal half of the caudal fin densely scaled (except in *T. portillorum*) (*vs*. more than the basal half or more densely scaled) (Fig. 5A); by the absence of a humeral spot (*vs*. humeral spot present); by the origin of the dorsal fin positioned at a vertical line posterior to the origin of the anal fin (*vs*. origin of the dorsal fin positioned at a vertical line slightly anterior to the origin of the anal fin); by long epiotic processes, extending beyond the second vertebra (*vs*. short epiotic processes, not extending beyond the first vertebra).

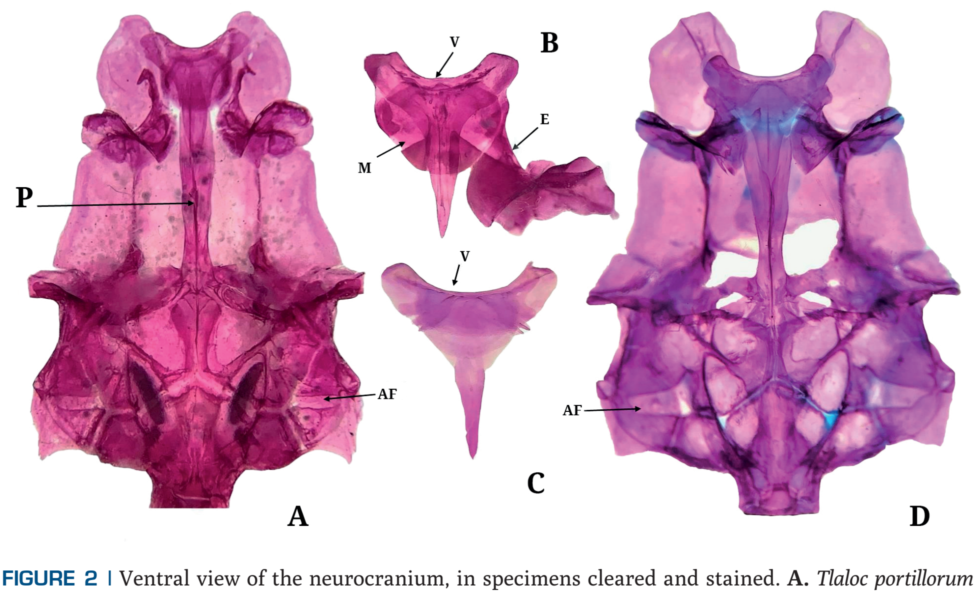

FIGURE 2 | Ventral view of the neurocranium, in specimens cleared and stained. **A.** *Tlaloc portillorum* (MZ-UNICACH 7222, 70.5 mm SL); **B.** Vomer region of *T. candalarius* (MZ-UNICACH 3899, 61.7 mm SL); **C.** Vomer region of *Profundulus kreiseri* (MZ-UNICACH 7214, 59.6 mm SL); and **D.** Neurocranium of *P. mixtlanensis* (MZ-UNICACH 6716, 55.6 mm SL). Abbreviations: V, vomer (Y-shaped); E, lateral ethmoid; M, mesethmoid; P, parasphenoid; AF, autopterotic fossa.

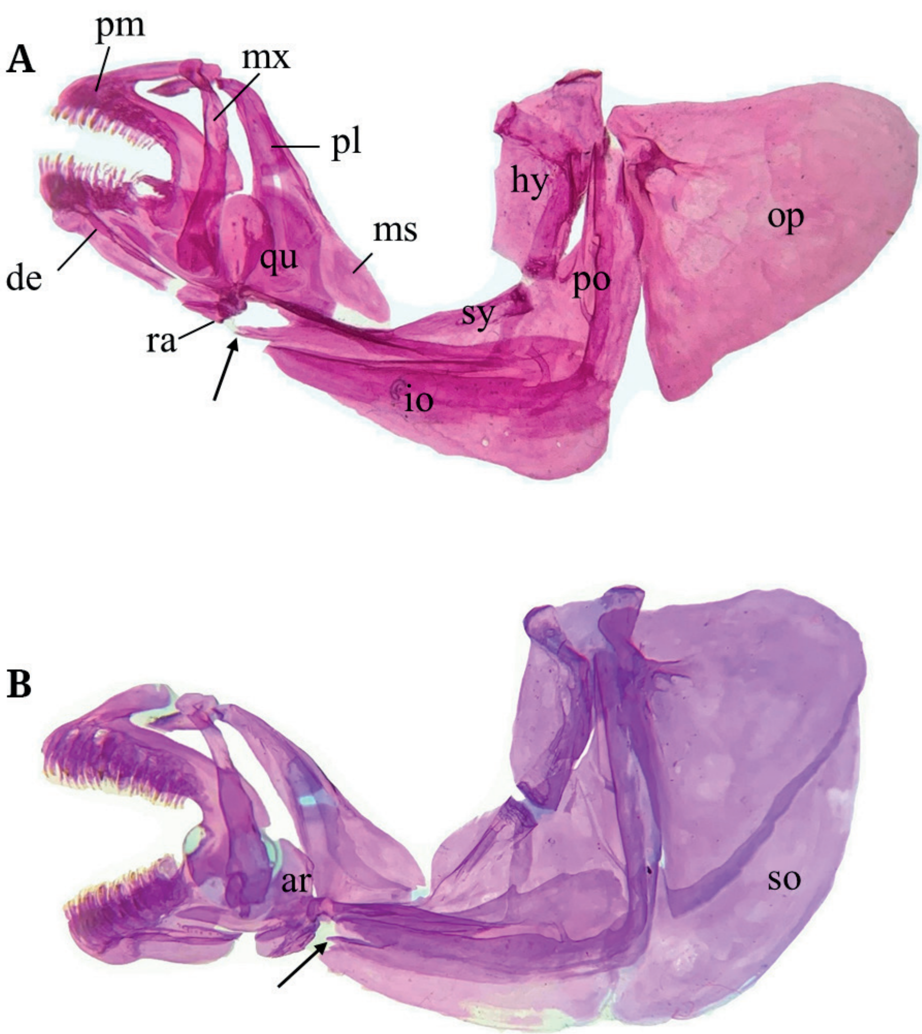

FIGURE 3 | Lateral view of left jaws, suspensorium and opercular series in specimens cleared and stained. **A.** *Tlaloc portillorum* (MZ-UNICACH 7222, 70.5 mm SL); **B.** *Profundulus mixtlanensis* (MZ-UNICACH 6716, 55.6 mm SL). Arrow points to dorsal margin of the interoperculum, with a long or short extension. Abbreviations: de, dentary; pm, premaxilla; ra, retroarticular; mx, maxilla; pl, palatine; qu, quadrate; ar, articular; ms, mesopterygoid; io, interopercle; sy, sympletic; hy, hyomandibula; po, preopercle; op, opercle; so, subopercle.

Description. Morphometric data appear in Tab. 1. Body uniformly slender; head compressed, moderately large (22.4–36.7%). Mouth subterminal to terminal. In *T. hildebrandi* and *T. portillorum*, the lower jaw broad, heavy, and protruding so that the upper jaw is included, whereas in *T. labialis* and *T. candalarius* both equal in forward projection, or the lower jaw is included in the upper jaw. Greatest body depth in the vertical just posterior to pectoral fin (20.0–32.6%). The females are elongated, and the males are more robust than the females. Dorsal and anal fins located posterior to the half of body length. Caudal peduncle relatively large (16.2–26.4%). Median hypural plate divided into subequal parts by an open groove.

TABLE 1 | Morphometric data of *Tlaloc* and *Profundulus* species. Asterisk mark the number of specimens analyzed, in parenthesis the average values.

	Tlaloc portillorum 58*	*T. hildebrandi* 63*	*T. labialis* 58*	*T. candalarius* 100*	*Profundulus punctatus* 196*	*P. guatemalensis* 26*
Standard length (mm)	37.6–71.4 (50.4)	37.9–111.5 (58.2)	33.4–101.9 (53.1)	38.8–99.2 (51.6)	36.2–82.2 (50.3)	38.4–83.9 (51.8)
Percents of standard length						
Head length	25.7–32.0 (28.9)	26.8–32.2 (28.3)	22.4–31.6 (26.9)	26.3–36.7 (29.4)	26.1–32.6 (29.1)	27.0–31.1 (28.9)
Predorsal length	66.1–73.6 (69.6)	64.2–68.5 (66.3)	65.0–70.4 (67.4)	63.6–73.8 (69.7)	62.2–74.7(68.0)	65.5–71.5 (68.4)
Prepelvic length	47.7–55.2 (51.1)	45.8–51.8 (48.9)	46.8–54.7 (50.6)	48.9–61.1 (53.7)	47.0–57.6 (52.2)	49.8–53.6 (51.5)
Anal origin to caudal base	29.0–36.7 (33.4)	36.3–41.9 (39.1)	32.3–41.8 (36.1)	27.3–39.7 (33.3)	19.3–37.4 (33.2)	31.9–36.7 (34.5)
Body, greatest depth	20.0–27.8 (25.2)	22.1–29.7 (24.6)	20.2–29.9 (24.4)	20.7–32.6 (27.7)	21.0–33.6 (28.5)	25.7–31.5 (29.0)
Body, greatest width	11.8–17.0 (14.5)	12.5–17.6 (14.8)	10.6–18.1 (14.3)	11.5–19.5 (15.6)	14.3–22.8 (18.3)	10.8–18.2 (14.7)
Caudal peduncle, length	16.3–23.5 (19.8)	20.3–26.4 (23.3)	17.8–23.6 (21.5)	16.2–24.0 (19.5)	13.7–21.8 (18.3)	15.5–22.1 (18.8)
Caudal peduncle, Least depth	12.6–15.9 (14.3)	12.0–15.1 (13.4)	12.6–15.1 (13.5)	11.4–16.6 (13.5)	13.9–18.3 (15.7)	14.2–16.1 (15.2)
Dorsal fin, basal length	11.1–16.5 (14.1)	11.7–17.6 (14.1)	11.6–16.4 (14.0)	11.1–17.7 (13.9)	11.1–18.3 (15.0)	12.5–16.6 (14.7)
Anal fin, basal length	12.1–17.4 (14.3)	14.0–19.1 (16.0)	12.7–19.5 (15.5)	12.3–17.5 (14.5)	11.6–20.1 (15.7)	14.3–18.6 (16.0)
Percents of head length						
Head depth	55.6–98.0 (67.3)	53.3–85.4 (62.5)	57.5–76.2 (67.0)	56.6–100.1 (68.5)	56.5–94.9 (72.7)	64.8–101.7 (86.0)
Head width	49.3–72.9 (59.6)	49.2–71.0 (64.6)	54.8–70.6 (62.1)	49.2–70.0 (60.7)	58.8–80.6 (68.7)	55.8–75.8 (64.3)
Interorbital, least bony width	37.3–48.7 (42.1)	40.0–48.7 (45.2)	41.1–51.7 (46.2)	34.9–48.3 (42.9)	40.0–53.2 (47.2)	43.3–54.1 (47.3)
Orbit length	21.1–28.6 (24.5)	18.0–28.9 (24.8)	24.9–32.7 (28.6)	19.5–30.6 (26.5)	19.0–29.9 (25.4)	21.6–29.2 (24.0)
Snout length	28.8–35.6 (32.7)	29.8–39.7 (34.9)	29.3–39.7 (33.7)	27.5–38.3 (32.8)	25.6–37.4 (32.3)	28.6–36.9 (33.3)
Upper jaw length	23.9–32.9 (28.3)	26.3–35.3 (31.0)	22.1–31.4 (27.6)	21.5–32.3 (27.7)	16.9–31.7 (25.3)	20.7–33.2(29.6.3)

TABLE 1 | (Continued)

	P. oaxacae 28*	*P. balsanus* 22*	*P. kreiseri* 52*	*P. parentiae* 40*	*P. mixtlanensis* 59*	*P. adani* 73*	*p. chimalapensis* 38*
Standard length (mm)	35.0–63.2 (45.5)	34.2–64.7 (49.7)	37.2–72.7 (49.4)	36.8–73.9 (52.7)	39.0–70.6 (49.7)	36.7–77.9 (53.7)	35.9–80.3 (45.6)
Percents of standard length							
Head length	26.3–30.5 (28.7)	24.1–30.8 (26.8)	26.2–31.6 (28.8)	26.9–35.3 (29.4)	26.8–35.3 (29.1)	26.1–33.9 (28.6)	27.4–33.4 (30.8)
Predorsal length	65.5–72.2 (69.0)	61.9–71.7 (65.5)	64.1–69.8 (67.0)	63.7–69.3 (66.9)	63.9–70.5 (67.1)	64.7–73.5 (68.2)	66.3–77.4 (69.4)
Prepelvic length	47.9–57.3 (52.2)	48.1–55.5 (51.4)	48.2–54.0 (51.7)	49.2–54.4 (51.5)	51.0–57.2 (53.8)	49.0–57.6 (53.3)	50.2–56.4 (53.9)
Anal origin to caudal base	25.2–32.6 (29.1)	29.2–37.1 (33.4)	29.7–36.8 (34.0)	29.0–37.4 (33.3)	30.8–37.8 (34.0)	29.4–37.9 (33.3)	27.1–35.6 (31.2)
Body, greatest depth	23.5–30.8 (26.6)	25.2–31.0 (27.8)	21.2–30.0 (25.7)	26.3–33.8 (30.2)	23.7–31.2 (26.9)	20.4–31.0 (26.1)	24.3–30.8 (27.5)
Body, greatest width	14.4–18.6 (16.5)	11.9–22.2 (17.4)	10.8–18.7 (14.2)	13.2–21.4 (17.8)	10.6–18.6 (15.0)	11.3–20.8 (15.1)	15.4–19.4 (17.5)
Caudal peduncle, length	11.1–19.6 (14.8)	15.5–20.8 (17.2)	15.5–21.7 (18.5)	14.3–20.0 (17.9)	17.3–23.2 (19.7)	15.5–21.9 (18.0)	14.2–19.9 (17.0)
Caudal peduncle, Least depth	11.9–16.6 (14.4)	11.8–15.9 (13.8)	12.4–16.2 (14.4)	14.1–16.9 (15.3)	11.9–15.9 (13.7)	11.7–15.4 (13.6)	13.9–17.4 (15.3)
Dorsal fin, basal length	12.8–17.7 (15.2)	12.5–19.2 (15.2)	13.3–18.1 (15.5)	11.6–18.6 (15.0)	11.9–17.2 (14.2)	11.7–18.3 (14.7)	12.5–16.5 (14.7)
Anal fin, basal length	11.7–18.5 (14.7)	13.2–21.0 (16.1)	13.7–18.3 (15.8)	13.2–19.0 (16.1)	12.7–18.9 (15.3)	13.5–19.4 (16.2)	12.6–18.9 (15.2)
Percents of head length							
Head depth	66.4–101.5 (81.0)	56.1–80.6 (69.3)	60.1–90.7 (75.0)	58.3–83.3 (70.5)	59.7–82.9 (73.2)	59.0–80.2 (71.9)	59.9–70.5 (65.8)
Head width	60.1–72.3 (65.0)	57.9–75.5 (68.1)	44.5–70.8 (60.9)	53.8–77.6 (68.5)	52.9–72.2 (65.7)	54.8–97.5 (67.6)	61.0–71.7 (65.6)
Interorbital, least bony width	41.5–48.3 (44.3)	38.7–55.9 (50.3)	38.1–48.5 (44.1)	38.9–58.7 (50.2)	38.2–52.7 (45.1)	38.9–50.2 (46.0)	45.9–52.7 (48.7)
Orbit length	21.2–26.3 (23.8)	21.4–28.9 (25.0)	20.4–31.3 (25.2)	21.5–28.9 (25.4)	23.1–30.0 (26.3)	20.5–28.5 (23.6)	22.0–32.6 (28.0)
Snout length	24.0–32.2 (28.8)	15.4–34.9 (25.3)	27.2–38.5 (32.5)	22.2–34.2 (29.2)	27.3–37.8 (32.6)	26.6–38.2 (33.5)	28.7–37.9 (33.1)
Upper jaw length	21.8–36.1 (26.9)	11.1–23.9 (16.5)	24.3–34.4 (28.7)	11.2–30.0 (18.4)	24.3–35.9 (29.7)	21.1–36.6 (33.5)	23.5–32.0 (26.4)

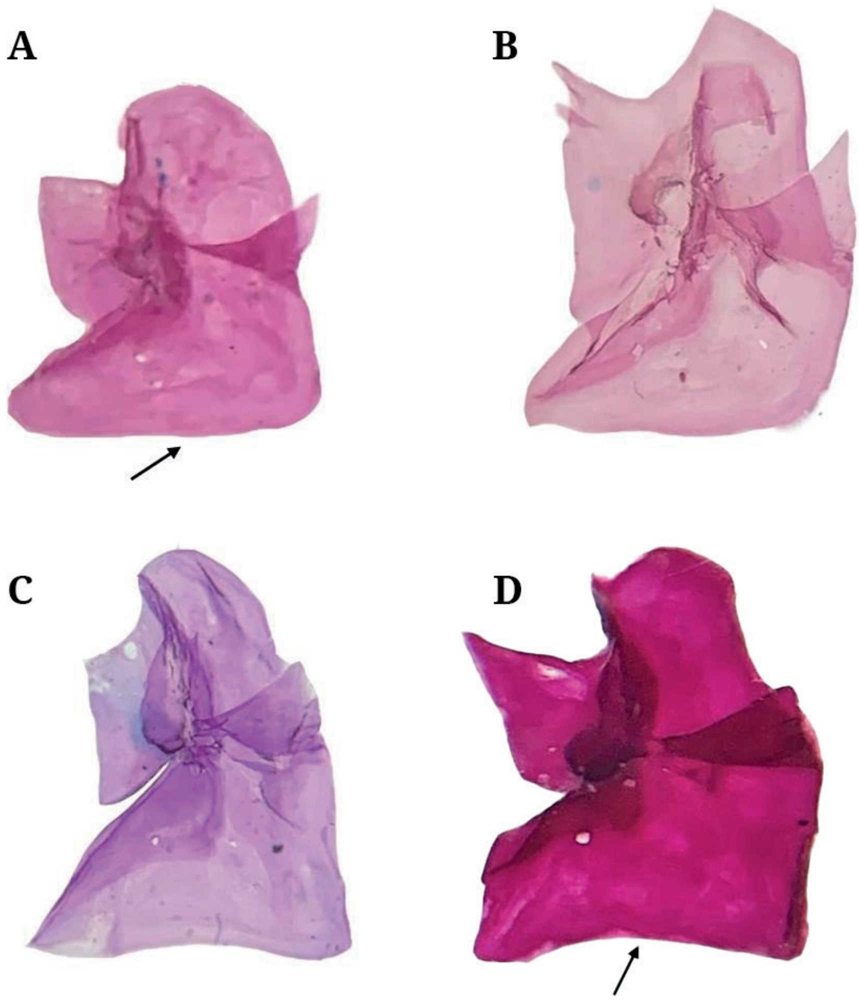

FIGURE 4 | Ventral view of left lacrimal. **A.** *Tlaloc portillorum* (MZ-UNICACH 7222, 70.5 mm SL); **B.** *T. hildebrandi* (MZ-UNICACH 2266, 75.1 mm SL); **C.** *Profundulus mixtlanensis* (MZ-UNICACH 6716, 55.6 mm SL); and **D.** *P. punctatus* (MZ-UNICACH 6632, 67.3 mm SL). Arrow point to ventral margin of the lacrimal.

The branching pattern of the cephalic latero-sensory canals in *Tlaloc* is similar to the general pattern of the Cyprinodontiformes. The supraorbital series follows the Type II designation of Gosline (1949), with canals between pores 1–2a, 2b–4a, 4b–7; preopercular pores 6–7 (mode = 7); preorbital pores 3–5 (mode = 4); mandibular pores 4–5 (mode = 5); in addition, there are 2 to 4 rostral pores usually developed.

Meristic characters are as follows (Tab. 2): anal: 9–18; dorsal: 7–14; pelvic: 5–7; pectoral: 13–20; caudal: 16–23; vertebrae totals: 33–38; gill rakers on anterior arm of the first arch: 13–19; branchiostegal rays: 6; scales lateral series: 29–39; scales predorsal: 19–26; scales around body: 25–36; scales around peduncle: 16–28.

Coloration. The coloration varies strongly among individuals and ontogenetically. The skin of the head and body may show golden reflections, especially in the opercular region and mid flank. The form and coloration of the nuptial adult male and female are shown in Fig. 6. Unpaired fins (dorsal and anal) are orange in males, with irregular black markings on the dorsal fin, evident in *Tlaloc candalarius*.

TABLE 2 | Meristic data of *Tlaloc* and *Profundulus* species. Asterisk mark the number of specimens analyzed, in parenthesis the modal values.

Character	*T. labialis* 58*	*T. candalarius* 102*	*T. hildebrandi* 63*	*T. portillorum* 58*	*P. punctatus* 202*	*P. guatemalensis* 26*
Dorsal rays	10–14	9–14 (11)	10–14 (11)	7–14 (11)	10–14 (12)	11–13 (12)
Anal rays	13–18 (16)	11–16 (14)	11–16 (15)	9–14 (13)	11–16 (14)	12–15 (14)
Pectoral rays	16–20 (18)	14–19 (15)	15–18 (16)	13–17 (15)	14–19 (17)	16–18 (17)
Caudal rays	20–23 (20)	16–23 (20)	17–23 (22)	17–23 (20)	18–24 (21)	18–24 (21)
Pelvic rays	5–7 (6)	5–7 (6)	5–7 (6)	5–7 (6)	5–7 (6)	6–7 (6)
Lateral scales	33–39 (37)	30–39 (34)	33–37 (36)	29–34 (33)	29–34 (33)	30–33 (33)
Scales predorsal	21–26	19–26 (23)	20–24 (22)	21–26 (23)	18–24 (20)	20–23 (22)
Scales around body	28–36	25–35 (31)	27–33 (30)	25–31 (28)	24–30 (26)	26–29 (28)
Scales around peduncle	18–22 (21)	16–21 (18)	16–21 (18)	16–22 (19)	17–25 (20)	18–23 (19)
Vertebrae	37–38 (37)	33–36 (35)	36–37 (36)	33–34 (33)	32–34	32–33 (33)
Gill rakers	13–18 (16)	14–19 (17)	14–19 (16)	13–17 (15)	15–21 (17)	15–19 (17)

TABLE 2 | (continued)

Character	*P. oaxacae* 35*	*P. balsanus* 22*	*P. kreiseri* 50*	*P. parentiae* 41*	*P. mixtlanensis* 60*	*P. adani* 71*	*P. chimalapensis* 38*
Dorsal rays	11–13 (12)	11–13 (12)	10–14 (12)	10–13 (12)	10–13 (11)	10–12 (11)	11–14 (13)
Anal rays	13–15 (14)	15–16 (15)	12–16 (14)	13–16 (15)	13–16 (14)	13–16 (14)	14–16 (15)
Pectoral rays	15–18 (16)	15–17 (16)	14–17 (16)	15–17 (16)	15–18 (16)	15–18 (16)	15–18 (17)
Caudal rays	17–22 (20)	18–20 (20)	19–23 (21)	18–22 (20)	18—3 (21)	18–23 (20)	18–23 (20)
Pelvic rays	6 (6)	6 (6)	5–6 (6)	6–7 (6)	6 (6)	6–7 (6)	6 (6)
Lateral scales	29–31 (30)	33 (33)	32–35 (34)	31–33 (33)	31–34 (33)	32–35 (33)	29–32 (31)
Scales predorsal	22–29 (25)	21–24 (24)	18–23 (21)	18–22 (22)	21–25 (22)	23–28 (26)	18–21 (19)
Scales around body	23–31 (27)	26–29 (28)	23–30 (27)	25–29 (29)	26–34 (28)	25–35 (30)	25–30
Scales around peduncle	16–22 (19)	18–21 (19)	17–21 (19)	17–21 (19)	16–21 (17)	15–18 (17)	17–21 (20)
Vertebrae	31–33	33–34 (33)	33–34 (34)	31–32 (32)	33–34 (33)	33–34 (33)	33
Gill rakers	15–18 (16)	14–18 (15)	14–17 (16)	14–22 (18)	16–19 (18)	16–20 (17)	16–19 (18)

FIGURE 5 | Male general morphology and caudal fin squamation, life colour patterns in: **A.** *Tlaloc labialis*; and **B.** *Profundulus punctatus*. Solid arrow points to the squamation of the caudal fin, dashed arrow points to the humeral spot.

Sexual dimorphism and contact organs. There is little sexual dimorphism in species of the genus *Tlaloc*. Males are slightly larger than females; the largest specimen recorded was a male from *Tlaloc hildebrandi* (111.49 mm SL), whereas the maximum size recorded in a female was in *Tlaloc labialis* (101.93 mm SL). The shape of the anal fin, however, shows a marked sexual difference: the anterior anal rays of the male are not greatly longer than the posterior ones, giving the distal margin of the fin an evenly rounded edge. However, in the female, since the medial rays, from about the sixth to the tenth, are much longer than either the anterior or the posterior rays, the distal margin of the fin is lobate when expanded. Males have contact organs or spinules, articulated with the lateral surfaces of the anal fin rays with some of them conspicuously long; this is the most notable, though not striking difference between males and females of all *Tlaloc* species (Fig. 7).

Geographical distribution. Restricted to the Atlantic slope of Middle America (Fig. 8). From the border between Oaxaca and Chiapas, Mexico, to the center of Honduras, with the exception of *Tlaloc portillorum*, this is located on both slopes of Honduras, Atlantic and Pacific.

Etymology. *Tlaloc* in reference to Tlaloc, a deity of water in Aztec mythology (Álvarez, Carranza, 1951).

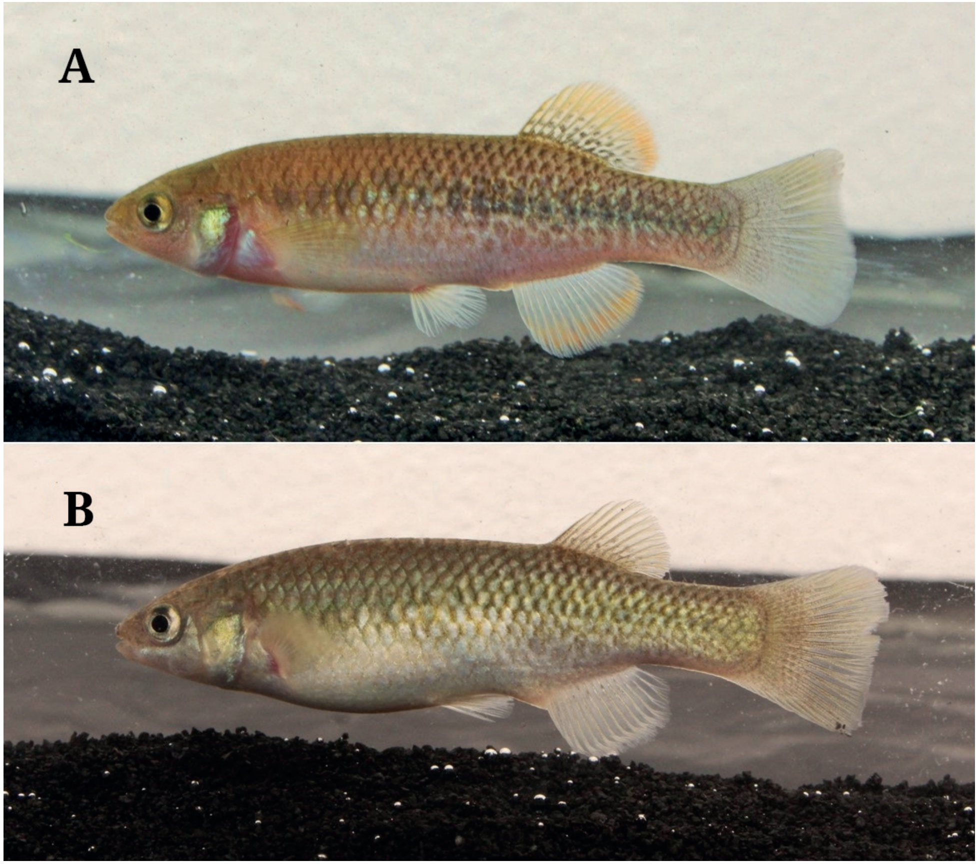

FIGURE 6 | *Tlaloc candalarius*. **A.** Male (MZ-UNICACH 7567, 71.4 mm SL); **B.** Female (MZ-UNICACH 7567, 78.8 mm SL); note the orange coloration of the dorsal and anal fins in the male.

FIGURE 7 | Bony spinules in fin rays of male *Tlaloc labialis*, indicated by arrow (MZ-UNICACH 6740, 75.7 mm SL), articulated with the lateral surfaces of the anal fin rays.

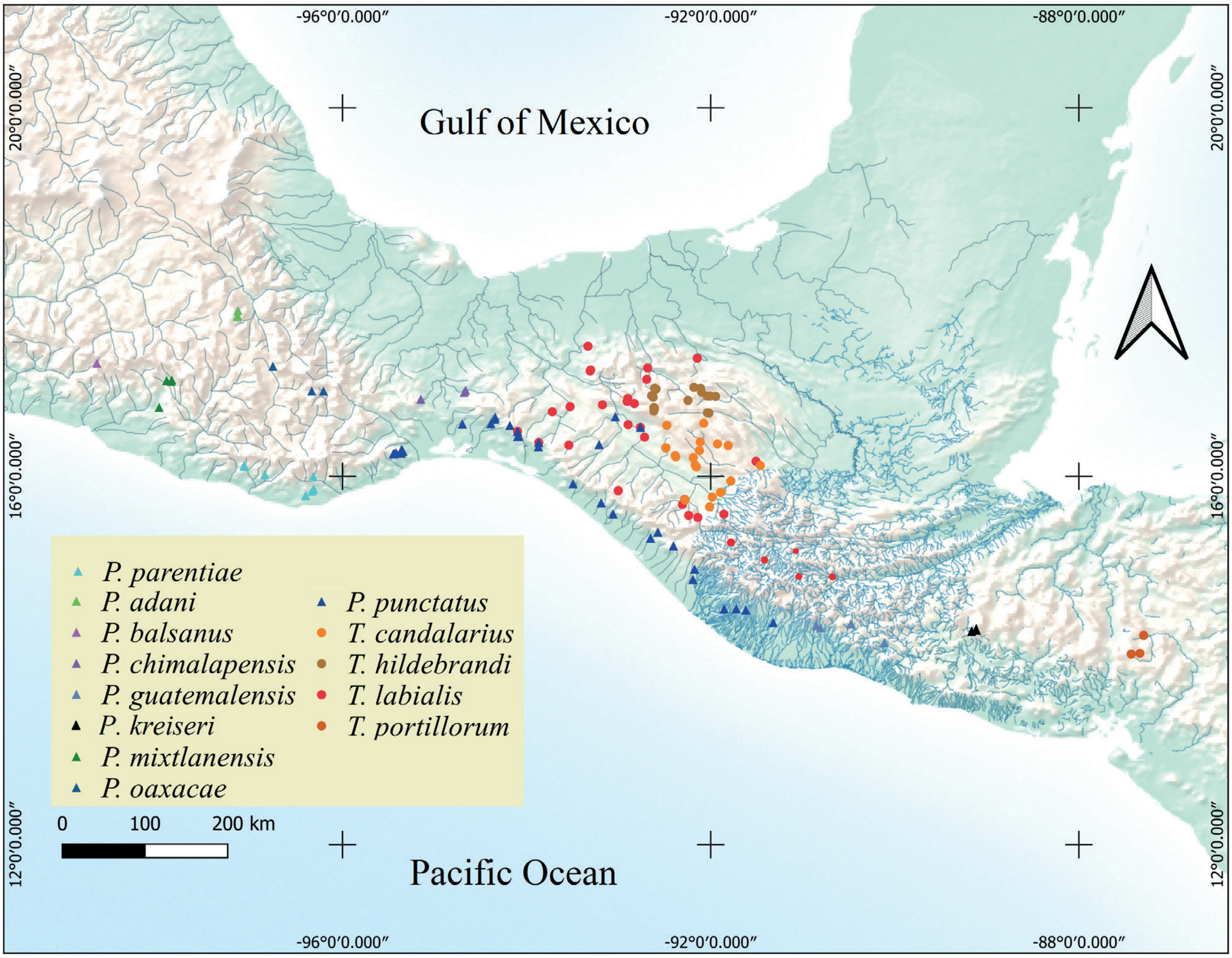

FIGURE 8 | Geographical distribution of species of the genera *Tlaloc* and *Profundulus* in southern Mexico and Central America.

Nine species are recognized in the genus *Profundulus* (Morcillo *et al*., 2016; Del Moral-Flores *et al*., 2020; Domínguez-Cisneros *et al*., 2021): *P. punctatus* (Günther, 1866), *P. guatemalensis* (Günther, 1866), *P. oaxacae* (Meek, 1902), *P. balsanus*, *P. kreiseri* Matamoros, Schaefer, Hernández & Chakrabarty, 2012, *P. mixtlanensis* Ornelas-García, Martinez-Ramírez & Doadrio, 2015, *P. parentiae* Matamoros, Dominguez-Cisneros, Velázquez-Velázquez & McMahan, 2018, *P. chimalapensis* Del Moral-Flores, López-Segovia & Hernández- Arellano, 2020, and *P. adani* Dominguez-Cisneros, Velázquez-Velázquez, McMahan & Matamoros, 2021.

Profundulus Hubbs, 1924

Profundulus Hubbs, 1924:12 (type species *Fundulus punctatus* Günther, 1866, by original designation).

Diagnosis. *Profundulus* is diagnosed here based on the following characters: The mesethmoid is small, crescent-shaped, and does not extend beyond the margin of the vomer (Figs. 2C–D); the vomer is greatly broadened anteriorly, lacks lateral processes and is in contact with the lateral ethmoids; the anterior portion of the parasphenoid is just in contact with the mesethmoid and does not extend beyond the center of the mesethmoid; the autopterotic fossa is large (Fig. 2D); the dorsal margin of the interoperculum, with a short extension, does not exceed the edge of the bone (Fig. 3B); the ventral margin of the lacrimal slightly concave (Figs. 4C–D). *Profundulus* is further distinguished from *Tlaloc* in having more than the basal half of the caudal fin densely scaled (except in *P. kreiseri*) (*vs*. less than the basal half of caudal fin densely scaled) (Fig. 5B); by a humeral spot (except in *P. adani*) (*vs*. humeral spot absent) (Fig. 5B); by the origin of the dorsal fin positioned at a vertical line slightly anterior to the origin of the anal fin (*vs*. origin of the dorsal fin positioned at a vertical line posterior to the origin of the anal fin); by short epiotic processes, not extending beyond the first vertebra (except in *P. parentiae*) (*vs*. long epiotic processes, extending beyond the second vertebra).

Description. Morphometric data appear in Tab. 2. Body rather robust, elongate; head compressed, large (24.1–35.3%); the interorbital broad (38.2–58.7%) and typically concave or nearly flat. Ascending premaxillary process short and broad and bluntly rounded at the tip. Mouth subterminal, lower jaw broad, heavy and protruding so that upper jaw is included. Dorsal fin rounded in both males and females with its basal length short (11.1–19.2%). Anal fins of males rounded, slightly elongated in females. Caudal peduncle relatively short (11.1–23.2%). Median hypural plate divided into subequal parts by an open groove.

Lateral-line system of sensory canals and pores on the head of *Profundulus*: The supraorbital series follows the Type II designation of Gosline (1949), with canals between pores 1–2a, 2b–4a, 4b–7; preopercular pores 6–8 (mode = 7); preorbital pores 3–5 (mode = 4); mandibular pores 4–5 (mode = 5); generally, there is a lack of rostral pores, exceptionally there may be 2 to 4 in some species.

Meristic traits are as follows (Tab. 2): anal: 11–17; dorsal: 10–15; pelvic: 5–7; pectoral: 13–19; caudal: 17–24; vertebrae totals: 31–35; gill rakers on anterior arm of the first arch: 14–22; branchiostegal rays, 6; scales lateral series: 29–35; scales predorsal: 18–29; scales around body: 23–35; scales around peduncle: 16–25.

Coloration. The form and coloration of the nuptial adult male are shown in Fig. 5B. Most of the body dark, often with irregular brown-dark spots on the scales, on the sides of the body on to the caudal fin. A golden yellow blotch covers the operculum and reaches the base of the pectoral fin.

Sexual dimorphism and contact organs. The sexual dimorphism is not very evident in species of the genus *Profundulus*. However, the males are slightly larger than females; the largest specimen recorded was a male from *P. guatemalensis* (83.9 mm SL), while the maximum size recorded in a female was in *P. adani* (77.9 mm SL). In males and females of all species of *Profundulus*, the dorsal and the anal fins have a similar morphology. Like *Tlaloc* (Fig. 7) the males of *Profundulus* have contact organs or spinules, articulated with the lateral surfaces of the anal fin rays with some of them conspicuously long; this is the most notable, though not striking difference between males and females of all *Profundulus* species.

Geographical distribution. On the Pacific slope, from the río Malinaltepec, río Papagayo basin, of Guerrero, southeastern Mexico, southward to the río Lempa in El Salvador and Honduras; on the Atlantic slope, from the upper reaches of the río Papaloapan of Oaxaca, Mexico, to the ríos Chamelecón and Ulúa in northwestern Honduras (Fig. 8).

Etymology. *Profundulus* in reference to its presumed primitive relationship to the genus *Fundulus* (Parenti, 1981).

Key to identification of Profundulidae species

1a. Humeral spot absent; dorsal fin origin posterior to a vertical through the anal fin origin; mesethmoid prominent and oval-shaped (c&s specimens), protruding from the posterior margins of the vomer (*Tlaloc*) 2

1b. Humeral spot present (except in *P. adani*); dorsal fin origin at or anterior to a vertical through the anal fin origin; mesethmoid small and crescent-shaped (c&s specimens), not protruding from the body of the vomer (*Profundulus*) 5

2a. Lower jaw broad, heavy, and protruding, so that the upper jaw is included 3

2b. Jaws equal, or the lower jaw is included in the upper jaw 4

3a. Thirty-six or 37 vertebrae in total; dark spot at the base of the caudal fin; 36 scales in lateral series (range: 33 to 37); origin of the anal fin to the base of the caudal fin relatively long (36.3–41.9% in the SL). Interior basin of the Chiapas highlands, Mexico (endemic) .... *T. hildebrandi*

3b. Thirty-three or 34 vertebrae in total; 33 scales in lateral series (range: 29 to 34); origin of the anal fin to the base of the caudal fin relatively short (29.0–36.7% in SL). Interior basin of the highlands of Honduras (endemic) *T. portillorum*

4a. Jaws equal; 33 to 36 vertebrae in total; dorsal fin in males with two or three series of black points; middle rays of the anal fin in females, similar in size to that of males. Interior basin, Comitán River and adjacent basins of Mexico and spring at Candelaria, Guatemala .... *T. candalarius*

4b. Upper jaw larger than the lower jaw; 37 to 38 vertebrae in total; middle rays of the anal fin in females, much more elongated than that of males. Interior basins of Chiapas, Mexico, and Guatemala .... *T. labialis*

5a. Scales on lateral line usually 30 (29–31); predorsal scales 25 (22–29); origin of the anal fin to the caudal-base, relatively short (25.2–32.6% in SL); pattern on the sides of the body with delineated, faint, vertical marks. Pacific slope, upper Verde River basin, Oaxaca, Mexico (endemic) .... *P. oaxacae*

5b. More than 30 scales on the lateral line; predorsal scales 19–24 (except in *P. adani*); origin of the anal fin to the caudal-base, relatively large (31.2–37.1% in SL) 6

6a. Less than basal half of caudal fin densely scaled; head width relatively narrow, its mean value is 60.9% in HL (range 44.5–70.8%). Inland basin of Honduras and Guatemala .... *P. kreiseri*

6b. Basal half or more of caudal fin densely scaled; head width relatively large, its mean value varies between 64.3 to 68.7% in HL..7

7a. Predorsal scales usually 26 (23–28); pronounced snout, lower jaw strongly forward projected; relatively large upper jaw (21.1–36.6% in HL). Atlantic slope, upper Papaloapan River basin, Oaxaca, Mexico (endemic) .... *P. adani*

7b. Less than 25 predorsal scales; snout is not pronounced, lower jaw is not strongly forward projected..8

8a. Long epiotic processes, surpassing the first epipleural ribs; robust and deep body (26.3–33.8% in SL). Pacific slope, Huatulco River, Oaxaca, Mexico (endemic)...*P. parentiae*

8b. Short epiotic processes, not reaching the first epipleural ribs; slender and deep body (21–31.5% in SL (except in *P. punctatus*)...9

9a. Body of the adult fish with brown spots on the scales, aligned in such a way that they form a longitudinal band on the sides of the body; humeral spot evident...10

9b. Body of the adult fish without brown spots on the scales on the sides of the body; humeral spot inconspicuous 11

10a. Third neural spine of the caudal complex much thinner than the second; base of the narrow anal fin less than the length of the caudal peduncle. Pacific slope, from the Isthmus of Tehuantepec, Mexico, to Champerico, Guatemala and Atlantic slope, upper Grijalva River basin, Chiapas,Mexico..*P. punctatus*

10b. Third neural spine of the caudal complex, as wide as the second; anal-base fin equal to or greater than the length of the caudal peduncle. Atlantic slope, upper basin of the Coatzacoalcos river (Chimalapas region), Oaxaca, Mexico (endemic) ....*P. chimalapensis*

11a. Head typically rectangular and more arched, its dorsal surface generally very rounded; dark band on the sides of the body extending from the vertical of the dorsal fin to the base of the caudal; 4 to 5 preorbital pores. Interior basin of Guatemala and El Salvador, Pacific slope .... *P. guatemalensis*

11b. Head conical, its dorsal surface concave to nearly flat; without dark band on the sides of the body; four preorbital pores. Interior basins of Guerrero and Oaxaca, Mexico. Pacific Slope 12

12a. Relatively long upper jaw (24.3–35.9% in HL); 31 to 34 scales on the lateral midline. Pacific slope, upper basin of the Mixteco river, Oaxaca, Mexico (endemic).. *P. mixtlanensis*

12b. Relatively short upper jaw (11.1–23.9% in HL); scales on the lateral midline invariably 33. Pacific slope, Papagayo river basin, Guerrero, Mexico (endemic)..*P. balsanus*

Material examined. *Profundulus adani*: **Mexico**: CNPE-IBUNAM 23796, holotype, 64.7 mm SL, Santa Maria Ixclatlan, Oaxaca, 17°51'03"N 97°11'57.4"W, 19 Jun 2018, E. Velazquez & M. J. Anzueto. CNPE-IBUNAM 23797, paratypes, 3, 39.0–59.1 mm SL, Santa Maria Ixcatlan, Oaxaca, 17°51'03"N 97°11'57.4"W, 19 Jun 2018, E. Velazquez & M. J. Anzueto. CNPE-IBUNAM 23798, paratypes, 3, 42.7–48.5 mm SL, Arroyo Nodon, San Miguel Huatla, Oaxaca, 17°47'59"N 97°08'11.9"W, 20 Jun 2018, E. Velazquez & M. J. Anzueto.

FMNH 145002, paratypes, 3, 43.1–58.9 mm SL, Santa Maria Ixcatlan, Oaxaca, 17°51'03"N 97°11'57.4"W, 19 Jun 2018, E. Velazquez & M. J. Anzueto. FMNH 145003, paratypes, 3, 67.8–75.0 mm SL, Rio Huatla, San Miguel Huatla, Oaxaca, 17°44'28"N 97°20'15.4"W, 20 Jun 2018, E. Velazquez & M. J. Anzueto. MZ-UNICACH 7382, paratypes, 44 (3 c&s), 36.6–68.2 mm SL, Santa Maria Ixcatlan, Oaxaca, 17°47'57.59"N 97°08'10.40"W, 19 Jun 2018, E. Velazquez & M. J. Anzueto. MZ-UNICACH 7342, paratypes, 18 (2 c&s), 38.3–60.8 mm SL, Arroyo Nodon, San Miguel Huatla, Oaxaca, 17°47'59"N 97°08'11.9"W, 20 Jun 2018, E. Velazquez & M. J. Anzueto. MZ-UNICACH 7343, paratypes, 11, 52.3–77.9 mm SL, Rio Huatla, San Miguel Huatla, Oaxaca, 17°44'28"N 97°20'15.4"W, 20 Jun 2018, E. Velazquez & M. J. Anzueto. *Profundulus balsanus*: **Mexico**: MZ-UNICACH 6712, topotypes, 22 (7 c&s), 34.2–64.6 mm SL, Rio Malinaltepec, Guerrero, 17°13'38.03"N 98°40'6.31"W, 26 Apr 2014, M. J. Anzueto. *Profundulus chimalapensis*: **Mexico**: MZ-UNICACH 7559, 38 (7 c&s), 35.8–80.3 mm SL, Arroyo Piedra del Rio el Corte, Santa Maria Chimalapa, Oaxaca, 20 Jan 2022, E. Velazquez & M. J. Anzueto. MZ-UNICACH 7560, topotype, 1, 35.1 mm SL, Arroyo la Aurora, Santo Domingo Petapa, Oaxaca, 16°50'17.9"N 95°08'59.8"W, 17 Oct 2021, E. Velazquez & S. Dominguez. *Profundulus guatemalensis*: **Guatemala**: LSUMZ 17906, 1 c&s, 52.2 mm SL, Rio las Cabezas, Sanarate, 20 Nov 2014, W. Matamoros. MZ-UNICACH 7194, 12 (4 c&s), 38.3–83.8 mm SL, Balneario el cantil, Rio Cantil, Escuintla, 10 Apr 2017, W. Matamoros & A. E. Gonzalez. MZ-UNICACH 7195, 9 (2 c&s), 38.7–50.3 mm SL, Caserío las Cañas, Arroyo tributario del rio Achihuate, Escuintla, 10 Apr 2017, M. Matamoros & A. E. Gonzalez. MZ-UNICACH 7197, 2, 41.6–42.0 mm SL, Puente la Concha, Arroyo la Concha, Jocotillo Villa Canales, 11 Apr 2017, M. Matamoros & A. E. Gonzalez. MZ-UNICACH 7198, 3, 39.4–57.3 mm SL, Las Cabezas, Puente de las Marias, Santa Rosa Oratoria, 11 Apr 2017, M. Matamoros & A. E. Gonzalez. *Profundulus kreiseri*: **El Salvador:** LSUMZ 15105, 2 (1 c&s), 41.57 mm SL, Quebrada Casco de la Hacienda, Parque Nacional Monte Cristo, Santa Ana, 7 Jun 2011, W. Matamoros. MZ-UNICACH 7205, 26 (3 c&s), 37.1–72.6 mm SL, Quebrada los Tecomates, tributario del rio Lempa, Chalatenango, 12 Apr 2017, W. Matamoros & A. E. Gonzalez. MZ-UNICACH 7214, 22 (2 c&s), 38.6–63.3 mm SL, Rio Onuapa, tributario del rio Lempa, Chalatenango, 12 Apr 2017, W. Matamoros & A. E. Gonzalez. MZ-UNICACH 7231, 5, 39.1–4.19 mm SL, Desembocadura del rio Negro, Perquín, 12 Apr 2017, W. Matamoros & A. E. Gonzalez. *Profundulus mixtlanensis*: **Mexico**: CIDOAX-300-F1228, 2, 39.0–41.1 mm SL, Yosondúa, Tlaxiaco, Oaxaca, 14 Jun 2014, E. Martinez. CIDOAX-301-F1229, 2, 45.6–49.2 mm SL, Ojo de Agua, Yutanicani, Oaxaca, 14 Jun 2014, E. Martinez. MZ-UNICACH 6716, 26 (9 c&s), 39.3–60.7 mm SL, Ranchería la Soledad, Rio San Isidro, Putla, Oaxaca, 29 Apr 2015, M. J. Anzueto & E. Velazquez. MZ-UNICACH 6717, 3, 53.6–65.5 mm SL, Arroyo tributario del Río Atoyac, colonia Nuevo Tenochtitlan, Putla, Oaxaca, 29 Apr 2015, M. J. Anzueto & E. Velazquez. MZ-UNICACH P 6718, 4, 39.5–53.8 mm SL, Puente Tierra Azul, Putla, Oaxaca, 29 Apr 2015, M. J. Anzueto & E. Velazquez. *Profundulus oaxacae*: **Mexico**: MZ-UNICACH 6714, 27 (4 c&s), 35.0–63.1 mm SL, Rio Salado, subcuenca Atoyac, Mitla, Oaxaca, 27 Apr 2015, M. J. Anzueto. MZ-UNICACH 6715, 22 (2 c&s), 39.2–70.5 mm SL, Arroyo Grande tributario del Río la Hormiga, Mitla, Oaxaca, 27 Apr 2015, M. J. Anzueto. *Profundulus parentiae*: **Mexico**: CNPE-IBUNAM 28804, holotype, 65.9 mm SL, Rio Huatulco, Santa Maria Huatulco, Oaxaca, 15°50'24.56"N 96°19'48.75"W, 25 Apr 2015, W. Matamoros, M. J. Anzueto, J. A. Jamangape & I. Aguilar. CNPE-IBUNAM 22805, paratypes, 3, 26.9–35.3 mm SL, Rio Huatulco, Santa Maria Huatulco, Oaxaca, 15°50'24.56"N 96°19'48.75"W, 25 Apr 2015, W. Matamoros, M. J. Anzueto, J. A. Jamangape & I. Aguilar. FMNH 131755, paratypes, 2, 26.9–35.3 mm SL, Rio Huatulco, Santa María Huatulco, Oaxaca, 15°50'24.56"N 96°19'48.75"W, 25 Apr 2015, W. Matamoros, M. J. Anzueto, J. A. Jamangape & I. Aguilar. MZ-UNICACH 6574, 6, 27.5–50.2 mm SL, Puente Hondura de Toro, Rio Huatulco, Santa María Huatulco, Oaxaca, 21 Apr 2015, W. Matamoros, M. J. Anzueto, J. A. Jamangape & I. Aguilar. MZ-UNICACH 6575, 10 (5 c&s), 50.3–68.3 mm SL, Toma de Agua, Rio Huatulco, Santa María Huatulco, Oaxaca, 25 Apr 2015, W. Matamoros, M. J. Anzueto, J. A. Jamangape & I. Aguilar. MZ-UNICACH 6576, paratypes, 10 (3 c&s), 40.2–67.7 mm SL, Arroyo de la calle central, colonia San Miguel Figueroa, Pochutla, Oaxaca, 15°47'24.1"N 96°24'03.9"W, 21 Apr 2015, W. Matamoros, M. J. Anzueto, J. A. Jamangape & I. Aguilar. MZ-UNICACH 6713, paratypes, 10 (4 c&s), 42.5–53.2 mm SL, Camino a Comitlan, Rio la Loma, Santa Maria Colotepec, Oaxaca, 16°01'08.1"N 96°50'41.3"W, 22 Apr 2015, W. Matamoros, M. J. Anzueto, J. A. Jamangape & I. Aguilar MZ-UNICACH 6721, 2 c&s, 44.8–39.3 mm SL, Rio del Rancho Flor de Café, San Gabriel Mixtepec, Oaxaca, 30 Apr 2015, M. J. Anzueto. MZ-UNICACH 7351, 6, 46.3–73.9 mm SL, Puente Mateo Piña, camino a Huatulco, San Mateo Piña, Oaxaca, 22 Sep 2018, E. Velazquez & M. J. Anzueto. *Profundulus punctatus*: **Guatemala**: MZ-UNICACH 7169, 32, 37.9–72.6 mm SL, Rio Batza, Colonia Campolla, puente Batza, Quetzaltenango, 9 Apr 2017, A. E. Gomez & E. Velazquez. MZ-UNICACH 7182, 16, 36.3–75.0 mm SL, Rio Nil, puente Nil, El Acintal, Retalhuleo, 9 Apr 2017, A. E. Gomez & E. Velazquez. MZ-UNICACH 7186, 14, 39.4–82.1 mm SL, Rio el Puentecito, Caserio, Retalhuleo, 9 Apr 2017, A. E. Gomez & E. 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2015, E. Velazquez. *Tlaloc labialis*: **Guatemala**: MZ-UNICACH 7233, 2 c&s, 35.5–65.6 mm SL. Rio Selegua, Huehuetan, 20 Apr 2017, W. Matamoros. **Mexico**: MZ-UNICACH 1402, 1, 64.1 mm SL, Rio Negro, Pueblo Viejo, Cintalapa, Chiapas, 11 Oct 2007, E. Velazquez & M. J. Anzueto. MZ-UNICACH 1305, 16, 41.5–79.7 mm SL, Rio Negro Santa Maria, Cintalapa, Chiapas, 12 Jul 2007, M. J. Anzueto & A. E. Gomez. MZ-UNICACH 3467, 16 (2 c&s), 55.5–73.5 mm SL, Rio Zacalapa, Copainala, Chiapas, 6 Aug 2009, M. J. Anzueto & E. Velazquez. MZ-UNICACH 5274, 1, 67.0 mm SL, Rio Frio, Chiapilla, Chiapas, 1 Oct 2014, E. Velazquez. MZ-UNICACH 5353, 1 c&s, 89.4 mm SL, Rio Ojo de Agua, Emiliano Zapata, Chiapas, 2 Oct 2014, M. J. Anzueto. MZ-UNICACH 6607, 7, 38.9–101.9 mm SL, Rio Mazantic, El Bosque, Chiapas, 8, Mar 2015, A. E. Gomez. MZ-UNICACH 6740, 2 c&s, 64.5–75.7 mm SL, Rio La Venta, Ocozocoautla, Chiapas, 23 Apr 2015, M. J. Anzueto & E. Velazquez. MZ-UNICACH 7563, 26, 33.4–53.1 mm SL, Rio Hondo, Ixtapa, Chiapas, 20 Sep 2019, M. J. Anzueto & E. Velazquez. *Tlaloc portillorum*: **Honduras**: LSUMZ 31597, topotypes, 14 (3 c&s), 49.8–70.7 mm SL, Rio Calan, Quebrada Potrerillos, Comayagua, 14°32'31"N 87°52'55"W, 5 Dec 2007, W. Matamoros. MZ-UNICACH 7220, 21 (4 c&s), 40.8–62.9 mm SL, Puente de Piedra a Lepaterique, Francisco Morazan, 15 Apr 2017, W. Matamoros & A. E. Gomenz. MZ-UNICACH 7222, 28 (2 c&s), 37.5–71.3 mm SL, Rio Nacaome, Las Tablas, Francisco Morazan, 15 Apr 2017, W. Matamoros & A. E. Gomez.

DISCUSSION

This study based on morphological characters supports relationships found between genera of Profundulidae as proposed in molecular analyses. Recently Morcillo *et al*. (2016) resurrected the genus *Tlaloc*, based on molecular evidence, recognizing the monophyly of the group. Monophyly of *Tlaloc* is supported in this study by five unique morphological characters: the mesethmoid is prominent and oval in shape, protruding from the posterior margins of the vomer, encompassing the posterior medial extension and making contact with the lateral ethmoids; the upper portion of the parasphenoid makes contact with the mesethmoid and does extent beyond the medial part of this last bone; the autopterotic fossa is reduced; the ventral margin of the lacrimal is straight; the dorsal margin of the interoperculum, with a long extension, exceeds the edge of the bone.

Profundulus was erected and diagnosed by Hubbs (1924), based on following diagnostic characters: The lateral rims of the genital aperture of the adult female are scarcely pronounced, surrounding not more than the first anal ray; the anal fin in the adult male is lower, instead of higher, than in either the young or the adult female. Miller (1955) in a review study of *Profundulus* (Cyprinodontidae) include these two traits and provided three new characters to characterize *Profundulus*: The shape of the premaxillary process, the nature of the hypural plate (divided into subequal parts by an open groove), and the number of gill rakers. Parenti (1981) distinguished *Profundulus* (representing the family Profundulidae) from all other cyprinodontoids by a large autopterotic fossa and a high number of gill rakers on the anterior arm of the first arch (14–23). With the reclassification of *Profundulus* in two genera, *Profundulus* and *Tlaloc* (Morcillo *et al*., 2016), the diagnostic character of a large autopterotic fossa is now limited to *Profundulus*. We here add five characters to distinguish *Profundulus* from *Tlaloc*: The mesethmoid is small, crescent-shaped, and does not exceed the margins of the vomer; the vomer is greatly broadened anteriorly, lacks lateral processes and is in contact with the lateral ethmoids; the upper portion of the parasphenoid, just in contact with the mesethmoid, does not extend beyond the medial part of this last bone; the dorsal margin of the interoperculum, with a short extension, does not exceed the edge of the bone; the ventral margin of the lacrimal is slightly concave.

Miller (1955) erected two subgenera based on the presence in *Profundulus* or absence in *Tlaloc* of conspicuously embedded scales in the preorbital region, the basal half or more of the caudal fin densely scaled, and the presence of a humeral spot in *Profundulus* or absence in *Tlaloc*. These characters were found in the analysis of only five described species. Although with most species these characters allow the separation of genera; in our review, including the 13 species currently described, none of these characters functioned as unique characters to diagnose genera.

González-Díaz *et al.* (2014) described eight osteological differences between the subgenera *Profundulus* and *Tlaloc* (seven of the skull and one of the axial skeleton), based on the analysis of only six species. Again, we observed only two characters to be considered of generic significance: the mesethmoid (small *vs*. large; our analyses corroborate the findings that were previously described by Uyeno, Miller, 1962), and the dorsal margin of the interoperculum (long *vs*. short extension). The form of the vomer (Y-shaped) was described by Costa (1989) as a character that defines the family Profundulidae; this character was described by González-Díaz *et al*. (2014) as a triangular-shaped character in *Profundulus* and Y-shaped in *Tlaloc*. We however observed Y-shaped vomers in both genera (not triangular) (Figs. 2B–C), so we agree with the description of Costa (1998).

The current study provides sufficient empirical evidence to confirm the separation and diagnosis of the genera *Tlaloc* and *Profundulus*. Analysis of morphological-osteological characters support the clades previously defined by molecular data. The comparative morphology has played an important role in the reconstruction of the evolutionary history and classification of cyprinodontiform fishes, often providing useful phylogenetic information at different taxonomic levels. For this reason, it would be important to incorporate this information to assess alternative hypotheses among members of the family Profundulidae and other groups within the Cyprinodontoidei suborder.

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AUTHORS' CONTRIBUTION

Sara E. Domínguez-Cisneros: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing-original draft.

Omar Domínguez-Domínguez: Funding acquisition, Resources, Supervision.

Ernesto Velázquez-Velázquez: Conceptualization, Writing-review and editing.

Rodolfo Pérez-Rodríguez: Methodology, Resources, Supervision.

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Not applicable.

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The author declares no competing interests.

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