Short note

The first occurrence of a freshwater percomorph fish (Actinopterygii: Teleostei) in the Ixtapa Formation (Miocene), Chiapas, southeastern Mexico

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ABSTRACT

In this paper we describe a single and incomplete fossil fish specimen collected in the Ixtapa fossiliferous site, located at the Ixtapa municipality, near Tuxtla Gutiérrez City, Chiapas, southeastern Mexico. The Ixtapa site contains ashfall sediments deposited under fluvio-lacustrine conditions, which belong to the Upper Miocene continental sediments of the Ixtapa Formation. The fossil assemblage previously recovered in this formation includes abundant angiosperm leaves, charophytes, and aquatic gastropods, as well as terrestrial mammals including horses, rhinoceros, and proboscideans. This first fossil fish from Ixtapa is considered a member of the Subdivision Percomorphaceae because its dorsal and anal fins have unsegmented spines and its caudal fin lacks the ural centrum 2. The imperfect preservation of this specimen impedes a taxonomical determination at species level; however, this fossil reveals the occurrence of primary freshwater percomorphs in the southern end of Mexico since the Miocene–Pliocene. Hence, the present discovery constitutes an important complement to understand the freshwater fish diversity in this region through time.

Keywords: Percomorph, Freshwater, Cenozoic, Ixtapa, Chiapas, Mexico.

RESUMEN

Aquí se describe un único e incompleto pez fósil colectado en los depósitos fluvio-lacustres del sitio fosilífero de Ixtapa, localizado en el Municipio del mismo nombre, cerca de la ciudad de Tuxtla Gutiérrez, Chiapas, en el sureste de México. En este sitio se exponen cenizas del Mioceno superior pertenecientes a la Formación Ixtapa. La asociación fósil recuperada en esta formación incluye una amplia diversidad de hojas de angiospermas, algas carofitas, gasterópodos acuáticos y también registros de mamíferos terrestres cómo, por ejemplo, caballos, rinocerontes y proboscidios. Este es el primer registro de un pez fósil en la localidad Ixtapa y es considerado como un miembro de la Subdivisión Percomorphaceae por la presencia de espinas no-segmentadas en las aletas dorsal y anal, además de la ausencia de centro ural 2 en el esqueleto caudal. La imperfecta preservación no permite una determinación taxonómica más precisa, sin embargo, este fósil desvela la presencia de peces percomorfos dulceacuícolas en el sur de México desde el Mioceno-Plioceno. Por lo tanto, el presente descubrimiento constituye un complemento importante para comprender la diversidad de peces dulceacuícolas en esta región a través del tiempo.

Palabras clave: Percomorfo, Dulceacuícola, Cenozoico, Ixtapa, Chiapas, México.

1. Introduction

The Ixtapa fossiliferous site is located at the coordinates 16°48′42.31″N, 92°54′33.58″W, 28 km east from Tuxtla Gutiérrez City. This site is exposed at the east side of the Soyaló-Ixtapa highway (State Road 195), next to the bridge that goes through the Río Hondo, one-kilometer North from downtown Ixtapa (Figure 1).

The Ixtapa Formation is Late Miocene in age and is deposited in low-energy fluvio-lacustrine conditions, over the Middle Miocene continental sandstones of the Coyolar Formation and the Eocene marine limestones of the El Bosque Formation. The Ixtapa Formation is covered by the Pliocene–Pleistocene volcanic deposits of the Punta de Llano Formation (*e.g.*, Ferrusquía-Villafranca, 1996; Martínez-Amador *et al.*, 2004; Hernández-Villalba *et al.*, 2013).

The fossil-bearing rocks of the Ixtapa site belong to the volcano-sedimentary sequence known as the Ixtapa Formation, an Upper Miocene geological unit which was originally named by González-Alvarado (1965). According to Ferrusquía-Villafranca (1996), the Ixtapa Formation is a sequence of pyroclastic materials interbedded with calcite pebbly gravels and tuffs. Tuffs are more frequent towards the base of the formation, forming part of interbedded layers of conglomerates, sandstones, and clays, where crystalline and calcareous conglomerates are sporadically present.

Martínez-Hernández (1992) reported that, at the base of the formation, the thick and thin well-stratified tuff–shales bear carbonized remains of leaves and stems of angiosperms, as well as gastropods and charophytes oogonia; whereas above, dark-gray conglomerates preserve remains of silicified wood and mammal remains, such as teeth of horses, rhinoceros, and proboscideans (*e.g.*, Daily and Durham, 1966; Menezes-Rocha, 2001; Hernández-Villalba *et al.*, 2013).

The most abundant fossils at the base of the Ixtapa Formation are carbonized leaves; therefore, the finding of a fish in this unit was unexpected. The aim of the present paper is to describe this fossil fish, which despite not being well preserved, could be an important clue to understand the paleobiogeographic patterns of the percomorph fishes in the extreme south of North and Central America. This fossil also represents the oldest primary freshwater percomorph fish known in Mexico.

2. Material and methods

The specimen described here is deposited in the National Collection of Paleontology of Mexico (Colección Nacional de Paleontología), at the Autonomous National University of Mexico (Universidad Nacional Autónoma de México). This fossil fish preserves partially both part and counterpart and contains only undefined isolated bones on the head. Furthermore, it lacks the anterior portion of the vertebral column, the pectoral and pelvic fins, and the tip of the dorsal, anal, and caudal fins.

The olive gray sediments, formed by volcanic tuff rocks, cover the skeleton. The small patches of rock matrix over many parts of the body were mechanically removed with thin excavators and needles, and chemically removed with punctual brushstrokes and 5% sulfamic acid. To obtain better contrast between the bones and the sediment, the specimen was coated with magnesium smoke.

A total of 11 anatomic measures and 10 counts compose the morphometric and meristic data of the specimen. The bone nomenclature follows the classic works on acanthomorph osteology (*e.g.*, Stiassny, 1986; Johnson and Patterson, 1993). The interpretation from the Upper Miocene to the Lower Pliocene of the Ixtapa Formation follows previous paleontological and geological studies of the area (*i.e.*, Martínez-Hernández, 1992; Ferrusquía-Villafranca, 1996; Hernández-Villalba *et al.*, 2013).

All the taxa used for comparison belong to the same institution of the species here described and include the Paleocene species *Eekaulostomus cuevasae* Cantalice and Alvarado-Ortega, 2016 (IGM 4716); *Kelemejtubus castroi* Cantalice and

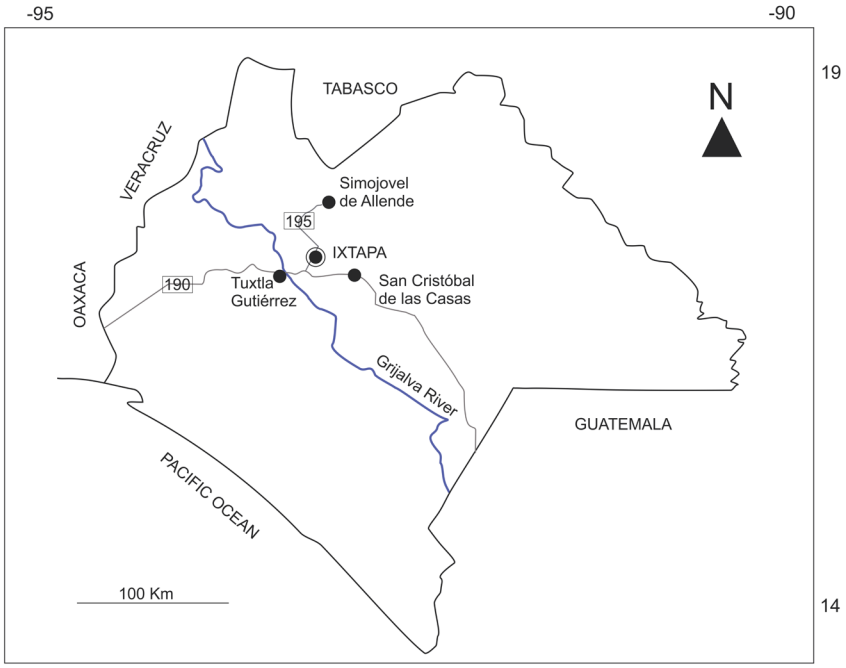

Figure 1 **Map of the State of Chiapas, showing the Ixtapa fossiliferous site (black and white circle) and nearby municipalities (black circles). Modified of Hernández-Villalba *et al.* (2013).**

Alvarado-Ortega, 2015 (IGM 4864-67, 4908-09); *Paleoserranus lakamhae* Cantalice, Alvarado-Ortega, and Alaniz-Galvan, 2018 (IGM 9469-9477; IHNFG 6876), from Chiapas State; *Tapatia occidentalis* Álvarez and Arriola-Longoria, 1972 (IGM 7966), from the Pliocene of Barranca de Santa Rosa locality, at Amatitlán, Jalisco State; and the dubious cyprinodontiform (IGM 7967; see discussion below) of Oligocene outcrops of Ahuehuetes, at Tepexi de Rodriguez, Puebla (Espinosa-Pérez *et al.*, 1991).

3. Results

3.1. SYSTEMATIC PALEONTOLOGY

Class ACTINOPTERYGII Woodward, 1891
Infraclass TELEOSTEI Müller, 1845
Subsection ACANTHOMORPHATA
(*sensu* Wiley and Johnson, 2010)
Subdivision PERCOMORPHACEAE
(= PERCOMORPHACEA, *sensu* Wiley and Johnson, 2010)
Family *INCERTAE SEDIS*
Gen. and sp. undetermined

Referred specimen. IGM 7968, incomplete specimen preserved in part and counterpart. The anterior third (including the head, pectoral, and pelvic fins), as well as the antero-ventral portion of the body, are not preserved (Figure 2). The posterior extremity of the rays that composes the dorsal, anal, and caudal fin is also lost.

Type locality and horizon. Ixtapa locality, Upper Miocene tuff sediments at the base of the Ixtapa Formation (Ferrusquía-Villafranca, 1996), Ixtapa Municipality, Chiapas, Mexico.

Morphological sources of taxonomic characters. This fossil fish belongs to the Subsection Acanthomorphata (or only acanthomorphs) because it has true unsegmented spines before soft rays on both dorsal and anal fins. Inside acanthomorphs, the species here described belongs to the Subdivision Perco-

morphaceae to have autogenous haemal spine on the second preural centrum (PU2); five autogenous hypural plates on the caudal skeleton; and the caudal fin with seventeen principal rays, with the pattern I+8—7+I.

Description

General features. Although not complete, it is possible to observe that the specimen is a small and cylindrical fish, with the body relatively low, but not flattened. Its estimated standard length is about 31.2 mm (Table 1). The head, jaws, and pelvic and pectoral fins are not preserved. The dorsal fin is continuous and seems to be slightly notched. The beginning of the anal fin is almost parallel to the end of the caudal fin. The caudal peduncle is relatively deep, occupying about 45% of the body height without the dorsal and anal fins.

Axial skeleton. The anterior portion of the axial skeleton is not preserved. No prezygapophysis or apophysis is observed. By the presence of ribs and anterior neural spines, it is possible to suggest that the axial skeleton has at least 28 vertebrae, 13 abdominals (or more) and 15 caudal (Table 2). The antero-ventral portion of the axial skeleton includes 13 pairs of long and thin ribs. The anterior ribs are partially preserved; while the posteriors are curved to the posterior portion of the body. The vertebral centra are progressively smaller and more elongated. The haemal spines of the two centra anterior the origin of the anal fin vertebrae are stout and short. The others, similar to all neural spines visible, are thin and long structures, curved towards the posterior portion of the body.

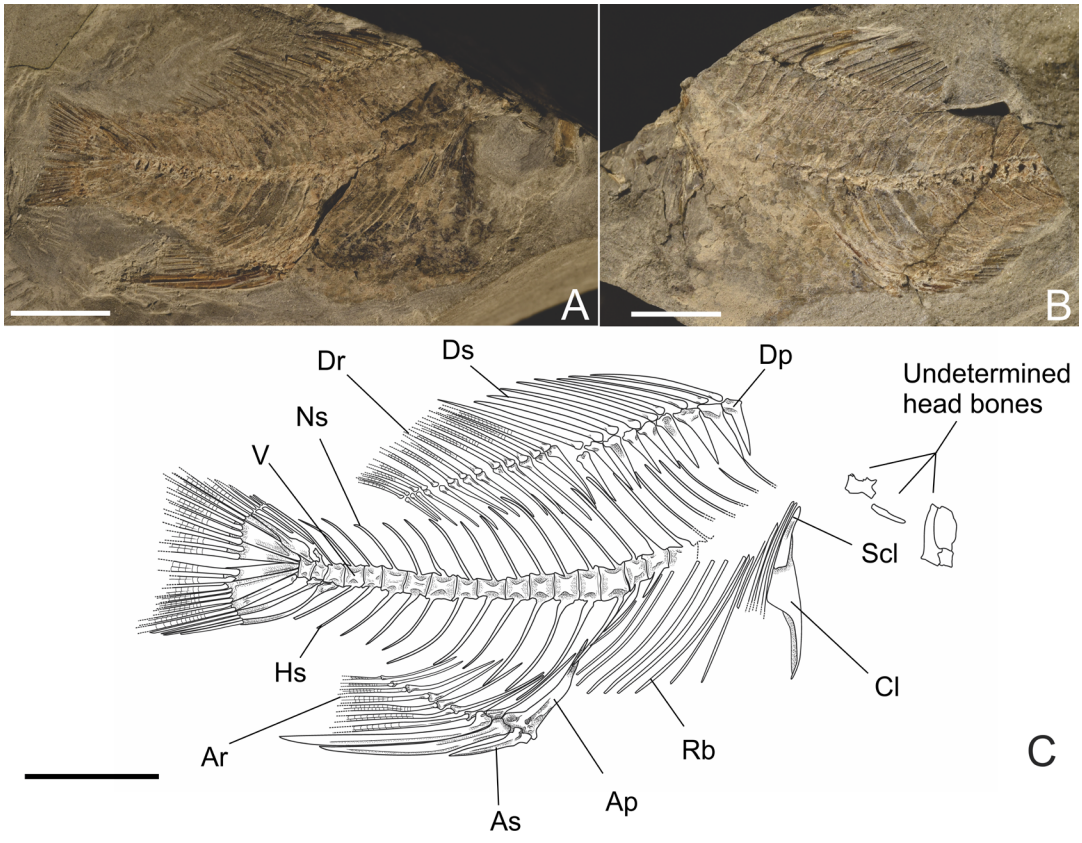

Figure 2 IGM 7968, a percomorph fish from the Miocene of Ixtapa, Chiapas, Mexico: A) right side; B) left side; C) schematic drawing based on both sides. Abbreviations: Ap, Anal fin pterygiophore; Ar, anal fin rays; As, anal fin spine; Cl, cleithrum; Dp, dorsal fin pterygiophore; Dr, dorsal fin rays; Ds, dorsal fin spines; Hs, haemal spine; Ns, neural spine; Rb, ribs; Scl, supracleithrum. The scales indicate 5 mm.

Pectoral girdle. This portion is very deteriorated. Only the supracleithrum and the cleithrum bones are preserved. The first is cylindrical and has its dorsal tip rounded; while the last seems to be strongly curved posteriorly, with its ventral tip pointed.

Dorsal fin. The supraneural bones and the first spines on the dorsal fin are lost. At least 10 spines and 15 soft rays, supported by a total of 22 pterygiophores, compose the dorsal fin. It seems to be continuous, with a slight notch before the last dorsal spine.

Anal fin. The anal fin is on the third posterior portion of the body. There are three stout spines, followed by seven soft rays; all supported by nine pterygiophores (Table 2). The first pterygiophore is the biggest bone of the series and supports the two first spines. Posteriorly, one thin and ventrally expanded pterygiophore supports the longest third spine, as well in the soft rays.

Caudal skeleton. The caudal skeleton is relatively well preserved; only the posterior portion of the caudal fin rays, and some procurrent rays on the lower lobe, are lost. This bone complex shows the preural centra (Pu) 3 and 2, urostyle, parhypural, five autogenous hypural plates, one uroneural (stegural), and two epurals (Table 2). The haemal spines of both Pu3 ad and Pu2 are autogenous, and the neural spine of Pu2 is very reduced (Figure 3).

The parhypural is spatulate; its anterior portion is not well preserved and, hence, it is not possible to observe the hypurapophysis, commonly found on percomorphs. The hypural plates are triangular and not fused to the urostyle. The hypural plates 1 to 3 have almost the same size, while hypural 4 is wide, and the hypural 5 is extremely reduced. The urostyle, a structure found in many acanthomorphs, represents a fusion between the preural centra 1 and the ural centra 1. The stegural is anteriorly wide and covers partially the urostyle and the hypural plates 4 and 5. Posteriorly, the stegural is thin and placed between the hypural 5 and the epurals. The two epurals are thin and elongated bones placed between the neural spine of Pu3 and the stegural.

Scales. The scales are big and most of them are cycloid; however, there are some ctenoid scales on the anterior and middle portion of the body. This last kind of scales is almost quadrangular and the ctenii portion is small, seemingly composed by only one series of spines.

Table 1. Measurements of the specimen IGM 7968 of the Ixtapa Formation (in millimeters). The plus sign indicates an estimation based on the minimum measure found.

Measurements	IGM 7968
Estimated standard length	+31.22
Body height	15.65
Body height without fins	11.06
Estimated dorsal length	+13.85
Dorsal fin height	5.34
Post dorsal length	5.13
Anal fin length	5.90
Anal fin height	8.77
Post anal length	5.88
Estimated caudal length	+3.11
Caudal peduncle height	5.03

Table 2. Counts of the specimen IGM 7968 of the Ixtapa Formation. The plus sign in bold indicate an estimation based on the minimal value found.

Counts	IGM 7968
Ribs	13
Vertebrae	28+(+13+15)
Dorsal fin	+X+15
Dorsal fin pterygiophores	+22
Anal fin	III+7
Anal fin pterygiophores	9
Caudal fin formula	I+8-7+I
Epurals	2
Uroneral	1
Hypural plates formula	H1/H2/H3/H4/H5

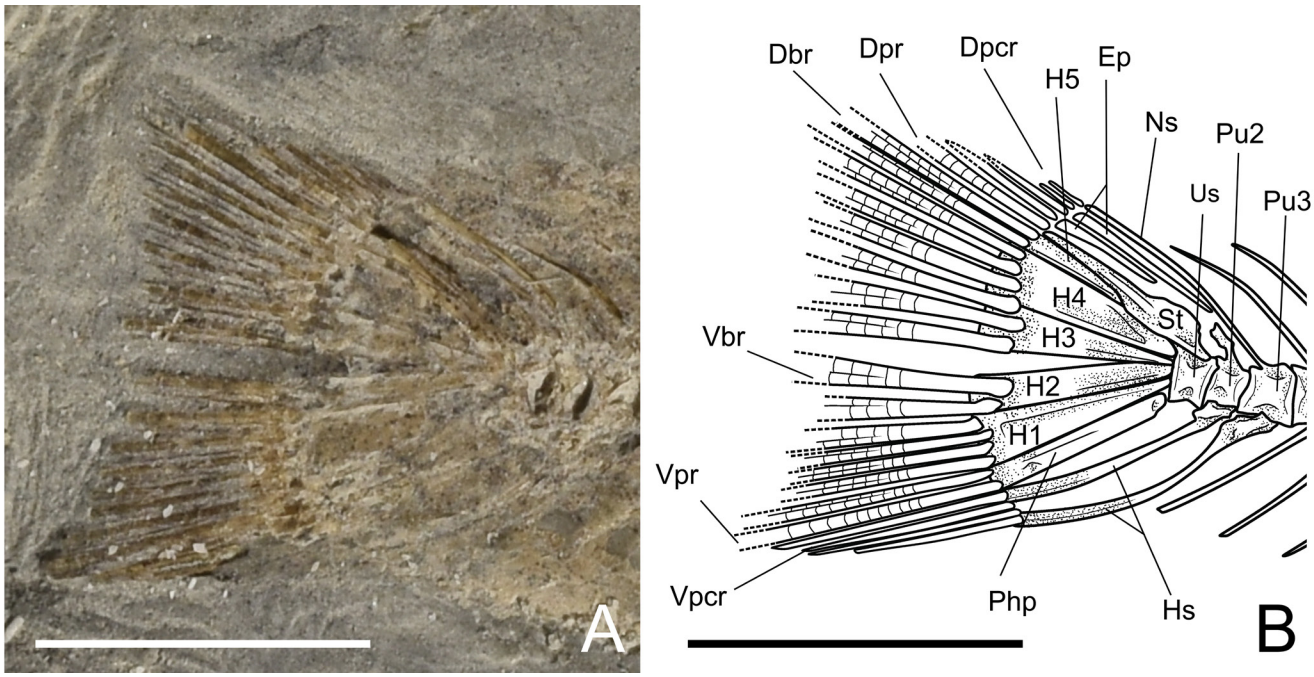

Figure 3 Schematic drawing of the caudal fin skeleton of IGM 7968. Abbreviations: Dbr, dorsal branched ray; Dpcr, dorsal procurrent ray; Dpr, dorsal principal ray; Ep, epural; H1-5, hypural plates; Hs, haemal spine; Ns, neural spine; Pu2-3, preural central; St, stegural; Us, urostyle. The scale indicates 5 mm.

4. Discussion and Conclusions

Cenozoic freshwater fish localities containing spiny-rayed fishes are scarce in Mexico. Most of the fossil beds with percomorph fossil records represent marine environments and belong to the Paleogene of Chiapas or to the Neogene of the Baja California peninsula (González-Rodríguez *et al.*, 2013; Alvarado-Ortega *et al.*, 2015; Guzmán, 2015). Inside the Paleogene strata, currently, are known flute-mouth fishes, sea basses, and some undetermined percomorphs (Alvarado-Ortega *et al.*, 2015; Cantalice and Alvarado-Ortega, 2017; Cantalice *et al.*, 2018). The body shape and the presence of three spines on the anal fin of the fossil herein described resembles the serranid *Paleoserranus lakamhae*; however, the anal spines of this last species are stouter, and the second anal fin spine is the biggest. Furthermore, the number of vertebrae in *P. lakamhae* is only 24, but in the percomorph of Ixtapa it is at least 28. In the Paleogene, there is also a small bony fish fossil found in Tepexi de Rodriguez, Puebla. This fish was recovered in the Oligocene continental strata of Ahuehuetes locality and was originally considered a percomorph member of the Order Cyprinodontiformes (Espinosa-Pérez *et al.*, 1991; Guzmán, 2015), which could be considered the oldest percomorph record restricted to freshwater environments in Mexico. Nevertheless, we revised the material and the specimen seems to have some morphological features (*i.e.*, the well-developed ceratobranchial 5 with ankylosed teeth) that could indicate some affinities with the ostariophysians of the Order Cypriniformes, such as first mentioned by González-Rodríguez *et al.* (2013). Unfortunately, this fossil specimen, for the moment, does not allow the proper classification in any subgroup of bony fishes; thus, it is best considered as Teleostei *incertae sedis* until a more detailed revision. However, the species herein described is easily distinguished with true spines on both dorsal and anal fin, a greater number of dorsal and anal rays preserved, and the body height and caudal peduncle slightly deeper.

After refuting the presence of primary percomorph fossil fish in the Paleogene, we can suggest that the early diversification of derived endemic freshwater perch-like fish in Mexico started in the Neogene. In this Period, the oldest Mexican percomorph record is *Tapatia occidentalis*, an extinct species of the family Goodeidae from the Pliocene locality of Barranca de Santa Rosa, Amatitlán, Jalisco (Guzmán *et al.*, 1998; González-Rodríguez *et al.*, 2013, Guzmán, 2015). The percomorph fish from Ixtapa distinguish from *T. occidentalis* by the absence of gonopodium on the anal fin (see Guzmán, 2015: 663).

From the Late Pliocene–Early Pleistocene deposits of the Lake Chapala Basin, Jalisco, Mexico, is reported the percomorph member of the family Centrarchidae *Micropterus relictus* Smith, Cavender and Miller, 1975. This species preserves only jaw elements (Near and Koppelmann, 2009), which are not preserved in the percomorph of Ixtapa, making the anatomical comparison between these species impossible. Finally, in the Quaternary Period is found the biggest diversity of extinct freshwater fish fauna of Mexico; however, most of the species are non-percomorph teleost (except for *Micropterus relictus*, mentioned above), differing considerably from the Ixtapa species.

Although the specimen studied herein does not allow a more detailed identification than the Subdivision Percomorphaceae, its Miocene Epoch and the localization provide new insights about the diversification of the group in continental waters of Mexico. To date, the known restricted freshwater fossil percomorphs are cyprinodontifom species of the family Goodeidae, recovered from the Pliocene to Holocene (Guzmán, 2015). Therefore, the specimen here described is the oldest and southernmost record of a perch-like fish in Mexico, suggesting, thus, an increase of about 6 Ma for the early diversification of primary freshwater percomorph in Mexico, and that this group already occupied lakes and rivers in the southwestern portion of the country before the establishment of endemic species in the central region of Mexico.

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References

Alvarado-Ortega, J., Cuevas-García, M., del Pilar Melgarejo-Damián, M., Cantalice, K.M., Alaniz-Galvan, A., Solano-Templos, G., Than-Marchese, B.A., 2015, Paleocene fishes from Palenque, Chiapas, southeastern Mexico: Palaeontologia Electronica, 18(2), 1–22. https://doi.org/10.26879/536

Álvarez, J., Arriola-Longoria, J., 1972, Primer goodeido fósil procedente del Pliocene Jaliscense (Pisces, Teleostomi): Boletín de la Sociedad de Ciencias Naturales de Jalisco, 6, 6–15.

Cantalice, K.M., Alvarado-Ortega, J., 2016, *Eekaulostomus cuevasae* gen. and sp. nov., an ancient armored trumpetfish (Aulostomoidea) from Danian (Paleocene) marine deposits of Belisario Domínguez, Chiapas, southeastern Mexico: Palaeontologia Electronica, 18(3), 1–24. https://doi.org/10.26879/682

Cantalice, K.M., Alvarado-Ortega, J., 2017, *Kelemejtubus castroi* gen. et sp. nov., an ancient percomorph (Teleostei, Actinopterygii)

from the Paleocene marine deposits near Palenque, Chiapas, southeastern Mexico: Journal of Vertebrate Paleontology, 37, 12 e1383265. https://doi.org/10.1080/02724634.2017.1383265

Cantalice, K.M., Alvarado-Ortega, J., Alaniz-Galvan, A., 2018, *Paleoserranus lakamhae* gen. et sp. nov., a Paleocene seabass (Perciformes: Serranidae) from Palenque, Chiapas, southeastern Mexico: South American journal of earth sciences, 83, 137–146, https://doi.org/10.1016/j. jsames.2018.01.010.

Daily F.K., Durham J.W., 1966, Miocene charophytes from Ixtapa, Chiapas, Mexico: Journal of Palentology, 40(5), 1191–1199.

Espinosa-Pérez, H., González-Rodríguez, K., Applegate, S.P., 1991, Nuevos Registros de Peces Dulceacuícolas Fósiles en México, *in* II Congreso Nacional de Ictiología, San Nicolás de Los Garza, Nuevo León, México, Abstract book, 33.

Ferrusquía-Villafranca, I., 1996, Contribución al conocimiento geológica de Chiapas - el área Ixtapa-Soyaló: Instituto de Geología, Universidad Nacional Autónoma de México, 109, 130.

González-Alvarado, I., 1965, Geología del área Ixtapa-San Cristóbal de las Casas, Chiapas: Petróleos mexicanos, Zona Sur, Informe geológico 507.

González-Rodríguez, K.A., Espinosa- Arrubarrena, L., González-Barba, G., 2013, An overview of the Mexican fossil fish record *in* Arratia G., Schultze, H-P., Wilson, V.H. (eds.) Mesozoic fishes 5 – Global Diversity and Evolution: Germany, Verlag Dr. Friedrich Pfeil, 9–34.

Guzmán, A.F., Stinnesbeck, W., Robles-Camacho, J., Polaco, O., 1998, El Paleolago de Amatitán, Jalisco: estratigrafía, sedimentología y paleontología de la localidad tipo de *Tapatia occidentalis* (Osteichthyes: Goodeidae): Revista de la Sociedad Mexicana de Paleontología, 8(2), 127–134.

Guzmán, A.F., 2015, El registro fósil de los peces mexicanos de agua dulce: Revista Mexicana de Biodiversidad, 86(3), 661–673. https://doi.org/10.1016/j.rmb.2015.05.003

Hernández-Villalba, D.V., Calvillo-Canadell, L., Cevallos-Ferriz S.R.S., 2013, Inferencia del paleoclima de la Formación miocénica en Ixtapa Chiapas, utilizando la fisionomía foliar de los fósiles: Paleontología Mexicana, 63, 48–65.

Johnson, D.G., Patterson, C., 1993, Percomorph phylogeny: a survey of acanthomorphs and a new proposal: Bulletin of Marine Science, 52(1), 554–626.

Martínez-Amador, H., Rosendo-Brito, B., Fitz-Bravo, C., 2004, Carta Geológico–Minera Tuxtla Gutiérrez E15-11, estados de Chiapas y Oaxaca, escala 1:250 000. Pachuca, Hidalgo, México: Consejo de Recursos Minerales, 172.

Martínez-Hernández, E., 1992, Caracterización ambiental del Terciario de la región de Ixtapa, Estado de Chiapas—un enfoque palinoestratigráfico: Revista del Instituto de Geología, Universidad Nacional Autónoma de México, 10, 54–64.

Menezes-Rocha, J.J., 2001, Tectonic evolution of the Ixtapa graben, an example of a strike-slip basin in southeastern Mexico: Implications for regional petroleum systems, i*n* Bartolini, C.; Buffler, R.T., Cantú, A. (eds.), The western Gulf of Mexico Basin: Tectonics, sedimentary basins, and petroleum systems: AAPG Memoir 75, 183–216.

Müller, J., 1845, Untersuchungen über die Eingeweide der Fische: Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin, 109-170, 5 láms.

Near, T.J., Koppelman, J.B., 2009, Species diversity, phylogeny, and phylogeography of Centrarchidae *in* Cooke, S.J., Philipp, D.P. (eds.), Centrarchid Fishes: Diversity, Biology, and Conservation: London, Blackwell Science, 1–38.

Smith, M.L., Cavender, T.M., Miller, R.R., 1975, Climatic and biogeographic significance of a fish fauna from the Late Pliocene-Early Pleistocene of the Lake Chapala Basin (Jalisco, Mexico): Papers on Paleontology the Museum of Paleontology University of Michigan 12, 29–38.

Stiassny, M.L., 1986, The limits and relationships of the acanthomorph teleosts. Journal of Zoology, 1(2), 411–460. https://doi.org/10.1111/j.1096-3642.1986.tb00644.x

Wiley, E.O., Johnson, G.D., 2010, A teleost classification based on monophyletic groups, *in* Nelson, J.S., Schultze, H.-P., Wilson, M.V.H. (eds.), Origin and Phylogenetic Interrelationships of Teleosts: Germany, Verlag Dr. Friedrich Pfeil, 123–182.

Woodward, A.S., 1891, Catalogue of fossil fishes in the British Museum (Natural History), Part II: London, Trustees of the British Museum (Natural History), 567.