

# The paleoichthyofauna housed in the Colección Nacional de Paleontología of Universidad Nacional Autónoma de México

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## Abstract

Fishes are a paraphyletic group composed by craniates except for the four-limbed clade Tetrapoda. This group was the only vertebrate representative until the Devonian but now comprises almost half of the vertebrate species, dominating nearly all aquatic environments. The fossil record is the key to understand the ancient paleobiodiversity and the patterns that lead the modern fish fauna, and paleontological collections play a fundamental role in providing accommodation, maintenance, and access to the specimens and their respective metadata. Here we present a systematic checklist of fossil fishes housed in the type collection of the Colección Nacional de Paleontología which is located at the Instituto de Geología of Universidad Nacional Autónoma de México. Currently housed in the type collection are 14 chondrichthyan specimens, belonging to two superorders, five orders, seven families, 10 genera, and five nominal species, and 361 osteichthyan specimens, belonging to eight orders, nine families, nine genera, and 26 nominal species. These fossils come from 32 localities and 15 geological units, which range temporally from the Jurassic to the Pleistocene. The paleoichthyofauna housed in the type collection of the Colección Nacional de Paleontología is remarkable for its singularity and reveals new insights about the origin and diversification of many groups of fishes. The recovery and curation of this fossil material indicates that knowledge of Mexican fossil fish diversity and its role in understanding lower vertebrate evolution are just emerging and reaffirms the importance of the biological and paleontological collections to the future biodiversity research.

## Key Words

Collection, diversity, fishes, paleontology, taxonomy, Mexico

## Introduction

Fishes are craniate animals that have gill arches and use fins for locomotion in aquatic environments (Berra 2007; Nelson et al. 2016; Clarke and Friedman 2018). Among vertebrates, fishes exhibit incomparable diversity in morphology, behavior, physiology, and distribution (Nelson et al. 2016). Currently, the extant fishes are classified in four distinct classes: Myxini (hagfishes), Petromyzontida (lampreys), Chondrichthyes (cartilaginous fishes, such as sharks and stingrays), and Osteichthyes. The last class is

divided into ray-finned (Actinopterygii) and lobe-finned fishes, Dipnoi and Actinistia, respectively (Helfman et al. 1997). Nevertheless, if we consider the extinct ichthyofauna, the number of classes at least doubles (see Nelson et al. 2016).

In the current understanding of vertebrate systematics, fishes constitute a paraphyletic group (Gill and Mooi 2002; Berra 2007) because it excludes the four-limbed osteichthyan clade Tetrapoda, which shares a common ancestor

with lobe-finned fishes (Zhu and Yu 2002). Nevertheless, with at least 32,000 species, fishes represent one-half of the world's living vertebrates and the study of fishes contributes to many subjects of scientific natural history knowledge, such as ontogeny, distribution, speciation, and diversification through space and time (Kornfield and Smith 2000; Peñáz 2001, Cavin et al. 2008; Nelson et al. 2016).

Fossils are physical evidence that helps in the recognition and interpretation of biological patterns and processes on Earth through time (Cavin et al. 2008). Nevertheless, by its composition, fossil material is so fragile that specific care is required for good long-term preservation, and museums and academic institutions are responsible for protecting and conserve this material (Allmon 1994, 2005; Llorente-Bousquets et al. 1994).

Paleontological collections not only have the responsibility of accommodating and storing the fossil record but also of providing the care and good conditions to use these materials for scientific research purposes and entertainment (Llorente-Bousquets et al. 1994; Cristín and Perrilliat 2011). Good practices in museum curation, such as the collection of specimens in appropriate spaces and conditions, the creation of systematic catalogues, and regulations for the proper use of fossils, are essential to generate and validate the information on which the advance of science is possible (Allmon 2005). Furthermore, paleontological collections have an important social and teaching role in spreading the scientific discoveries accessible to the public (Suarez and Tsutsui 2004).

The Colección Nacional de Paleontología of Universidad Nacional Autónoma de México (CNP-UNAM) is remarkable by its number of specimens collected in many regions of the country from various geological ages (e.g. Perrilliat 1993; Cristín and Perrilliat 2011; Perrilliat and Castañeda-Posadas 2013; Rojas-Zúñiga and Gio-Argáez 2016). Although the birth of CNP-UNAM was at the end of the 19<sup>th</sup> century, its formal consolidation inside the Institute of Geology occurred between 1978 and 1986. Only in 2004 did this collection become recognized as the National Collection of Paleontology and given the designation as the “Museum María del Carmen Perrilliat”. All fossils housed at the CNP-UNAM have the acronym (IGM) and began to be incorporated in 1978. Previous fossil records are in other institutions or are lost.

Today, the CNP-UNAM has five sections: geographic reference, foreign materials, Recent materials, molds, and the collection of types (Perrilliat et al. 1986; Carreño and Montellano-Ballesteros 2005). The type collection includes: 1) specimens belonging to type series and 2) voucher specimens, which are recorded in this collection as hypotypes. This section comprises about 10,000 specimens of microfossils, plants, invertebrates, and vertebrates, ranging from the end Precambrian to the Quaternary period of the Cenozoic (e.g. Perrilliat 1993; Perrilliat and Castañeda-Posadas 2013).

After 25 years since the last report about the fossil vertebrates housed in the type collection of CNP-UNAM (Perrilliat 1993), fossil fish specimens have been incre-

mentally added and many changes in fish taxonomy and classification have occurred. Therefore, following Article 72 of the International Code of Zoological Nomenclature, we present the systematic list of fishes currently housed in this collection and their respective localities. Furthermore, we provide information about the implications of these discoveries to understanding the taxonomy, biogeography, and early evolutionary history of some taxa and highlight the importance of biological collections to future research on paleodiversity in Mexico.

## Methods

All fish fossils housed in the CNP-UNAM type collection were reviewed. Information on the taxonomy, age, and distribution are from both the collection database and the literature. For each species, we include the catalogue number (IGM), taxonomic classification, and respective distribution and age. Nomenclature on extinct Chondrichthyes follows Nelson et al. (2016) and Van de Laan (2018), while nomenclature on Recent Osteichthyes follows Betancur-R. et al. (2017) and Fricke et al. (2019). The nomenclature of extinct bony fishes follows Nelson et al. (2016), Van der Laan (2018), and original references. The maps were created with QGIS software version 2.18.19 (QGIS Development Team 2018) and the fossil fish localities were plotted using the software ArcView version 3.3 (Environmental Systems Research Institute, Inc., Redlands, California). Most of the taxonomic database used is available under open access at Unidad Informática para la Paleontología of UNAM (UNIPALEO; <http://www.unipaleo.unam.mx>).

## Results

### 1. Systematic checklist list of CNP-UNAM fossil fishes

Subphylum Vertebrata Cuvier, 1812  
 Infraphylum Gnathostomata Zittel, 1879  
 Class Chondrichthyes Huxley, 1880  
 Subclass Elasmobranchii Bonaparte, 1838  
 Cohort Euselachii Hay, 1902  
 Order †Hybodontiformes Maisey, 1975  
 Superfamily †Hybodontoidea Owen, 1846  
 Family †Hybodontidae Agassiz, 1843  
 Genus †*Planohybodus* Rees & Underwood, 2008  
 †*Planohybodus* indet.

**Referred specimen.** IGM 9316, IGM 9317 (Alvarado-Ortega et al. 2014).

**Locality and age.** Llano Yosobé, Sabinal Formation, Tlaxiaco, Oaxaca; Jurassic (Kimmeridgian-Tithonian).

Subcohort Neoselachii Compagno, 1977  
 Superorder Galeomorphii Compagno, 1973  
 Order Carcharhiniformes Compagno, 1973

**Carcharhiniformes indet.**

**Referred specimen.** IGM 6990 (Ferrusquía-Villafranca et al. 1999).

**Locality and age.** Rancho el Jobo, San Juan Formation, Tuxtla Gutiérrez, Chiapas; Middle Eocene.

Family Carcharhinidae Jordan & Evermann, 1896  
 Genus *Galeocerdo* Müller & Henle, 1837

†*Galeocerdo rosaliensis* Applegate, 1978

**Referred specimen.** IGM 5854 (holotype).

**Locality and age.** Tirabuzón Formation, Santa Rosalía, Baja California Sur; Pliocene.

***Galeocerdo* indet.**

**Referred specimen.** IGM 6989 (Ferrusquía-Villafranca et al. 1999).

**Locality and age.** Rancho el Jobo, San Juan Formation, Tuxtla Gutiérrez, Chiapas; Middle Eocene.

Family Hemigaleidae Hasse, 1878  
 Genus *Hemipristis* Agassiz, 1843

***Hemipristis* indet.**

**Referred specimen.** IGM 6988 (Ferrusquía-Villafranca et al. 1999).

**Locality and age.** Rancho el Jobo, San Juan Formation, Tuxtla Gutiérrez, Chiapas; Middle Eocene.

Order Lamniformes Berg, 1958  
 Family Lamnidae Bonaparte, 1835  
 Genus *Carcharodon* Smith, 1938

†*Carcharodon auriculatus* Jordan, 1923

**Referred specimen.** IGM 6986 (Ferrusquía-Villafranca et al. 1999).

**Locality and age.** Rancho el Jobo, San Juan Formation, Tuxtla Gutiérrez, Chiapas; Middle Eocene.

Genus *Isurus* Rafinesque, 1810

†*Isurus cf. praecursor* Leriche, 1902

**Referred specimen.** IGM 6985 (Ferrusquía-Villafranca et al. 1999).

**Locality and age.** Rancho el Jobo, San Juan Formation, Tuxtla Gutiérrez, Chiapas; Middle Eocene.

Family Odontaspidae Müller & Henle, 1839

Genus *Carcharias* Rafinesque, 1810

***Carcharias* indet.**

**Referred specimen.** IGM 6983 (Ferrusquía-Villafranca et al. 1999).

**Locality and age.** Rancho el Jobo, San Juan Formation, Tuxtla Gutiérrez, Chiapas; Middle Eocene.

Genus *Odontaspis* Agassiz, 1838

***Odontaspis* indet.**

**Referred specimen.** IGM 6984 (Ferrusquía-Villafranca et al. 1999).

**Locality and age.** Rancho el Jobo, San Juan Formation, Tuxtla Gutiérrez, Chiapas; Middle Eocene.

Genus †*Striatolamia* Glikman, 1964

†*Striatolamia macrota* (Agassiz, 1843)

**Referred specimen.** IGM 6982 (Ferrusquía-Villafranca et al. 1999).

**Locality and age.** Rancho el Jobo, San Juan Formation, Tuxtla Gutiérrez, Chiapas; Middle Eocene.

Family †Otodontidae Glikman, 1964

†**Otodontidae indet.**

**Referred specimen.** IGM 6987 (Ferrusquía-Villafranca et al. 1999).

**Locality and age.** Rancho el Jobo, San Juan Formation, Tuxtla Gutiérrez, Chiapas; Middle Eocene.

Order Orectolobiformes Compagno, 1973  
 Suborder Orectoloboidei Regan, 1908  
 Family Ginglymostomatidae Gill, 1862  
 Genus *Nebrius* Rüppel, 1837

*Nebrius* indet.

**Referred specimen.** IGM 6981 (Ferrusquía-Villafranca et al. 1999).

**Locality and age.** Rancho el Jobo, San Juan Formation, Tuxtla Gutiérrez, Chiapas; Middle Eocene.

Superorder Batoidea Compagno, 1973  
 Order Rhinopristiformes Last, Serét & Naylor, 2016

Family *incertae sedis*

Genus †*Tlaloebatos* Brito, Villalobos-Segura & Alvarado-Ortega, 2019

†*Tlaloebatos applegatei* Brito, Villalobos-Segura & Alvarado-Ortega, 2019

**Referred specimens.** IGM 5853 (holotype).

**Locality and age.** Tlayúa quarry, Tlayúa Formation, Tepexi de Rodríguez, Puebla; Cretaceous (Albian).

Megaclass Osteichthyes Huxley, 1880  
 Class Actinopterygii Woodward, 1891  
 Subclass Neopterygii Regan, 1923

Order *incertae sedis*

Family *incertae sedis*

Genus †*Cipactlichthys* Brito & Alvarado-Ortega, 2013

†*Cipactlichthys scutatus* Brito & Alvarado-Ortega, 2013

**Referred specimens.** IGM 6605 (holotype), IGM 6606 (paratype).

**Locality and age.** Tlayúa quarry, Tlayúa Formation, Tepexi de Rodríguez, Puebla; Cretaceous (Albian).

Order †Aspidorhynchiformes Bleeker, 1859  
 Family †Aspidorhynchidae Bleeker, 1859  
 Genus †*Vinctifer* Jordan, 1919

†*Vinctifer ferrusquiai* Cantalice, Alvarado-Ortega & Brito, 2018

**Referred specimen.** IGM 8873 (holotype).

**Locality and age.** Llano Yosobé, Sabinal Formation, Tlaxiaco, Oaxaca; Jurassic (Kimmeridgian-Tithonian).

Order †Pycnodontiformes Berg, 1937  
 Suborder †Pycnodontoidei Nursall, 1966  
 Family †Pycnodontidae Agassiz, 1833

†Pycnodontidae indet.

**Referred specimen.** IGM 3143 (Carranza-Castañeda and Applegate 1994).

**Locality and age.** Cerro los Mendoza, El Doctor Formation, Zimapán, Hidalgo; Cretaceous (Albian-Cenomanian).

Subfamily †Pycnodontinae (Agassiz, 1833)  
 Genus †*Pycnodus* Agassiz, 1833

†*Pycnodus* indet.

**Referred specimen.** IGM 4551 (Alvarado-Ortega et al. 2015).

**Locality and age.** Belisario Domínguez quarry, Tenejapa-Lacandón geological unity; Salto de Agua, Chiapas; Paleocene (Danian).

Genus †*Tepexichthys* Applegate, 1992

†*Tepexichthys aranguthyrorum* Applegate, 1992

**Referred specimens.** IGM 3286 (holotype), IGM 3288-IGM 3289, IGM 3291-IGM 3300, IGM 3455, IGM 3513, IGM 3587, IGM 3689, IGM 3690, IGM 4052-IGM 4122 (paratypes).

**Locality and age.** Tlayúa quarry, Tlayúa Formation, Tepexi de Rodríguez, Puebla; Cretaceous (Albian).

Suborder †Gyrodontoidei Nursall, 1966  
 Family †Gyrodontidae Berg, 1940  
 Genus †*Gyrodus* Agassiz, 1833

†*Gyrodus* indet.

**Referred specimens.** IGM 9318, IGM 9319 (Alvarado-Ortega et al. 2014).

**Locality and age.** Llano Yosobé, Sabinal Formation, Tlaxiaco, Oaxaca; Jurassic (Kimmeridgian-Tithonian).

Infraclass Holostei Müller, 1845  
 Division Ginglymodi Cope, 1871  
 Order †Semionotiformes Arambourg & Bertini, 1958 (*sensu* López-Arbarello 2012)  
 Family †Semionotidae Woodward, 1890  
 Genus †*Tlayuamichin* López-Arbarello & Alvarado-Ortega, 2011

†*Tlayuamichin itzli* López-Arbarello & Alvarado-Ortega, 2011

**Referred specimens.** IGM 6716 (holotype), IGM 6717-IGM 6720 (paratypes).

**Locality and age.** Tlayúa quarry, Tlayúa Formation, Tepexi de Rodríguez, Puebla; Cretaceous (Albian).

Family †Macrosemiidae Wagner, 1860  
 Genus †*Notagogus* Agassiz, 1843

†*Notagogus novomundi* González-Rodríguez & Reynoso, 2004

**Referred specimen.** IGM 8172 (holotype), IGM 8173-IGM 8181 (paratypes).

**Locality and age.** Tlayúa quarry, Tlayúa Formation, Tepexi de Rodríguez, Puebla; Cretaceous (Albian).

Genus †*Macrosemiocotzus* González-Rodríguez, Applegate & Espinosa-Arrubarrena, 2004

†*Macrosemiocotzus americanus* González-Rodríguez, Applegate & Espinosa-Arrubarrena, 2004

**Referred specimens.** IGM 8163 (holotype), IGM 8164-IGM 8171 (paratypes).

**Locality and age.** Tlayúa quarry, Tlayúa Formation, Tepexi de Rodríguez, Puebla; Cretaceous (Albian).

Order Lepisosteiformes Hay, 1929

Lepisosteiformes indet.

**Referred specimens.** IGM 9321, IGM 9322 (Alvarado-Ortega et al. 2014).

**Locality and age.** Llano Yosobé, Sabinal Formation, Tlaxiaco, Oaxaca; Jurassic (Kimmeridgian-Tithonian).

Family Lepidotidae Owen, 1860  
 Genus *Scheenstia* López-Arbarello & Sferco, 2011

*Scheenstia* indet.

**Referred specimen.** IGM 9320 (Alvarado-Ortega et al. 2014).

**Locality and age.** La Lobera, “Caliza con *Cidaris*”, Tlaxiaco, Oaxaca; Jurassic (Oxfordian-Early Kimmeridgian).

Superfamily Lepisosteioidea López-Arbarello, 2012

Family Lepisosteidae Agassiz, 1832

Lepisosteidae indet.

**Referred specimens.** IGM 7657-IGM 7662 (Rodríguez De la Rosa and Cevallos-Ferriz 1998).

**Locality and age.** El Pelillal, Cerro del Pueblo Formation, Coahuila; Cretaceous (Campanian).

Genus †*Nhanulepisosteus* Brito, Alvarado-Ortega & Meunier, 2017

†*Nhanulepisosteus mexicanus* Brito, Alvarado-Ortega & Meunier, 2017

**Referred specimens.** IGM 4898 (holotype), IGM 4899-IGM 4902 (paratypes).

**Locality and age.** Llano Yosobé, Sabinal Formation, Tlaxiaco, Oaxaca; Jurassic (Kimmeridgian-Tithonian).

Division Halecomorphi Cope, 1872  
 Order †Ionoscopiformes Grande & Bemis, 1998

Family †Ionoscopidae Lehman, 1966  
 Genus †*Quetzalichthys* Alvarado-Ortega & Espinosa-Arrubarrena, 2008

†*Quetzalichthys perrillatae* Alvarado-Ortega & Espinosa-Arrubarrena, 2008

**Referred specimen.** IGM 8592 (holotype), IGM 8593-IGM 8596 (paratypes).

**Locality and age.** Tlayúa quarry, Tlayúa Formation, Tepexi de Rodríguez, Puebla; Cretaceous (Albian).

Family †Ophiopsidae Bartram, 1975

Genus †*Teoichthys* Applegate, 1988

†*Teoichthys kallistos* Applegate, 1988

**Referred specimen.** IGM 3460 (holotype), IGM 4126 (paratype).

**Locality and age.** Tlayúa quarry, Tlayúa Formation, Tepexi de Rodríguez, Puebla; Cretaceous (Albian).

†*Teoichthys brevipina* Machado, Alvarado-Ortega, Machado & Brito, 2013

**Referred specimens.** IGM 6741 (holotype), IGM 6742 and IGM 6744 (paratypes), IGM 6604, IGM 6743, IGM 6745-IGM 6747 (Machado et al. 2013).

**Locality and age.** Tlayúa quarry, Tlayúa Formation, Tepexi de Rodríguez, Puebla; Cretaceous (Albian).

Order Amiiformes Hay, 1929

Family Amiidae Bonaparte, 1837

Subfamily †Vidalamiinae Grande & Bemis, 1998

Genus †*Pachyamia* Chalifa & Tchernov, 1982

†*Pachyamia mexicana* Grande & Bemis, 1998

**Referred specimens.** IGM 7379 (holotype), IGM 7380-IGM 7387 (paratypes).

**Locality and age.** Tlayúa quarry, Tlayúa Formation, Tepexi de Rodríguez, Puebla; Cretaceous (Albian).

Genus †*Melvius* Bryant, 1987

†*Melvius* indet.

**Referred specimens.** IGM 7663, IGM 7664 (Rodríguez De la Rosa and Cevallos-Ferriz 1998).

**Locality and age.** El Pelillal, Cerro del Pueblo Formation, Coahuila; Cretaceous (Campanian).

Infraclass Teleostei Müller, 1845

Order †Pholidophoriformes Wagner, 1860

Family †Pleuropholidae Saint-Seine, 1949

Genus †*Pleuropholis* Egerton, 1858

†*Pleuropholis cinerosorum* Alvarado-Ortega & Brito, 2016

**Referred specimens.** IGM 4733 (holotype), IGM 4734, IGM 4735, IGM 9323 (paratypes).

**Locality and age.** Llano Yosobé, Sabinal Formation, Tlaxiaco, Oaxaca; Jurassic (Kimmeridgian-Tithonian).

Order †Ichthyodectiformes Bardack & Sprinkle, 1969

†Ichthyodectiformes indet.

**Referred specimen.** IGM 9048 (Alvarado-Ortega et al. 2007).

**Locality and age.** Tlayúa quarry, Tlayúa Formation, Tepexi de Rodríguez, Puebla; Cretaceous (Albian).

Suborder †Ichthyodectoidei Maisey, 1991

Family †Ichthyodectidae Crook, 1892

Genus †*Unamichthys* Alvarado-Ortega, 2004

†*Unamichthys espinosai* Alvarado-Ortega, 2004

**Referred specimens.** IGM 8373 (holotype), IGM 8374-IGM 8376 (paratypes).

**Locality and age.** Tlayúa quarry, Tlayúa Formation, Tepexi de Rodríguez, Puebla; Cretaceous (Albian).

Megacohort Elopocephalai Arratia, 1999

Cohort Elopomorpha Greenwood, Rosen, Weitzman & Myers, 1966

Order Anguilliformes Goodrich, 1909

Anguilliformes indet.

**Referred specimen.** IGM 4547 (Alvarado-Ortega et al. 2015).

**Locality and age.** Belisario Domínguez quarry, Tenejapa-Lacandón geological unity, Salto de Agua, Chiapas; Paleocene (Danian).

Megacohort Osteoglossocephalai Betancur-R., Broughton, Wiley, Carpenter, López, Holcroft, Arcila, Sanciangco, Cureton, Zhang, Borden, Rowley, Reneau, Hough, Lu, Grande, Arratia & Ortí, 2013 (=Osteoglossocephala *sensu* Arratia 1999)

Supercorhort Osteoglossomorpha Greenwood, Rosen, Weitzman & Myers, 1966

Order Osteoglossiformes Berg, 1940

Suborder Osteoglossoidei Regan, 1909

Family Osteoglossidae Bonaparte, 1832

Subfamily Osteoglossinae Nelson, 1968

Genus †*Phaerodus* Leidy, 1873

†*Phaerodus* indet.

**Referred specimen.** IGM 4549 (Alvarado-Ortega et al. 2015).

**Locality and age.** División del Norte quarry, Tenejapa-Lacandón geological unity, Palenque, Chiapas; Paleocene (Danian).

Supercohort Clupecocephala Patterson & Rosen, 1977

Order †Crossognathiformes Taverne, 1989

Suborder †Pachyrhizodontoidei Forey, 1977

†Pachyrhizodontoidei indet.

**Referred specimen.** IGM 9049 (Alvarado-Ortega et al. 2007).

**Locality and age.** Tlayúa quarry, Tlayúa Formation, Tepexi de Rodríguez, Puebla; Cretaceous (Albian).

Family *incertae sedis*

Genus †*Michin* Alvarado-Ortega, Mayrinck & Brito, 2008

†*Michin cernai* Alvarado-Ortega, Mayrinck & Brito, 2008

**Referred specimens.** IGM 9028 (holotype), IGM 9029-IGM 9033 (paratypes).

**Locality and age.** Tlayúa quarry, Tlayúa Formation, Tepexi de Rodríguez, Puebla; Cretaceous (Albian).

Cohort Otomorpha Wiley & Johnson, 2010

Subcohort Clupei Wiley & Johnson, 2010

Order †Ellimmichthyiformes Grande, 1982

Family †Paraclupeidae Chang & Chou, 1974

†*Paraclupea seilacheri* Alvarado-Ortega & Melgarejo-Damián, 2017

**Referred specimens.** IGM 4717 (holotype), IGM 4718-IGM 4723 (paratypes).

**Locality and age.** Tlayúa quarry, Tlayúa Formation, Tepexi de Rodríguez, Puebla; Cretaceous (Albian).

Order Clupeiformes Rafinesque, 1810

Suborder Clupeoidei Rafinesque, 1810

Family *incertae sedis*

†*Ranulfoichthys dorsonudum* Alvarado-Ortega, 2014

**Referred specimens.** IGM 9034 (holotype), IGM 9467, IGM 9468 (paratypes); IGM 9035-IGM 9047 (Alvarado-Ortega, 2014).

**Locality and age.** Tlayúa quarry, Tlayúa Formation, Tepexi de Rodríguez, Puebla; Cretaceous (Albian).

Family Clupeidae Cuvier, 1817

Clupeidae indet.

**Referred specimen.** IGM 4548 (Alvarado-Ortega et al. 2015).

**Locality and age.** División del Norte quarry, Tenejapa-Lacandón geological unity, Palenque, Chiapas; Paleocene (Danian).

Subcohort Ostariophysa Lord, 1922

Section Otophysa (=Series Otophysa sensu Rosen & Greenwood, 1970)

Superorder Cypriniphysae Fink & Fink, 1981

Order Cypriniformes Rafinesque, 1810

Superfamily Cobitoidea Swainson, 1839

Family Catostomidae Agassiz, 1850

Subfamily Ictiobinae Smith, 1992

Genus *Ictiobus* Rafinesque, 1820

†*Ictiobus aguilerai* Alvarado-Ortega, Carranza-Castañeda & Álvarez-Reyes, 2006

**Referred specimens.** IGM 8444 (holotype), IGM 8445-IGM 8591 (paratypes).

**Locality and age.** La Cementera, La Viga, Tecalco, and El Hoyo, Tarango Formation, Tula de Allende, Hidalgo; Pliocene.

Order Siluriformes Rafinesque, 1810

Suborder Siluroidei Rafinesque, 1810

Superfamily Bagroidea Bleeker, 1858

Family Ariidae Bleeker, 1858

Ariidae indet.

**Referred specimen.** IGM 5318, IGM 5319 (Hernández-Junquera 1977).

**Locality and age.** Laguna de la Media Luna, Río Verde, San Luis Potosí; Pleistocene.

Cohort Euteleosteomorpha Greenwood, Rosen, Weitzman & Myers, 1966

Subcohort Neoteleostei Nelson, 1969

Infracohort Eurypterygia Rosen, 1973

Section Ctenosquamata Rosen, 1973

Subsection Acanthomorpha Rosen, 1973

Division Acanthopterygii Rosen & Patterson, 1969

Subdivision Percomorphaceae Betancur-R., Broughton, Wiley, Carpenter, López, Holcroft,

Arcila, Sanciangco, Cureton, Zhang, Borden, Rowley, Reneau, Hough, Lu, Grande, Arratia & Ortí, 2013 (=Percomorphacea sensu Wiley & Johnson, 2010)

**Percomorphaceae indet.**

**Referred specimen.** IGM 7968 (Cantalice and Alvarado-Ortega in press).

**Locality and age.** Ixtapa locality, Ixtapa Formation, Ixtapa, Chiapas; Miocene.

Genus †*Kelemejtubus* Cantalice & Alvarado-Ortega, 2017

†*Kelemejtubus castroi* Cantalice & Alvarado-Ortega, 2017

**Referred specimens.** IGM 4864 (holotype), IGM 4865-IGM 4867, IGM 4908, IGM 4909 (paratypes).

**Locality and age.** Belisario Domínguez and División del Norte quarries, Tenejapa-Lacandón geological unity, Salto de Agua and Palenque, Chiapas; Paleocene (Danian).

Series Syngnatharia Betancur-R., Wiley, Bailly, Miya, Lecointre et al., 2014

Order Syngnathiformes Berg, 1940

Suborder Syngnathoidei Regan, 1909

Superfamily Aulostomoidea Greenwood, Rosen, Weitzman & Myers, 1966

Family †Eekaulostomidae Cantalice & Alvarado-Ortega, 2016

Genus †*Eekaulostomus* Cantalice & Alvarado-Ortega, 2016

†*Eekaulostomus cuevasae* Cantalice & Alvarado-Ortega, 2016

**Referred specimen.** IGM 4716 (holotype).

**Locality and age.** Belisario Domínguez quarry, Tenejapa-Lacandón geological unity, Salto de Agua, Chiapas; Paleocene (Danian).

Series Carangaria Betancur-R., Broughton, Wiley, Carpenter, López, Holcroft, Arcila, Sanciangco, Cureton, Zhang, Borden, Rowley, Reneau, Hough, Lu, Grande, Arratia & Ortí, 2013 (=Carangimorpha sensu Li et al. 2009)

Order Istiophoriformes Betancur-R., Broughton, Wiley, Carpenter, López, Holcroft,

Arcila, Sanciangco, Cureton, Zhang, Borden, Rowley, Reneau, Hough, Lu, Grande, Arratia & Ortí, 2013

Family Istiophoridae Rafinesque, 1815

**Istiophoridae indet.**

**Referred specimens.** IGM 7885-IGM 7887, IGM 7890-IGM 7892, IGM 7894 (Fierstine et al. 2001).

**Locality and age.** La Angostura and Rancho Algodones, Trinidad Formation, Baja California Sur; Upper Miocene.

Genus *Makaira* Lacépède, 1802

*Makaira nigricans* Lacépède, 1802

**Referred specimens.** IGM 7882-IGM 7884, IGM 7888, IGM 7889, IGM 7893 (Fierstine et al. 2001).

**Locality and age.** La Angostura, Los Dientes Grandes, Cañada de En medio, and Rancho Algodones, Trinidad Formation, Baja California Sur; Upper Miocene.

Series Ovalentaria Wainwright, Smith, Price, Tang, Sparks, Ferry, Kuhn, Eytan & Near, 2012  
Superorder Atherinomorphae Betancur-R., Wiley, Arratia, Acero, Bailly, Miya, Lecointre & Ortí, 2017 (=Atherinomorpha sensu Greenwood et al. 1996)

Order Cyprinodontiformes Berg, 1940

**Cyprinodontiformes indet. (sensu Espinosa-Perez et al. 1991)**

**Referred specimen.** IGM 7967 (Cantalice and Alvarado-Ortega in press)

**Locality and age.** Los Ahuehuetes, Pie de vaca Formation, Tepexi de Rodríguez, Puebla; Oligocene.

Suborder Cyprinodontoidei Dyer & Chernoff, 1996

Family Goodeidae Jordan & Gilbert, 1883

Genus †*Tapatia* Álvarez & Arriola-Longoria, 1972

†*Tapatia occidentalis* Álvarez & Arriola-Longoria, 1972

**Referred specimen.** IGM 7966 (Cantalice and Alvarado-Ortega in press).

**Locality and age.** Barranca de Santa Rosa, Amatitán, Jalisco; Pliocene.



Series Eupercaria Sanciango, Carpenter & Betancur-R., 2016  
 Order Perciformes Rafinesque, 1810  
 Suborder Serranoidei Imamura & Yabe, 2002  
 Family Serranidae Swainson, 1839  
 Genus †*Paleoserranus* Cantalice, Alvarado-Ortega & Alaniz-Galvan, 2018

†*Paleoserranus lakamhae* Cantalice, Alvarado-Ortega & Alaniz-Galvan, 2018

**Referred specimens.** IGM 4550 (holotype), IGM 9469-IGM 9477 (paratypes).

**Locality and age.** Belisario Domínguez and División del Norte quarries, Tenejapa-Lacandón geological unity, Salto de Agua and Palenque, Chiapas; Paleocene (Danian).

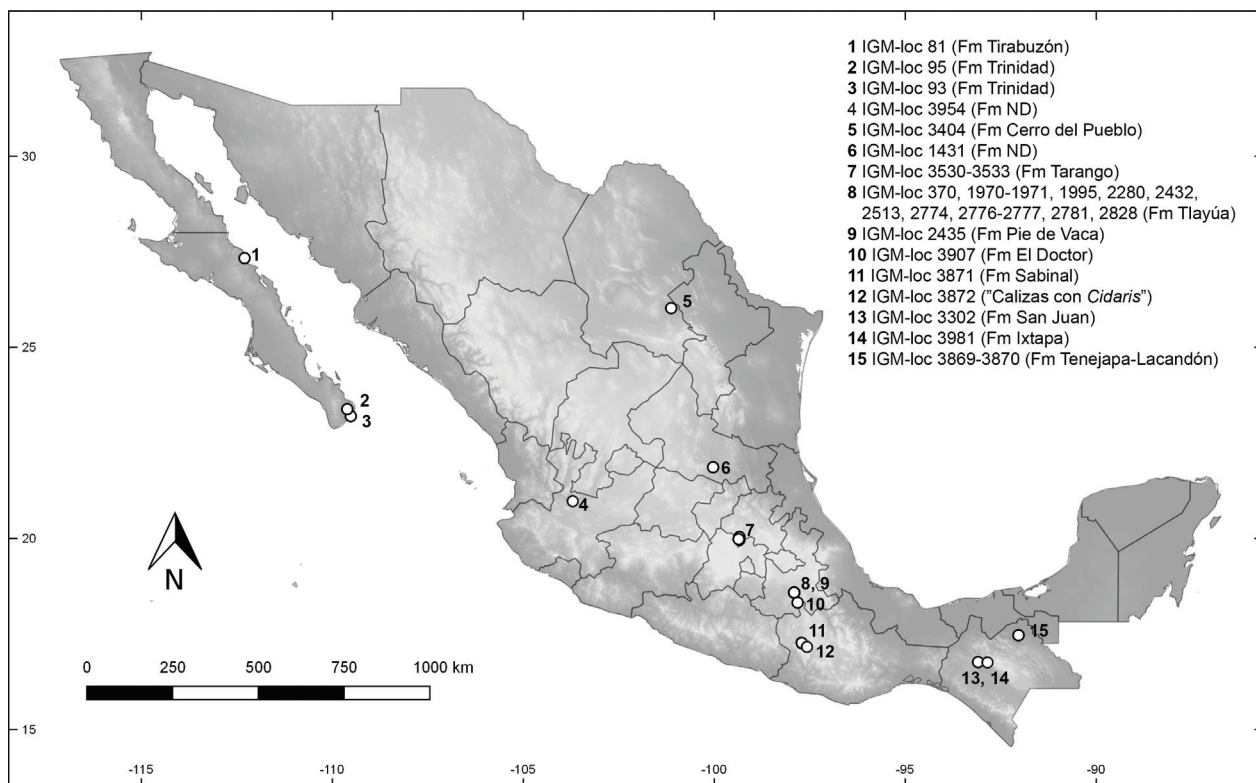
## 2. CNP-UNAM fossil fish localities

The fossil fishes catalogued into the Type Collection of CNP-UNAM are from 32 paleontological localities belonging to four undefined geological units (Fig. 1; Suppl. material 1), seven marine formations, and five freshwater formations. The oldest strata found is from Oxfordian “Caliza con *Cidaris*” geological unit, Oaxaca, while the youngest fish fossil beds are from the Pleistocene of La-

guna de Media Luna (San Luis Potosí), the Tarango Formation, near Tula (Hidalgo), and Pie de Vaca, near Tepexi de Rodríguez (Puebla) (Fig. 2). This range represents approximately the last 150 million years of Earth’s history. Below are the main features of these Mexican lithostratigraphic units.

### The Tirabuzón Formation

This geological unit was first known as the Gloria Formation and based on an outcrop exposed few kilometers away from Santa Rosalía town, Baja California Sur (Wilson 1948). Given that this last name was pre-occupied for a unit of Jurassic rocks from Coahuila (Imlay 1936), Applegate and Espinosa-Arrubarrena (1981) suggested the name of Cañada Gloria Formation for the rocks of Baja California Sur; however, the name of this geological unit changed to Tirabuzón Formation (Carreño 1981), based on Wilson (1948) and on nomenclatural incongruences present in the previous suggestions. The stratotype of the Tirabuzón Formation is inside the Bole Basin, at Santa Rosalía, Baja California Sur (Wilson 1948; Carreño 1981) and is a discontinuous basal conglomerate covered with potentially fossiliferous marine sandstone sediments that are overlaid with conglomerate strata containing a gradual lateral transition to littoral, deltaic, and nonmarine facies (Carreño 1981; Ortlieb and Colleta 1984; Carreño and Smith 2007). The abundant fossil content in this formation includes ichnofossils, foraminifers,



**Figure 1.** Map of Mexico, showing the localities currently catalogued at CNP-UNAM.

Cenozoic	Quaternary	Holocene		
		Pleistocene	Upper	Fm ND
			Middle	
		Pliocene	Calabrian	
			Gelasian	Fm Trinidad
	Piacenzian		Fm Tirabuzón, Fm Tarango	
	Neogene	Miocene	Zanclean	Fm ND
			Messinian	
		Oligocene	Tortonian	
			Serravallian	Fm Ixtapa
			Langhian	
			Burdigalian	
			Aquitanian	
	Paleogene	Eocene	Chattian	Fm Pie de Vaca
			Rupelian	
		Eocene	Priabonian	
			Bartonian	
			Lutetian	Fm San Juan
		Paleocene	Ypresian	
Danian			Fm Tenejapa-Lacandón	
Mesozoic	Cretaceous	Maastrichtian		
		Upper	Campanian	Fm Cerro del Pueblo
			Santonian	
			Coniacian	
			Turonian	
			Cenomanian	Fm El Doctor
	Lower	Albian	Fm Tlayúa	
		Aptian		
		Barremian		
		Hauterivian		
		Valanginian		
		Berriasian		
		Jurassic	Upper	Tithonian
Kimmeridgian	Fm Sabinal			
Middle	Oxfordian		"Calizas con <i>Cidaris</i> "	
	Callovian			
	Bathonian			
Lower	Bajocian			
	Aalenian			
	Toarcian			
		Pliensbachian		
		Sinemurian		
		Hettangian		

**Figure 2.** Partial chronostratigraphic chart correlating each formation catalogued in CNP-UNAM that contains fossil fishes and its respective geological age.

mollusks, echinoderms and cetaceans (Wilson 1948; Applegate 1978; Carreño 1981; Ortlieb and Colleta 1984; Quiroz-Barroso and Perrilliat 1989; Barnes 1998; Carreño and Smith 2007; Shroat-Lewis 2007). The age of the unit is Late Miocene-Early Pliocene based on planktonic foraminifers (Carreño 1981), nannofossils (Ortlieb and Colleta 1984), and the shark fauna (Applegate 1978).

### The Trinidad Formation

Pantoja-Alor and Carrillo-Bravo (1966) first described this unit which is also located in Baja California Sur. Its stratotype is near the intersection of the Coyote and La Trinidad Streams, in the western margin of the Coyote Stream;

however, these outcrops are from both San José del Cabo and Los Barriles Basins (Pantoja-Alor and Carrillo-Bravo 1966; Martínez-Gutiérrez and Sethi 1997; Schwennicke et al. 2017). The unit mainly has a fine-grained sandstone, siltstone, and mudstone but is also composed of gray-greenish, laminated, fine to medium marine sandstone, shale and siltstone, and some diatomite laminate toward the center of the San José del Cabo Basin (Martínez-Gutiérrez and Sethi 1997; Schwennicke et al. 2017). The age of the Trinidad formation range from the middle Miocene to upper Pliocene and its depositional environment has three distinct types of strata: 1) a basal nearshore-lagoon deposit; 2) a deep marine environment; 3) a high-energy, shallow marine waters, which they relate to inner shelf shoals and bars (Martínez-Gutiérrez and Sethi 1997; McCloy 1984; Carreño 1992; Fierstine et al. 2001; Schwennicke et al. 2017). The fossil record of the unit comprises nanoplanktons (Schwennicke et al. 2017), foraminifers and diatomite (McCloy 1984; Carreño 1992), mollusks (Martínez-Gutiérrez and Sethi 1997) fishes (Fierstine et al. 2001), and trace fossils (Schwennicke et al. 2017).

### The Cerro del Pueblo Formation

Located in Coahuila state, this formation was described at the beginning 20<sup>th</sup> century (Imlay 1936); however, its formal description as Cerro del Pueblo Formation was later (Murray et al. 1962). Belonging to the Difunta Group (Eberth et al. 2004), its stratotype is northeast to Saltillo City, and its outcrops are in several localities in the Parras Basin (Murray et al. 1962). The lithology of the unit is mainly composed of mudstone and sandstone but also of lesser amounts of limonite, conglomerates, and limestone (McBride et al. 1974; Kirkland et al. 2000). The unit contains a vast fossil record, comprising plants (fruiting structures, palm fronds, conifer cones), rudists, bivalves, gastropods, cephalopods, elasmobranchs, bony fishes, dinosaurs, crocodiles, turtles (Kirkland et al. 2000), and insects (Cifuentes-Ruiz et al. 2006). There are seven distinct facies, and sediments were laid down in a low coastal plain and shallow marine conditions which were strongly influenced by frequent changes in the relative sea-level or coastal physical processes (Eberth et al. 2004). Hence, the paleoenvironment is a cyclic alternation of marine, estuarine, and freshwater environments (Cifuentes-Ruiz et al. 2006). The age of the formation ranges from uppermost late Campanian to Maastrichtian (Kirkland et al. 2000).

### The Tarango Formation

This formation is in the Valley of Mexico (which includes the states of Ciudad de México, Estado de México, and Hidalgo) and was first proposed based on sediments exposed about 4 km southwest of Mixcoac, Mexico City (Bryan 1948; Ferrusquía-Villafranca et al. 2017). This geological unit is composed of sandstone and poorly cemented con-

glomerate, poorly cemented sandstone and interleaved clay, layers of clay, some layers of basalt interspersed with detrital units, lightly compacted conglomerate lenses, insulated limestone lenses, thin lenses of volcanic ash and tuff, and caliche nodules tuff, tuff-breccia, fluvial volcanic gravel, and thin pumice layers (Bryan 1948; Cervantes-Medel and Armienta 2004; Ferrusquía-Villafranca et al. 2017). The fossil record includes ostracods and diatoms (Ferrusquía-Villafranca et al. 2017), bony fishes (Alvarado-Ortega et al. 2006), and mammals of the genera *Equus* Linnaeus, 1758, *Cuvieronius* Osborn, 1923, *Mammuthus* Brookes, 1828, *Sylvilagus* Gray, 1867, *Canis* Linnaeus, 1758, and *Bison* Smith, 1827 (Castillo-Cerón et al. 1996). The depositional environment is a series of fluvial/lacustrine conditions with sandstone crossbedding which indicates deltaic conditions (Segerstrom 1962; Alvarado-Ortega et al. 2006; Ferrusquía-Villafranca et al. 2017). Based on the paleofauna, geochronology, and fault systems, the Tarango Formation is currently considered to present a Pliocene-Quaternary age (Castillo-Cerón et al. 1996; Suter et al. 2001).

### The El Doctor Formation

The El Doctor Formation outcrops from the eastern portion of Queretaro state to the western edge of Hidalgo (Wilson et al. 1955). Its type locality is in the north flank, near El Doctor village in the Sierra Gorda, Queretaro, northeastern Peña de Bernal (Wilson et al. 1955; Segerstrom 1961; Aguirre-Díaz et al. 2013). This unit has a large limestone bank of varied textures with some chert lenses, dolomite interbeds, and shale partings (Segerstrom 1961). Based on lithology, there are four subunits: 1) La Negra, deposited in the deep of the neritic zone; 2) San Joaquín, with the same sediments of La Negra but deposited at a depth and under storm wave action; 3) Cerro Ladrón, a calcareous bank formed in shallow waters; and 4) Socavón, with clastic sediments deposited not far from the input origin (Wilson et al. 1955). The fossil record found in the El Doctor Formation includes rudists (Wilson et al. 1955), miliolids, corals, oysters, gastropods, ammonites, echinoids (Segerstrom 1962), planktic and benthic foraminifers, radiolarians (Bravo-Cuevas et al. 2009), crustaceans (Feldmann et al. 2007), and fishes (Carranza-Castañeda and Applegate 1994; Bravo-Cuevas et al. 2009). Its deposits originate on a platform shelf followed by a transitional marine system, including open sea to deep shelf margin, with alternation of neritic and open oceanic waters and, occasionally, influx of near-shore waters, probably during storms (Wilson et al. 1955; Carrillo-Martínez 1981; Bravo-Cuevas et al. 2009). The age of this formation is Albian-Cenomanian (Wilson et al. 1955; Bravo-Cuevas et al. 2009).

### The Tlayúa Formation

The stratotype is a few kilometers north of Tepexi de Rodríguez town, Puebla state, eastern Mexico (Pantoja-Alor

1992). There is a subdivision of the Tlayúa Formation: 1) the Lower Member, formed by micritic limestones (mudstone to wackestone) with silica concretions and chert lenses; 2) the Middle Member, formed by red lithographic laminar limestone (mudstone) and chert lenses; and 3) the Upper Member, with layers of dolomite and dolomitic limestone (Pantoja-Alor 1992). The fossil record is preserved in the Middle Member and, by its abundance and exceptional quality of preservation, the Tlayúa Formation is currently considered the first fossil-*Lagerstätte* site found in Mexico (Alvarado-Ortega et al. 2007). The paleontological record are both marine and terrestrial fauna and flora, including rudists (Alencáster 1973), foraminifera, sponges, gorgonians, gastropods, ammonoids (Cantú-Chapa 1987), belemnoids (Seibertz and Buitrón 1987), bivalves, arthropods (Feldmann et al. 1998), asteroids (Buitrón-Sánchez et al. 2015), holothurians (Applegate et al. 1996), ophiuroids, fishes (Applegate 1987; Alvarado-Ortega 2004), lizards, crocodiles, turtles (Reynoso 1997, 2000), pterosaurs (Cabral-Perdomo and Applegate 1994), algae, and gymnosperms (Espinosa-Arrubarrena et al. 1996). The paleoenvironment is a double-enclosed shallow lagoon behind a barrier reef with stagnant, anaerobic, and hypersaline conditions and bounded by semi-arid land, on the other side, by a barrier bordering a deeper, well-oxygenated lagoon (Applegate 1987; Pantoja-Alor 1992; Espinosa-Arrubarrena and Applegate 1996). Nevertheless, some influences of an open sea have been proposed (Kashiyama et al. 2004). The age of Tlayúa quarry strata ranges between the Aptian and Albian stages in the Early Cretaceous between 125 and 100 Ma (Cantú-Chapa 1987; Seibertz and Buitrón 1987; Kashiyama et al. 2004).

### The Pie de Vaca Formation

The outcrops of the Pie de Vaca Formation are in the southern portion of Puebla, a few kilometers northeast of Tepexi de Rodríguez town very close to the Tlayúa Formation (Pantoja-Alor 1992). The lithology of the formation consists of continental deposits of fluvial-lacustrine and alluvial environments formed by conglomerates, gravel, silt, clay, marl, limestone, travertine, and volcanic rocks (Pantoja-Alor 1992). These are followed by micritic sandstone with siliciclastic bands and intraclasts of flint, limestone, and volcanic rocks (Cabral-Perdomo et al. 2018). The fossil records of the unit are ichnites belonging to birds, camelids, felids, proboscideans, small artiodactyls (Cabral-Perdomo 1995, 2013), and bony fishes (González-Rodríguez et al. 2013; Guzmán 2015). Fungus, leaves, leaflets, wood, and fruits of angiosperms are also well conserved in this unit, as well as ostracods and stromatolites (Beraldi-Campesi et al. 2006). The paleoenvironmental condition is a tropical paleolake which evolved from a basin with alluvial conditions to shallow, alkaline, and evaporitic lacustrine circumstances, indicating the gradual desertification of the environment

(Beraldi-Campesi et al. 2006). Although the palynological record indicates an Eocene-Oligocene age for this formation (Martínez-Hernández and Ramírez-Arriaga 1999), the paleobotanical and ichnological record with associated mammals indicates with more robustness an Oligocene-Pleistocene age (Cabral-Perdomo 1995, 2013; Cabral-Perdomo et al. 2018; Ramírez and Cevallos-Ferri 2002).

### The Sabinal Formation

The Sabinal Formation is in northeastern Oaxaca, with its outcrops (Yosobé and La Lobera) in the southern portion of Tlaxiaco Basin (López-Ticha 1985; Meneses-Rocha et al. 1994; Alvarado-Ortega et al. 2014). The lithology of the formation consists of a sequence of mudstone and wackestone clay, marl, and dark gray to black bituminous shale strata with abundant calcareous concretions arranged in thin laminar layers and showing abundant light oil impregnations (López-Ticha 1985; Felix 1891; Meneses-Rocha et al. 1994; Alvarado-Ortega et al. 2014). The fossil contents of the unit are microfossils (ostracods), plants, invertebrates (mostly ammonites), marine reptiles, and bony fishes (Alvarado-Ortega et al. 2014; Barrientos-Lara et al. 2015). The paleoenvironment is as a transitional environment under the marine influence (Alvarado-Ortega et al. 2014). A Kimmeridgian-Tithonian age is attributed to the Sabinal Formation based on the ammonite assemblage (Alvarado-Ortega et al. 2014).

### The “Caliza con *Cidaris*” geological unit

This Jurassic geological unit was informally named because it carries numerous remains of urchins belonging to the genus *Cidaris* Leske, 1778. Main outcrops of this unit are present between Tlaxiaco and Mixtepec in Oaxaca State (Buitrón 1970). This includes the outcrops in “La Titana” hills, near Tlaxiaco, firstly reported by Felix (1891) (also see Alvarado-Ortega et al. 2014). The numerous marine invertebrates recovered in the gray marls and limestones interbedded with shales present in this site suggest that its age could extend from the Late Callovian to the Early Kimmeridgian (Buitrón 1970). Besides the first fossil fishes from the Lobera site reported by Alvarado-Ortega et al. (2014), where “Caliza con *Cidaris*” sediments outcrops; the fossils already documented in this geological unit include three bivalves, echinoids, calcareous sponges, gastropods, annelids, crinoids, a brachiopod (Buitrón 1970; Felix 1891).

### The San Juan Formation

Located to the northwest of Tuxtla Gutiérrez in Chiapas state (Licari 1960; Allison 1967; Ferrusquía-Villafranca 1996), the San Juan Formation have light-brown shales and yellowish-brown fine-grained calcarenite, composed

of conglomerates, sandstone, siltstone, limestone, marl, and coquina (Ferrusquía-Villafranca 1996; Perrilliat et al. 2003). The fossil record in the unit contains foraminifers (Ferrusquía-Villafranca 1996; Perrilliat et al. 2003), calcareous algae, wood, bivalves, corals, annelids, gastropods, nautiloids, bivalves, echinoderms (Perrilliat et al. 2003), crustaceans, bony fishes (Vega et al. 2001), and sharks (Ferrusquía-Villafranca et al. 1999). The paleoenvironments are episodes of shallow, marine waters with high organic productivity and low terrigenous influence, combined with well-oxygenated shallow waters influenced by continental sedimentation and, probably, with marsh conditions from a deltaic lagoon system (Ferrusquía-Villafranca 1996; Perrilliat et al. 2003). Based on the foraminifer fossil record, the age assigned to the San Juan Formation is middle Eocene (Ferrusquía-Villafranca 1996; Perrilliat et al. 2003).

### The Ixtapa Formation

Also located in Chiapas, the Ixtapa Formation is 28 km east from Tuxtla Gutiérrez City and its outcrops mainly at the east side of the Soyaló-Ixtapa highway (State Road 195) next to the bridge that crosses the Río Hondo 1 km north of Ixtapa Municipality (Langenheim and Frost 1963; Ferrusquía-Villafranca 1996). This unit has a sequence of pyroclastic materials interbedded with calcitic pebbly gravels and tuffs, which become more frequent towards the base of the unit forming part of interbedded layers of conglomerates, sandstones, and clays where crystalline and calcareous conglomerates are sporadically present (Langenheim and Frost 1963; Martínez-Hernández 1992). The fossil record in Ixtapa Formation is diverse and includes charophytes, foraminifers, mollusks (Daily and Durham 1966), palynomorph assemblages (e.g. dinoflagellates and mangrove pollen), proboscides, horses, rhinoceros (Langenheim and Frost 1963; Daily and Durham 1966), freshwater turtles (Ferrusquía-Villafranca 1996), and only one record of a bony fish (Cantalice and Alvarado-Ortega in press). The Ixtapa Formation was formed under a low-energy fluvial-lacustrine conditions over the Middle Miocene continental sandstones of the Coyolar Formation and is below the Pliocene-Pleistocene volcanic deposits of the Punta de Llano Formation (Ferrusquía-Villafranca 1996; Martínez-Amador et al. 2004; Hernández-Villalva et al. 2013). The paleoenvironment is a continental lacustrine or a brackish transitional environment near the coast (Daily and Durham 1966; Martínez-Hernández 1992). The age assigned to this Formation ranges from the Middle to Late Miocene (Ferrusquía-Villafranca 1996).

### The Tenejapa-Lacandón geological unity

The Tenejapa-Lacandón geological unity was first mentioned by Islas-Tenorio et al. (2005). This layer represents the union of two contemporary and laterally continuous formations: Tenejapa, first described from outcrops of San Cristóbal de las Casas City (Quezada-Muñetón

1987), and Lacandón, primary known from Petén, Guatemala (Vinson 1962; Fourcade et al. 1999). Because it is not possible to determine the boundaries between the two Formations and the proper identity of each unit is poorly understood, here we interpret both formations as a single element, the Tenejapa-Lacandón geological unity (see Alvarado-Ortega et al. 2015). This layer outcrops in diverse portions of Chiapas state (Islas-Tenorio et al. 2004, 2005); however, the fossils housed in the CNP are from the División del Norte and Belisario Dominguez quarries. The first one is approximately 2 km southeast of the archeological site of Palenque City, while the last is 9.5 km from Palenque City. Both strata are limestone marls deposited in laminated and parallel strata, which show yellowish-creamy colors with some dark-grey silicified bands and nodules (Alvarado-Ortega et al. 2015; Cantalice et al. 2018a). The fossil specimens are many poor-preserved impressions of plant remains and a singular paleoichthyofauna (Alvarado-Ortega et al. 2015; Cantalice and Alvarado-Ortega 2016, 2017; Cantalice et al. 2018a). The number of well-preserved specimens (mostly on massive mortality) makes this geological unity a fossil-Lagerstätte site. The paleoenvironment of Tenejapa-Lacandón geological unity is a marine platform with influences of external conditions to the west, originating the Tenejapa Formation, and to the east, shallow waters influenced by primarily internal conditions composes the Lacandón Formation (Quezada-Muñetón 1987; Alvarado-Ortega et al. 2015). Studies based on stable strontium isotopes indicate a Paleocene (Danian) age for this geological unity (Alvarado-Ortega et al. 2015).

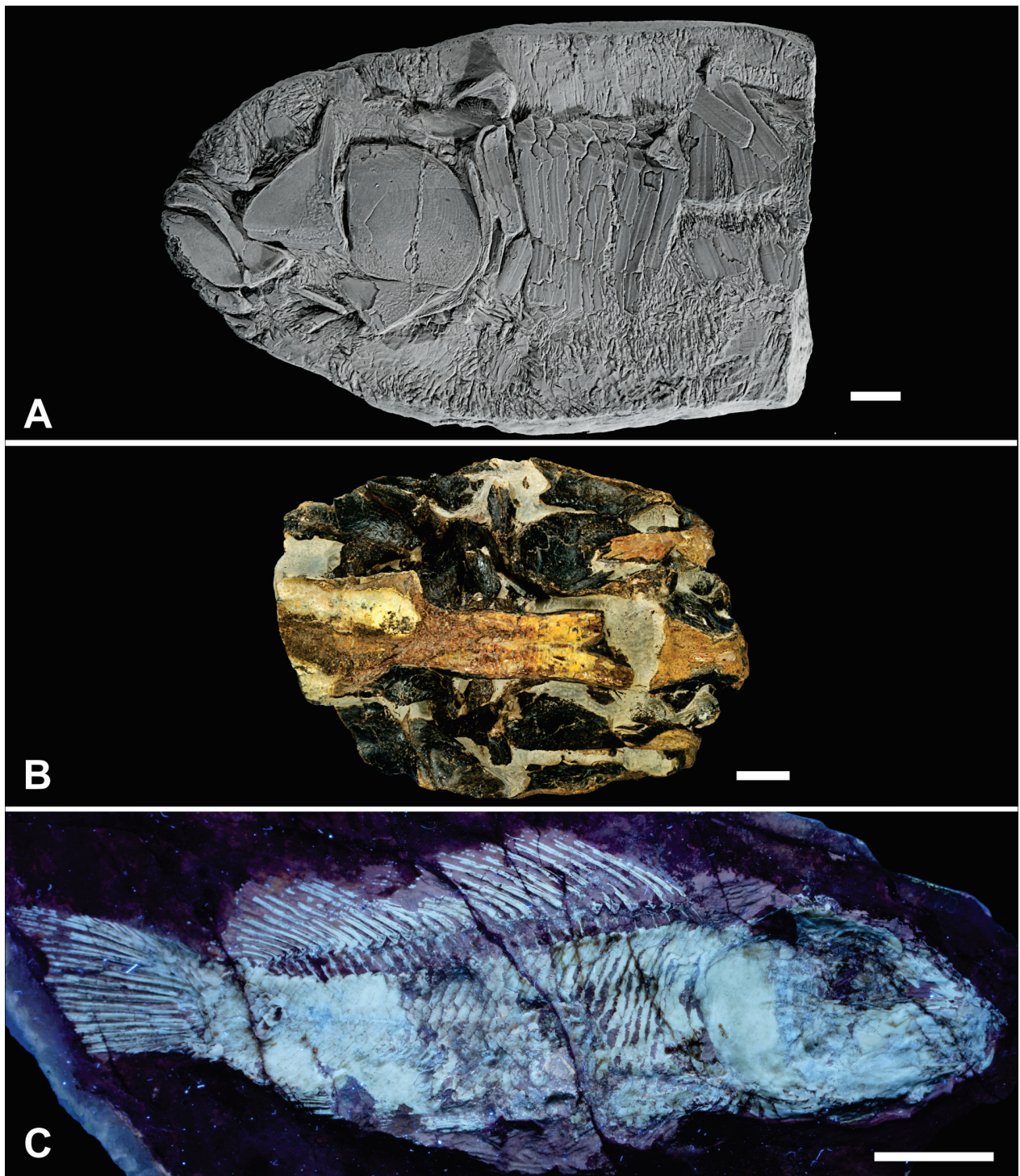
## Discussion

Since the last systematic review of the vertebrates housed on the CNP-UNAM (Perrilliat 1993), the number of specimens of fossil fishes has increased from five to 375, and the number of valid species raised from two to 27, including 20 new to science. This means that the number of fossil fishes species housed in the collection is currently 11 times greater than previously, not considering, however, the fossils that were are not determinable to species, which represent almost one-half of the palaeoichthyological material currently housed in the type collection. These numbers show a great increment in the knowledge of Mexican fossil fishes over the last two decades.

Many of the species housed in CNP-UNAM are the oldest record of its respective group and the first report of the taxon in North America (Table 1). These represent not only an increase of the knowledge about the fish diversity but also constitute valuable tools to a new understanding of the historical biogeography of fishes. This is the case of †*Vinctifer ferrusquiai* (Fig. 3A), from Kimmeridgian-Tithonian marine deposits from Oaxaca, which is the oldest fossil record and the first report of a member of the genus †*Vinctifer* outside the Cretaceous Period (Cantalice et al. 2018b). Its age and distribution suggest that the family Aspidorhynchidae under went a

**Table 1.** Remarks of outstanding Mexican species housed at the CNP-UNAM. Abbreviation: A. America; L. last occurrence; N. North America; O. oldest occurrence. The asterisk means the oldest generic occurrence.

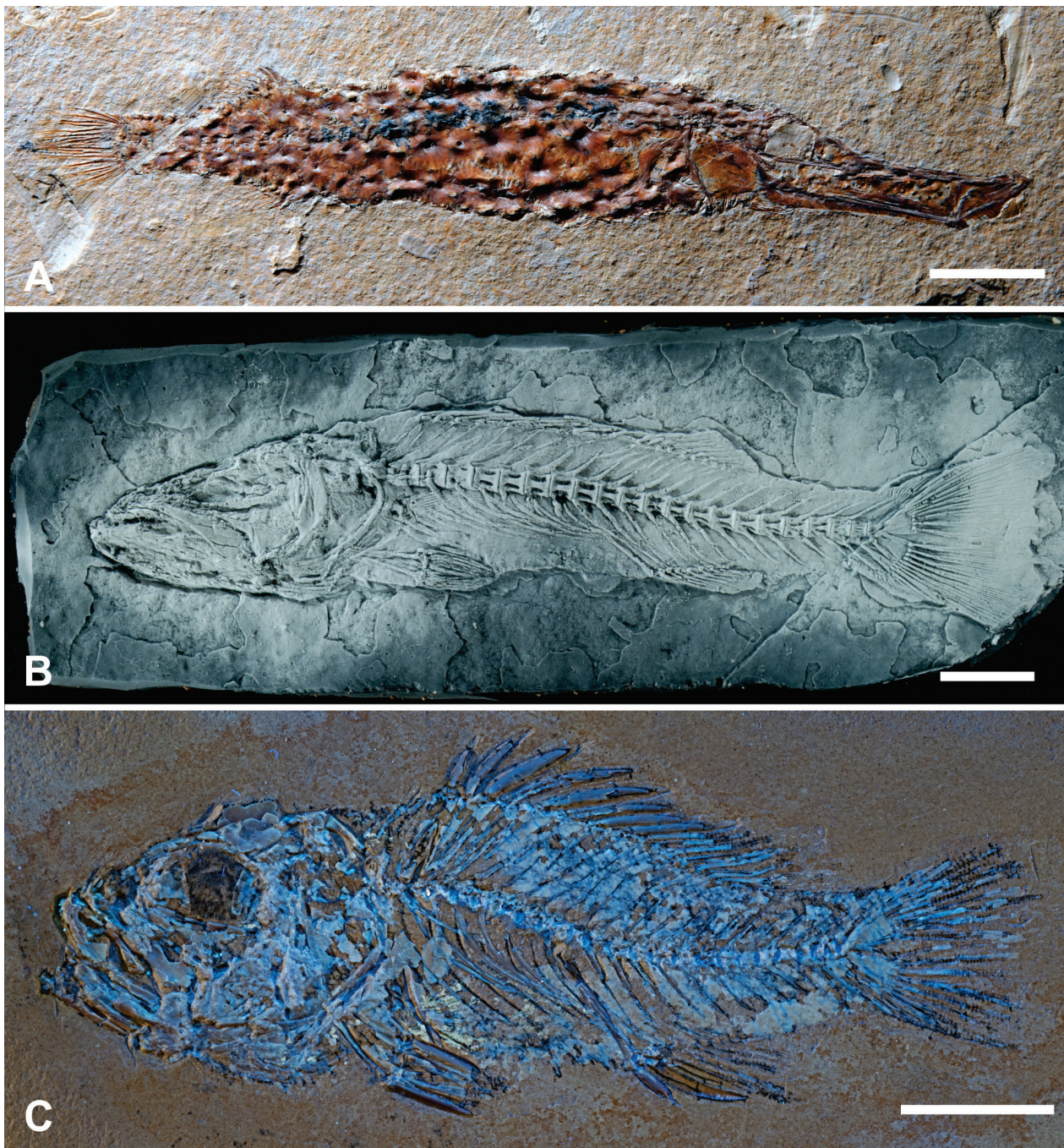
Taxon	Oldest or Last occurrence	First report	Apparent endemism
Class CHONDRICHTHYES			
Order †HYBODONTIFORMES			
Family †HYBODONTIDAE			
† <i>Planohybodus</i> indet.		N	
Order CARCHARHINIFORMES			
Family CARCHARHINIDAE			
† <i>Galeocerdo rosaliensis</i>			X
Order RHINOPRISTIFORMES			
Family incertae sedis			
† <i>Tlalobatos applegatei</i>			X
Class ACTINOPTERYGII			
Order incertae sedis			
Family incertae sedis			
† <i>Cipactlichthys scutatus</i>			X
Order †ASPIDORHYNCHIFORMES			
Family †ASPIDORHYNCHIDAE			
† <i>Vinctifer ferrusquiai</i>	O*		X
Order †PYCNODONTIFORMES			
Family †PYCNODONTIDAE			
† <i>Pycnodus</i> sp.	O	A	
† <i>Tepeichthys aranguthyorum</i>			X
Division GINGLYMODI			
Order †SEMIONOTIFORMES			
Family †SEMIONOTIDAE			
† <i>Tlayuamichin itzli</i>			X
Family †MACROSEMIIDAE	L	A	
† <i>Notagogus novomundi</i>			X
† <i>Macrosemiocotzus americanus</i>			X
Order LEPISOSTEIFORMES			
Family LEPIDOTIDAE			
<i>Scheenstia</i> sp.		A	
Family LEPISOSTEIDAE	O	A	
† <i>Nhanulepisosteus mexicanus</i>			X
Division HALECOMORPHI			
Order †IONOSCOPIFORMES			
Family †IONOSCOPIIDAE	L	A	
† <i>Quetzalichthys perillatae</i>			X
Family †OPHIOPSIDAE	L	A	
† <i>Teoichthys kallistos</i>			X
† <i>Teoichthys brevipina</i>			X
Order AMIIFORMES			
Family AMIIDAE	O	A	
† <i>Pachyamia mexicana</i>	O*		X
Order †PHOLIDOPHORIFORMES			
Family †PLEUROPHOLIDAE			
† <i>Pleuropholis cinerosorum</i>		A	X
Order †ICHTHYODECTIFORMES			
Family †Ichthyodectyidae			
† <i>Unamichthys espinosai</i>			X
Order OSTEOGLOSSIFORMES			
Family OSTEOGLOSSIDAE			
† <i>Phaerodus</i> indet.	O*		
Order †CROSSOGNATHIFORMES			
Family incertae sedis			
† <i>Michin csernai</i>			X
Order †ELLIMMICHTHYIFORMES			
Family †PARACLUPEIDAE			
† <i>Paraclupea seilacheri</i>		A	
Order CLUPEIFORMES			
Family incertae sedis			
† <i>Ranulfoichthys dorsonudum</i>			X
Order CYPRINIFORMES			
Family CATOSTOMIDAE	O		
† <i>Ictiobus aguilerai</i>			X
Division ACANTHOPTERYGII			
Order incertae sedis			
Family incertae sedis			
† <i>Kelemejtubus castroi</i>			X
Order SYNGNATHIFORMES	O		
Family †EKAULOSTOMIDAE			
† <i>Eekaulostomus cuevasae</i>			X
Order CYPRINODONTIFORMES			
Family GOODEIDAE	O		
† <i>Tapatia occidentalis</i>			X
Order PERCIFORMES			
Family SERRANIDAE	O		
† <i>Paleoserranus lakamhae</i>			X



**Figure 3.** Some species housed in the CNP-UNAM type collection. **A.** †*Vinctifer ferrusquiai* Cantalice, Alvarado-Ortega & Brito, 2018; **B.** †*Nhanulepisosteus mexicanus* Brito, Alvarado-Ortega & Meunier, 2017; both being the most ancient species of their families to date; **C.** †*Macrosemiocotzus americanus* González-Rodríguez, Applegate & Espinosa-Arrubarrena, 2004, the first report of Macrosemiidae in North America. Scale bars: 10 mm.

rapid diversification and had a wide distribution during the Late Jurassic (Cantalice et al. 2018b). Another example is the earliest known lepisosteoid, †*Nhanulepisosteus mexicanus* (Fig. 3B), which raises the origin of modern gars to the Late Jurassic (Brito et al. 2017). Furthermore, the Paleocene fossil fishes from Chiapas (Fig. 4) push back the absolute age of origin of many acanthomorph

groups (e.g. seabasses and flutemouth fishes) to the early Cenozoic, just after the K/Pg boundary (Late Paleocene, 63 Ma). These finds reveal that the Caribbean Region is an important place for the origin and diversification of some modern ray-finned fish lineages (Alvarado-Ortega et al. 2015; Cantalice and Alvarado-Ortega 2016, 2017; Cantalice et al. 2018a).

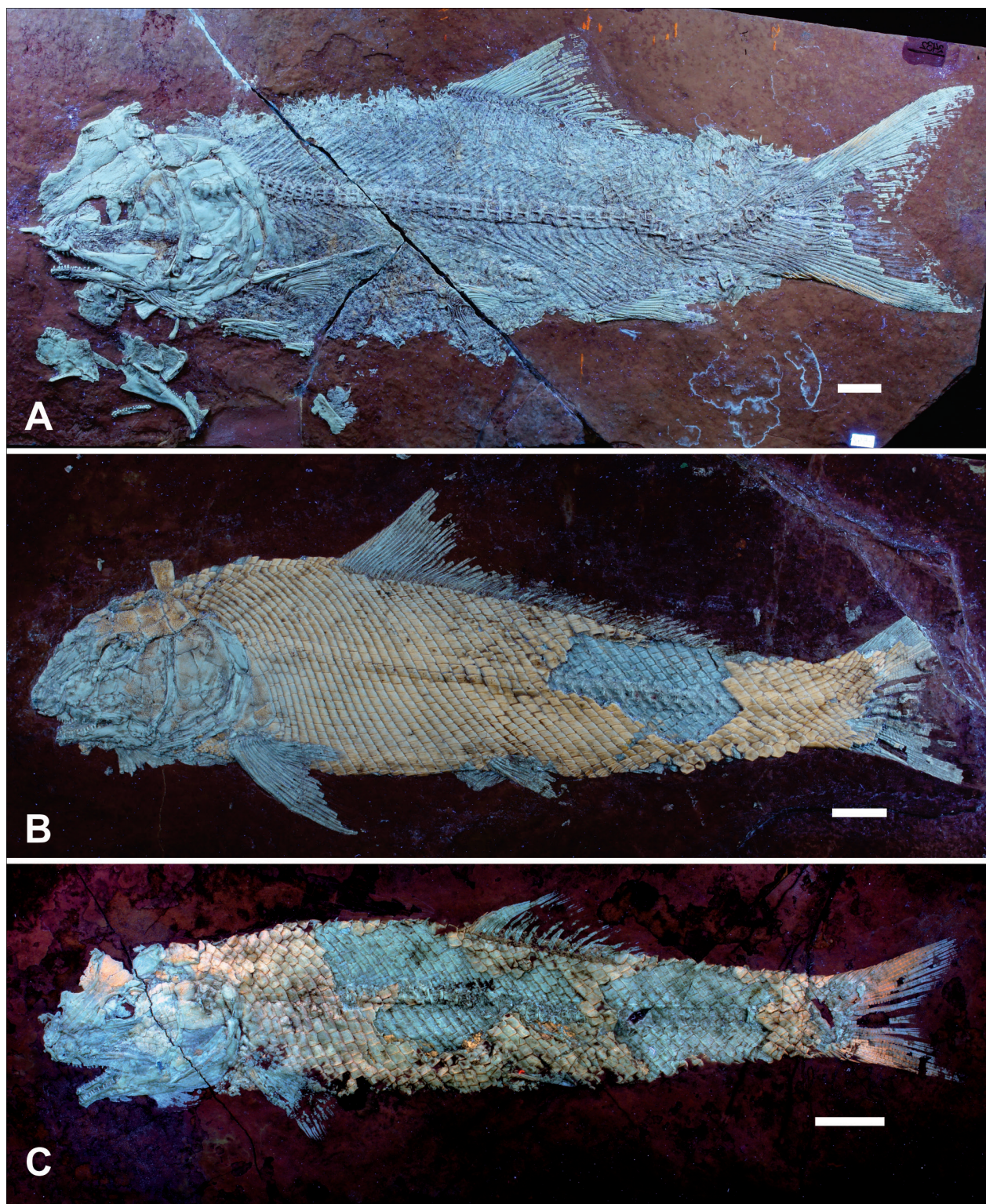


**Figure 4.** Paleocene fossil fishes found in marine outcrops of Chiapas housed in CNP-UNAM **A.** †*Eekaulostomus cuevasae* Cantalice & Alvarado-Ortega, 2016; **B.** †*Kelemejtubus castroi* Cantalice & Alvarado-Ortega, 2017; **C.** †*Paleoserranus lakamhae* Cantalice, Alvarado-Ortega & Alaniz-Galvan, 2018. Scale bars: 10 mm.

When included in a phylogenetic context, some species housed in CNP-UNAM offer valuable details that help understanding the morphological and ecological changes that occurred in some groups of fishes through time. One example is the aulostomoid †*Eekaulostomus cuevasae* (Fig. 4A), which is considered the stem group of Recent flutemouth fishes and reveals that reduction of body scutes size and enlargement of the snout, trunk, and fin rays are evolutionary trends of aulostomoids (Cantalice and Alvarado-Ortega 2017). These morphological modifications are possibly related to improvements in

predation in extant species (Cantalice and Alvarado-Ortega 2017). Moreover, including CNP-UNAM species in phylogenetic analyses also provide support to solve some incongruences on fish classification, such as †*Quetzalichthys* and †*Teoichthys* (Fig. 5), two genera collected in Tlayúa quarry (Puebla), which when included in the phylogeny of the order Ionoscopiformes proved the monophyly of the families Ophiopsidae and Ionoscopidae (Alvarado-Ortega and Espinosa-Arrubarrena 2008).

Mexico has been in the tropical region since the Jurassic, the period of the oldest fossil fish records report-



**Figure 5.** Cretaceous fossil fishes from Tlaúa quarry, Puebla, housed in CNP-UNAM **A.** †*Quetzalichthys perrillatae* Alvarado-Ortega & Espinosa-Arrubarrena, 2008; **B.** †*Teoichthys kallistos* Applegate, 1988; **C.** †*Teoichthys brevipina* Machado, Alvarado-Ortega, Machado & Brito, 2013. Scale bar: 10 mm.

ed at CNP to date (Scotese 2014). The 150 million years since the Jurassic to present day could explain the diversification of several groups of fishes and the richness of possible Mexican endemic fauna (Table 1). Therefore, the continual collection and increases in knowledge of

the paleoichthyofauna housed at CNP is fundamental to understand the patterns of fish diversity through the geological ages and highlights the Mexican fossil records as essential to understanding biogeographic patterns and current global diversity.



## Conclusions

After 25 years since the last vertebrate catalogue (Perilliatt 1993), we present the first fossil fish catalogue of the species housed in the type collection of the Colección Nacional de Paleontología of Universidad Nacional Autónoma de México (CNP-UNAM). The increase of knowledge of fossil fish diversity, as its biological and biogeographical implications, are evidence that maintaining a proper collection of the Mexican fossil record is necessary for understanding the complex evolutionary history of fishes. The knowledge of the Mexican paleoichthyofauna is emerging. The formal description of many specimens housed in the geographic reference section is still necessary and increasing with periodic fieldwork. Palaeoichthyology is a promising research area in Mexican paleontology.

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## Supplementary material 1

### Supplementary Information

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Data type: locality data

Explanation note: Table with essential information about the distinct geological localities containing fishes catalogued in the CNP-UNAM.

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