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An overview of the Mexican fossil fish record

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Abstract

The fossil fish record of Mexico is poorly known despite numerous recent discoveries of new localities that represent different ages and environments. The stimulus for a new era in Mexican paleoichthyology occurred in 1976, with the arrival of Shelton P. APPLEGATE in the country. Before "Shelly's" time, the study of fossil fishes was delegated to geologists and paleontologists mostly interested in geological exploration for oil and other resources, not vertebrate paleontology. The diverse geological episodes that occurred in Mexico during millions of years generated a large array of different environments that supported a great diversity of biotas, including fishes. Paleozoic ichthyological records in Mexico are scarce, represented only by three reports of the shark *Helicoprion*. Early Mesozoic fishes have not yet been discovered, but Late Jurassic deposits contain halecomorphs, pycnodontiforms and ichthyodectiforms. So far, the most abundant records correspond to Cretaceous marine fishes. Some localities such as Tlayúa (Puebla), Vallecillo (Nuevo León), El Chango (Chiapas), and El Rosario (Coahuila) are Konservat-Lagerstätten. Some others were discovered more recently and, although their entire diversity is still unknown, certain families such as Macrosemiidae and Ichthyotringidae have already been reported for the first time in the New World. Mexican Cenozoic records, discovered mainly in the Baja California Peninsula, include abundant marine shark and ray teeth but only a few teleost remains. Freshwater teleost records are almost entirely confined to central Mexico and, according to the known records, they seem to be biased towards the Neogene (following the final episodes of the Sierra Madre Occidental and the formation of the Mexican Volcanic Belt). Study of Mexican fossil fishes will help us to understand the patterns of distribution and the phylogenetic relationships of the groups present in this part of the world, and the collaboration of international paleoichthyologists will increase our knowledge of the fossil fishes of Mexico.

Introduction

The known Mexican fossil fish record has increased considerably during the last twenty years. This significant improvement is owing to the discovery of many new localities of different ages that cover an important array of paleoenvironments, never reported before in Mexico. ALVARADO-ORTEGA et al. (2006d) published a fine assessment of the Mexican Mesozoic osteichthyans. Although this work was fairly complete and even included a section related to the history of Mexican paleoichthyology, we believe that it is important to bring this information up to date and to add information on chondrichthyans. The records presented in this work represent the product of two centuries of research; nevertheless, it must be mentioned that the major stimulus for paleoichthyology in Mexico was the arrival of Shelton P. APPLEGATE (Figs. 1, 2B, 3) at the University of Mexico (UNAM) in 1976, when he established a Mexican school of paleoichthyologists (ALVARADO-ORTEGA et al. 2006d).

Part of the information presented here was known by the time of the 60th Annual meeting of the Society of Vertebrate Paleontology held in Mexico City in 2000. At that time, K. GONZÁLEZ-RODRÍGUEZ and S. P. APPLEGATE participated in several extended talks, describing the work that had been done in the country, mainly in the Baja California Peninsula, during the last century. Today, almost ten years later, the fossil record has increased considerably. Many studies are in progress and an increasing number of new localities are discovered each year. To provide an overview of what has been the outcome of all these studies, we will discuss the most important known fish localities in Mexico, starting with work done since the middle of the 19th Century.

Fig. 1.
Shelton P. APPLEGATE ("Shelly") on the top of the Popocatepetl Mountain, central Mexico. Photograph by Edward WILSON (1975).

Institutional abbreviations: CPC, Paleontological Collection of Coahuila, Museo del Desierto, Saltillo, Coahuila State, Mexico; **IGM**, Paleontological Museum of the Geological Institute of the National Autonomous University of Mexico, Mexico City; **UAHMP**, Paleontological Museum of the Autonomous University of Hidalgo, Pachuca, State of Hidalgo, Mexico; **UNAM**, National Autonomous University of Mexico, Mexico City.

Discoveries during the 19th Century and first half of the 20th Century

The discovery and study of Mexican fossil fishes was sporadic during the 19th Century and the first part of the 20th Century. Historical events such as the Mexican Revolution in 1910 affected the development of many scientific areas, and paleontology was no exception. The main paleontological discoveries occurred together with the geological exploration of the territory during this time. The study of fossil fishes started with Hermann von MEYER (1840), who described *Carcharodon mexicanus* in the state of Michoacán in western Mexico. During the 19th Century, the most important works were those of COPE (1871) (Fig. 4A), who described the first Mexican osteichthyan, *Prymnetes longiventer* from the state of Chiapas, and FELIX (1891) (Fig. 4B), who described *Thrissops* sp., *Otomitla speciosa*, and *Belonostomus ornatus* from Lower Cretaceous rocks of Cerro de la Virgen, Oaxaca, southeastern Mexico. Later, in the first decade of the 20th Century, the major contributor was AGUILERA (1906, 1907) (Fig. 4C), a renowned Mexican geologist, who reported the presence of *Ptychodus* and *Ceratodus* teeth in the Cretaceous sediments of Los Peyotes, Coahuila, northern Mexico, as part of his foundational work on the geology of Mexico.

In the same time period, BÖSE (Fig. 4D), a German paleontologist, collected Cenozoic elasmobranchs in Baja California (today the northern state). WITTICH (1913) reported the presence of numerous elasmobranch remains from the same region; he published a list of genera of different localities. Other scientists such as JORDAN & GILBERT (1919), JORDAN & HERTLEIN (1926), HERTLEIN & JORDAN (1927), HANNA & HERTLEIN (1927), and HERTLEIN (1966), were also interested in the material (mainly shark teeth) discovered in the Baja California Peninsula. They explored the whole region and published several studies. DICKERSON & KEW (1917) studied fossil shark material from Veracruz State of eastern Mexico; and two decades later, LERICHE (1938) reported the presence of *Carcharodon megalodon* from the Eocene-Oligocene of Tabasco, southeastern Mexico.

More than 30 years after AGUILERA's work, another Mexican investigator of the Instituto Geológico Mexicano (Mexican Geological Institute) named Federico K. G. MÜLLERRIED restarted paleoichthyological studies in Mexico. He reported shark teeth from Cretaceous sediments of Sierra de San Miguel in the state of Hidalgo in 1939. He described also *Helicoprion mexicanus*, the first Paleozoic shark of Mexico, found in Las Delicias County, Coahuila State, in 1945.

During the first half of the 20th Century, Manuel MALDONADO-KOERDELL (Fig. 2A) and David H. DUNKLE were the foremost contributors to Mexican paleoichthyology. MALDONADO-KOERDELL (1948a, b) published two catalogues of elasmobranchs, and in 1949 he reviewed all teleost records known

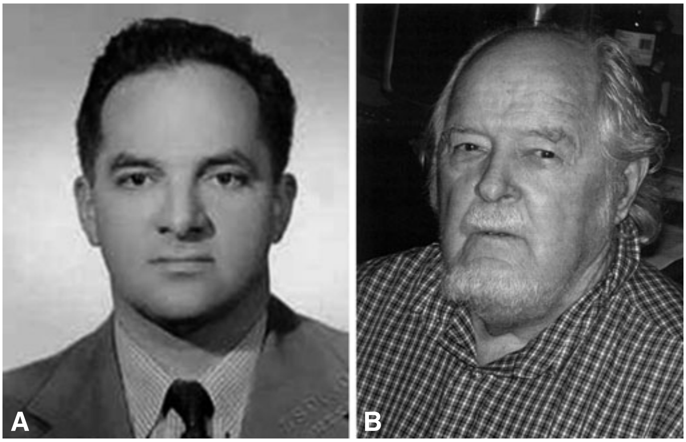

Fig. 2.
In the second half of the 20th century, Manuel MALDONADO-KOERDELL (**A**) and Shelton P. APPLEGATE (**B**) contributed to the development of Mexican Paleoichthyology.

to that time, including the works of FELIX (1891), COPE (1871), and AGUILERA (1906). The catalogues that resulted from this effort document 25 chondrichthyans (one Paleozoic, three Mesozoic and 21 Cenozoic) and eight Mesozoic osteichthyans. A few years later, DUNKLE & MALDONADO-KOERDELL (1953) described *Gyrodus* cf. *G. macrophthalmus* (Jurassic) and *Leptolepis tamanensis* (Early Cretaceous) from San Luis Potosí State. Later, MALDONADO-KOERDELL (1956) described a late Turonian ichthyofauna from Xilitla, San Luis Potosí State, represented by *Hemiptychodus mortoni*, *Xiphactinus molossus*, and *Ichthyodectes* sp. MÜLLERRIED (1945), BÖSE (1913), and BÖSE & CAVINS (1928) reported teleosts in Cretaceous rocks. Some of these researchers were geologists of Petróleos Mexicanos. Others worked for the Geological Institute of Mexico, but most were foreign paleontologists.

Although many of these discoveries were critical, Mexican science was still without any legal control or ethical standards regarding the collection of paleontological material. Only a limited number of fossil fishes collected by Mexican geologists were deposited in the collections of the Geological Institute of Mexico, and after 1952 their study was assigned to DUNKLE. Unfortunately most of the material was taken out of the country and was deposited in museums around the world, including the Smithsonian Institution in U.S.A. More data about the history of these first discoveries can be found in ALVARADO-ORTEGA et al. (2006d).

Fig. 3.
S. P. APPLEGATE and some of his students during the Mexican Paleontological Meeting held in Guadalajara, Jalisco, Mexico in 2002. From left to right: Francisco ARANDA-MANTECA, Luis ESPINOSA-ARRUBARRENA, Jesús ALVARADO-ORTEGA, Katia GONZÁLEZ-RODRÍGUEZ, and Gerardo GONZÁLEZ-BARBA.

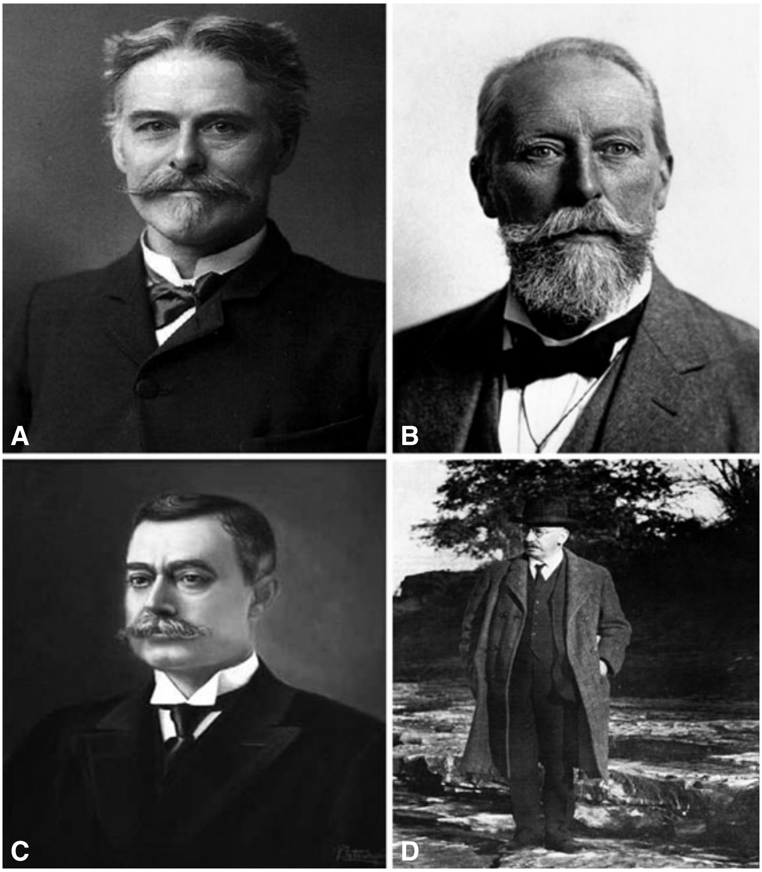

Fig. 4.
During the 19th Century, Edward D. COPE (**A**), Johannes FELIX (**B**), José G. AGUILERA (**C**), and Emil BÖSE (**D**), collected and studied the first Mexican fossil fish.

Discoveries during the second half of the 20th Century

The Baja California Peninsula was widely explored for petroleum, minerals, water, etc. during the second part of the 20th Century. The Los Angeles County Museum, now called the Natural History Museum of Los Angeles County, organized several paleontological prospecting trips in the peninsula, and as a result of these expeditions, much fossil material was collected. Although the recovered specimens were initially incorporated into the LACM collections, in about 1980, through the assertive negotiations of a (then) young generation of Mexican paleontologists, the Baja California materials were returned to Mexico and today they are housed at the Paleontological Museum of the Geological Institute of the National Autonomous University of Mexico (Colección Nacional de Paleontología-IGM).

The copper deposits at Santa Rosalía in the northeastern part of the state of Baja California Sur have been widely exploited since 1868, and investigated for the presence of fossil shark teeth since the 1960's. APPLEGATE, Harley GARBANI and Pat ROYCE were directed to a site named Corkscrew Hill (Loma del Tirabuzón in Spanish; see below section on Cenozoic Records, Fig. 8: 7) by some residents of the town of Santa Rosalía in 1965. The locality is a paradise for fossil hunters, as it contains thousands of shark teeth, as well as remains of fishes and marine mammals. APPLEGATE (1978) described *Galeocerdo rosaliensis*, a new species of the middle Pliocene ancestor of the present day "tiger shark" *Galeocerdo cuvier*, from these beds. This discovery triggered a new era of paleoichthyological research, undertaken by APPLEGATE, MORRIS, FERRUSQUÍA and ESPINOSA-ARRUBARRENA, supported by the National Geographic Society, the Los Angeles County Museum, and to a large extent by the University of Mexico (encompassing the decades of the 60's, 70's and 80's).

APPLEGATE, together with some students involved in the study of Recent and fossil sharks, started to revise the Cenozoic fossil shark record in Mexico. He pioneered a group interested in elasmobranch research (e. g., biology, conservation, evolution and all its paleontological implications). The group was dubbed "CIPACTLI" (taken from the Nahuatl name of the representation of a possible shark that appears in the FEJÉVÁRY-MAYER Codex). The members of the CIPACTLI group, including several paleontologists, biologists and many students, such as Luis ESPINOSA-ARRUBARRENA (Fig. 3), Fernando SOTELO, Jaime ALVARADO, René HERNÁNDEZ, and Víctor TORRES, among many others, together with S. APPLEGATE, continued to explore and collect in Baja California. This work resulted in a vast new collection of shark and ray teeth that, together with teleosts, mammals and other fossils, led to many papers (e. g., APPLEGATE 1978, 1979, 1986, 1993; APPLEGATE & WILSON 1976; APPLEGATE et al. 1979; APPLEGATE & ESPINOSA-ARRUBARRENA 1981; ESPINOSA-ARRUBARRENA & APPLEGATE 2000), and of some unpublished theses, describing the diversity of fishes in the Baja California Peninsula during the Cenozoic.

The discovery of the Tlayúa quarry in 1981, by far the most important fossil fish locality in Mexico, inspired APPLEGATE to train new paleoichthyologists (Fig. 3) specialized in the morphology, evolution, paleoecology and paleogeography of osteichthyans. Since then, the richness of the fish fauna in the Tlayúa quarry has caught the attention of many foreign and Mexican specialists of the fish groups present in the "tlayuan" ichthyofauna, but in recent years more fish localities representing a large array of geological ages have been discovered and new taxa are in need of description. The next years should be very exciting for Mexican paleoichthyology. As a contribution to the Fifth International Meeting of Mesozoic Fishes (2010) and in memory of "Shelly" APPLEGATE, we here discuss all these new records that certainly were stimulated by his original investigations.

Paleozoic record

The geological framework in which the Mexican continental crust developed is highly complex and strongly biased towards middle Mesozoic to Cenozoic rock exposures, as against the near absence of older Precambrian and Paleozoic units. Although the geological record of the Paleozoic includes almost all of the Paleozoic periods, and there are at least ten states in which rocks of these ages outcrop in Mexico (MORÁN-ZENTENO 1986, 1994; ORTEGA-GUTIÉRREZ et al. 1992, 1995), rocks of Paleozoic age are scarce enough to bear only a very few localities with fossil fishes.

In general terms, according to ORTEGA-GUTIÉRREZ et al. (2000), the Paleozoic paleogeography and tectonic episodes of the northwestern part of the country correspond to extensive epicontinental seas and their characteristic calcareous platforms, associated with a passive continental margin having clear Laurentian (North American) affinities, as opposed to the eastern and southern areas of Mexico, which seem to correspond to geological processes recorded in the eastern part of Laurentia, and more importantly to the northern margins of Gondwana (Oaxaquian affinities).

Paleozoic fish localities

Among Paleozoic fish localities, the Cerro Puntiagudo locality, east of San Salvador Patlanoaya in the state of Puebla (central Mexico) yielded one broken symphysial tooth whorl of *Helicoprion* sp., described by SOUR-TOVAR et al. (2000). There are two previous reports of *Helicoprion* from Mexico. One specimen was found in the state of Coahuila, near Delicias County, and described as *H. mexicanus* by MÜLLERIED (1945). Unfortunately, the description was incomplete, and the holotype is lost. The second report came from central-west Chihuahua (BRIDGES & DEFORD 1962), but the specimen was not formally named, and the material is lost as in the first case (SOUR-TOVAR et al. 2000). Therefore, the Pueblan *Helicoprion* sp. of Leonardian age represents not only the oldest fish record, but the oldest vertebrate to be found in Mexico as well as the southernmost evidence of this taxon in the Western Hemisphere (SOUR-TOVAR et al. 2000).

Early Mesozoic (Triassic and Jurassic)

A large part of the Mexican continental crust already existed during the development of Pangaea, although the exact position of many areas is still under investigation (ORTEGA-GUTIÉRREZ et al. 1992, ORTEGA-GUTIÉRREZ et al. 2000). Concerning the stratigraphic record of the Triassic, there are eight states with continental outcrops and only half that number with marine rocks that have yielded Middle to Late Triassic fossils, mainly invertebrates, but as yet no fishes (ALVARADO-ORTEGA et al. 2006d). These states (Sonora, San Luis Potosí, and Zacatecas) represent excellent areas to prospect for marine fossil fishes.

During Late Triassic and Early Jurassic times (as the process of disaggregation of Pangaea took place), Mexico was mostly an emerged territory with only a few narrow bays (BURCKHARD 1930, ERBEN 1957, IMLAY 1980). This scenario became particularly important when the opening of the Gulf of Mexico (PADILLA Y SÁNCHEZ 2007) was accompanied by a series of marine transgressions that started the development of wide marine platforms, typical of epicontinental seas.

From these Late Jurassic deposits in the Kimmeridgian section of the Tamán beds near the Moctezuma River in Tamán, San Luis Potosí state (Fig. 5: 2), an incomplete right mandible of *Gyrodus* cf. *G. macrophthalmus* was discovered and described by DUNKLE & MALDONADO-KOERDELL (1953). A second Jurassic specimen, corresponding to an impression of *Thrissops* sp., was collected in the Mazapil beds of the Zacatecas State (Fig. 5: 1). This deposit belongs to the La Caja Formation of early Kimmeridgian age (VILLASEÑOR-MARTÍNEZ et al. 2006). These authors also reported the presence of a halecomorph caudal fin of uncertain affinity in the Kimmeridgian beds of the La Casita Fm. in Galeana, Nuevo León State, northern Mexico.

As the marine transgressions continued, large parts of the Mexican territory were gradually covered, occupying low areas in ancient (Paleozoic and Triassic) topography, whereas the highlands stood as peninsulas or islands (REYNOSO 2006, ALVARADO-ORTEGA et al. 2006d, GARCÍA-BARRERA 2006).

Cretaceous

Throughout the Early Cretaceous, seas covered most of the territory with the exception of a wide fringe that extended from southern to northwestern Mexico, with only a few highlands in the states of Chiapas, Guerrero, and Oaxaca remaining exposed (MORÁN-ZENTENO 1986, GARCÍA-BARRERA 2006). During Albian and Cenomanian times, the seas reached their maximum extension, nearly covering all of the country. Most of the Mesozoic marine fish localities in Mexico come from these deposits and those deposited later, towards the end of the Cretaceous Period.

In the Albian-Cenomanian interval, the shallow water deposits dramatically increased and teemed with rudistid "reefs" and associated biotas according to ALENCÁSTER (1987), KAUFFMAN (1973), and COATES (1973). These calcareous platforms included broad areas reaching from the state of Jalisco (west-central Mexico) to Chiapas in the southern part of the country. During the Turonian stage, the sea retreated from part of the Mexican territory, leaving extensive land areas generated by elevation, folding and exhumation of large volumes of intrusive rocks (MORÁN-ZENTENO 1994, ORTEGA-GUTIÉRREZ et al. 1992). These tectonic events mark the start of the rise (orogeny) of the Sierra Madre Occidental that eventually generated profuse amounts of terrigenous deposits together with intense volcanic activity. The marine regressions, like several others,were comparatively slow but continuous during the Late Cretaceous and lasted until the end of the Cenozoic, by which time the entire continent was exposed as seen today (GARCÍA-BARRERA 2006).

Chondrichthyan records

The Cretaceous record of chondrichthyans in Mexico does not begin until the middle of the period, but beginning at that time, an increasing number of middle–Late Cretaceous sites contain shark and ray materials. These sites include: the Muhi Quarry with the Albian–Cenomanian El Doctor Formation, in Hidalgo (Fig. 5: 13), the Jaboncillos locality within the Cenomanian–Turonian Boquillas Formation in northwest Coahuila (Fig. 5: 6), the Vallecillo quarry within the Turonian Agua Nueva Formation in Nuevo León (Fig. 5: 10), the quarries within the Turonian–Maastrichtian Mexcala Formation in Guerrero (Fig. 5: 18), the localities within the Santonian Aguja Formation in Chihuahua (Fig. 5: 5), the localities within the Campanian-Maastrichtian Difunta Group including the Parras, the Cerro del Pueblo, and the Rancho Nuevo formations in southern Coahuila State (Fig. 5: 9), the localities within the Maastrichtian Rosario

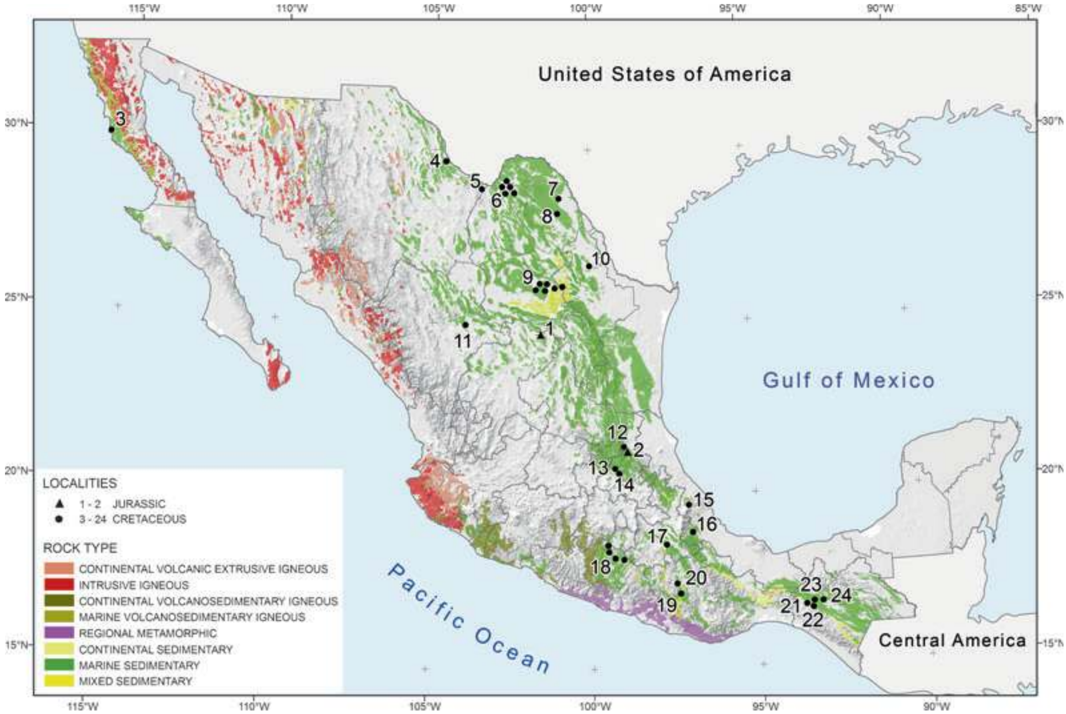

Fig. 5.
Jurassic and Cretaceous fish localities in Mexico of marine origin.
Jurassic outcrops: **1**, Mazapil, Zacatecas; **2**, Tamán, San Luis Potosí.
Cretaceous localities: **3**, El Rosario, Baja California Norte; **4**, Ojinaga, Chihuahua; **5**, Los Altares, Chihuahua; **6**, Múzquiz outcrops (La Mula, Los Temporales, San Miguel, Jaboncillos, Jicotecas, Los Pilotes Ranch), Coahuila; **7**, El Rosario, Coahuila; **8**, Los Peyotes, Coahuila; **9**, Difunta Group localities, Coahuila; **10**, Vallecillo quarry, Nuevo León; **11**, Carranza, Durango; **12**, Xilitla, San Luis Potosí; **13**, Muhi quarry, Hidalgo; **14**, Cerro Los Mendoza, Hidalgo; **15**, Jilotepec, Veracruz; **16**, Córdoba, Veracruz; **17**, Tlayúa quarry, Puebla; **18**, Mexcala Formation quarries (Arroyo Las Bocas, Taxco Viejo, Temalac, Tepetlapa), Guerrero; **19**, Cerro de la Virgen, Oaxaca; **20**, Huajuapan de León, Oaxaca; **21**, El Espinal quarry, Chiapas; **22**, El Chango quarry, Chiapas; **23**, Ocozocoautla, Chiapas; **24**, Tuxtla Gutiérrez, Chiapas.
The Cretaceous sites **3**, **5–10**, **13**, **17**, **18**, **23** and **24** include shark and bony fish, whereas the Cretaceous sites **4**, **11**, **12**, **14–16** and **19–22** only include teleost remains.

Formation in Baja California (Fig. 5: 3), the localities within the Maastrichtian Escondido and Pen formations in Coahuila and the Maastrichtian Potrerillos Formation in La Popa Basin, Nuevo León (Fig. 5: 9), and the quarries of the Maastrichtian Ocozocoautla Formation in Chiapas (Fig. 5: 23).

The Albian-Cenomanian elasmobranch fauna of the El Doctor Formation from the Muhi Quarry near Zimapán, Hidalgo (Fig. 5: 13) includes *Ptychodus* sp. and *Squalicorax* sp. as well as rajiform remains (GONZÁLEZ-RODRÍGUEZ & FIELITZ 2009). From the same geographical area (Hidalgo state) MÜLLERRIED (1939) in MALDONADO-KOERDELL (1948a) reported a fragmented tooth of the Lamnidae from the Sierra de San Miguel de la Cal in Actopan, Valle del Mezquital, from beds that also belong to the El Doctor Formation.

The Cenomanian-Turonian Boquillas Formation in northern Coahuila (Fig. 5: 6) has yielded: *Ptychodus mammillaris anonymus*, *P. decurrens decurrens*, *P. concentricus*, *P. marginalis*, *Carcharias* sp., *Scapanorhynchus raphiodon*, *Anomotodon* sp., *Cretoxyrhina mantelli*, *Cretolamna appendiculata*, *Paleoanacorax falcatus*, *Hemiscyllium* sp., *Rhinobatus incertus*, and *Ischirhiza avonicola* (GONZÁLEZ-BARBA & ESPINOSA-CHÁVEZ 2005). The Upper Turonian strata in División Peyotes, Sierra Peyotes, northern Coahuila (Fig. 5: 8), have yielded: *Lamna* sp., *Oxyrhina* sp., *Ptychodus mortoni*, and *P. whipplei* (AGUILERA 1907, MALDONADO-KOERDELL

1948b). A partial skeleton of *Squalicorax falcatus* was also recovered from the Temporales quarry (Fig. 5: 6), within the Turonian Eagle Ford Formation, northwestern Coahuila (GONZÁLEZ-BARBA & PORRAS-MÚZQUIZ 2010).

The Turonian Vallecillo Member of the Agua Nueva Formation at the Vallecillo quarries (Fig. 5: 10), has yielded teeth of *Ptychodus mortoni* and *P. decurrens* as well as several articulated scyliorhinid and lamnid vertebrae that were found on slabs, in which the preservation includes partial body impressions (BLANCO et al. 2001; BLANCO-PIÑON et al. 2005; GIERSCH et al. 2008, 2010c; IFRIM et al. 2010). The Turonian Agua Nueva Formation also includes *Ptychodus mortoni* (MALDONADO-KOERDELL 1956) in Xilitla, San Luis Potosí State (Fig. 5: 12).

The Turonian-Maastrichtian Mexcala Formation in Guerrero state (Fig. 5: 18) is exposed at various sites with abundant shark teeth. The Temalac locality of early Maastrichtian age produced *Ptychodus mortoni*, *Squalicorax* cf. *S. falcatus*, and *Cretoxyrhina mantelli*; the Turonian Taxco el Viejo locality includes *P. decurrens*, and the early Maastrichtian Tepetlapa locality yields *Serratolamna serratae* (ALVARADO-ORTEGA et al. 2006c).

The Pen Formation in northwestern Coahuila (Fig. 5: 6) of Late Santonian/Early Campanian age has yielded *Cretoxyrhina mantelli*, *Cretalamna apendiculata*, *Scapanorhynchus texanus*, and *Squalicorax kaupi* (GONZÁLEZ-BARBA & RIVERA-SYLVA 2010).

The Difunta Group in the Parras Basin, southern Coahuila (Fig. 5: 9) of Campanian-Maastrichtian age, has yielded *Ischyrhiza mira*, from the Parras Formation (upper Campanian), *Serratolamna serrata* and *Schizorhiza stromeri* in the Rincón Colorado area from the Cerro del Pueblo Formation (Campanian), *Serratolamna serrata*, *Scapanorhynchus texanus*, *Pseudocorax* sp, and *Schizorhiza* sp. from the El Barril Canyon in the Maastrichtian Rancho Nuevo Formation, *Carcharias* sp., *Anomotodon* sp. *Cretalamna appendiculata*, *Cretalamna maroccana*, *Serratolamna serrata*, *Squalicorax kaupi*, and *Ptychotrygon* sp. in the Rancho Los Robledo locality from the Maastrichtian Escondido Formation (HERNÁNDEZ-RIVERA 1998, AGUILLÓN-MARTÍNEZ et al. 1998, KIRKLAND et al. 2000, KIRKLAND & AGUILLÓN-MARTÍNEZ 2002, GONZÁLEZ-BARBA et al. 2010).

Hybodus, *Chiloscyllium*, *Ginglymostoma*, *Cretorectolobus*, *Odontaspis*, *Carcharias*, *Scapanorhynchus*, *Cretolamna*, *Squalicorax*, *Rhinobatos*, *Protoplatyrhina*, *Squatirhina*, I*schyrhiza*, and *Ptychotrygon* have been recovered from the Santonian Aguja Formation in the Los Altares locality (Fig. 5: 5) of Chihuahua State (COPE et al. 2003).

The Maastrichtian localities and faunas are the most abundant Late Cretaceous records in Mexico. The El Rosario Formation in the Mesa La Sepultura of Baja California state (Fig. 5: 3) has yielded: *Scapanorhynchus* sp., *Squalicorax* sp., and *Brachyrhizodus wichitaensis*. The Potrerillos Formation (Difunta Group) in the La Popa Basin of Nuevo León (Fig. 5: 9) has yielded: *Carcharias* sp., *Cretalamna appendiculata*, *Serratolamna serrata*, *Squalicorax kaupi*, and *Ischyrhiza mira*. The Ocozocoautla Formation in Chiapas (Fig. 5: 23) has yielded: *Carcharias* sp., *Cretoxyrhina* sp., *Serratolamna serrata*, *Squalicorax pristodontus* and *Rhombodus binkhorsti* (GONZÁLEZ-BARBA et al. 2001).

Osteichthyan records

Osteichthyan records are most abundant from the Cretaceous in Mexico due to the vast area of Cretaceous rocks. As mentioned above, the first recorded Cretaceous localities bearing fishes were discovered by national and foreign geologists during the 19th Century. The first confirmed osteichthyan Cretaceous record comes from the Lower Cretaceous rocks of Cerro de la Virgen, Oaxaca State (Fig. 5: 19), from where FELIX (1891) described *Thrissops* sp., *Otomitla speciosa*, and *Belonostomus ornatus*. ALVARADO-ORTEGA et al. (2011) have prospected this area in recent years. They found semionotiforms, pycnodontiforms, and *Otomitla mexicana*. The second recorded Cretaceous fish and the only lungfish from Mexico, *Ceratodus* sp., was collected in the Cretaceous sediments of Los Peyotes, Coahuila (Fig. 5: 8), by AGUILERA (1907). Following these initial discoveries in Mexico, the Early Cretaceous *"Leptolepis" tamanensis* was reported from San Luis Potosí State (DUNKLE & MALDONADO-KOERDELL 1953), and *Xiphactinus molossus* and *Ichthyodectes* sp. were reported from the upper Turonian Xilitla sediments (Fig. 5: 12) of San Luis Potosí (MALDONADO-KOERDELL 1956). Almost fifty years later, from the same Xilitla area, BLANCO-PINÓN et al. (2006) collected *Enchodus* sp., *Tselfatia* sp., *Rhynchodercetis* sp., and various ichthyodectiform vertebrae and scales from the Agua Nueva Formation. Also from San Luis Potosí, and possibly from the vicinity of the Xilitla area, AGUILERA (1896) reported *Syllaemus* sp. and *Diplomystus* sp. from two Cretaceous localities. Regrettably, these records have not been confirmed and the specimens, as in other cases, were lost.

During 1990, the first author made a survey of the fishes deposited in the Colección Nacional de Paleontología-IGM of the University of Mexico. The objective of this investigation was to trace any evidence of Cretaceous specimens in the collection, especially those reported in BARRIOS-RIVERA (1985). As a result of this search, several badly preserved teleost specimens were located corresponding to localities in the states of Chihuahua, Coahuila, Durango, San Luis Potosí, Veracruz, Chiapas, and Puebla. In addition to the Colección Nacional de Paleontología-IGM, in the same database, BARRIOS-RIVERA (1985) also listed some fish reports from the states of Coahuila, Tamaulipas, Hidalgo, and Oaxaca, deposited in the National Institute of Anthropology and History (INAH) and in the Museum of Natural History of Mexico. These teleost fishes have never been formally described, but these reports have led to prospecting in some of these areas.

The most important Cretaceous localities bearing osteichthyans that are currently under study include: Tlayúa quarry in Puebla State of Albian age (Fig. 5: 17), Vallecillo quarry in Nuevo León State (Fig. 5: 10) of early Turonian age, Muhi quarry in Hidalgo State (Fig. 5: 13) of Albian-Cenomanian age, El Espinal (Fig. 5: 21) and El Chango quarries (Fig. 5: 22) in Chiapas State of Cenomanian age, Mexcala Formation quarries in Guerrero State (Fig. 5: 18) of Turonian-Maastrichtian age, and La Mula quarry (Fig. 5: 6), El Rosario quarry (Fig. 5: 7) and Los Pilotes Ranch (Fig. 5: 6) in Coahuila State, all of Turonian age.

The Tlayúa, Vallecillo, El Chango, and El Rosario quarries are considered Konservat-Lagerstätten characterized by a very diverse fauna (BLANCO-PIÑÓN et al. 2002, STINNESBECK et al. 2005, ALVARADO-ORTEGA et al. 2011). A list of the fish taxa recorded in each locality and discussion of some aspects of the diversity and paleoenvironments are provided below.

The Tlayúa quarry (Fig. 5: 17) is the most important locality discovered in Mexico and the most studied. The quarry belongs to the Middle Member of the Tlayúa Formation of Albian age (PANTOJA-ALOR 1992, APPLEGATE et al. 2006). There are different interpretations concerning the depositional paleoenvironment of the fossils (PANTOJA-ALOR 1992, ESPINOSA-ARRUBARRENA & APPLEGATE 1996, FELDMANN et al. 1998, KASHIYAMA et al. 2004, APPLEGATE et al. 2006), but it is evident that the fishes come from different environments that include shallow, deep, and brackish waters.

Since the discovery of the Tlayúa quarry in 1981, many taxa have been described. During the Fifth International Meeting on Mesozoic Fishes in Saltillo (2010), a field trip to the outcrop was organized and a list of the currently identified taxa was compiled (ESPINOSA-ARRUBARRENA & ALVARADO-ORTEGA 2010). The osteichthyans comprise numerous taxa of Actinopterygii and one of Actinistia. For each order, the named taxa are in brackets: Amiiformes (*Pachyamia mexicana* GRANDE & BEMIS, 1998; cf. *Amblysemius*), Ionoscopiformes (*Teoichthys kallistos* APPLEGATE, 1988 [Fig. 6A]; *Quetzalichthys perrilliatae* ALVARADO-ORTEGA & ESPINOSA-ARRUBARRENA, 2008), Semionotiformes (*Tlayuamichin itztli* LÓPEZ-ARBARELLO & ALVARADO-ORTEGA, 2011), Macrosemiiformes (*Macrosemiocotzus americanus* GONZÁLEZ-RODRÍGUEZ et al., 2004; *Notagogus novomundi* GONZÁLEZ-RODRÍGUEZ & REYNOSO, 2004 [Fig. 6B], genus A and B?), Pycnodontiformes (*Tepexichthys aranguthyorum* APPLEGATE 1992 [Fig. 6C], *Neoproscinetes* sp. ?), Aspidorhynchiformes (*Belonostomus* sp., *Vinctifer* sp.), 'Pholidophoriformes', Crossognathiformes *(Michin scernai* ALVARADO-ORTEGA et al. 2008, *Notelops* sp., cf. *Rhacolepis)*, Ichthyodectiformes (*Unamichthys espinosai* ALVARADO-ORTEGA, 2004), Elopocephala incertae sedis (Araripichthyidae [*Araripichthys* sp.]), Elopiformes (cf. *Brannerion*, cf. *Megalops*, cf. *Paraelops*), Osteoglossomorpha (cf. *Lycoptera*), Tselfatiiformes (cf. *Bananogmiu*s), Ellimmichthyiformes (*Elimmichthys* sp.), Gonorynchiformes, Aulopiformes (cf. *Yabrudichthys*), and Beryciformes (ESPINOSA-ARRUBARRENA & ALVARADO-ORTEGA 2010), and one member of the Actinistia (*Axelrodichthys* cf. *A. araripensis* [ESPINOSA-ARRUBARRENA et al. 1996]).

The Muhi quarry (Fig. 5: 13) of Hidalgo State in central Mexico, of Albian-Cenomanian age, belongs to the El Doctor Formation and represents an open shelf to deep shelf-margin paleoenvironment (BRAVO-CUEVAS et al. 2009) where invertebrates, fishes, and reptiles were deposited. Because of its fossil richness it was recently proposed as a fossil concentrate Lagerstätte by BRAVO-CUEVAS et al. (2012). The fish assemblage of the Muhi quarry comprises the chondrichthyans mentioned above and numerous osteichthyans including Aspidorhynchiformes, Crossognathiformes (Pachyrhizodontidae), Ichthyodectiformes, Elopiformes, Clupeomorpha, Dercetidae (GONZÁLEZ-RODRÍGUEZ & BRAVO-CUEVAS 2005, GONZÁLEZ-RODRÍGUEZ & FIELITZ 2009) Enchodontidae (*Enchodus zimapanensis* FIELITZ & GONZÁLEZ-RODRÍGUEZ 2010 [Fig. 6D]), Ichthyotringoidea (*Ichthyotringa mexicana* FIELITZ & GONZÁLEZ-RODRÍGUEZ 2008 [Fig. 6E]), Halecoidea, Tselfatiiformes, Euteleostei indet., Acanthomorpha (*Muhichthys cordobai* GONZÁLEZ-RODRÍGUEZ & FIELITZ 2008 [Fig. 6F]), and new miniature armored acanthomorphs described in this volume.

Aside from the diversity of the fish assemblage discovered in the Muhi quarry, the presence of taxa not previously reported in America, such as the shrimp *Aeger hidalguensis* (FELDMANN et al. 2007), and the aulopiform *Ichthyotringa mexicana* FIELITZ & GONZÁLEZ-RODRÍGUEZ 2008, let this locality appear

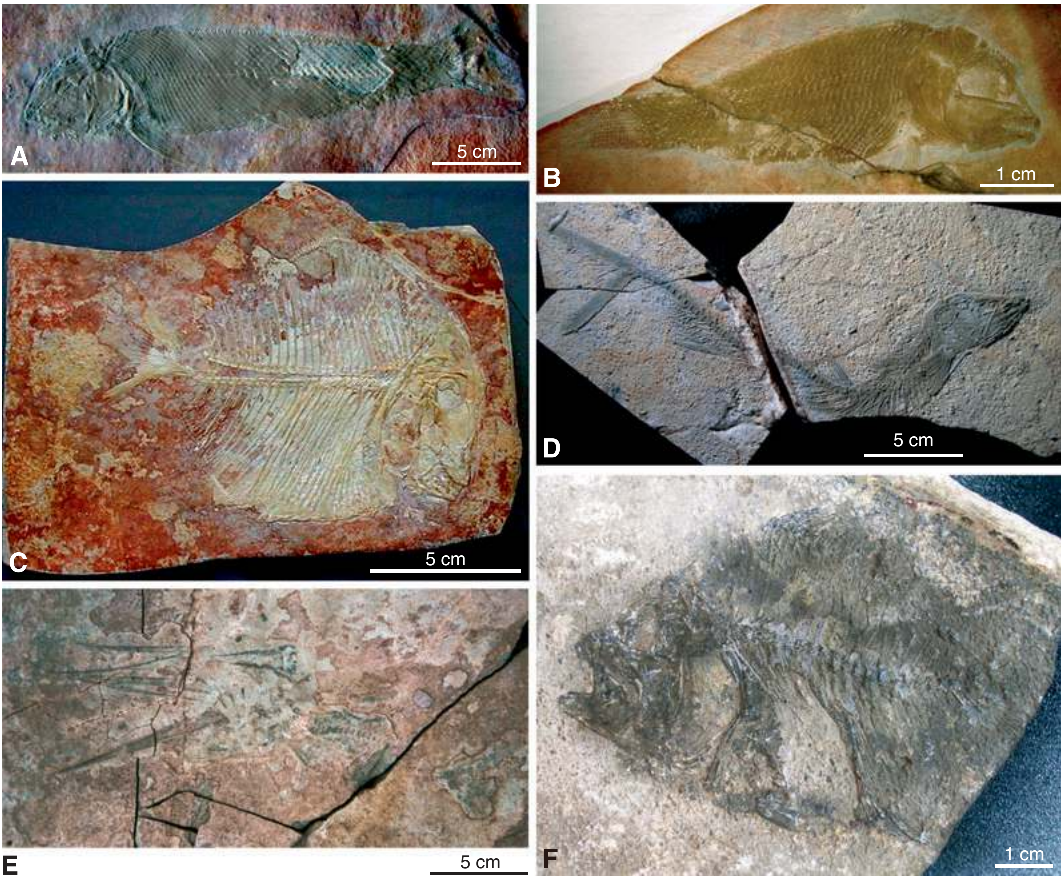

Fig. 6.
Some of the most important Cretaceous fish taxa first described in Mexico within the last 25 years. **A,** *Teoichthys kallistos* APPLEGATE 1988 (IGM-3460), from the Albian Tlayúa quarry, Puebla State; **B,** *Notagogus novomundi* GONZÁLEZ-RODRÍGUEZ & REYNOSO 2004 (IGM-8173), Albian Tlayúa quarry, Puebla; **C,** *Tepexichthys aranguthyorum* APPLEGATE 1992 (IGM-3286), Albian Tlayúa quarry, Puebla; **D,** *Enchodus zimapanensis* FIELITZ & GONZÁLEZ-RODRÍGUEZ 2010 (UAHMP-679), Albian–Cenomanian Muhi quarry, Hidalgo State; **E,** *Ichthyotringa mexicana* FIELITZ & GONZÁLEZ-RODRÍGUEZ 2008 (UAHMP-2067), Albian–Cenomanian Muhi quarry, Hidalgo; **F,** *Muhichthys cordobai* GONZÁLEZ-RODRÍGUEZ & FIELITZ 2008 (UAHMP-2068), Albian–Cenomanian Muhi quarry, Hidalgo.

as an important center of endemism in Mexico. Also from the El Doctor Formation, but in the Cerro Los Mendoza, Progreso, near the Muhi quarry, CARRANZA-CASTAÑEDA & APPLEGATE (1994) reported a pycnodont vomerine plate.

El Espinal (Fig. 5: 21) and El Chango (Fig. 5: 22) quarries in Chiapas State of the Sierra Madre Formation (Aptian-Santonian) have yielded Pycnodontiformes, Macrosemiiformes, Clupeomorpha (*Triplomystus applegatei* ALVARADO-ORTEGA & OVALLES-DAMIÁN 2008, and a *Paraclupea*-like form), an unnamed ichthyodectoid, Alepisauriformes (*Saurorhamphus* sp., and *Enchodus* sp.), a gonorynchid, and some unidentified forms (ALVARADO-ORTEGA et al. 2009). The age of these outcrops is controversial because there is not complete stratigraphic control. Based on invertebrates, VEGA et al. (2006) reported an Albian age for the El Espinal quarry, but according to the fish assemblage, ALVARADO-ORTEGA et al. (2009) appraised a Cenomanian age. The study of the fish fauna is in progress and the identification of some forms such as macrosemiids is so far to be confirmed. GONZÁLEZ-RODRÍGUEZ et al. (2002) identified the only macrosemiid specimen found at that time and assigned it to *Macrosemius* cf. *M. fourneti*, but later

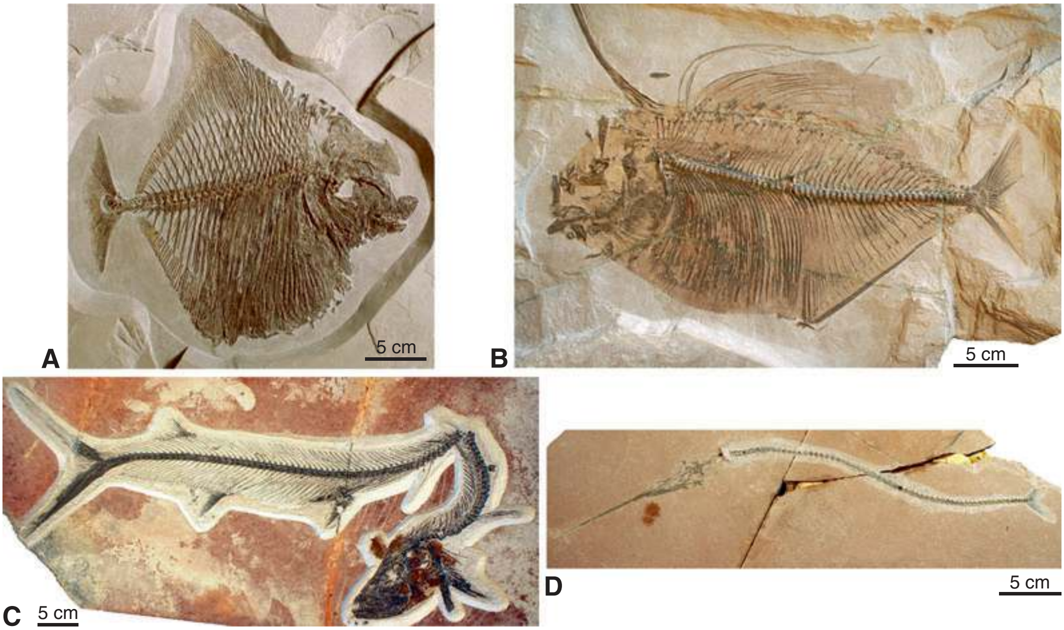

Fig. 7.
Some fishes described from the Turonian Vallecillo quarry, Nuevo León State. **A.** *Nursallia gutturosum* (CPC-302); **B,** *Tselfatia formosa* (CPC-429); **C,** *Vallecillichthys multivertebratum* BLANCO & CAVIN 2003 (CPC-438); **D,** *Rhynchodercetis regio* BLANCO-PIÑON & ALVARADO-ORTEGA 2006 (CPC-435). Photographs are courtesy of C. IFRIM and S. GIERSCH.

ALVARADO-ORTEGA et al. (2009) described it as *Macrosemiocotzus americanus*. A full discussion of the identification of this fish is in preparation by the first author of this paper.

The Vallecillo quarry (Fig. 5: 10) of Nuevo León State, northeastern Mexico, belongs to the Vallecillo Member of the lower Turonian Agua Nueva Formation. Many papers concerning the fish fauna have been published recently (BLANCO et al. 2001; BLANCO-PIÑON et al. 2002; BLANCO & CAVIN 2003; BLANCO-PIÑÓN & ALVARADO-ORTEGA 2005a, 2006; BLANCO-PIÑÓN et al. 2005, 2007, 2008; GIERSCH et al. 2010a–c; SCHULTZE et al. 2010).

According to IFRIM et al. (2005, 2007, 2010) the fish-bearing strata were deposited on an open shelf, a conclusion that is supported by the pelagic nature of the assemblage and the absence of submarine barriers in the region around Vallecillo, Nuevo León. In addition, a complete review of the Vallecillo fish fauna was also presented in the abstract book of the Fifth International Meeting on Mesozoic Fishes in Saltillo by IFRIM et al. (2010). In addition to the chondrichthyan taxa mentioned above, the osteichthyan fauna is represented by Pachycormiformes, Pycnodontiformes (*Nursallia gutturosum* ARAMBOURG, 1955 [Fig. 7A]), Aspidorhynchiformes (*Belonostomus* sp.), Crossognathiformes (*Goulmimichthys roberti* BLANCO & CAVIN, 2003, *Pachyrhizodus caninus* COPE, 1872 in GIERSCH et al. 2010a, *Tingitanichthys* sp. GIERSCH et al. 2010b), Tselfatiiformes (*Tselfatia formosa* ARAMBOURG, 1955 [Fig. 7B]), Ichthyodectiformes (*Gillicus arcuatus* COPE, 1875), *Vallecillichthys multivertebratum* BLANCO & CAVIN, 2003, BLANCO-PIÑON & ALVARADO-ORTEGA 2007 [Fig. 7C], cf. *Heckelichthys* GIERSCH et al. 2010b), Aulopiformes (*Rhynchodercetis regio* BLANCO-PIÑÓN & ALVARADO-ORTEGA, 2006 [Fig. 7D]), *Robertichthys riograndensis* BLANCO-PIÑÓN & ALVARADO-ORTEGA, 2005a, *Araripichthys* sp. IFRIM et al. 2007, 2010), and Latimerioidei (SCHULTZE et al. 2010).

Additional Upper Cretaceous quarries have been discovered during recent years in northern Mexico. The sequences of La Mula quarry and Los Pilotes Ranch (Fig. 5: 6) near Múzquiz, Coahuila State, belong to the Turonian Eagle Ford Formation (BLANCO & ALVARADO-ORTEGA 2005b, ALVARADO-ORTEGA & PORRAS-MÚZQUIZ 2009). The La Mula quarry yields numerous elasmobranchs and actinopterygians such as *Laminospondylus* sp., *Nursallia* sp., *Goulmimichthys* sp., *Saurodon* sp., *Tselfatia* sp., *Enchodus* sp., and some unidentified remains (BLANCO & ALVARADO-ORTEGA 2005b, ALVARADO-ORTEGA et al. 2006a). Los Pilotes Ranch has yielded *Laminospondylus* sp., *Gillicus arcuatus*, *Enchodus* sp., an *Omosoma*-like fish, some complete unidentified clupeomorphs, and abundant isolated scales (ALVARADO-ORTEGA & PORRAS-MÚZQUIZ 2009).

The El Rosario quarry in northern Coahuila (Fig. 5: 7) is another Upper Cretaceous locality belonging to the Austin Group of late Turonian–early Coniacian age, containing invertebrates and vertebrates with anatomical details of soft tissues preserved and some specimens conserved in 3D. These fossils were deposited in an open marine-shelf environment near the southern opening of the Western Interior Seaway, several hundred kilometers south of the present North American coastline (STINNESBECK et al. 2005). Osteichthyans include at least Pycnodontiformes, Ichthyodectiformes, Tselfatiiformes, ?Cimolichthyoidei, ?Enchodontoidei, ?Prionolepididae, and Acanthomorpha indet. (STINNESBECK et al. 2005). Likewise, the Aguja Formation exposed in the Las Jicotecas locality (Fig. 5: 6), northwestern Coahuila, has yielded lepisosteid scales of late Campanian age (RIVERA-SYLVA et al. 2009).

Additional Late Cretaceous osteichthyan records come from the Turonian-Maastrichtian Mexcala Formation, which crops out in at least six localities of Guerrero State (Fig. 5: 18), southwestern Mexico. In these localities, *Pachyrhizodus* cf. *P. caninus*, Ichthyodectiformes, *Tselfatia* sp., *Enchodus* sp., dercetids, and several unidentified taxa have been discovered (ALVARADO-ORTEGA et al. 2006c). The six localities represent different paleoenvironments that vary from a deltaic plane to a pelagic marine environment (AGUILERA-FRANCO 2000).

Cenozoic

The geological evolution of Mexico during the Cenozoic is a continental story that had a significant influence on the development and distribution of the flora and fauna that lived there during (at least) the last 50 million years.

According to CEVALLOS-FERRIZ & GONZÁLEZ-TORRES (2006), the main geological processes that have been recognized in Mexico can be grouped as follows:

1) Development of large magmatic provinces (Sierra Madre Occidental, Mexican volcanic Belt and Sierra Madre del Sur). The evolution of these provinces is one of the most remarkable features of the Cenozoic in Mexico; 2) Formation (deposition) and uplift of the eastern orogenic belt (Sierra Madre Oriental). The Laramide orogeny is linked to the marine regression that started in the Late Cretaceous and ended in the middle Eocene. The territory that emerged increased the surface area of the land almost 100 %, offering to the continental biota a large array of new habitats to colonize and thrive; 3) A series of marine regressions that formed the current contour of Mexico, already discussed above; 4) Fragmentation and displacement of continental terranes in the Cenozoic. This includes the opening of the Gulf of California and the displacement of the Chortis Block. The formation of the Baja California Peninsula and the opening of the Gulf of California involved fragmentation and displacement of a large part of continental western Mexico during middle-late Neogene times. The opening of the Gulf of California resulted from a right lateral movement between the Pacific and North American plates. On the other hand, the displacement of the Chortis Block from the southern Pacific margin of Mexico to northern Central America during the time from Late Cretaceous to late Pliocene), was important in the formation of a land bridge between North and South America (CEVALLOS–FERRIZ & GONZÁLEZ-TORRES 2006).

Chondrichthyan records

The Baja California Peninsula contains a great diversity of marine Cenozoic shark and ray materials (mainly teeth). Many sites are also characterized by the presence of diverse teleost remains that include scales and complete specimens. The Baja California Cenozoic chondrichthyan records include a sequence of Paleogene and Neogene localities, taxa from which had been listed by GONZÁLEZ BARBA & THIES (2000), but previous studies were also made during the "APPLEGATE" era (APPLEGATE 1978, 1979, 1986, 1993; APPLEGATE & WILSON 1976; APPLEGATE et al. 1979; APPLEGATE & ESPINOSA-ARRUBARRENA 1981; ESPINOSA-ARRUBARRENA & APPLEGATE 2000). The marine Cenozoic chondrichthyan localities are shown in Figure 8 and the known records are listed in Appendix 1.

The Paleocene (Danian) Sepultura Formation (Fig. 8: 3) represents the oldest Paleogene record (GONZÁLEZ-BARBA & THIES 2000). There are also Ypresian (Fig. 8: 8) (GONZÁLEZ-BARBA 2004), Priabonian (GONZÁLEZ-BARBA 2002), Rupelian (GONZÁLEZ-BARBA 2008), and Chattian outcrops in the peninsula. The Chattian (El Cien Formation) localities (Fig. 8: 10, 11, 13, 14, 15, 16) are exposed in the San Hilario area (APPLEGATE 1986) and in the San Juan de la Costa area (GONZÁLEZ-BARBA 2006).

Miocene outcrops include the Tortugas Formation in the Vizcaino Peninsula (Fig. 8: 4, 5, 6), the Trinidad Formation (Fig. 8: 17) in the San José del Cabo Basin, Arroyo La Muela, Mesa La Cantina, La Salada Formation (Fig. 8: 12, 18), and The Rosarito Beach Formation (Fig. 8: 1, 2). The Pliocene Gloria Formation is exposed in Santa Rosalía (Fig. 8: 7, 9) (APPLEGATE 1978); the Almejas Formation (Fig. 8: 5, 6) and the Refugio Formation (Fig. 8: 19) occur in the San José del Cabo basin (GONZÁLEZ BARBA & THIES 2000).

Additional Cenozoic chondrichthyan records include those of *Carcharodon* sp. in the Miocene of the Ferrotepec mine (Fig. 8: 23) of Michoacán (APPLEGATE 1979), *Hemipristis serra* in the Miocene of Tuxpan, Veracruz (DICKERSON & KEW 1917) (Fig. 8: 21), *Carcharodon megalodon* in the Eocene-Oligocene of Tabasco (LERICHE 1938), *Aetobatus* sp. in the Eocene of the state of Tamaulipas (MALDONADO-KOERDELL 1948a) (Fig. 8: 20), *Nebrius* sp., *Strilatolamnia macrota*, *Carcharias* sp., *Odontaspis* sp., *Isurus praecursor*, *Carcharodon auriculatus*, *Hemipristis curvatus*, *Hemipristis* sp., and *Galeocerdo* sp. in the middle Eocene San Juan Formation of the Mesa de Copoya in Chiapas State (FERRUSQUÍA-VILLAFRANCA et al. 1999, GONZÁLEZ-BARBA et al. 2004) (Fig. 8: 24), and *Carcharocles angustidens* in the upper Oligocene La Quinta Formation of the state of Chiapas (GONZÁLEZ-BARBA et al. 2002).

Osteichthyan records

Most of the Cenozoic fish localities discovered in Mexico represent marine environments as shown by the chondrichthyan records above, but some also come from fresh-water environments. Cenozoic marine osteichthyans are mainly recovered from the Baja California Peninsula. MINCH et al. (1970) reported an indeterminate fish belonging to Scombridae from the middle Miocene Rosarito Beach Formation in the Mesa de La Misión locality (Fig. 8: 1). ARANDA-MANTECA (1990, 1994) described additional fish remains from the same locality some years later; he assigned them to the following families: Acipenseridae, Clupeidae, Ariidae, Syngnathidae, Sebastidae, Polyprionidae, Serranidae, Carangidae, Lutjanidae, Sciaenidae, Oplegnathidae, Labridae, Sphyraenidae, Trichiuridae, Scombridae, Balistidae, and Diodontidae.

From the central and southern parts of Baja, FIERSTINE et al. (2001) described the fossil blue marlin *Makaira nigricans* from the Trinidad Formation (upper Miocene to upper Pliocene) of San José del Cabo Basin, Baja California Sur (Fig. 8: 17). GONZÁLEZ-BARBA & ALVARADO-ORTEGA (2009) reported Clupeiformes from the upper Oligocene San Gregorio and El Cien formations (Fig. 8: 14). From other areas of the country, Miocene otoliths belonging to Sciaenidae were reported by LERICHE (1938) from the Rio Coatzacoalcos basin in Veracruz (Fig. 8: 22), and WEILER (1959) described otoliths of Sciaenidae and Gobiidae from the same state.

Finally, in a very recent investigation performed in southern Mexico, ALANIZ-GALVÁN & ALVARADO-ORTEGA (2009) and ALANIZ-GALVÁN (2011) reported the presence of Paleocene perciforms around the archeological Maya zone in Chiapas (Fig. 8: 25), as well as Pycnodontiformes, Osteoglossiformes, Clupeiformes, Anguilliformes, and Gonorhynchiformes.

Cenozoic freshwater fish localities

During the Cenozoic, several important geological processes generated a large number of lakes, in which many endemic fresh-water fish species were established (BARBOUR 1973, ALVAREZ DEL VILLAR 1978, MILLER & SMITH 1986, ARROYO-CABRALES et al. 2008). The known record of these fresh-water taxa started in the Miocene and continued throughout the rest of the Neogene (MINCKLEY et al. 2005). According to ARROYO-CABRALES et al. (2008) and BARRIOS-RIVERA (1985), these species consists of up to 30 taxa distributed in the states of Sonora, Chihuahua, Zacatecas, Jalisco, Guanajuato, San Luis Potosí, Estado de Mexico, Puebla, Hidalgo, Tlaxcala, and Distrito Federal.

It is not surprising that the fossil record of Cenozoic fresh-water fishes is sparse and very young (e.g., Miocene), considering the development of large magmatic provinces (Sierra Madre Occidental, Mexican Volcanic Belt, and Sierra Madre del Sur), that produced large areas covered by volcanic material. For example, according to ORTEGA-GUTIÉRREZ et al. (1992), and McDOWELL & CLABAUGH (1979), during the Oligocene episode of the Sierra Madre Occidental, the volcanic activity became so intense that it produced what is today the largest ignimbrite deposit on the planet.

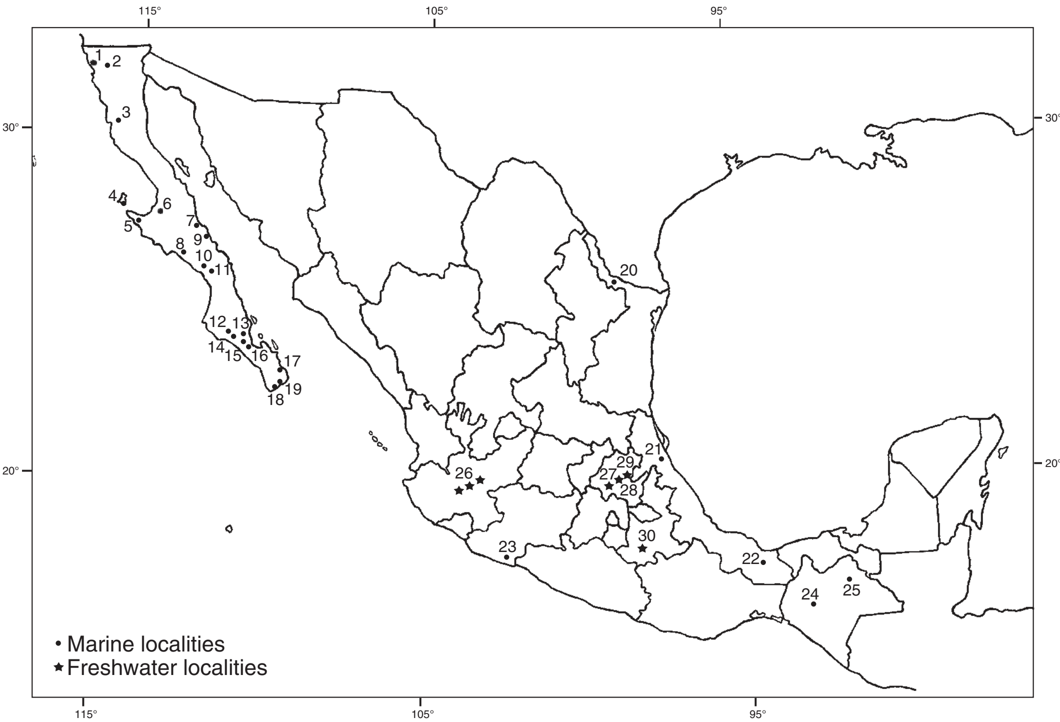

Fig. 8.
Some of the most important Cenozoic localities in Mexico. Marine sites (**1–25**) contain shark, ray and teleost remains; the freshwater localities (**26–30**) are restricted to teleost records. **1**, La Misión, Baja California Peninsula (=BC); **2**, Mesa de los Indios (BC); **3**, Mesa de la Sepultura (BC); **4**, Isla Cedros (BC); **5**, Bahía Tortugas (BC); **6**, Guerrero Negro (BC); **7**, Loma del Tirabuzón "Corkscrew Hill" (BC); **8**, Bateque (BC); **9**, Santa Rosalía (BC); **10**, La Cocina (BC); **11**, La Purísima (BC); **12**, El Rifle (BC); **13**, Harley's Hideaway (BC); **14**, El Cien (BC); **15**, Ten minute locality (BC); **16**, San Juan de la Costa (BC); **17**, La Trinidad (BC); **18**, Rancho Algodones (BC); **19**, El Refugio (BC); **20**, Presa del Azúcar, Tamaulipas; **21**, Tuxpan, Veracruz; **22**, Cuenca Río Coatzacoalcos, Veracruz; **23**, Mina Ferrotepec, Michoacán; **24**, Mesa de Copoya, Chiapas; **25**, Palenque, Chiapas; **26**, Chapala lake localities, Jalisco; **27**, Tula, Hidalgo; **28**, Atotonilco el Grande, Hidalgo; **29**, Zacualtipán, Hidalgo; **30**, Los Ahuehuetes, Hidalgo.

Cenozoic freshwater fish records

The geological processes during the Late Cenozoic in Mexico resulted in fragmentation of drainages and subsequent isolation of fish populations, causing speciation through vicariance (MILLER & SMITH 1986). Many ancient lakes ranging in age from Miocene to late Pleistocene were formed in central Mexico and the continuously changing drainage configuration (BARBOUR 1973) generated patterns of fish diversification and speciation that can be observed in past and present Mexican fish species.

The Cenozoic outcrops (Fig. 8) around the recent lakes of the state of Jalisco (Fig. 8: 26) in central Mexico are the best studied. ALVAREZ & ARRIOLA (1972) described *Tapatia occidentalis*, the oldest record of the endemic Mexican teleostean family Goodeidae from the Pliocene Barranca de Santa Rosa, Amatitlán, Jalisco. Furthermore, from the same geographical area, mid to late Pleistocene goodeids comprising *Alloophorus robustus*, *Goodea atripinnis*, *Chapalichthys encaustus*, *Ameca splendens* (SMITH et al. 1975), and the late Pleistocene *Girardinichthys viviparous* (ALVAREZ & MONCAYO 1976) have been commonly reported. Today 41 species of goodeids are distributed in lakes and rivers in the Mexican Central Plateau (encompassing at least 15 states), but many species have suffered local extinctions because of environmental changes (DOMÍNGUEZ-DOMÍNGUEZ et al. 2008).

Also from Jalisco (Fig. 8: 26), ALVAREZ (1966, 1974) and SMITH (1987) reported Pleistocene cyprinids

(*Algansea rubeescens*, *Yuriria alta*, *Xistrosus popoche*, *Falcularis chapalae*, and *Notropis* sp.), ictalurids *(Ictalurus dugesi*, *Ictalurus spodius)*, and atherinids (*Chirostoma* sp.). SMITH et al. (1975) studied *Micropterus relictus* and *Moxostoma* sp. CAVENDER & MILLER (1982) also reported *Ictalurus* sp., *Micropterus relictus*, *Oncorhynchus* sp., and *Salmo australis*.

There are some other published records from the upper Pleistocene outcrops of Tlapacoya in the state of Mexico, from where ALVAREZ & MONCAYO (1976) described cranial bones of *Notropis aztecus*, *Algansea ticella*, *Evarra* sp. and various species of *Chirostoma*. In the state of Puebla, ESPINOSA-PÉREZ et al. (1991) reported the presence of a small cyprinid from the Oligocene Ahuehuetes locality in Tepexi de Rodríguez (Fig. 8: 30). CASTILLO-CERÓN et al. (1996) recovered numerous Miocene otoliths and scales from Zacualtipán, Hidalgo (Fig. 8: 29), and ALVARADO-ORTEGA et al. (2006b) described *Ictiobus aguilerai* from the Pliocene (Blancan) La Cementera locality near Tula, Hidalgo (Fig. 8: 27), where also *Ictalurus* sp. remains have been collected. Moreover, BECERRA-MARTÍNEZ (2002) reported Pliocene goodeids from the Atotonilco el Grande Formation in Hidalgo (Fig. 8: 28). As can be seen in this overview, the study of fossil freshwater fishes in Mexico is in its infancy. The challenge is to describe the emerging taxa and to unravel the evolutionary patterns that have been generated in the last 50 million years.

Conclusions

The geological evolution of Mexico shows that the present day geography of the country is the result of complex geological processes, in which Mexico was at the confluence of major events that produced a great diversification of flora and fauna, including fishes.

Only a few Paleozoic and Triassic fossil-fish localities have been reported until now, but after the opening of the Gulf of Mexico and the Proto-Caribbean seaways (in the Late Jurassic), and once the active Circum-Tropical marine current (during the Early Jurassic) were established (ITURRALDE-VINENT 2006), fishes became more abundantly represented in the fossil record of Mexico. Nevertheless, the scarce localities found until now have delayed knowledge of the real fish diversity. Many of the published papers are devoted to the report of new localities and faunas, but few are dedicated to the description of these new species, and most of the fauna has not been studied yet. There must be many fossil sites yet to be discovered in Mexico. The information derived from new fieldwork all over the country will reveal much more about the real diversity of fossil fishes in the Mexican territory.

During the last few years, we have seen that the Early and "mid" Cretaceous fish localities of Mexico show more affinities with some of the sites reported from the eastern Tethys Sea, such as the ones from Morocco, Namoura and Ein-Yabrud (GONZÁLEZ-RODRÍGUEZ & REYNOSO 2004, ALVARADO-ORTEGA & ESPINOSA-ARRUBARRENA 2007, ALVARADO-ORTEGA et al. 2009, GONZÁLEZ-RODRÍGUEZ & FIELITZ 2009, BRAVO-CUEVAS et al. 2012), but the outcrops of Late Cretaceous age in northern Mexico have, in addition, affinities with North American Western Interior Seaway localities (GONZÁLEZ-BARBA & ESPINOSA-CHÁVEZ 2005, STINNESBECK et al. 2005). These resemblances can be explained in turns of a connection between the Paleo-Gulf of Mexico and the Western Interior Seaway, mainly through northwestern Texas. According to STEPHENSON & REESIDE (1938), this was well established in late Early to early Late Cretaceous.

Even though many fishes have been found but not yet studied in Mexico, the presence of the first records of several taxa in America is remarkable and some Mexican new records have also increased the geochronological ranges of taxa. Particular groups reported for the first time in the New World include: Macrosemiidae (GONZÁLEZ-RODRÍGUEZ et al. 2004, GONZÁLEZ-RODRÍGUEZ & REYNOSO 2004), Ichthyotringoidea (FIELITZ & GONZÁLEZ-RODRÍGUEZ 2008), and the first finding of miniature armored acanthomorphs in the Cretaceous (GONZÁLEZ-RODRÍGUEZ et al. this volume). On the other hand, as studies are completed, taxa such as *Pachyrhizodus*, *Tselfatia*, and *Enchodus*, which are some of the most common forms present in the "mid"-Cretaceous fossil record (CAVIN 2008) are also very common in Mexico. However, when some of these genera are studied in detail, many new species appear; such is the case with *Enchodus zimapanensis* FIELITZ & GONZÁLEZ-RODRÍGUEZ, 2010, from Hidalgo State.

If the paleontological record of "mid" and Late Cretaceous fishes in Mexico is still limited, the number of Cenozoic localities and specimens known so far is even more so. Marine osteichthyans and sharks in some western states and mainly in the Baja Peninsula are more abundant than elsewhere in Mexico, but still their abundance cannot compare with the Cretaceous records. Without a doubt the most interesting Cenozoic fish remains are the freshwater sites, particularly those of late Paleogene and Neogene ages, which document speciation events produced by important geological events of that time.

The discovery and study of more Mexican fossil fishes will help us to understand the patterns of distribution and the phylogenetic relationships of many groups present in this part of the world that, to this time, have been unknown to science. The study of the different paleoenvironments inhabited by the fossil fishes will add to understanding of the conditions that prevailed during their lifetime.

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Appendix 1

Chondrichthyan Cenozoic records from Baja California Peninsula

	Paleocene		Eocene	Oligocene		Miocene		Pliocene
	Early	Late	Middle	Middle	Late	Middle	Late	
HEXANCHIDAE								
Hexanchus primigenius				X				
Hexanchus microdon		X						
Hexanchus gigas							X	
Hexanchus griseus								X
Hexanchus sp.						X		
Notorhynchus sp.							X	X
HEPTRANCHIDAE								
Heptranchias sp.						X		
ECHINORHINIDAE								
Echinorhinus sp.						X		

	Paleocene		Eocene	Oligocene		Miocene		Pliocene
	Early	Late	Middle	Middle	Late	Middle	Late	
SQUALIDAE								
Centrophorus sp.							X	
Squalus sp.			X			X		X
Isistius sp. cf. *I. triangulus*							X	
SQUATINIDAE								
Squatina sp.			X	X	X	X	X	
HETERODONTIDAE								
Heterodontus sp.			X	X		X	X	X
GINGLYMOSTOMATIDAE								
Ginglymostoma angolense		X						
Ginglymostoma bequaerti		X						
Ginglymostoma sp.								X
Nebrius obliquus		X		X	X			
RHINCODONTIDAE								
Rhincodon sp. aff. *R. typus*					X			
LAMNIFORMES								
ODONTASPIDIDAE								
Odontaspis ferox								X
Striatolamia macrota			X					
Striatolamia striata	X							
Carcharias acutissima				X				X
Carcharias cuspidata				X				
Carcharias hopei	X	X						
Carcharias vicenti		X						
Carcharias sp.			X		X		X	
LAMNIDAE								
Carcharodon carcharias							X	X
*Carcharodon megalodon**							X	X
Isurolamna lerichei		X						
Isurolamna rupeliensis				X				
Isurus desori				X	X			
Isurus hastalis						X	X	
Isurus oxyrinchus						X	X	X
Isurus paucus						X		
Isurus planus						X	X	
Isurus praecursor			X					
Isurus retroflexus						X		
Isurus sp.	X							
Lamna rupeliensis					X			
Lamna sp.			X				X	
Xiphodolamia eocaena		X	X					
CRETOXYRHINIDAE								
Cretolamna appendiculata		X						
Palaeocarcharodon orientalis		X						
OTODONTIDAE								
Carcharocles angustides				X				
Carcharocles angustidens-turgidus					X			
Carcharocles auriculatus-sokolowi			X					
Carcharocles sp. aff. *C. chubutiensis*						X		
Otodus obliquus		X						
Otodus sp.			X					
Parotodus benedeni							X	X

	Paleocene		Eocene	Oligocene		Miocene		Pliocene
	Early	Late	Middle	Middle	Late	Middle	Late	
ALOPIIDAE								
Alopias exigua				X	X			
Alopias latidens			X	X	X	X		
Alopias pelagicus								X
Alopias sp. aff. *A. denticulatus*				X				
Alopias sp. aff. *A. pelagicus*								
Alopias sp.			X			X		
CETORHINIDAE								
Cetorhinus sp.						X	X	X
MEGACHASMIDAE								
Megachasma sp.						X		
SCYLIORHINIDAE								
Galeus sp.			X					
Scyliorhinus sp.			X				X	
TRIAKIDAE								
Galeorhinus minor		X						
Galeorhinus sp.			X	X		X		X
Mustelus sp.							X	X
Triakis sp.			X					
Pachygaleus lefevrei		X						
HEMIGALEIDAE								
Hemipristis curvatus			X					
Hemipristis serra				X	X	X	X	X
CARCHARHINIDAE								
Abdounia beaugei			X					
Carcharhinus albimarginatus							X	X
Carcharhinus altimus							X	X
Carcharhinus brachyurus							X	X
Carcharhinus falciformis							X	X
Carcharhinus galapagensis							X	X
Carcharhinus leucas							X	X
Carcharhinus limbatus							X	X
Carcharhinus obscurus							X	X
Carcharhinus porosus								X
Carcharhinus velox							X	X
Carcharhinus sp. aff. *C. brachyurus*				X	X			
Carcharhinus sp. aff. *C. falciformis*				X	X			
Carcharhinus sp. aff. *C. egertoni*						X		
Carcharhinus sp. aff. *C. priscus*						X		
Carcharhinus sp.				X		X	X	
Galeocerdo aduncus						X	X	
Galeocerdo contortus					X			
Galeocerdo cuvieri								X
Galeocerdo latidens			X					
Galeocerdo rosaliensis							X	X
Galeocerdo sp.			X	X		X		
Nasolamia velox								
Negaprion brevirostis								X
Negaprion fronto						X	X	X
Negaprion sp.			X	X	X		X	
Physogaleus sp.			X	X	X	X		
Prionace glauca							X	X
Rhizoprionodon longurio							X	X
Rhizoprionodon sp.			X	X		X	X	

	Paleocene		Eocene	Oligocene		Miocene		Pliocene
	Early	Late	Middle	Middle	Late	Middle	Late	
SPHYRNIDAE								
Sphyrna lewini							X	X
Sphyrna media							X	X
Sphyrna mokarran							X	X
Sphyrna zygaena							X	X
Sphyrna sp. aff. *S. lewini*						X		
Sphyrna sp. aff. *S. zygaena*				X	X	X	X	
RHINOBATIDAE								
Rhinobatos sp.			X		X	X	X	X
RAJIDAE								
Raja sp.			X	X			X	X
DASYATIDAE								
Dasyatis sp.		X		X	X	X	X	X
GYMNURIDAE								
Gymnura sp.			X			X	X	
PRISTIDAE								
Propristis schweinfurthi				X				
Pristis sp. aff. *P. lathami*			X					
Pristis sp.								
DASYATOIDEA incertae sedis.								
Coupatezia sp.			X					
Heterotorpedo sp.			X					
MYLIOBATIDAE								
Aetobatus sp.			X	X		X	X	X
Myliobatis sp.	X		X	X	X	X	X	X
RHINOPTERIDAE								
Rhinoptera sp.				X		X		
MOBULIDAE								
Burnhamia sp.						X		
Mobula sp.						X	X	
CHIMAERIDAE								
Hydrolagus sp.							X	

The taxonomic position of taxa follows CAPPETTA (2004), except **Carcharodon megalodon* (= *Carcharocles megalodon*), which follows APPLEGATE & ESPINOSA-ARRUBARRENA (1996), and *Carcharias*, which follows NELSON (2006). **Early Paleocene:** Sepultura Formation; **late Paleocene:** Tepetate Formation; **middle-late Eocene:** Tepetate and Bateque Formations; **middle-late Oligocene:** San Gregorio and El Cien formations, San Juan member of the El Cien Formation; **late Oligocene:** San Gregorio and El Cien formations, San Juan member of the El Cien Formation; **middle-early Miocene:** San Isidro Formation; **middle Miocene:** Playa Rosarito and San Ignacio formations; **late Miocene:** Tortugas, Almejas, and Trinidad formations; **Pliocene:** San Diego, Tirabuzón, Carmen, La Salada, and Refugio formations; **middle Pliocene:** Gloria Formation (APPLEGATE 1978, APPLEGATE & ESPINOSA-ARRUBARRENA 1981, APPLEGATE et al. 1979, ESPINOSA-ARRUBARRENA & APPLEGATE 1981, GONZÁLEZ-BARBA & THIES 2000, LOZANO-CARREÑO 1990).

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