The fossil record of turtles and tortoises (Testudines) of Mexico, Central America and the Caribbean Islands, with comments on its taxonomy and paleobiogeography: a bibliographic review

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ABSTRACT

Testudines is the crown-group that includes all living forms of turtles and their closest extinct relatives. This group is known to exist starting in the Middle Jurassic. The fossil record of Testudines in Mexico is scarce but has been previously compiled in several papers. In this paper, we are presenting an update that includes all osteological and ichnological records of Mexico, and we have added fossil records of turtles and tortoises from Central America and the Caribbean Islands. In Mexico, the Testudines fossil record extends from the Late Jurassic to the Pleistocene, and widely abundant during the late Pleistocene. Kinosternon and Gopherus are the best represented taxa, known from the late Miocene to the late Pleistocene. In Mexico, records of fossil turtles show a wide distribution, except in the areas around the states of Campeche and Quintana Roo in the east; Colima, Guerrero, and Sinaloa in the west, and Querétaro, and Mexico City in the center. Ichnological records are known only in Coahuila, Puebla and Zacatecas. Reports of fossil turtles in Central America include El Salvador, Honduras, Costa Rica, Nicaragua and Panama--the latter being the country with the most records--and in the Caribbean Islands including Cuba, Dominican Republic, Jamaica, the United States Islands of Puerto Rico and Navassa, and the British Island of Sombrero in Anguilla. Seven fossil turtles have been described as new species in Mexico (Notoemys tlaixiacoensis, Yelmocheys rosarioae, Mexichelys couhuilaeensis, Allaeocheys liliae, Gopherus donaloi, G. auffenbergi and G. pargensis, of which G. auffenbergi is synonymous with G. berlandieri, and G. pargensis is considered a nomen vanum); two from Panama (Rhinoclemmys panamaensis and Staurotypus moschus); one from Costa Rica (Rhinoclemmys nicoyana); two from Cuba (Notoemys oxfordensis and Chelonoidis cubensis); one from the Dominican Republic (Chelonoidis marcanoi), one from Puerto Rico (Chelonoidis monensis), and one from Sombrero Island, Anguilla (Chelonoidis sombrerensis).

Key words: Cryptodira; Pleurodira; Mesozoic; Paleogene; Neogene; Cenozoic; Mexico; Central America.

RESUMEN

Testudines se refiere al grupo-corona que incluye a todas las formas de tortugas vivientes y sus ancestros más cercanos. Este grupo apareció en el Jurásico Medio. El registro fósil de Testudines en México es escaso y ha sido previamente compilado en diversos escritos. Aquí se presenta una recopilación actualizada, con las evidencias osteológicas e icnológicas de México, además del registro de tortugas fósiles de América Central y las islas del Caribe. En México, el registro fósil de Testudines abarca desde el Jurásico Tardío hasta el Pleistoceno tardío, siendo más abundantes en esta última época. Kinosternon y Gopherus son las taxones mejor representados y se conocen desde el Mioceno tardío hasta el Pleistoceno tardío. En México, las tortugas fósiles tienen una distribución muy amplia, excluyendo solamente los estados de Campeche, Ciudad de México, Colima, Guerrero, Querétaro, Quintana Roo y Sinaloa; y los registros icnológicos

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INTRODUCTION

Testudines refers to the crown-group that includes all forms of living and fossil turtles and their closest relatives (Joyce et al., 2004). Morphological and molecular studies show that turtles are diapsids closely related to Archosauromorpha (Rieppel and deBraga, 1996; Crawford et al., 2012; Field et al., 2014; Shaffer et al., 2017), and not anapsid sauropsids as previously thought. Basal forms (Testudinata), are mainly known for the Late Triassic and Early Jurassic (Broin, 1984; Gaffney, 1990; Gaffney and Kitching, 1994, 1995; Li et al., 2008; Szczygiel and Sulej, 2016; Joyce, 2017), the true turtles (Testudines) appeared by the Middle Jurassic (Joyce, 2017), and since then the lineage has survive and evolved worldwide.

The Testudines fossil record in Mexico, Central America and the Caribbean Islands is scarce. Mexican turtle fossil fauna has been previously compiled in several works. The first known compilation was the unpublished undergraduate thesis of Barrios Rivera (1985), who elaborated the most extensive review of Mexican fossil vertebrates until then. This compendium has been the base of all following reappraisals. Flores-Villela (1993) when analyzing the herpetofauna of Mexico summarizes the fossil records of amphibians and reptiles from the Eocene to the Pleistocene in a table; however, he does not specify exact locations or bibliographic sources. The most complete published review of fossil turtles was that of Reynoso (2006), who compiled research on fossil turtles in Mexico, Central America and the Caribbean Islands dated as late Holocene were not included.

METHOD

We conducted a detailed and extensive review of Mexican, Central America, and the Caribbean Islands fossil turtle literature and lists (e.g. Barrios Rivera, 1985; Flores-Villela, 1993; Reynoso, 2006; Cadena et al., 2012; Chávez Galván et al., 2013; Albury et al., 2018), supplemented by recent reports in scientific literature, book chapters, and some grey literature as well as thesis and abstracts at academic meetings. When several publications refer to the same taxa in the same locality, we used the original source, in order to avoid data redundancy. Additionally, we consulted Mexican and Central American Paleontological Collections to obtain specimen records not reported in the literature. Generic and specific names were used as they were first published and the validity of some assignments is discussed in the related section.

In the catalog we used the traditional definition of a fossil, which are the remains of organisms that lived in the geological past, older than 10000 years (Buitrón et al., 2010). Because of this, reports from some islands in the Caribbean Islands dated as late Holocene were not included.

RECORDS BY COUNTRY AND GEOLOGICAL AGE

A total of 86 localities with fossil record of turtles and tortoises were found for Mexico, Central America and Caribbean Islands (Figure 1). Of these localities, 59 are in Mexico, 12 in Central America and 15 in the Caribbean Islands. In Mexico we found one Jurassic, 12 Cretaceous, one Eocene, three Oligocene, five Miocene and 31 Pleistocene localities. In El Salvador, there are three localities of the Pleistocene, in Honduras and Costa Rica one of the Miocene and one of the Pleistocene each; in Nicaragua one Pleistocene, and in Panama one Oligocene and three Miocene localities.

In Mexico, Central America and Caribbean Islands, 22 families –of which ten are extinct– have been found. The highest diversity at the family level is from the Mesozoic with 14 families recorded.

Many of the fossils mentioned in specialized literature only have been identified at the family or generic level, while many other specimens have not been adequately described, and others have not been illustrated. This is caused by the lack of knowledge of turtles themselves or because the difficulty in assigning partial bone elements to more specific taxa.

Costa Rica

Paleogene

The first turtle record in Costa Rica was Testudo costarricensis from Peralta de Limón, Cartago Province (Segura, 1944), dated as Oligocene-Miocene or Eocene age. Currently, this record is considered invalid (Lichtig et al., 2018).

Neogene

Remains of Apalone sp. (Figure 2a) from the El Limoncito (Late Miocene) were reported from the west of San Vito, Canton de Coto Brus, Puntarenas Province (Laurito et al., 2005), where still unidentified turtle remains have been recovered recently (Laurito, 2017, com. pers.).

Quaternary

Rhinoclemmys nicoyana (Figure 2b) was described by Acuña-Mesén and Laurito-Mora (1996) based on a nuchal bone and plastral elements collected from the riverbed of the Nacoame River in Barra Honda, Nicoya (Late Pleistocene), Guanacaste Province.
Figure 1. Map showing the locations of fossil remains of Testudines in Mexico, Central America and Caribbean islands. Mexico: 1) Tlaxiaco, Oaxaca (Kimmeridgian); 2) Tlayua Quarry, Puebla (Albian); 3) Parras Basin, Coahuila (Turonian); 4) Mezquital, Nuevo León (Turonian); 5) San Carlos Fm., Coahuila, Maestrac (Turonian); 6) Oxxaca Group, Sonora (Maestrac); 7) El Gallo Fm., Baja California Sur (late Miocene); 8) Proterozoic, El Gallo Fm., Baja California Sur (late Miocene); 9) Baja California Sur, late Oligocene; 10) Bahia de los Angeles, Baja California Sur (late Oligocene); 11) Los Arenales, Baja California Sur (late Oligocene); 12) La Freida, Baja California Sur (late Oligocene); 13) La Casa Blanca, Baja California Sur (late Oligocene); 14) San Carlos Fm., Chihuahua (late Oligocene); 15) Cerro del Pueblo Fm., Coahuila (late Oligocene); 16) San Buenaventura Nealtican, Puebla (late Oligocene); 17) Mejicanas, Mexico (late Oligocene); 18) Cueva del Diablo, Mexico (late Oligocene); 19) La Goleta Fm., Michoacán (late Oligocene); 20) Agua Fria, Baja California Sur (late Oligocene); 21) Yucatán Fm., Yucatán (late Oligocene); 22) Cueva de los Muertos, Yucatán (late Oligocene); 23) La Cueva de los Muertos, Yucatán (late Oligocene); 24) Cueva de los Muertos, Yucatán (late Oligocene); 25) Cueva de los Muertos, Yucatán (late Oligocene); 26) Cueva de los Muertos, Yucatán (late Oligocene); 27) Cueva de los Muertos, Yucatán (late Oligocene); 28) Cueva de los Muertos, Yucatán (late Oligocene); 29) Cueva de los Muertos, Yucatán (late Oligocene); 30) Cueva de los Muertos, Yucatán (late Oligocene); 31) Cueva de los Muertos, Yucatán (late Oligocene); 32) Cueva de los Muertos, Yucatán (late Oligocene); 33) Cueva de los Muertos, Yucatán (late Oligocene); 34) Cueva de los Muertos, Yucatán (late Oligocene); 35) Cueva de los Muertos, Yucatán (late Oligocene); 36) Cueva de los Muertos, Yucatán (late Oligocene); 37) Cueva de los Muertos, Yucatán (late Oligocene); 38) Cueva de los Muertos, Yucatán (late Oligocene); 39) Cueva de los Muertos, Yucatán (late Oligocene); 40) Cueva de los Muertos, Yucatán (late Oligocene); 41) Cueva de los Muertos, Yucatán (late Oligocene); 42) Cueva de los Muertos, Yucatán (late Oligocene); 43) Cueva de los Muertos, Yucatán (late Oligocene); 44) Cueva de los Muertos, Yucatán (late Oligocene); 45) Cueva de los Muertos, Yucatán (late Oligocene); 46) Cueva de los Muertos, Yucatán (late Oligocene); 47) Cueva de los Muertos, Yucatán (late Oligocene); 48) Cueva de los Muertos, Yucatán (late Oligocene); 49) Cueva de los Muertos, Yucatán (late Oligocene); 50) Cueva de los Muertos, Yucatán (late Oligocene); 51) Cueva de los Muertos, Yucatán (late Oligocene); 52) Cueva de los Muertos, Yucatán (late Oligocene); 53) Cueva de los Muertos, Yucatán (late Oligocene); 54) Cueva de los Muertos, Yucatán (late Oligocene); 55) Cueva de los Muertos, Yucatán (late Oligocene); 56) Cueva de los Muertos, Yucatán (late Oligocene); 57) Cueva de los Muertos, Yucatán (late Oligocene); 58) Cueva de los Muertos, Yucatán (late Oligocene); 59) Cueva de los Muertos, Yucatán (late Oligocene); 60) Cueva de los Muertos, Yucatán (late Oligocene); 61) Cueva de los Muertos, Yucatán (late Oligocene); 62) Cueva de los Muertos, Yucatán (late Oligocene); 63) Cueva de los Muertos, Yucatán (late Oligocene); 64) Cueva de los Muertos, Yucatán (late Oligocene); 65) Cueva de los Muertos, Yucatán (late Oligocene); 66) Cueva de los Muertos, Yucatán (late Oligocene); 67) Cueva de los Muertos, Yucatán (late Oligocene); 68) Cueva de los Muertos, Yucatán (late Oligocene); 69) Cueva de los Muertos, Yucatán (late Oligocene); 70) Cueva de los Muertos, Yucatán (late Oligocene); 71) Cueva de los Muertos, Yucatán (late Oligocene); 72) Cueva de los Muertos, Yucatán (late Oligocene); 73) Cueva de los Muertos, Yucatán (late Oligocene); 74) Cueva de los Muertos, Yucatán (late Oligocene); 75) Cueva de los Muertos, Yucatán (late Oligocene); 76) Cueva de los Muertos, Yucatán (late Oligocene); 77) Cueva de los Muertos, Yucatán (late Oligocene); 78) Cueva de los Muertos, Yucatán (late Oligocene); 79) Cueva de los Muertos, Yucatán (late Oligocene); 80) Cueva de los Muertos, Yucatán (late Oligocene); 81) Cueva de los Muertos, Yucatán (late Oligocene); 82) Cueva de los Muertos, Yucatán (late Oligocene); 83) Cueva de los Muertos, Yucatán (late Oligocene); 84) Cueva de los Muertos, Yucatán (late Oligocene); 85) Cueva de los Muertos, Yucatán (late Oligocene); 86) Cueva de los Muertos, Yucatán (late Oligocene).
The marine turtle *Caribemys oxfordiensis* was described based on a nearly complete shell recovered in the Jagua Formation (Upper Jurassic, Oxfordian), near Viñales, Pinar del Río Province (De la Fuente and Iturralde-Vinent, 2001). Later, Cadena Rueda and Gaffney (2005) reassigned the species to *Notoemys*.

**Neogene**

Unidentified Pelomedusoides turtle has been reported from the Lagunitas Formation (early Miocene) in Domo de Zaza, Sacti Spiritus Province (MacPhee et al., 2003.).

**Quaternary**

*Testudo cubensis* was described by Leidy (1868) based on a costal plate. It was found together with the lower jaw of a giant sloth at Ciego Montero, Cienfuegos Province. Additional material (plates and a femur) assigned to *T. cubensis* came from a tar pit near Hato Nuevo, Matanzas Province (Williams, 1950). Also, several remains referred to *Pseudemys cf. P. decussata* were recovered from Sierra de Jatibonico, and Ciego Montero localities, and fragments of plastral and carapace.
assigned just to *Pseudemys* were recovered from Daiquiri, Oriente Province, and Cueva de los Machos near Cienfuegos, Santa Clara Province (Williams, 1950).

**Dominican Republic**

**Quaternary**

The first record of large tortoises in Dominican Republic was documented based on shell fragments and limb elements collected at a cave near Bayaguana in San Cristóbal Province, in the Los Haitises region, and referred to *Geocheleon* (Franz and Woods, 1983). *Chelonoidis marcanoi* was described based on several remains, making up at least seven individuals from Quaternary sediments at several cave sites in Pedernales Province, southern Dominican Republic (Turvey et al., 2017). Also, *Chelonoidis dominicensis* was described based on one specimen that conserved the skull, the shell nearly complete, and appendicular skeleton recovered from the Oleg’s Bat Cave in La Alttagracia Province, southeastern Dominican Republic (Albury et al., 2018).

**El Salvador**

**Quaternary**

*Hesperotestudo crassiscutata, Kinosternon* sp. and an unidentified Emydidae were recovered from the Tomatey river (Middle-late Pleistocene) (Cisneros, 2005). *Hesperotestudo (=Geochelone)* was also reported at Barranca del Sisimico locality (Early-Middle Pleistocene), San Vicente Department, and El Hormiguero locality (late Pleistocene), San Miguel Department (Webb and Perrigo, 1984).

**Honduras**

**Neogene**

*Rhinoclemmys* sp. and *Geochelone* sp. were recovered from the Gracias Formation (Late Miocene), near the Gracias town in the Department of Lempira. *Rhinoclemmys* is known from an isolated nuchal bone that combines diagnostic morphological features for the genus: narrow anteromedian scute, strong midsagittal keel, and strong posteroomedian concavity (Webb and Perrigo, 1984). *Geochelone* based on one large shell and several shell fragments, however, diagnostic features have been not provided (Webb and Perrigo, 1984).

**Quaternary**

*Rhinoclemmys* sp. was recovered from Orillas del Humuya (Late Pleistocene), Comayagua Department, in association with the toxodont *Mixotoxodon laresensis*, the ground sloths *Eremotherium* sp. and *Megalonyx* sp., the mammoth *Mammuthus columbi*, the horse *Equus* sp., and the capybara *Hydrochaerus* sp. (Webb and Perrigo, 1984).

**Jamaica**

**Quaternary**

Several fossil remains referred to *Pseudemys terrapen* have been recovered from Late Pleistocene deposits at Wallingford Roadside Cave, in St. Elizabeth Parish, and from Lluidas Vale Cave, St. Catherine Parish (Williams, 1950).

**Mexico**

**Mesozoic**

**Late Jurassic.** *Notoemys tlaxiacoensis* (Platychelyidae) comprises the oldest turtle record in Mexico described from partial shell, preserving part of the carapace and plastron (Figure 3a) from Sabinal Formation (Kimmeridgian) of Yosobé, Tlaxiaco, Oaxaca (López-Conde et al., 2016).

**Cretaceous.** We know of Cretaceous fossil turtles in Baja California, Chiapas, Coahuila, Chihuahua, Puebla, Nuevo León and Sonora (see Figure 1). In the Early Cretaceous the turtle record is represented by tracks assigned to the ichnogenus *Emydiphus* found in the San Juan Raya Formation (lower Aptian) in Santa Ana Teloxtoc, Tehuacán, Puebla (Rodríguez-de la Rosa et al., 2017). The ichno fossil found was associated with traces of marine invertebrates, crocodyliforms, pterosaurs and non-avian dinosaurs. Two specimens referred to *Araripemydidae* (Pleuridora, Pelomedusoidei) (García and Reynoso-Rosales, 2006), as well as other specimens not yet determined (Figure 3e; Reynoso et al., 2000) are known from the Tlayúa Quarry (Albian), Puebla.

In the Late Cretaceous *Trionyx* sp. was reported by José Aguilera (1869), from the Division Parras, Parras, Coahuila (early Turonian). This report is the first known record of a fossil turtle for Mexico. Two protostegids, *Desmatochelys lowii*, and an undetermined form possibly belonging to a new taxon were reported from the Eagle Ford Formation (Turonian) from Múzquiz, Coahuila (Delgadillo-Escobar and Rodríguez-de la Rosa, 2011; Rodríguez-de la Rosa et al., 2011). Two unidentified turtle specimens were reported from Agua Nueva Formation (Turonian), in Vallecillo, Nuevo León (Blanco et al., 2001). One of these specimens is believed to be a *Desmatochelys* (Figure 3b). For the Coniacian there is a single report of turtle tracks in the sandstone of the Caracol Formation, exposed on the wall of an abandoned mine located within the municipalities of Mazapil and Concepción del Oro, Zacatecas (González-Romo et al., 2012; Figure 4a). Another protostegid specimen, referred as *Desmatochelys cf. D. lowii*, from the San Carlos quarry (Austin Formation, Campanian) was recently described (López-Conde et al., 2019; Figure 3d). This specimen preserves both articulated hindlimbs, elements not described before in *D. lowii* (López-Conde et al., 2019). Many fossil turtles have been reported at Cerro del Pueblo Formation, Coahuila (Campanian). From this formation *Toxochelys latiremis, Yelmocheles rosarioae*, *Euclastes coahuilaensis* (Figure 3c), *Chedghaii sp., Bothremys sp., Compsemys sp. Neurankylus sp., Adocus sp., Hoplochelys sp. have been reported, as well as unidentified specimens referred to Chelydridae, Pleurosternidae, Adocidae and Trionychidae (Rodríguez-de la Rosa and Cevallos-Ferriz, 1998; García and Reynoso-Rosales, 2002; Brinkman and Rodríguez-de la Rosa, 2006; Brinkman et al., 2009; Rivera-Sylva et al., 2011; Rodríguez-de la Rosa et al., 2011; Brinkman et al., 2016). On this locality, turtle tracks not related to any known ichnogenus and associated with theropod and pterosaur (*Pterachnium*) footprints were also reported in El Pelilal, Coahuila (Rodríguez-de la Rosa, 2003; Figure 4b). *Naomicheles* was reported for the “El Gallo” Formation in Baja California (Late Campanian) based on costal bone and plastron fragments that showed typical cylindrical tubers ornamentation (Rodríguez-de la Rosa and Aranda-Manteca, 2000). Additional taxa have been recently described at this Formation by López-Conde et al. (2018) that includes *Compsemys victa* and *Basilemys* sp., as well as fragment specimens referred to Trionychidae indeterminate and cf. Chelydridae. The first known turtle ichnos fossil record was reported at the Cañón del Tule Formation (Campanian), in the Ramos Arizpe municipality, Coahuila (Rodríguez-de la Rosa and Dávila-Rodríguez, 1998). Additional remains referred to Trionychidae have been found in Aguja Formation (Late Campanian), Javelina Formation (Maastrichtian) and San Carlos Formation (Coanacian-Maastrichtian), on the border between Chihuahua and Coahuila; and in the Corral del Enmedio Formation and Packard Formation, Cabullona Group (Late Campanian-Maastrichtian) in Sonora (Lucas et al., 1995;
Hoplochelys sp., the species *Yelmochelys rosarioae* and Trionychidae are also known for Cañón del Tule Formation, Coahuila (Maastrichtian) (Brinkman and Rodríguez-de la Rosa, 2006; Brinkman et al., 2016). In Southern Mexico, about seven carapace and plastron fragments and one femur from the Ocozocoautla Formation (Maastrichtian) have been reported (Figure 3f); however, the specimens have not been studied in detail and therefore their taxonomic identity is still unknown (Carbot-Chanona and Ovalles-Damián, 2013).

**Neogene**

**Miocene.** A new species of the family Carettochelyidae, *Allaeochelys liliae* (Figure 2c; Carbot-Chanona et al., 2020) from a single specimen recovered from the amber mines in the Simojovel (Mazantic Shale, lower Miocene) is known. Dermochelys, Mesochelonia and Syllomus have been reported from the Rosarito Beach Formation (middle Miocene) (Aranda Manteca, 2013). *Pseudemys* sp. and *Stylemys* sp. were reported in Potrero Zietla (late Miocene), Hidalgo (Castillo Cerón et al., 1996). Isolated carapace and plastron plates assigned to Testudinidae and Trionychidae were collected in a sequence of lacustrine sediments from the Tecolotlán Basin, Jalisco (late Miocene, Hemphillian) (Aguilar Cabrera et al., 2013). *Gopherus*, from Tecolotlán Basin was
also reported, but the exact locality where the specimen was found is not known (McDonald and Carranza-Castañeda, 2017). A shell referred to as cf. *Trachemys* sp. was collected at San Nicolás Formation, San Luis Potosí (late middle to late Miocene; Ferrusquía-Villafranca et al., 2014). Turtle shell remains, possibly belonging to *Geochelone* were found in Los Gigantes Basin (late Miocene), in Nayarit (Carranza-Castañeda, 2006). Remains of turtles assigned to Dermatemydidae and Trionychidae were recovered in Puente Ixcán (late Miocene) in Marqués de Comillas, Chiapas (Carbot-Chanona, 2011).

*Pliocene. Geochelone* sp. was recovered from Las Tunas, in Santa Anita, Los Cabos, Baja California (Miller, 1980); *Gopherus berlandieri* from El Fronton locality, Atotonilco, Hidalgo (Nájera Hernández, 2006); cf. *Gopherus* sp. from Yepomera, Chihuahua (Brattstrom, 1961); *Gopherus or Hesperotestudo* from San José de Pimas, La Colorada, Sonora (White et al., 2010); and *Testudo* sp., and *Kinosternon* sp. from La Goleta, Michoacán (Brattstrom, 1955). *Kinosternon* sp. from La Viga de Tula, Hidalgo (Castillo Cerón et al., 1996) was also reported. Brattstrom (1961) reported an unidentified turtle from Río Virgenes Village [sic], in Nuevo León.

Quaternary

**Pleistocene.** The turtle fossil record in the Pleistocene is the most abundant and diverse. *Kinosternon* and *Gopherus* are the genus with the most records. For *Kinosternon, K. scorioides* was reported from Los Tanques, Zacatecas (Guzmán and Polaco, 1998); Arroyo Cedazo, Aguascalientes (Mooser, 1986); Cueva Encantada, Chimualacatlán, Morelos (Arroyo-Cabales et al., 2004) and La Simpatía, Villa Corzo, Chiapas (Luna-Espinosa and Carbot-Chanona, 2009); *K. integrum* from Guílã Naquitz, Valles Centrales, Oaxaca (Flannery and Wheeler, 1986) and Jocotepec, Jalisco (Barrios Rivera, 1985); cf. *K. integrum* from Los Tanques, Zacatecas (Guzmán and Polaco, 2000); *K. hirtipes* from Jocotepec, Jalisco (Barrios Rivera, 1985); *K. hirtipes/integrum* from Santiago Chazumba, Oaxaca (Cruz et al., 2009); *K. flavescens* and *K. sonoriense* from La Brisa, Sonora (Van Devender et al., 1985); K. cf. *cruentatum/creaseri* for Actun Xpukil cave system, Yucatán (Barrios Rivera, 1985). *Kinosternon* sp. has been reported from Chihuahua (Chacón-Soria and Aguilar, 2010; White et al., 2010); Los Tanques, Zacatecas (Guzmán and Polaco, 1998, 2000); Rancho La Amapola and Laguna de la Media Luna, San Luis Potosí (Hernández Junquera, 1977; Lorenzo and Mirambell, 1986); La Cinta-Portalitos, in the Cintas-Politalito, in the Michoacán–Guanaajuato boundary (Moreno-Flores et al., 2017); Cueva Encantada, Chimualacatlán, Morelos (Arroyo-Cabales et al., 2004); Cerro Tlapacoya, Estado de México (Álvarez and Huerta, 1975); Potrero Zietla local fauna, Hidalgo (Castillo Cerón et al., 1996; López et al., 2002), and Santa Cruz Nuevo, Puebla (Tovar and Montellano, 2006; Tovar et al., 2007), and cf. *Kinosternon* sp. in Chimualacuatla, Estado de México (Barrios Rivera, 1985). *Gopherus. G. agassizi* from the Sonora coast was reported (Moodie and Van Devender, 1979); the new species *G. auffenbergi* (Figure 2d) from El Cedazo, Aguascalientes (Mooser, 1972); *G. berlandieri* from the Cañón Tecoral, in Tehuacán, Puebla; Actopán, Epazoyucan, and San Agustín Tlaxiaca, in Hidalgo (Nájera Hernández, 2006; Castillo-Cerón et al., 2009; and Cueva Santa María Chilchotla, in Oaxaca (Flannery, 1967); *Gopherus* cf. *G. berlandieri* from Santa Cruz Nuevo, Puebla (Tovar and Montellano, 2006; Tovar et al., 2007), *G. donalai* (Figure 2e) was described as a new species from Ejido San Lázaro, Villagrán, Tamaulipas (Yáñez and Montellano-Ballesteros, 2004); *G. flavomarginatus* for the Cedazo local fauna, Aguascalientes; Cerro Hervideros, Durango and Los Tanques, Zacatecas (Mooser, 1980, Guzmán and Polaco, 1998, 2000); *Gopherus* cf. *G. flavomarginatus* from Jiménez Cave, Chihuahua (Messing, 1986); *G. pargensis* was described as a new species from El Cedazo, Aguascalientes (Mooser, 1980), and *Gopherus* sp. from El Carrizal-Santa Rita–El Rifle area, Baja California Sur (Ferrusquía-Villafranca and Torres-Roldán, 1980); San Agustín Tlaxiaca, Hidalgo (Bravo-Cuevas, 2001); Santiago Chazumba, Oaxaca (Cruz et al., 2009); Pitiquito and Hermosillo, Sonora (White et al., 2010), and La Cinta-Portalitos, in the Michoacán–Guanaajuato boundary (Moreno-Flores et al., 2017).

*Trachemys* is another turtle with a good number of records in Pleistocene sediments from Mexico. *Trachemys scripta* has been reported in Atoyac, Veracruz (Peña-Serrano and Miranda-Flores, 2006), and La Simpatía, Villa Corzo municipality, Chiapas (Luna-Espinosa and Carbot-Chanona, 2009). *Trachemys* sp. have records in Los Tanques, Zacatecas (Guzmán and Polaco, 2000); San Buenaventura Nealtican, Puebla (Herrera-Flores, 2009) and Loltún cave, Yucatán (Cruz et al., 2016).

Other taxa that have been reported are *Claudius angustatus* for Atoyac, Veracruz (Peña-Serrano and Miranda-Flores, 2006); *Chelonia* sp. in Baja California Sur (González-Barba et al., 1998); *Terrapene culturatus* in Jocotepec, Jalisco (Barrios Rivera, 1985); cf. *Terrapene* sp. from Rancho La Brisa, Sonora (Van Devender et al., 1985); *Geochelone* sp. in Potrero Zietla local fauna, Hidalgo (Nájera Hernández and Castillo Cerón, 2004), El Cedazo, Aguascalientes (Mooser, 1980) and El Golfo, Sonora (Barrios Rivera, 1985); *Hesperotestudo* sp. in Puerto...
Peñasco and La Colorada, Sonora (White et al., 2010) and Epazoyucan, Hidalgo (Castillo-Cerón et al., 2009); Testudo sp. in El Cedazo, Aguascalientes (Mooser, 1958); Barranca de Acatlán, Tequisquiacc, Estado de México (Hibbard, 1955) and Atepetzingo, Valsequillo, Puebla (Güenthner, 1968); cf. Staurotypus sp. in La Simpatia, Villa Corzo, Chiapas (Luna-Espinosa and Carbot-Chanona, 2009); Rhinoclemmys sp. in Santa Cruz Nuevo, Puebla (Tovar and Montellano, 2006; Tovar et al., 2007); Chrysemys scripta in El Golfo, Sonora (Barrios Rivera, 1985); Pseudemys scripta for the Rancho Brisa locality, in Sonora (Van Devender et al., 1985) and Pseudemys sp. in Jocotepac, Jalisco and Teapa, Tabasco (Polaco-Ramos, 1981; Barrios Rivera, 1985), as well as Chelydridae and Trionychidae in Térapa, Sonora (Moscato and Jasinski, 2016).

Navassa Island, United States of America

Quaternary

Auffenberg (1967) reported several fragments remains of turtles and tortoises recovered from brecciated deposit at the top of a sink hole near the Navassa lighthouse that he referred to as Geochelone and Pseudemys.

Nicaragua

Quaternary

At El Bosque locality (Pleistocene), southwest of Pueblo Nuevo, Esteli Department, a turtle and a tortoise were documented, associated to megatheriid and megalonychid ground sloth, gomphotheres, horses, deer and toxodonts (Lucas et al., 2008).

Panama

Paleogene

Podocnemididae is known for the Gatunillo site, Gatunillo Formation (Late Eocene-Early Oligocene), Colón Province (Cadena et al., 2012).

Neogene

Testudinidae and Podocnemididae were recovered from the Culebra Formation (early Miocene), while Rhinoclemmys panamaensis (Figure 2f), Rhinoclemmys sp., Staurotypus moschus (Figure 2g), Testudinidae, Trionychidae and Podocnemididae were recorded in Cucaracha Formation (early Miocene), Centenario Bridge, in the Panama Canal basin, and Cheloniiidae from the Gatun Formation (late Miocene) (Cadena et al., 2012).

Puerto Rico

Paleogene

A fragmentary pelomedusid shell was described by Wood (1972) and assigned to Oligocene age. The specimen apparently comes from an uncertain locality along the highway between San Sebastian and Lares municipalities.

Quaternary

Testudo (Monachelys) monensis was described based on cranial, postcranial and appendicular remains from Lirio Cave, in Mona Island (Williams, 1952).

Sombrero Island, Anguilla

The only evidence of tortoise or turtles in the Sombrero Island is Emys sombreroensis, that was named based on plastron and carapace remaines recovered at Sombrero guano, a site rich in lime phosphate (Leidy, 1868). Additional material of this taxon was described by Julien (1878) and Auffenberg (1967).

DISCUSSION

Taxonomy

Today, 13 genera and two ichnogenera have been identified for the Mesozoic of Mexico, including three new species: Notoemyx tlaxiacensis, Yelmolchelys rosarioae and Euclastes coahuilaensis (Brinkman et al., 2009; Brinkman et al., 2016; López-Conde et al., 2016). Of these taxa, only the taxonomic status of E. coahuilaensis has changed, since Parham and Pyenson (2010), based on the results of their cladistic analyzes, found that E. coahuilaensis is separated from the Cenozoic species Euclastes wielandi and E. platyops, for which they erected the name Mexichelys, to include the species coahuilaensis.

Trionyx is another taxon reported for the Cretaceous of Coahuila (Aguilera, 1869). Meylan (1897) mentioned that Trionyx has served as a “garbage basket” since there has been a tendency to synonymize Trionychidae with the generic name. Today, Trionyx is considered a genus restricted to Africa and Asia (Rhodin et al., 2017) and it is not expected to be present in the American Continent. Then, the specimen described by Aguilera (1869), should be referred to Trionychidae. Similarly, the specimen determined as Bothremys sp. from the Cerro del Pueblo Formation, Coahuila (García and Reynoso-Rosas, 2002) was tentatively referred to as Chedighaii by Gaffney et al. (2006). However, the new taxonomic assignment was based on photographs of the specimens but it was not possible to observe diagnostic features that differentiate Bothremys from Chedighaii, such as the presence/absence of holes in the crushing surface of the maxilla-jugal (Gaffney et al., 2006). Recent work on the specimen by García and Reynoso (in prep.) suggests that the specimen may represent a new genus and species of Bothremyidae.

Among Cenozoic turtles, Pseudemys, Chrysemys and Trachemys have been reported at several Pleistocene localities. Reynoso (2006) pointed out that the fossils reported in Mexico as Pseudemys and Chrysemys are in fact Trachemys. Molecular studies show that Pseudemys, Chrysemys and Trachemys are distinct valid genera (Wiens et al., 2010; Guillon et al., 2012). As it is considered today, Pseudemys and Chrysemys are restricted to Canada and the US, but these taxa do not extend their distribution far south into Mexico. To have a proper species assignment in the Mexican fossils it is necessary to review in detail the morphology of the known material. Trachemys remains from Atoyac, Veracruz (Peña-Serrano and Miranda-Flores, 2006) and La Simpatia, Chiapas (Luna-Espinosa and Carbot-Chanona, 2009) were referred to T. scripta. Historically, Trachemys scripta was divided into several subspecies, but recently those subspecies were elevated to the rank of species (Fritz et al., 2012). So, Trachemys scripta’s distribution ranges from the southeastern part of the US, to as far south as northern Nuevo León, Mexico. The species from Atoyac can be easily assigned to T. venusta, based on distribution, but the remains from La Simpatia, Chiapas may be referred either to T. grayi or T. venusta which overlap distribution in Chiapas (Fritz et al., 2012; Rhodin et al., 2017). However, remains need to yield good diagnostic features in order to be reassigned to particular taxa. In the absence of diagnostic morphological characters in fossil specimens of both Veracruz and Chiapas, we recommended naming these specimens only at the genus level, Trachemys sp. as suggested by Reynoso (2006). Likewise, Pseudemys terrapen from Jamaica and Pseudemys cf. P. decussata from Cuba (Williams, 1950), should be referred to Trachemys, as indicated by Morgan (1993).
Terrapene culturatus reported in Jocotepec, Jalisco referred by Barrios Rivera (1985) is not a valid name since this species has never been described. Based on the recent distribution of Terrapene in Mexico (Rhodin et al., 2017), we believe it is possible that records of Jocotepec in Jalisco, and Rancho La Brisa in Sonora, may belong to Terrapene nelsoni.

A recent review of the specimens referred as cf. Hadrianus sp. and Stylenys sp. from the Oligocene Iniyoo Local Fauna, Oaxaca (Jiménez-Hidalgo et al., 2015), show that these specimens should be referred to as a different taxon (Carbot-Chanona et al., work in progress).

Gopherus is a taxonomically complicated genus that includes six extant and seven extinct species (Edward et al., 2016, Rhodin et al., 2017; Vlachos, 2018). Bramble (1982) synonymized the Irvingtonian G. auffenbergi of El Cedazo in Aguascalientes (Mooser, 1972), with G. berlandieri. Similarly, Gopherus pargensis (Mooser, 1980) was considered invalid because the species was described based on a shell fragment with no diagnostic morphological characters (Reynoso and Montellano-Ballesteros, 2004). However, Vlachos (2018) considered G. pargensis a junior synonym of G. auffenbergi, because both species share the singular costal morphology that characterizes G. auffenbergi.

Meylan (1995) argued that all North American fossil forms referred to Geochelone should be called Hesperotestudo, since Geochelone is a restricted genus for India, Pakistan, Sri Lanka and Myanmar (Rhodin et al., 2017). Meylan (1995) also suggested that small size Hesperotestudo should be referred to subgeneric Hesperotestudo and large size ones to Caudochelys. Then Geochelone sp. from Las Tunas fauna in Baja California Sur, El Golfo in Sonora, El Cedazo in Aguascalientes, Atotonilco in Hidalgo, the Gracias Formation in Honduras, and Barranca del Sisimico and El Hormiguero in El Salvador (Miller, 1980; Mooser, 1980; Barrios Rivera, 1985; Webb and Perrigo, 1984; Nájera Hernández and Castillo Cerón, 2004), should be referred to as Hesperotestudo. The specimens from Tomayate river in El Salvador referred to as Hesperotestudo crassiscutata (Cisneros, 2005), must be updated, as this taxon has only been reported in Pleistocene deposits from Florida, Georgia and Texas (Meylan, 1995; Hulbert and Pratt, 1998; Powell et al., 2016).

Testudo is another genus distributed only in southern Europe, northern Africa and Middle East (Rhodin et al., 2017). Then, the specimens reported for Pleistocene localities of El Cedazo in Aguascalientes, Barranca de Acatlán in Estado de Mexico, and Atetpetzingo in Puebla (Hibbard, 1955; Mooser, 1958; Güenther, 1968) and for the Pliocene locality La Goleta Formation in Michoacán (Brattstrom, 1955) should belong either to Gopherus or Hesperotestudo, but material needs to be reviewed.

“Testudo” costarricensis was considered evidence of a migration of tortoises from North America to South America and the antecessor of the genus Chelonoides (Segura, 1944). This taxon was later reclassified as Geochelone costarricensis (Auffenberg, 1971). It was even considered in a phylogenetic analysis (Coto Rojas and Acuña Mesen, 1986), however, “Testudo” costarricensis was based on an incorrect reconstruction of their carapace and plastron, and an reexamination of the holotype by Lichting et al. (2018) shows it to be identical to the tortoise Oligophorus laticuneus from the Oligocene of North America. Vlachos (2018) considers that “Testudo” costarricensis differs from Oligophorus laticuneus in the absence of a contact between marginal VI and pleural III, the rounded anterior plastral lobe, and the overlap of the pectoral scutes on the posterior part of the entoplastron, concluding that T. costarricensis should be referred as a different genus other than those named for North America.

The species from the Caribbean Islands, originally assigned to genus Testudo (e.g. T. cubensis and T. monensis), are now considered to belong to genus Chelonoidis (Franz and Franz, 2009).

Spatial and temporal distribution

In Mexico, turtle remains have been found in 24 states, excluding Campeche, Mexico City, Colima, Guerrero, Querétaro, Quintana Roo and Sinaloa, and only Coahuila, Puebla and Zacatecas have ichnological records. For Central America, there are fossil turtles in El Salvador, Honduras, Costa Rica and Panama (Figure 1). In the Caribbean Islands there are turtle remains in Cuba, Dominican Republic, Jamaica, the United States islands of Puerto Rico and Navassa, and the British Island of Sombrero in Anguilla. The temporal range includes from Late Jurassic to late Pleistocene (Figure 5).

Notoemys seems to be restricted to the American Continent. Four species have been described: N. oxfordensis from the Jagua Formation (Late Jurassic, Oxfordian), Cuba (de la Fuente and Iturralde-Vinent, 2001); N. zapataoensis of the Rosablanca Formation (Lower Cretaceous, Valanginian), Colombia (Cadena and Gaffney, 2005); N. laticentralis of the Vaca Muerta Formation, Argentina (Late Jurassic-Early Cretaceous, Tithonian-Berriasian) (Lapparent de Brion et al., 2007; Cadena and Joyce, 2015) and N. tlaxiacoensis of the Sabinal Formation (Late Jurassic, Kimmeridgiano), Mexico (López-Conde et al., 2016). Notoemys extends from the Oxfordian to the Valanginian and it appears to have a wide distribution range within the continent, from Colombia to Argentina (including the Caribbean islands), and N. tlaxiacoensis extended the geographic range to North America.

In the Aptian-Albian there are records of Araripemysidae only in central Mexico, and the family seems to be restricted for this interval of time worldwide. Araripemys was first described from gondwanic deposits: Araripemys barretoi from the Santana Formation (Lower Cretaceous, Aptian-Albian) in Brazil (Price, 1973; Meylan, 1996); and, Taquetochelys decorate from the basin of the Ténéré Desert (Lower Cretaceous, Aptian) in Niger (Broin, 1980; Pérez-García, 2019). It is possible that distribution in Mexico would extend its range to North America.

In the Upper Cretaceous of Mexico there are 13 families present: Adocidae, Baenidae, Bothremyidae, Cheloniiidae, Chelydridae, Compsemyidae, Helochelydridae, Kinosternoidae, Nanhsiungchelyidae, Pleurosternidae, Protostegidae, Solemyidae, and Trionychidae. Protostegidae is the only family with records in the Turonian and all other families are present in the Campanian. Cheloniiidae and Chelydridae are also known for the Maastrichtian, although these families extend their temporal range to the Recent (Ernst and Barbour, 1989; Meylan and Meylan, 2000). It is likely that the high diversity of families during the late Cretaceous of Mexico corresponds to the extension of the Western Interior Seaway and the predominance of warm global temperatures (Wrigth, 1987; Upchurch et al., 1998), factors that favored emergence of tropical ecosystems, which undoubtedly influenced the diversification of ectothermic sauropsids, such as turtles. In contrast, the few records and low diversity during the Paleocene of Mexico and Central America could be a consequence of the K-Pg extinction, or maybe, due to the little paleontological work has been done in these countries.

During the Neogene Testudines diversity rose again. Trionychidae, Emydidae and Testudinidae became the most extended families with the most records. Trionychidae was well represented from the Turonian to the Maastrichtian in northern Mexico (Aguilar, 1869; Rodríguez-de la Rosa and Cevallos-Ferriz, 1998; Brinkman and Rodríguez-de la Rosa, 2006; Brinkman, 2014; Brinkman et al., 2016). During the Paleogene, Trionychidae has been reported from the Early to the late Miocene, as far north as Jalisco in western Mexico, to Panamá (Aguilar Cabrera et al., 2013; Carbot-Chanona, 2011; Laurito et al., 2005; Cadena et al., 2012). The distribution of Trionychidae today extends as far north as in Mexican states bordering the United States (Legler and Vogt, 2013;
Rhodin et al., 2017), suggesting that the family went extinct in north central Mexico and Central America after the Miocene.

The fossil record of Testudinidae appears by the end of Paleogene in Mexico, consistent with those of the United States; however, in Central America this family appears by the early Neogene, and in the Caribbean Islands in the Pleistocene, but today, this family is extinct in these islands. The greatest diversity of Testudinidae in Mexico and Central America occurred from the late Miocene to the late Pleistocene. Today, only *Gopherus* is restricted to North America, extending as far south as southern Tamaulipas and Durango, while only *Chelonoidis* is present in Central America (south of Panama) (Rhodin et al., 2017).

The extension of the distribution range of the Testudinidae species was possibly favored by the cooling during the Eocene-Oligocene transition (Liu et al., 2009) with environmental conditions that prevailed until the Pleistocene. *Hesperotestudo* has been reported from central Mexico to Costa Rica, but this genus faced extinction in the Pleistocene. Conversely, the genus *Gopherus* that was very successful from the Miocene, still survives with five living species, of which *G. berlandieri*, *G. evgoodei*, *G. flavomarginatus* and *G. morafkai* are distributed in northern Mexico (Rhodin et al., 2017). *Gopherus agassizzi* was reported for the Sonoran coast (Pleistocene) (Moodie and Van Devender, 1979), although currently this area is occupied by *G.
morafkai (Murphy et al., 2011). The original taxonomic assignment to G. agassizzi was done considering that at the time, G. agassizzi was the only species considered for western North America. According to recent Gopherus species distribution in the area, it is more probable that the turtle of Moodie and Van Devender (1979) belongs to G. morafkai, but a detailed review of the material should be done before drawing final conclusions.

Fossil remains assigned to Gopherus sp. are known farther south from current distribution area. The genus has been reported from Baja California Sur, the border between Michoacán and Guanajuato and Estado de Mexico (Ferrusquía-Villafranca and Torres-Roldán, 1980, Moreno-Flores et al., 2017), and as far south as Oaxaca (Cruz et al., 2009). Gopherus flavomarginatus, is currently distributed in southeastern Chihuahua, southwest of Coahuila and north of Durango (Ernst and Barbour, 1989), but in the late Pleistocene it extended its distribution south to Aguascalientes and Zacatecas (Mooser, 1980; Guzmán and Polaco, 1998, 2000). Gopherus berlandieri is found in eastern Coahuila, Nuevo León to southern Tamaulipas and San Luis Potosi (Ernst and Barbour, 1989; Rhodin et al., 2017), but during the late Pleistocene it extended its distribution to the states of Aguascalientes, Puebla, Hidalgo and Oaxaca (Flannery, 1967, Mooser, 1972, Tovar and Montellano, 2006, Tovar et al., 2007, Castillo-Cerón et al., 2009). Gopherus doniolai (Reynoso and Montellano-Ballesteros, 2004), is a valid species different from the giant Gopherus turtles of North America. It is the youngest record of the giant turtle lineage with the southernmost distribution. Its discovery explains that changes in carapace morphology in ontogeny are more related to changes on size rather than to sexual dimorphism (Reynoso and Montellano-Ballesteros, 2004).

Currently, Kinosternon (Kinosternidae) includes around twenty species extending from Central and southeast of USA to northern Brazil and Argentina (Bonin et al., 2006; Rhodin et al., 2017). Fossils are known in Mexico and Central America from the Late Miocene to the Late Pleistocene, extending geographically from northern Mexico to El Salvador. Fossils of several Kinosternon species have been reported outside their current distribution area. This includes Kinosternon scorpionis reported from Zacatecas, Aguascalientes, Morelos and Chiapas (Mooser, 1980, Guzmán and Polaco, 1998; Arroyo-Cabrales et al., 2004; Luna-Espinosa and Carbot-Chanona, 2009), K. flavescens from Sonora (Van Devender et al., 1985), and K. hirtipes from Oaxaca (Cruz et al., 2009). We believe this material needs to be updated since geographical evidence may indicate that they are not well determined, or that their distribution in the past was much more extensive than today.

Trachemys (Emydidae), currently extends from southeast of USA to Brazil (Bonin et al., 2006; Fritz et al., 2012). Reports of Trachemys sp. from Zacatecas and Puebla (Guzmán and Polaco, 2000; Herrera-Flores, 2009) also need to be revised since nowadays, the distribution of Trachemys does not encompass states on the high plateau of Mexico (Legler and Vogt, 2013). Fossils of this genus have been reported from the late Miocene to the Late Pleistocene in Mexico and Central America. Its restricted distribution during the Neogene and Quaternary could be caused by droughts derived from the gradual cooling in the global climate.

CONCLUSION

The fossil record of turtles in Mexico, Central America and the Caribbean Islands is scarce but important, because they document the history of a large area that has served as a transition between the rest of North America and South America. It ranges from the Late Jurassic to the Late Pleistocene. However, as expected, there are still hiatuses in the chronological record since the reports of the Paleocene are null and very scarce for the Eocene and Oligocene, mainly because few outcrops are known to date. The periods with the greatest fossil record of Testudines are the Campanian and Pleistocene, being this last epoch where more species have been recorded. Among all fossil turtle reports, Kinosternon and Gopherus are the best represented taxa. Guatemala and Belize, in Central America, do not have reports of fossil turtles, perhaps, because few paleontological works have been done in those countries.

Finally, there is a lack of specialists for the study of fossil Testudines in Mexico, Central America and the Caribbean Islands, compared to the large number of specimens in museum collections that has not been studied.

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