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Taxonomía y sistemática de los Testudines del Oligoceno-Mioceno del sur de México

QUE PARA OBTENER EL GRADO DE

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PRESENTA

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Con fundamento en la **opinión favorable** emitida por escrito por la Comisión Revisora que analizó el trabajo terminal presentado por usted, denominado ***Taxonomía y sistemática de los Testudines del Oligoceno-Mioceno del sur de México*** cuyo director de tesis es el Dr. Gustavo Rivera Velázquez, quien avala el cumplimiento de los criterios metodológicos y de contenido; esta Dirección General a mi cargo **autoriza** la impresión del documento en cita, para la defensa oral del mismo, en el examen que habrá de sustentar para obtener el **Grado de Doctor en Ciencias en Biodiversidad y Conservación de Ecosistemas Tropicales.**

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ATENTAMENTE
"POR LA CULTURA DE MI RAZA"

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DEDICATORIA

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RESUMEN

Las tortugas (clado Testudines) habitan en casi todos los continentes del planeta. En la actualidad se conocen 356 especies, incluidas en 94 géneros y 14 familias. Desafortunadamente, 148 especies se consideran oficialmente amenazadas a nivel mundial. Por ello, el conocer la diversidad de tortugas en el pasado, así como los procesos de especiación, dispersión y extinción que se han suscitado a lo largo del tiempo geológico, es fundamental para sumar componentes que ayuden en la conservación de las especies de tortugas Recientes.

Aunque existen innumerables evidencias fósiles de vertebrados terrestres provenientes de yacimientos del Paleógeno y Neógeno en diversas localidades del sur y sureste de México, estos han sido poco estudiados desde un enfoque filogenético y biogeográfico, especialmente los Testudines. Para comenzar a subsanar esto, primeramente, se realizó una actualización del registro fósil osteológico e icnológico de Testudines en México, Centroamérica y las islas del Caribe. En México, el registro se extiende desde el Jurásico tardío hasta el Pleistoceno, fue muy abundante durante el Pleistoceno tardío y abarca una amplia distribución en el país. Por su parte, los registros icnológicos se conocen sólo para el Cretácico tardío de Coahuila, Puebla y Zacatecas. Para Centroamérica, se conocen registros fósiles de tortugas en el Pleistoceno de El Salvador y Nicaragua, Mioceno tardío-Pleistoceno de Honduras y Costa Rica, y Eoceno tardío-Mioceno tardío de Panamá, siendo este último, el país con más registros. En las Islas del Caribe, se han documentado fósiles de este grupo en el Jurásico, Mioceno y Pleistoceno de Cuba, Pleistoceno Tardío de República Dominicana, Jamaica, Islas Navassa e Isla Sombrero, y Oligoceno y Pleistoceno de Puerto Rico. Posteriormente, se estudiaron dos ejemplares de tortugas provenientes del Oligoceno y Mioceno del sur de América del Norte. El primer ejemplar proviene de la Formación Chilapa, que aflora en los alrededores del poblado Santiago Yolomécatl, Oaxaca. Su estudio permitió erigir un género y especie nueva. El nuevo taxón exhibe caracteres morfológicos que apoyan su inserción como un miembro basal del clado Testudinidae. Las relaciones filogenéticas del nuevo taxón se evaluaron utilizando un enfoque de evidencia total (morfológico + molecular), usando tres tipos de análisis: Máxima Parsimonia con Ponderación Implícita (MPPI), Máxima Parsimonia Estándar (MPE) e Inferencia Bayesiana (IB). Los resultados obtenidos por MPPI y MPE recuperaron al nuevo taxón en una posición basal dentro del clado Testudinidae. La nueva tortuga del Oligoceno de Oaxaca representa la primera tortuga Paleógena y la más sureña descrita para México, así como el miembro más antiguo del clado Testudinidae conocido en el país. El segundo ejemplar estudiado se rescató de los Esquistos Mazantic, en Simojovel de Allende, Chiapas, de edad Mioceno más temprano. Este nuevo ejemplar fue referido como una nueva especie del género *Allaeochelys* (clado Carettochelyidae), *A. liliae*, con base en la ausencia de escudos en el carapacho y plastrón, así como por la posesión de un plastrón ancho. *Allaeochelys liliae* se diferencia de otras especies de *Allaeochelys* por la siguiente combinación caracteres: ornamentación en el carapacho levemente marcada, con tubérculos y orificios pequeños poco profundos, xiphiplastron e hipoplastrón ornamentados con orificios y surcos vermiculares distribuidos uniformemente en toda la superficie, suprapygal con forma semi-triangular, pero con cinco bordes de contacto, y costal ocho en contacto con las periféricas nueve y diez. *Allaeochelys liliae*, representa el primer registro del clado Carettochelyidae en el Neógeno del continente americano, además de representar la primera especie descrita de este clado para el Aquitaniano (Mioceno temprano) en todo el mundo. La presencia de nuevos taxones en Oaxaca y Chiapas soporta la hipótesis de la importancia que tuvo del sur de México en la diversificación y dispersión de los Testudines durante el Oligoceno-Mioceno.

Palabras clave: Testudines, América del Norte, Paleógeno, Neógeno, filogenia, biogeografía.

ABSTRACT

Turtles (clade Testudines) inhabit on almost every continent on the planet. At present, 356 species are known, included in 94 genera and 14 families. Unfortunately, 148 species are considered officially threatened globally. This is why knowing the diversity of turtles in the past, as well as evolutionary processes that have arisen over geological time, is essential to add components that help in the conservation of Recent turtle species.

Although there are innumerable fossil evidences of terrestrial vertebrates from Paleogene and Neogene deposits in various localities of southern and southeastern Mexico, these have been little studied from a phylogenetic and biogeographic approach, especially the Testudines. To advance in its study, first, an updated osteological and ichnological fossil record of Testudines in Mexico, Central America and the Caribbean islands was carried out. In Mexico, the record extends from the late Jurassic to the Pleistocene and was very abundant during the Late Pleistocene, covering a wide distribution in the country. On the other hand, the ichnological records are known only for the late Cretaceous of Coahuila, Puebla and Zacatecas. For Central America, fossil records of turtles are known in the Pleistocene of El Salvador and Nicaragua, the late Miocene-Pleistocene of Honduras and Costa Rica, and the late Eocene-late Miocene of Panama, the latter being the country with most records. In the Caribbean Islands, fossils of this group have been documented in the Jurassic, Miocene and Pleistocene of Cuba, late Pleistocene of the Dominican Republic, Jamaica, Navassa Islands and Sombrero Island, and Oligocene and Pleistocene of Puerto Rico. Subsequently, two specimens of tortoises from the Oligocene and Miocene of southern North America were studied. The first specimen comes from the Chilapa Formation, which outcrops around the Santiago Yolomécatl town, Oaxaca. Its study allowed the creation of a new genus and species. The new taxon exhibits morphological characters that support its insertion as a basal member of the clade Testudinidae. The phylogenetic relationships of new taxon were evaluated using a total evidence approach (morphological + molecular), using three types of analysis: Implied Weighted Maximum Parsimony (IWMP), Standard Maximum Parsimony (SMP), and Bayesian Inference (BI). The results obtained by IWMP and SMP recovered the new in a basal position within the clade Testudinidae. This new taxon represents the first Paleogene and southernmost tortoise described for Mexico, as well as the oldest member of the clade Testudinidae known in the country. The second specimen studied was recovered from the Mazantic Shale, in Simojovel de Allende, Chiapas, earlier Miocene age. The new specimen was referred as a new species of the genus *Allaeochelys* (clade Carettochelyidae), *A. liliae*, is based on the loss of carapacial and plastral scutes and a large plastron. *Allaeochelys liliae* differs from other *Allaeochelys* by the following unique combination of characters: slightly marked carapace ornamentation, with small shallow tubers and pits, xiphiplastron and hypoplastron ornamented with vermicular pits and grooves evenly distributed over the entire surface, suprapygal with semi-triangular shape, but with five contact edges, and eight ribs in contact with the peripherals nine and ten. It represents the first record of Carettochelyidae clade in the Neogene of the American continent, and it is the first *Allaeochelys* described for the Aquitanian (early Miocene) worldwide. The presence of new taxa in Oaxaca and Chiapas supports the hypothesis of the importance of southern of Mexico in the diversification and dispersal of the Testudines during the Oligocene-Miocene interval.

Keywords: Testudines, North America, Paleogene, Neogene, phylogeny, biogeography.

CAPÍTULO I

1.1. INTRODUCCIÓN GENERAL

Testudinata Klein 1760, es un grupo de saurópsidos que se define como el clado que posee un caparazón de tortuga completamente desarrollado (Joyce *et al*., 2021). Este grupo se determina por una serie de características morfológicas, como son: i) un escudo óseo dorsal (caparazón) formado por huesos costales fusionados con costillas endocondrales y huesos neurales fusionados con vértebras torácicas; ii) un escudo óseo ventral (plastrón) formado por la interclavícula, clavícula y de tres a cinco huesos fusionados entre sí; iii) lámina de la escapula por debajo de las costillas; iv) postparietal ausente; v) lagrimal pequeño o ausente; vi) maxilar, premaxilar y dentario edentados; vii) postfrontal ausente, y viii) supratemporal ausente (presente sólo en las formas basales como *Proganochelys*) (Gaffney y Meylan, 1988; Gaffney, 1990; Rieppel y Reiz, 1999; Carroll, 2013).

Los miembros basales de Testudinata incluyen a *Proganochelys quenstedti*, del Triásico superior (Noriano) de Alemania (Gaffney, 1990); *Proganochelys tenertesta* del Triásico superior (Noriano), del Condado Quay, Nuevo México, EUA (Joyce *et al*. 2009; Joyce, 2017); *Proganochelys ruchae* del Triásico superior (Noriano), de la Provincia Phetchabun, Tailandia (Broin, 1984); *Proterochersis robusta* y *Proterochersis limendorsa*, del Triásico superior (Noriano) de Baden-Württemberg, Alemania (Szczygielski & Sulej, 2016); *Proterochersis porebensis*, del Triásico superior (Noriano), de Silesian Voivodeship, Polonia (Szczygielski y Sulej, 2016; Joyce, 2017); *Palaeochersis talampayensis*, del Triásico superior (Noriano), de La Rioja, Argentina (Rougier *et al*., 1995) y *Australochelys africanus*, del Jurásico inferior (Hettangiano/Sinemuriano), Orange Free State, Sudáfrica (Gaffney y Kitching, 1994, 1995).

Por su parte, Testudines hace referencia al grupo-corona que incluye a todas las formas de tortugas vivientes y sus ancestros más cercanos (Joyce *et al.*, 2004). Este grupo era considerado como un grupo de saurópsidos anápsidos (Gaffney y Meylan, 1988). Sin embargo, estudios morfológicos y moleculares demuestran que son diápsidos estrechamente relacionados con Archosauromorpha (Rieppel y deBraga, 1996; Crawford *et al*., 2012; Field *et al*., 2014; Shaffer *et al*., 2017).

Las tortugas habitan en casi todos los continentes del planeta −excepto en la Antártida− debido a su enorme diversidad, que incluye formas terrestres, de agua dulce y marinas (Ernst y Barbour, 1989). En la actualidad se conocen 356 especies, incluidas en 94 géneros y 14 familias (Rhodin *et al*., 2017). Desafortunadamente, 148 especies se consideran oficialmente amenazadas a nivel mundial (En Peligro Crítico, En Peligro o Vulnerable; IUCN, 2016). Es por eso, que conocer la diversidad de tortugas en el pasado, así como los procesos de especiación, dispersión y extinción que se han suscitado a lo largo del tiempo geológico, es fundamental para sumar componentes que ayuden en la conservación de las especies de tortugas Recientes.

Esta tesis está estructura en cinco capítulos. El Capítulo I abarca la Introducción general, Justificación, Objetivos y un Marco Teórico Metodológico, este último, destinado a explicar los principios en los que se basan los programas utilizados en este trabajo, con los que se propusieron las hipótesis filogenéticas de los ejemplares aquí estudiados. En el Capítulo II se hace una recopilación del registro publicado de tortugas fósiles en México, Centroamérica y las Islas del Caribe, con el fin de entender sus patrones de distribución temporal y geográfico. De igual manera, en este capítulo se discute la validez de las asignaciones taxonómicas que se han realizado al estudiar el material de tortugas fósiles de estas tres regiones. En el Capítulo III se describe una nueva tortuga del Oligoceno temprano de Oaxaca y se explora su relación filogenética dentro del clado Testudinidae, utilizando una matriz de datos de evidencia total (morfológico + molecular). En el Capítulo IV se describe una especie nueva de tortuga del Mioceno temprano de Chiapas. La posición filogenética de la nueva especie se explora bajo un análisis de máxima parsimonia y su importancia biogeográfica es comentada. Por último, en el Capítulo V se plasma la discusión general y las conclusiones obtenidas con este trabajo.

1.1.2. Justificación

Diversos estudios demuestran que el sur-sureste de México ha sido un punto geográfico clave, donde han ocurrido procesos de especiación. Hasta ahora, los estudios se han centrado principalmente en crustáceos y peces del Cretácico tardío de Chiapas (*e.g*. Vega *et al.*, 2001, 2006, 2018; Alvarado-Ortega y Than-Marchese, 2012; 2013; Díaz-Cruz *et al*., 2016; 2019). Por el contrario, los yacimientos del Paleógeno y Neógeno del sur de México han sido poco explorados y los estudios enfocados en conocer la paleobiodiversidad del área apenas empiezan a tomar fuerza. Como consecuencia, varios grupos de vertebrados son poco conocidos, en especial el de los Testudines, que están representados por algunos ejemplares provenientes de las localidades Santiago Yolomecatl (NALMA Arikareeano, Oligoceno temprano), al noroeste de Oaxaca (Jiménez-Hidalgo *et al.*, 20015, 2019; Guerrero-Arenas *et al*., 2020) y Los Pocitos (Mioceno Inferior, Aquitaniano), Simojovel de Allende, norte de Chiapas, que no han sido descritos formalmente, por lo que su identidad taxonómica es desconocida. En consecuencia, al presente no se conoce el papel que desempeñó el sur de México en la evolución, diversificación y dispersión de los Testudines continentales.

Por tal motivo, es importante la descripción detallada de los ejemplares encontrados en las localidades de Oaxaca y Chiapas, identificarlos específicamente, e incluirlos en análisis que permitan reconstruir sus relaciones filogenéticas y paleobiogeográficas.

1.2. HIPÓTESIS

Los fósiles de Testudines rescatados en las localidades del Oligoceno temprano de Oaxaca y Mioceno de Chiapas, representan taxones nuevos, que servirán para entender el origen y evolución del grupo dentro de un contexto temporal y geográfico.

1.3. OBJETIVO

Describir y establecer las relaciones filogenéticas y paleobiogeográficas de los ejemplares de Testudines del Oligoceno-Mioceno de Oaxaca y Chiapas.

1.3.1. Objetivos particulares

- Describir a detalle los ejemplares de Testudines provenientes de las localidades del Oligoceno de Oaxaca y del Mioceno de Chiapas.

- Comparar morfológicamente los ejemplares del Oligoceno de Oaxaca y del Mioceno de Chiapas con taxones provenientes de otras localidades de América del Norte, con el fin de establecer sus particularidades y establecer si se trata de entidades taxonómicas nuevas o ya conocidas.

- Realizar análisis filogenéticos basados en caracteres morfológicos con el propósito de establecer las relaciones de los ejemplares de Testudines del Oligoceno de Oaxaca y del Mioceno de Chiapas.

- Plantear hipótesis paleobiogeográficas robustas basadas en la filogenia de los ejemplares estudiados, con el fin de establecer la importancia del sur de México en la diversificación y dispersión de los Testudines durante el Oligoceno-Mioceno de América de Norte.

1.4. MARCO TEÓRICO METODOLÓGICO

La cladística o sistemática filogenética es uno de los métodos más ampliamente utilizados en la taxonomía y se emplea básicamente para reconstruir clasificaciones naturales, además de que es aplicada en disciplinas como la biogeografía, la ecología, la etología, la conservación y la evolución (Morrone, 2013).

La sistemática cladística se basa en los principios de Henning (1966) y construye los cladogramas (árboles) usando el algoritmo de Wagner. Un árbol de Wagner es un árbol creado agregando secuencialmente los taxones en la rama más parsimoniosa disponible (Farris, 1970). En este método, solo se usa parte de los datos de cada punto durante la adición de taxones. Un taxón puede colocarse mejor en alguna parte del árbol cuando solo se usan algunos taxones, pero puede colocarse mejor en otro lugar cuando se incluyen todos los taxones. Por lo tanto, los taxones que se han agregado determinan el resultado de un árbol de Wagner para un conjunto de datos grandes, de modo que diferentes secuencias de adición conducirán, a resultados diferentes.

Debido a que parte central de este trabajo se basa en la generación de hipótesis filogenéticas, a continuación, se explican los principios en los que se basan los programas utilizados en esta tesis para la búsqueda de los cladogramas más parsimoniosos.

1.4.1. Análisis de parsimonia usando TNT (*Tree Analysis Using New Technology*)

Se han desarrollado diversas herramientas computacionales para construir cladogramas de forma eficiente y rápida, como Hennig86 (Farris, 1988), PAUP (Swofford, 2002), Nona (y sus descendientes; Goloboff, 1994, 1996a, 1996b) o Winclada (Nixon, 1999a). Sin embargo, estas herramientas han quedado a deber ante el incesante incremento del tamaño de los conjuntos de datos, que incluyen gran número de taxones terminales y caracteres morfológicos o moleculares. En respuesta nació TNT (*Tree Analysis Using New Technology*, Goloboff *et al*., 2008), una herramienta que incorpora nuevos algoritmos incorporados en el menú “New Technology” que permiten búsquedas de árboles más rápidos, aunque se usen juegos de datos grandes (hasta 50 veces más rápido que PAUP; Goloboff *et al*., 2008). Estos algoritmos incluyen *Ratchet*, *Tree Drifting*, *Sectorial Searches* y *Tree Fusing* (Goloboff *et al*., 2008).

1.4.1.1. Ratchet. Esta técnica fue desarrollada por Nixon (1999b) y funciona ponderando o eliminando de manera selectiva un porcentaje de los caracteres. Las topologías de los árboles se obtienen utilizando *Random Addition Sequence* (RAS [Secuencia de Adición Aleatoria]) y *Tree Bisection Reconnection* (TBR [Reconección de Árbol Biseccionado]). El TBR es una técnica ampliamente utilizada para hacer más eficiente el proceso de búsqueda de los árboles producidos por el método Wagner. Durante este proceso se intercambian ramas entre los árboles producidos, al tiempo que se evalúa la parsimonia de cada uno de estos después de cada reordenamiento. Si un nuevo árbol es más parsimonioso que el previo, este se conserva y lo reemplaza; contrariamente, si el nuevo árbol es menos parsimonioso, se deshecha y se continúa el proceso. El reordenamiento de ramas entre árboles se repite miles de veces hasta encontrar el árbol, o árboles, más parsimoniosos (Nixon, 1999b).

En el *Ratchet*, durante la fase de TBR, se llevan a cabo perturbaciones en los árboles de Wagner previamente encontrados. En cada perturbación se cambia el peso de los caracteres antes de realizar la búsqueda de los árboles más parsimoniosos. Estas fases de perturbación son de tres tipos: *original weight*, manteniendo el peso original; *upperweight*, aumentando el peso de ciertos caracteres y *under-weight,* disminuyendo el peso de los caracteres. Estas perturbaciones se alternan cada una con una fase de búsqueda (*search*) de los mejores árboles, entre los posibles nuevos árboles generados. Estas perturbaciones y búsquedas se realizan hasta cierto límite de sustituciones o hasta que un determinado porcentaje del proceso de reordenamiento de las ramas de los árboles generados se haya alcanzado, parámetros que pueden ser previamente definidos por el usuario.

1.4.1.2. Tree Drifting. Es un método de perturbación de árboles similar al *Ratchet* que se basa también en el proceso de reordenamiento de ramas. Sin embargo, en lugar de recalibrar el peso de los caracteres, calcula la diferencia de ajuste (*fit*) entre los árboles que sufren intercambio en la etapa del proceso de reordenamiento y el del árbol siguiente que se produce. Con esta medida, el programa sólo permitirá la realización de reordenamientos de ramas que generen los nuevos árboles más parecidos (árboles sub-óptimos) dentro del límite establecido por este ajuste (Goloboff, 1999).

El *fit* es un índice que se presenta de dos formas: el *fit* absoluto y el *fit* relativo. La diferencia entre dos *fit* absolutos se obtiene calculando la diferencia en el número de pasos entre dos cladogramas, mientras que la diferencia entre *fit* relativos (RFD) entre dos cladogramas (A y B) se calcula mediante la fórmula: RFD = (FC)/F, donde F es la suma de la diferencia entre el número de pasos de los caracteres que son más parecidos al cladograma A que el cladograma B y C, que a la suma de los caracteres que son más parecidos en el cladograma B con relación al cladograma A (Goloboff y Farris 2001).

1.4.1.3. Sectorial Search. Es una forma especial de reorganización de ramas que necesita un árbol como punto de partida. Se basa en seleccionar diferentes sectores del árbol, volviéndolos a analizar por separado; si se encuentra una mejor configuración, se reemplaza en todo el árbol. Los conjuntos de datos reducidos se pueden analizar muy rápidamente y se forman representando nodos internos por sus conjuntos de estados de primer paso (el nodo basal debe representarse por el conjunto de estados de primer paso calculado hacia arriba). Los sectores se pueden seleccionar de dos maneras, al azar o con base en un consenso (Goloboff, 1999).

1.4.1.4. Tree Fusing. Se basa en el intercambio de subgrupos entre diferentes árboles. Los subgrupos deben tener una composición idéntica. Estos cambios se realizan calculando el número de pasos del árbol resultante de esta fusión entre el subgrupo transferido y el árbol objetivo. Múltiples subgrupos se transfieren entre los árboles, generando nuevos árboles más parsimoniosos hasta alcanzar un patrón óptimo global. Los mecanismos de reordenamiento de ramas se realizan entonces en estos nuevos árboles, para encontrar patrones aún más parsimoniosos (Goloboff, 1999).

1.4.2. Análisis de parsimonia en TNT usando ponderación

Goloboff (1993, 1997) optimizó los métodos para ponderar caracteres de acuerdo con su homoplasia: Ponderación Implícita (*Implied Weighting*) y Optimización Auto-ponderada (*Self-weighted optimization*). La Ponderación Implícita da peso a los caracteres como un todo (Goloboff, 1993), mientras que la Optimización Auto-ponderada fue diseñada para ponderar las transformaciones entre los estados de los caracteres. Con frecuencia, la Optimización Auto-ponderada produce transformaciones de estado de carácter asimétricas, según el número de transformaciones entre cada estado de carácter (Goloboff, 1997). El análisis de Ponderación Implícita da peso a los caracteres como un todo usando un valor *K* que determina que tan fuerte serán los análisis de la homoplasia. A mayor valor de *K* se favorecen las apormofias y se disminuye el peso de las homoplasias (Goloboff, 1993, 1997); dando como resultado una mejor resolución de los árboles.

1.4.3. Inferencia Bayesiana en Mr-Bayes

La inferencia Bayesiana tiene ventaja sobre otros métodos de inferencia filogenética, principalmente en la fácil interpretación de resultados, la habilidad de incorporar información *a priori* y ventajas computacionales (Huelsenbeck y Ronquist, 2001). Aunque el método de inferencia Bayesiana fue propuesto para inferir filogenias usando datos moleculares, en los últimos años ha sido usado para reconstruir filogenias con datos morfológicos siguiendo las recomendaciones de Lewis (2001), las cuales describen una serie de pasos que modelan la evolución de los caracteres discretos en un marco simple, utilizando un mínimo de suposiciones. El modelo de Lewis (2001) asume que un carácter morfológico puede cambiar su estado en cualquier momento, con la misma probabilidad para todos los intervalos de tiempo a lo largo de una rama.

La principal característica de los modelos Bayesianos es el uso explícito de la probabilidad para cuantificar la incertidumbre en inferencias basadas en el análisis de datos estadísticos (Gelman *et al*., 2004). Este supuesto es utilizado en Mr-Bayes (Huelsenbeck y Ronquist, 2001), un software que utiliza el algoritmo *Markov chain Monte Carlo* (MCMC) para aproximar la probabilidad posterior de un árbol. Mr-Bayes lee archivos en formato NEXUS (ver Maddison *et al*., 1997) y funciona con una interfaz de línea de comandos, desde donde el usuario puede cambiar los modelos de sustitución y las preferencias del análisis. Aunque originalmente Mr-Bayes solo admitía modelos filogenéticos simples, la última versión puede trabajar con datos binarios, "estándar" (morfología), de nucleótidos y aminoácidos, así como con datos mixtos (Ronquist y Huelsenbeck, 2003). Estos últimos permiten trabajar con matrices donde se pueden combinar datos morfológicos y moleculares a través de particiones, cada una con parámetros vinculados o desvinculados entre sí (Ronquist *et al*., 2012).

El algoritmo MCMC es un método para tomar muestras válidas, aunque dependientes, de la distribución de probabilidad de interés (en este caso, las probabilidades posteriores de los árboles filogenéticos; Huelsenbeck y Ronquist, 2001). El algoritmo MCMC básico funciona de la siguiente manera: primero se propone un estado nuevo para la cadena mediante un mecanismo estocástico. Luego, se calcula la probabilidad de aceptación para este nuevo estado, tomando en cuenta que la probabilidad de aceptación de este nuevo estado es como mínimo igual a uno; donde la relación de probabilidad es la relación de las probabilidades del estado nuevo al estado anterior, la relación anterior es la relación de la probabilidad previa del estado nuevo al estado antiguo, y la relación propuesta es la relación entre la probabilidad de proponer un estado antiguo y la probabilidad de proponer un estado nuevo. Posteriormente, se extrae una variable aleatoria uniforme (0, 1). Si este número es menor que la probabilidad de aceptación, entonces se acepta el nuevo estado y se actualiza el estado de la cadena, de lo contrario, la cadena permanece en el estado anterior. Este proceso de proponer y aceptar/rechazar nuevos estados se repite miles o millones de veces. La proporción del tiempo que se visita un solo árbol durante el curso de la cadena es una aproximación válida de su probabilidad posterior (Huelsenbeck y Ronquist, 2001).

La implementación de análisis bayesianos usando datos morfológicos en grupos fósiles ha demostrado tener buenos resultados (*e.g.* Prieto-Márquez, 2010; Brusatte *et al*., 2016; Díaz-Cruz *et al*., 2019). Sin embargo, la implementación del modelo parece ser apropiada solo si se incluyen autapomorfías (Müller y Reisz, 2006).

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CAPÍTULO II

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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2.1. 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 Queretaro, 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 tlaxiacoensis*, *Yelmochelys rosarioae*, *Mexichelys coahuilaensis*, *Allaeochelys liliae*, *Gopherus donlaloi*, *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 nicoyama*); 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*).

Keywords: Cryptodira, Pleurodira, Mesozoic, Paleogene, Neogene, Cenozoic, Mexico, Central America.

2.2. 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 los 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 solamente existen en Coahuila, Puebla y Zacatecas. En América Central existen reportes de tortugas fósiles en El Salvador, Honduras, Costa Rica, Nicaragua y Panamá, siendo este último el país con más registros; y en las islas del Caribe incluye Cuba, República Dominicana, Jamaica, las islas de Puerto Rico y Navassa, ambos territorios estadounidenses y la isla británica de Sombrero en Anguila. Siete especies fósiles se han descrito como nuevas en México (*Notoemys tlaxiacoensis*, *Yelmochelys rosarioae*, *Mexichelys coahuilaensis*, *Allaeochelys liliae*, *Gopherus donlaloi*, *G. auffenbergi* y *G. pargensis*, de las cuales *G. auffenbergi* se sinonimizó con *G. berlandieri* y *G. pargensis* es considerado un *nomen vanum*), dos en Panamá (*Rhinoclemmys panamaensis* y *Staurotypus moschus*) y una en Costa Rica (*Rhinoclemmys nicoyama*), dos en Cuba (*Notoemys oxfordensis* and *Chelonoidis cubensis*); una en República Dominicana (*Chelonoidis*

marcanoi), una en Puerto Rico (*Chelonoidis monensis*) y una en la Isla Sombrero, Anguila (*Chelonoidis sombrerensis*).

Palabras clave: Cryptodira, Pleurodira, Mesozoico, Paleógeno, Neógeno, Cenozoico, México, América Central.

2.3. 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; Szczygielski 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 reptiles in Mexico until then. In that publication he mentioned 89 fossil turtle records from the Late Cretaceous to the Pleistocene, located all over Mexico. Later, Chávez Galván *et al*. (2013) created a synopsis of Quaternary Mexican herpetofauna extracted from paleontological and archeological sites; and most recently Brinkman (2014) compiled Mesozoic turtles of Mexico particularly focused on reports from the Cerro del Pueblo and Cañón del Tule formations in Coahuila, and the Cabullona Group in Sonora, but left out several turtle records reported in other locations. However, the Central American and Caribbean Islands fossil record of turtles has been left aside and has only been partially summarized by Cadena *et al*. (2012) and Albury *et al*. (2018).

To understand the patterns of temporal and spatial distribution of this group in the northern hemisphere, here we present a detailed compilation of fossil turtles in Mexico, Central America and the Caribbean Islands, including the ichnological record, previously ignored in former compilations. Once this information is available, we will have an updated overview of the raw paleobiodiversity of fossil turtles in the region.

2.4. 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; Chávez Galván *et al*., 2013; Cadena *et al*., 2012, 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 10,000 years (Buitrón *et al*., 2010). Because of this, reports from some islands in the Caribbean Islands dated as late Holocene, were not included.

2.5. 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, six Miocene, five Pliocene 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 Oligoene 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.

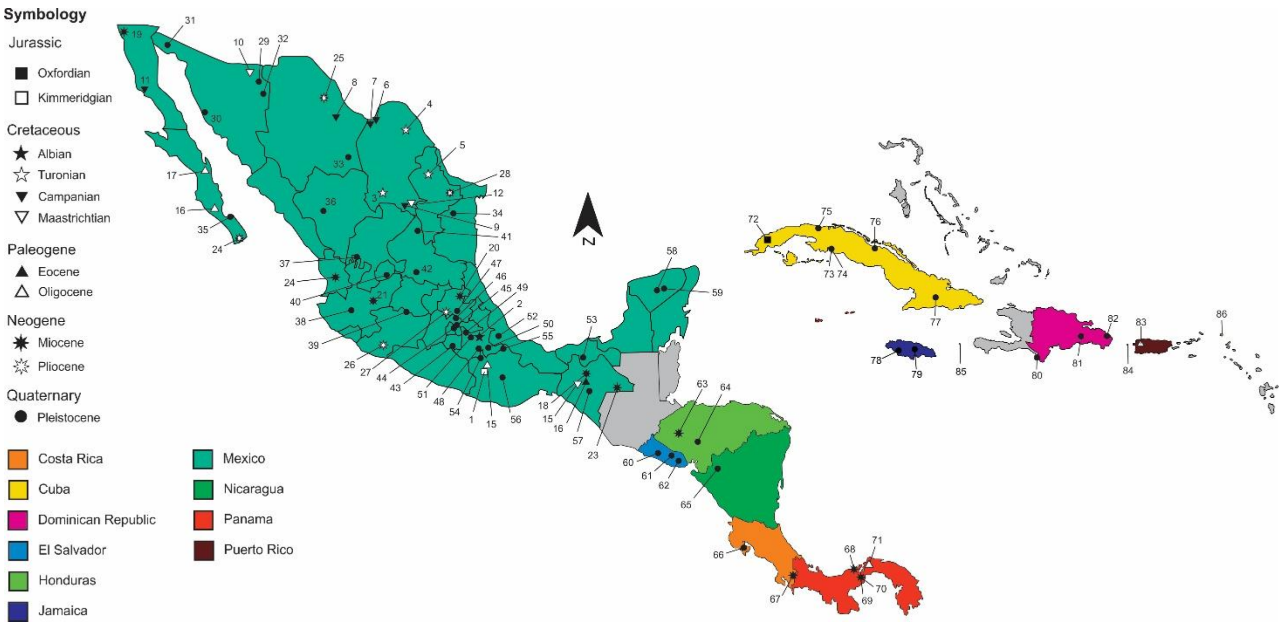

Figure 1. Map showing the locations of fossil remains of Testudines in Mexico, Central America and Caribbean islands. **Mexico**: 1) Tlaxiaco, Oaxaca (Kimmeridgian); 2) Tlayua Quarry, Puebla (Albian); 3) Parras Basin, Coahuila (Turonian); 4) Múzquiz, Coahuila (Turonian); 5) Vallecillo, Nuevo León (Turonian); 6) Javelina Fm., Coahuila (Campania); 7) Aguja Fm., Coahuila (Campanian); 8) San Carlos Fm., Chihuahua (Campanian); 9) Cerro del Pueblo Fm., Coahuila (Campanian); 10) Cabullona Group, Sonora (Maastrichtian); 11) "El Gallo" Fm., Baja California (Campanian); 12) Canyon del Tule Fm., Coahuila (Maastrichtian); 13) Ocozocoautla Fm., Chiapas (Maastrichtian); 14) Mesa de Copoya, Chiapas (middle Eocene); 15) Yolomécatl, Oaxaca (early Oligocene); 16) El Cien Fm., Baja California Sur (late Oligocene); 17) San Gregorio Fm., Baja California Sur (late Oligocene); 18) Simojovel, Chiapas (early Miocene); 19) Rosarito Beach Fm., Baja California (middle Miocene); 20) Protero Zietla, Hidalgo (late Miocene); 21) Tecolotlán Basin, Jalisco (late Miocene); 22) Los Gigantes Basin, Nayarit (late Miocene); 23) Puente Ixcán, Chiapas (late Miocene); 24) Santa Anita, Baja California Sur (Pliocene); 25) Yepomera, Chihuahua (Pliocene); 26) La Goleta Fm., Michoacan (Pliocene); 27) Vigo de Tula, Hidalgo (Pliocene); 28) Río Vírgenes, Nuevo León (Pliocene); 29) La Brisca, Sonora (Pleistocene); 30) Sonora coast (Pleistocene); 31) El Golfo, Sonora (Pleistocene); 32) Terapa, Sonora

(Pleistocene); 33) Jiménez Cave, Chihuahua (Pleistocene); 34) Ejido San Lázaro, Municipality of Villagrán, Tamaulipas (Pleistocene); 35) The Carrizal-Santa Rita-El Rifle, Baja California Sur (Pleistocene); 36) Cerro Hervideros, Durango (Pleistocene); 37) Los Tanques, Zacatecas (Pleistocene); 38) Jocotepec, Jalisco (Pleistocene); 39) La Cinta-Portalitos, Michoacán-Guanajuato boundary (late Pleistocene); 40) El Cedazo, Aguascalientes (Pleistocene); 41) Rancho La Amapola, San Luis Potosí (Pleistocene); 42) Laguna de la Media Luna, San Luis Potosí (late Pleistocene); 43) Cueva Encantada, Chimalacatlán, Morelos (Pleistocene); 44) Cerro Tlapacoya, Mexico State (Pleistocene); 45) Chimalhuacan, Mexico State (Pleistocene); 46) Barranca de Acatlán, Tequixquiac, Mexico State (Pleistocene); 47) San Agustín Tlaxiaca, Hidalgo (late Pleistocene); 48) Santa Cruz Nuevo, Puebla (Pleistocene); 49) San Buenaventura Nealtican, Puebla (Pleistocene); 50) Cañón Tecorral, Tehuacán, Puebla (Pleistocene); 51) Atepetzingo, Valsequillo, Puebla (late Pleistocene); 52) Atoyac, Veracruz (late Pleistocene); 53) Teapa, Tabasco (late Pleistocene); 54) Santiago Chazumba, Oaxaca (late Pleistocene); 55) Cueva Blanca, Oaxaca (Pleistocene); 56) Guilá Naquitz, Central Valleys, Oaxaca (Pleistocene); 57) La Simpatía, Villa Corzo, Chiapas (late Pleistocene); 58) Actun, Yucatán (late Pleistocene); 59) Loltún Cave, Yucatán (late Pleistocene). **El Salvador**: 60) Tomayate River (late Pleistocene); 61) Barranca El Sisimico (late Pleistocene); 62) El Hormiguero (late Pleistocene). **Honduras**: 63) Gracias Fm. (Miocene); 54) Orillas del Humuya, Comayagua (late Pleistocene). **Nicaragua**: 65) El Bosque, Pueblo Nuevo (late Pleistocene). **Costa Rica**: 66) Nacaome River, Barra Honda Nicoya (late Pleistocene); 67) El Limoncito, Puntarenas (late Miocene). **Panama**: 68) Gatum Fm. (late Miocene); 69) Culebra Fm., Gaillard Cut, Panama Canal Basin (early Miocene); 70) Cucaracha Fm., Gaillard Cut, Panama Canal Basin (early-middle Miocene); 71) Gatuncillo Fm., Gatun Locks, area of Colon, Panama Canal Basin (Oligocene). **Cuba**: 72) Jagua Fm., Viñales (Oxfordian); 73) Cueva de Los Machos, Cienfuegos, Santa Clara Province (late Pleistocene); 74) Ciego Montero, Cienfuegos, Santa Clara Province (late Pleistocene); 75) Hato Nuevo, Matanzas Province (late Pleistocene); 76) Sierra de Jatibonico (late Pleistocene); 77) Daiquiri, Oriente Province (late Pleistocene). **Jamaica**: 78) Wallingford Roadside Cave, St. Elizabeth Parish (late Pleistocene); 79) Lluidas Vale Cave, St. Catherine Parish (late Pleistocene). **Dominican Republic**: 80) Bayaguana, San Cristobal Province (late Pleistocene); 81) Pedernales Province (late Pleistocene); 82) Oleg's Bat Cave, La Altagracia Province (late Pleistocene). **Puerto Rico**: 83) Road between San Sebastian and Lares (Oligocene); 84) Lirio Cave, Mona Island (late Pleistocene). **Navassa Island**: 85) near the Navassa lighthouse (late Pleistocene). **Sombrero Island**: 86) Sombrero guano site (late Pleistocene).

2.5.1. Costa Rica

2.5.1.1. 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).

2.5.1.2. 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.).

2.5.1.3. Quaternary

Rhinoclemmys nicoyama (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 Nacaome river in Barra Honda, Nicoya (Late Pleistocene), Guanacaste Province.

2.5.2. Cuba

2.5.2.1. Jurassic

The marine turtle *Caribemys oxfordiensis* was described based on a nearly complete shell recovered in the Jagua Formation (Upper Jurassic, Oxfordian), near of Viñales, Pinar del Río Province (De la Fuente and Iturralde-Vinent, 2001). Later, Cadena Rueda and Gaffney (2005) reassigned the species to *Notoemys*.

2.5.2.2. Neogene

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

2.5.2.3. 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).

2.5.3. Dominican Republic

2.5.3.1. 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 Cristobal Province, in the Los Haitises region, and referred to *Geochelone* (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 Altagracia Province, southeastern Dominican Republic (Albury *et al*., 2018).

2.5.4. El Salvador

2.5.4.1. Quaternary

Hesperotestudo crassiscutata, *Kinosternon* sp. and an unidentified Emydidae were recovered from the Tomayate 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).

2.5.5. Honduras

2.5.5.1. 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 posteromedian 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).

2.5.5.2. Quaternary

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

2.5.6. Jamaica

2.5.6.1. 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).

2.5.7. Mexico

2.5.7.1. 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 *Emydhipus* found in the San Juan Raya Formation (lower Aptian) in Santa Ana Teloxtoc, Tehuacán, Puebla (Rodríguez-de la Rosa *et al*., 2017). The ichnofossil found was associated with traces of marine invertebrates, crocodyliforms, pterosaurs and non-avian dinosaurs. Two specimens referred to Araripemydidae (Pleurodira, Pelomedusoides) (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 undescribed 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 between 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*, *Yelmochelys rosarioae, Euclastes coahuilaensis* (Figure 3C), *Chedighaii* 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 (*Pteraichnus*) footprints, were also reported in El Pelillal, Coahuila (Rodríguez-De la Rosa, 2003; Figure 4b). *Naomichelys* 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 icnofossil 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 de Enmedio Formation and Packard Formation, Cabullona Group (Late Campanian-Maastrichtian) in Sonora (Lucas *et al*., 1995; Brinkman, 2014). *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 México, 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).

2.5.7.2. Paleogene

Eocene. A poorly preserved shell from the Mesa de Copoya (Middle Eocene), southwest of Tuxtla Gutiérrez, Chiapas, was reported by Mullerried (1943); currently, this material is lost.

Oligocene. Sea turtles associated with bony fishes, sharks, rays, dolphins, desmostilids and whales were reported in the El Cien Formation and in the central area of the San Gregorio Formation (Late Oligocene, Chattian) in San Juan de la Costa and La Purísima area, Baja California Sur (González Barba and Alvarado Ortega, 2009). Aff. *Hadrianus* sp. and *Stylemys* sp. were reported as part of the Iniyoo Local Fauna, near Santiago Yolomécatl, northwest Oaxaca (Jiménez-Hidalgo et al., 2015), recently dated as early Oligocene (Guerrero-Arenas *et al*., 2020).

2.5.7.3. 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 Rosarito Beach Formation (middle Miocene) (Aranda Manteca, 2013). *Pseudemys* sp. and *Kinosternon* 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 Virgines Village [sic], in Nuevo León.

2.5.7.4. 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. scorpioides* was reported from Los Tanques, Zacatecas (Guzmán and Polaco, 1998); Arroyo Cedazo, Aguascalientes (Mooser, 1980); Cueva Encantada, Chimalacatlán, Morelos (Arroyo-Cabrales *et al*., 2004) and La Simpatía, Villa Corzo, Chiapas (Luna-Espinosa and Carbot-Chanona, 2009); *K. integrum* from Guilá Naquitz, Valles Centrales, Oaxaca (Flannery and Wheeler, 1986) and Jocotepec, Jalisco (Barrios Rivera, 1985); *K.* cf. *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 Brisca, Sonora (Van Devender *et al*., 1985); *K.* cf. *cruentanum*/*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 Michoacán-Guanajuato boundary (Moreno-Flores *et al*., 2017); Cueva Encantada, Chimalacatlán, Morelos (Arroyo-Cabrales 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

Chimalhuacán, Estado de México (Barrios Rivera, 1985). *Gopherus*, *G. agassizii* 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 Tecorral, in Tehuacán, Puebla; Actopan, Epazoyucan, and San Agustín Tlaxiaca, in Hidalgo (Nájera-Hernández, 2006; Castillo-Cerón *et al*., 2009) and Cueva Blanca, 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. donlaloi* (Figure 2E) was described as a new species from Ejido San Lázaro, Villagrán, Tamaulipas (Reynoso 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-Guanajuato 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-Espinoza 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 Brisca, 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, Tequixquiac, Estado de México (Hibbard, 1955) and Atepetzingo, Valsequillo, Puebla (Güenther, 1968); cf. *Staurotypus* sp. in La Simpatía, 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 La Brisca locality, in Sonora (Van Devender *et al*., 1985) and *Pseudemys* sp. in Jocotepec, Jalisco and Teapa, Tabasco (Polaco-Ramos, 1981; Barrios Rivera, 1985), as well as Chelydridae and Trionychidae in Térapa, Sonora (Moscato and Jasinski, 2016).

2.5.8. Navassa Island, United States of America

2.5.8.1 Quaternary

Pleistocene. 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*.

2.5.9. Nicaragua

2.5.9.1. Quaternary

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

2.5.10. Panama

2.5.10.1. Paleogene

Podocnemididae is known for the Gatuncillo site, Gatuncillo Formation (Late Eocene-Early Oligocene), Colon Povince (Cadena *et al*., 2012).

2.5.10.2. Neogene

Miocene. 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 Cheloniidae from the Gatum Formation (late Miocene) (Cadena *et al*., 2012).

2.5.11. Puerto Rico

2.5.11.1. Paleogene

Oligocene. 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.

2.5.11.2. Quaternary

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

2.5.12. Sombrero Island, Anguilla

2.5.12.1. Quaternary

Pleistocene. The only evidence of tortoise or turtles in the Sombrero Island, is *Emys sombrerensis*, that was named based on plastron and carapace remains 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).

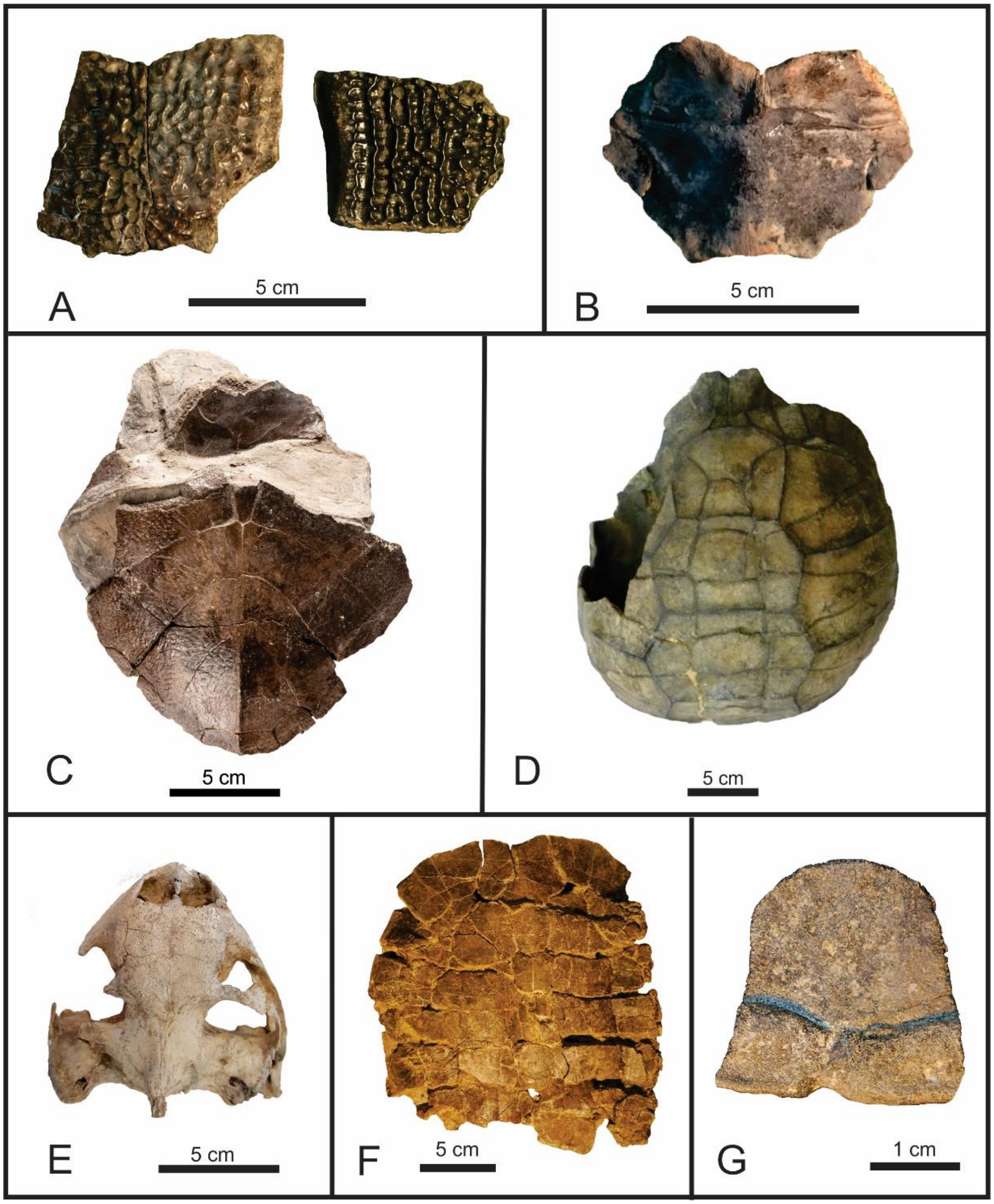

Figure 2**.** Neogene Testudines from Mexico and Central America. A) *Apalone* sp., El Limoncito (late Miocene), Costa Rica; B) *Rhinoclemmys nicoyama*, nuchal (holotype CFM 1311), Barra Honda Nicoya, Costa Rica; C) *Allaeochelys liliae* (holotype MALM-401), Los Pocitos mines, Simojovel, State of Chiapas, Mexico; D *Gopherus berlandieri* (=*G. auffenberger*) from the early Pleistocene of Aguascalientes; E) *Gopherus donlaloi* (holotype, IGM 6076), skull in dorsal view, late Pleistocene, Tamaulipas, Mexico; F) *Rhinoclemmys panamaensis*, carapace in dorsal view (holotype UF 237887), Cucaracha Formation (early Miocene), Panama; G) *Staurotypus moschus*, left peripheral (holotype UF 242076), Cucaracha Formation (early Miocene), Panama.

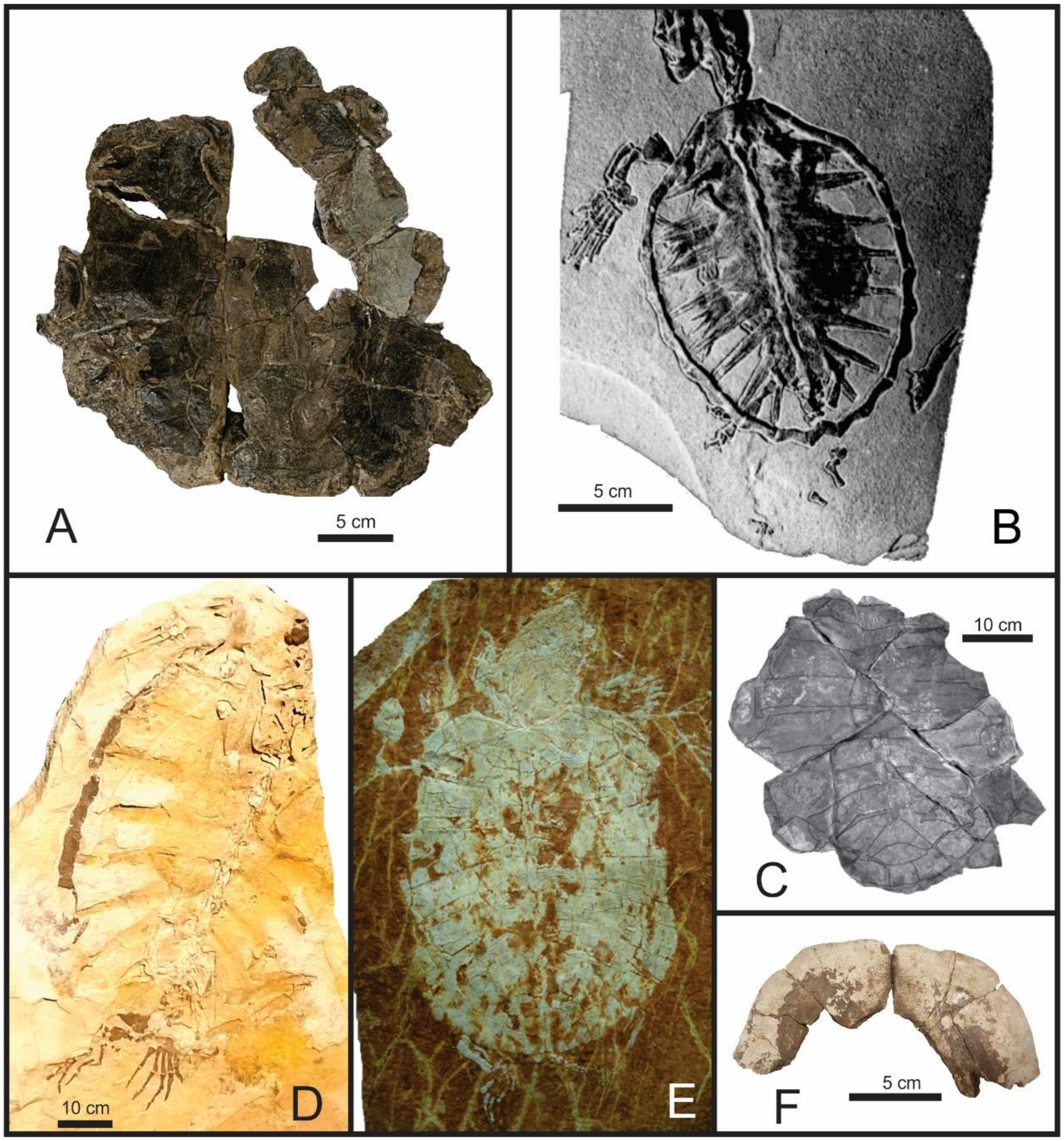

Figure 3. Mesozoic Testudines from Mexico. A) *Notoemys tlaxiacoensis*, carapace in dorsal view (holotype IGM 4861), Sabinal Formation (Kimmeridgian, Late Jurassic), Oaxaca; B) *Desmatochelys* sp., Vallecillo (Upper Cretaceous, Turonian), Nuevo León (taken from Blanco et al., 2001); C) *Mexichelys coahuilaensis*, carapace in dorsal view (paratype CPC 259), La Parrita, Cerro del Pueblo Formation (Upper Cretaceous, Campanian), Coahuila (taken from Brinkman, 2014); D) *Desmatochelys* cf. *D. lowii*, specimen in ventral view (MUZ-562), Austin Formation (Campanian) Jiménez, Coahuila; E) Araripemydidae indeterminate, Tlayúa Quarry (Early Cretaceous, Albian), Puebla; F) plastron fragment of the undetermined turtle in ventral view, Ocozocoautla Formation (Upper Cretaceous, Maastrichtian), Chiapas.

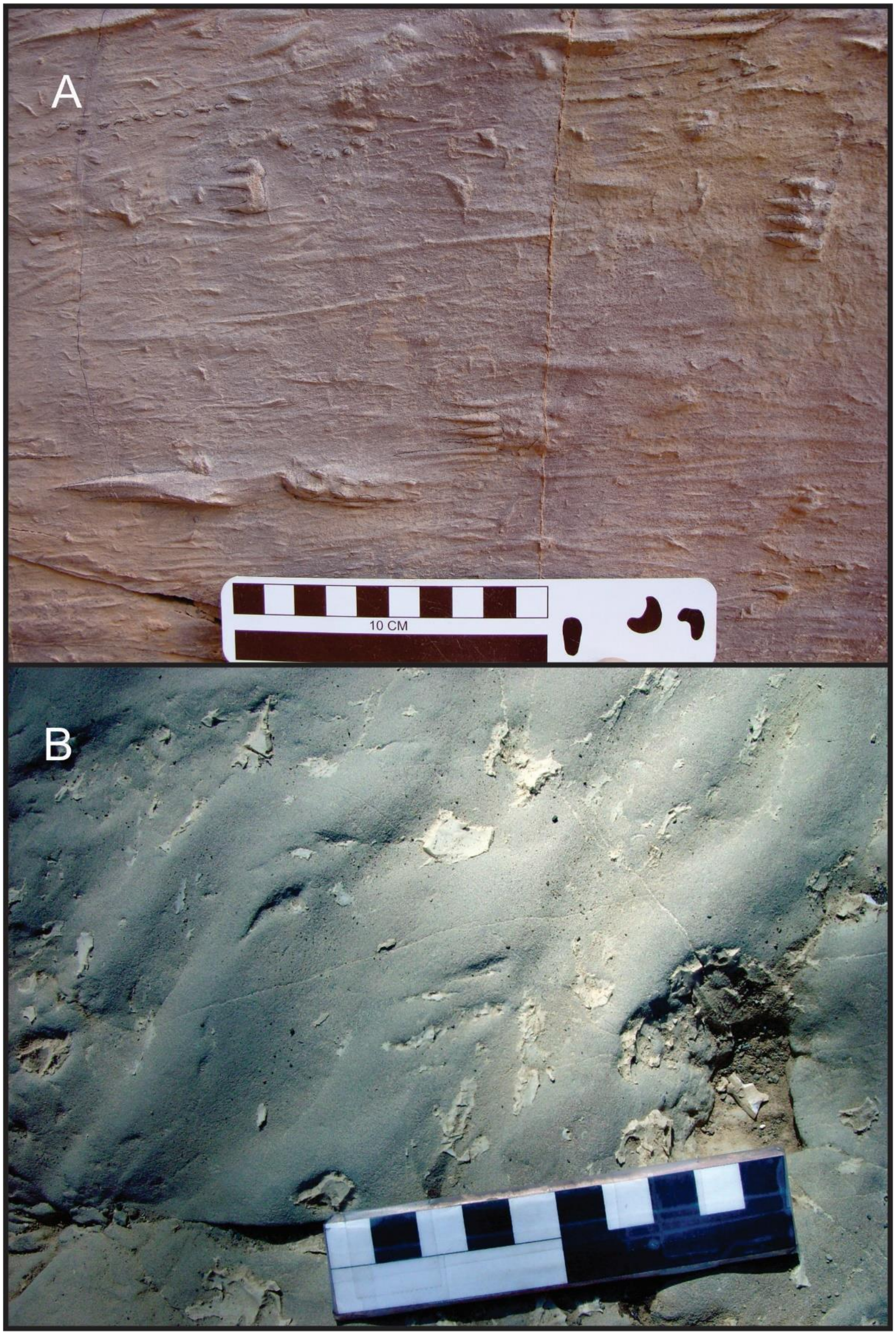

Figure 4. Cretaceous turtle footprints from Mexico. A) Impressions of anterior and posterior extremities found in the Caracol Formation (Late Cretaceous, Coniacian), north of Zacatecas. B) Partial impression of a turtle footprint found in the Cerro del Pueblo Formation (Late Cretaceous, Campanian), Coahuila.

2.6. Discussion

2.6.1. Taxonomy

Today, 13 genera and two ichnogenera have been identified for the Mesozoic of Mexico, including three new species: *Notoemys tlaxiacoensis*, *Yelmochelys 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 (1987) 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-Rosales, 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.) suggest that the specimen may represents a new genus and species of Bothremydidae.

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 Simpatía, Chiapas (Luna-Espinoza 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 Simpatía, 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 Brisca in Sonora, may belong to *Terrapene nelsoni*.

A recent review of the specimens referred as cf. *Hadrianus* sp. and *Stylemys* 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 (Edwards *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 synonymous 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 subgenus *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 Atepetzingo 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 *Oligopherus laticuneus* from the Oligocene of North America. Vlachos (2018) considers that "*Testudo*" *costarricensis* differs from *Oligopherus 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*), now are considered to belong to genus *Chelonoidis* (Franz and Franz, 2009).

2.6.2. 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. oxfordiensis* from the Jagua Formation (Late Jurassic, Oxfordian), Cuba (de la Fuente and Iturralde-Vinent, 2001); *N. zapatocaensis* of the Rosablanca Formation (Lower Cretaceous, Valanginian), Colombia (Cadena & Gaffney, 2005); *N. laticentralis* of the Vaca Muerta Formation, Argentina (Late Jurassic-Early Cretaceous, Tithonian-Berriasian) (Lapparent de Broin 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 Araripemydidae only in central Mexico, and the family seems to be restricted for this interval of time worldwide. Araripemids were 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.

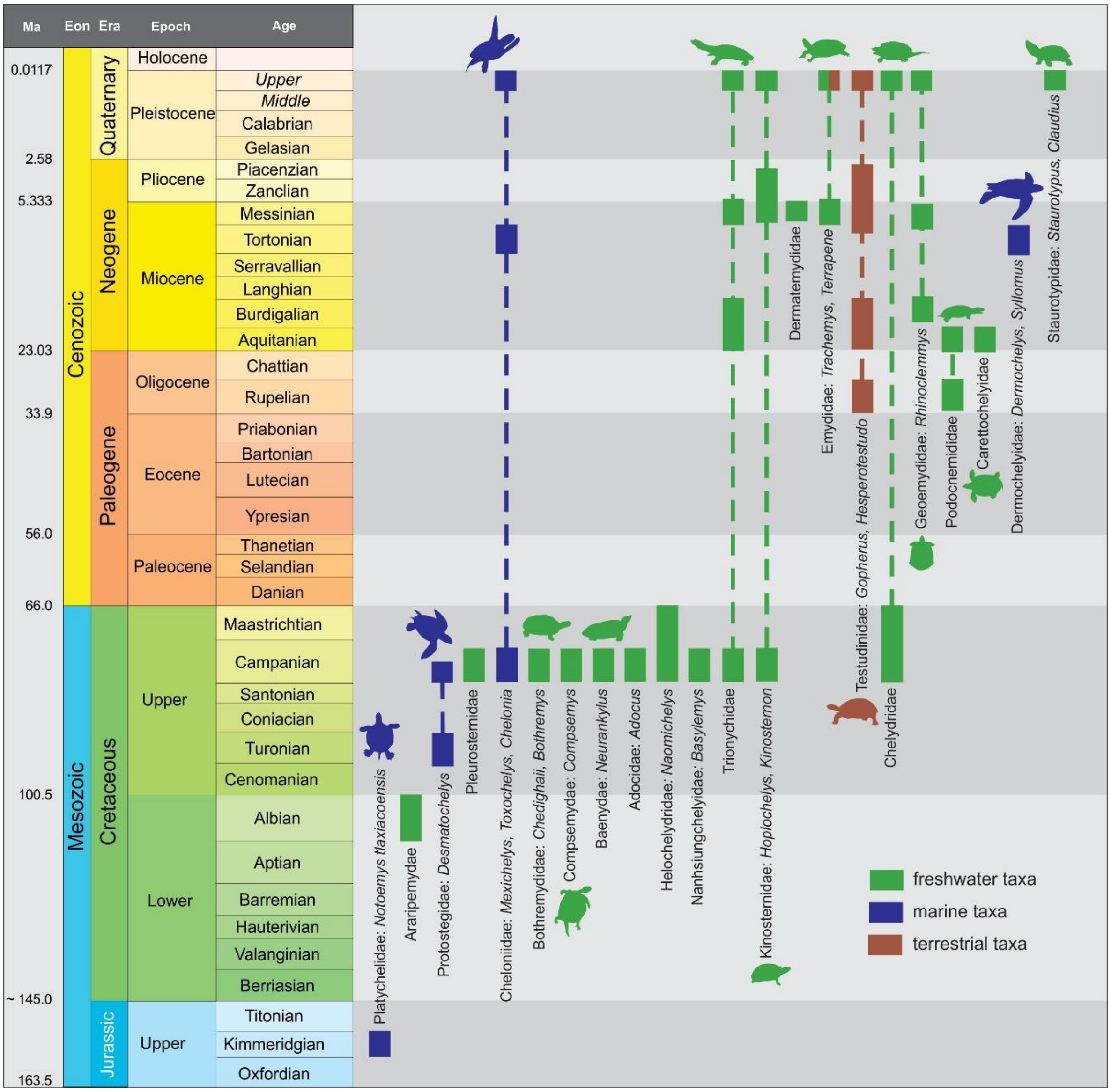

Figure 5. Geochronological range of Testudines families present in the fossil record of Mexico and Central America. Silhouettes drawn by Gerardo Carbot-Chanona.

In the Upper Cretaceous of Mexico there are 13 families present: Adocidae, Baenydae, Bothremydidae, Cheloniidae, Chelydridae, Compsemydae, Helochelydridae, Kinosternoidae, Nanhsiungchelyidae, Pleurosternidae, Protostegidae, Solemydae, and Trionychidae. Protostegidae is the only family with records in the Turonian and all other families are present in the Campanian. Cheloniidae 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 México (Aguilera, 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 assignation to *G. agassizii* was done considering that at the time, *G. agassizii* 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. morafkae*, 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 Potosí (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 donlaloi* (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 scorpioides* 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 these genus have been reported from the late Miocene to the Late Pleistocene in México 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.

2.7. Conclusion

The fossil record of turtles in Mexico, Central America and the Caribbeans 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* as 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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CAPÍTULO III

A new large Testudinidae tortoise from the early Oligocene (Arikareean NALMA) of Oaxaca, southern Mexico and its phylogenetic position within Pan-Testudinidae

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3.1. Abstract

Pan-Testudinidae is an extant clade of terrestrial tortoises with a past distribution range wider than today. Members of this clade have a rather scarce fossil record in Mexico and the few specimens known in scientific collections are poorly studied. In this work, we described a new genus and species of Testunididae, based on a single specimen from the early Oligocene deposits exposed in the marginal facies of the Chilapa Formation, Oaxaca, southern of Mexico. The new taxon species exhibits osteological characters that support its placement as a basal member of Testudinidae. The phylogenetic relationships of the new taxon were assessed using a total evidence approach (morphological + molecular) in a global Pan-Testudinidae context, using Implied Weighted Maximum Parsimony (IWMP), Standard Maximum Parsimony (SMP), and Bayesian Inference (BI). Although the BI consensus tree is not well resolved, the results obtained by IWMP and SMP retrieved the new taxon as a basal clade of Testudinidae. The differences between the topology of the three phylogenetic analyses, show that the position of several taxa within Testudinidae is affected by the kind of performed phylogenetic analyses. This new taxon also represents the first Paleogene and southernmost tortoise described from Mexico and the oldest Testudinidae known in the country.

Keyword. Pan-Testudinidae, phylogenetic analysis, Maximum Parsimony, Bayesian inference, Paleogene, Chilapa Formation

3.2. Introduction

Pan-Testudinidae is a clade of terrestrial tortoises, defined as the total clade of crown clade Testudinidae (Joyce et al. 2021). Molecular clock analysis suggested that Pan-Testudinidae and Pan- Geoemydidae split in the late Cretaceous, about 73.8 Ma (Pereira et al. 2017).

Pan-Testudinidae figures among the very first chelonians to be studied and named *Hadrianus majusculus* Hay, 1908, from the Wasatch beds (early Eocene) of New Mexico is the oldest-known genus of this clade (Hay 1908). Today, Pan-Testudinidae members are found in Africa, Southeast Asia, North America, and South America, including the Galapagos Archipelago; however, in the past it was more widespread with records in northern Europe and England, central Asia, and the West Indies (Ernst & Barbour 1989). There are 18 genera with about 67 extant species, including giant species with more than 1 m length, as the living *Chelonoidis* spp. (Bonin et al. 2006; Rhodin et al. 2017).

The fossil record of Testudinidae in Mexico is scarce and mostly come from late Miocene, Pliocene and Pleistocene deposits (Carbot-Chanona et al. 2020). *Gopherus* sp. has been reported from the late Miocene of the Tecolotlán Basin, Jalisco (McDonald & Carranza-Castañeda 2017), and from the late Pleistocene of El Carrizal-Santa Rita-El Rifle area, Baja California Sur; San Agustín Tlaxiaca, Hidalgo; Santiago Chazumba, Oaxaca; Pitiquito and Hermosillo, Sonora, and La Cinta-Portalitos, in the Michoacán-Guanajuato border (Ferrusquía-Villafranca & Torres-Roldán 1980; Cruz et al. 2009; White et al. 2010; Carbot-Chanona et al. 2020). *Gopherus berlandieri* is known from the Pliocene at El Fronton locality, Atotonilco, Hidalgo, and from the Late Pleistocene of the Cañón Tecorral, in Tehuacán and Santa Cruz Nuevo, Puebla; El Cedazo, Aguascalientes; Actopan, Epazoyucan, and San Agustín Tlaxiaca, Hidalgo; Cueva Blanca, at Santa María Chilchotla, Oaxaca (Flannery 1967; Mooser 1972; Tovar & Montellano 2006; Tovar et al. 2007; Carbot-Chanona et al. 2020). *Gopherus agassizii* was reported from the late Pleistocene of Sonora coast (Moodie & Van Devender 1979;), *G. flavomarginatus* from El Cedazo, Aguascalientes; Cerro Hervideros, Durango; Los Tanques, Zacatecas, and Jiménez Cave, Chihuahua (Mooser, 1980; Messing 1986; Reynoso & Montellano-Ballesteros 2004; Carbot-Chanona et al. 2020), and the extinct giant turtle *G. donlaloi* from Ejido San Lázaro, Villagrán, Tamaulipas (Reynoso & Montellano-Ballesteros 2004). *Hesperotestudo* is another extinct testudinid reported in Mexico, from the late Miocene at Los Gigantes Basin, Nayarit; the Pliocene of Las Tunas, Santa Anita, Los Cabos, Baja California, and the late Pleistocene of Potrero Zietla local fauna and Epazoyucan, Hidalgo; El Cedazo, Aguascalientes, and Puerto Peñasco and La Colorada, Sonora (Miller 1980; Carranza-Castañeda 2006; White et al. 2010; Carbot-Chanona et al. 2020).

Jiménez-Hidalgo et al. (2015) described the Iniyoo Local Fauna, from Santiago Yolomécatl, in northwestern Oaxaca. The faunal assemblage was originally assigned to the Late Eocene. The testudinids cf. *Hadrianus* sp. and *Stylemys* sp. were reported from this fauna (Jiménez-Hidalgo et al. 2015). New recent reexamination of that material allowed the recognition of a new genus and species of Testudinidae tortoise herein described. We also present a revision of the phylogenetic placement as inferred under different phylogenetic approaches and we comment their distribution in a paleobiogeographic context.

3.3. Geological setting

The specimen here described is part of the Iniyoo Local Fauna, and was collected in a fluviolacustrine fossiliferous sequence of 325 m thick of red-ochre to cream-colored fine-grained sand, clay, silt beds, with some conglomerate and silcrete beds that crop out in the surroundings of the town of Santiago Yolomécatl, in the northwestern part of the State of Oaxaca, southern Mexico (Jiménez-Hidalgo et al. 2015, 2021). This sequence was originally considered part of the Chilapa Formation with an Eocene–early Oligocene age (Santamaría-Díaz et al. 2008). Later, a late Eocene age was assigned to the fossiliferous beds based on radiometric dates (35.7 ± 1.0 and 32.9 ± 0.9 Ma) previously published for the Cañada María Andesite, nearby the study area (Jiménez-Hidalgo et al., 2015; Jiménez-Hidalgo et al. 2017). Guerrero-Arenas et al. (2020) provided a new age for the fossiliferous beds based on U-Pb detrital zircon geochronology estimated in 30.6 Ma, which corresponds to the Rupelian age (Oligocene). These authors also informally subdivided the fossiliferous beds into three sections: the “lower beds” conformed by limestone, silts, sands, and conglomerate intercalations; the “middle beds” consist of clayey silt and silty sand, with sand and conglomerate interbedding; and the “upper beds” conformed by clayey siltstone, silty sand, silcretes, sand and conglomerate strata (Guerrero-Arenas et al. 2020).

Although some authors have considered that the fossiliferous beds are part of the Yolomecatl Formation (e.g. Ferrusquía-Villafranca et al. 2016; Ferrusquía-Villafranca & Wang 2021), the most up-to-date geological work asserts that the unit is a marginal facies of the Chilapa Formation; also, an additional U-Pb maximum depositional age of 30.62 ± 0.67 Ma based on detrital zircon crystals collected from a sandstone that is approximately 9.2 m above the fossil vertebrate-bearing interval was also provided (see details in Jiménez-Hidalgo et al. 2021).

The fossil association present in the Iniyoo Local Fauna includes squamates (*Rhineura* sp.), carnivores, sciurid and geomyid rodents (e.g. *Gregorymys veloxikua*), leptochoerids (*Leptochoerus* sp.), merycoidodontids (*Merycoidodon* sp.), tayassuids (*Perchoerus probus*), protoceratids, camelids (*Poebrotherium* sp.), agriochoerids, hypertragulids (*Nanotragulus* sp.), chalicotheriids, equids (*Miohippus assinoboiensis*), amynodontid rhinoceros (cf. *Amynodontopsis* sp.) and rodent and insect ichnofossils (Jiménez-Hidalgo et al. 2015; Jiménez-Hidalgo et al. 2017; Guerrero-Arenas et al. 2018; Guerrero-Arenas et al. 2020). The age of the fauna is earliest Arikareean (Ar1) North American Land Mammal Age, based on the first appearance datum for the amphicyonid *Mammacyon* and the last appearance datums of the tayassuid *Perchoerus probus* and the rhinocerotid *Subhyracodon* (Jiménez-Hidalgo et al. 2021).

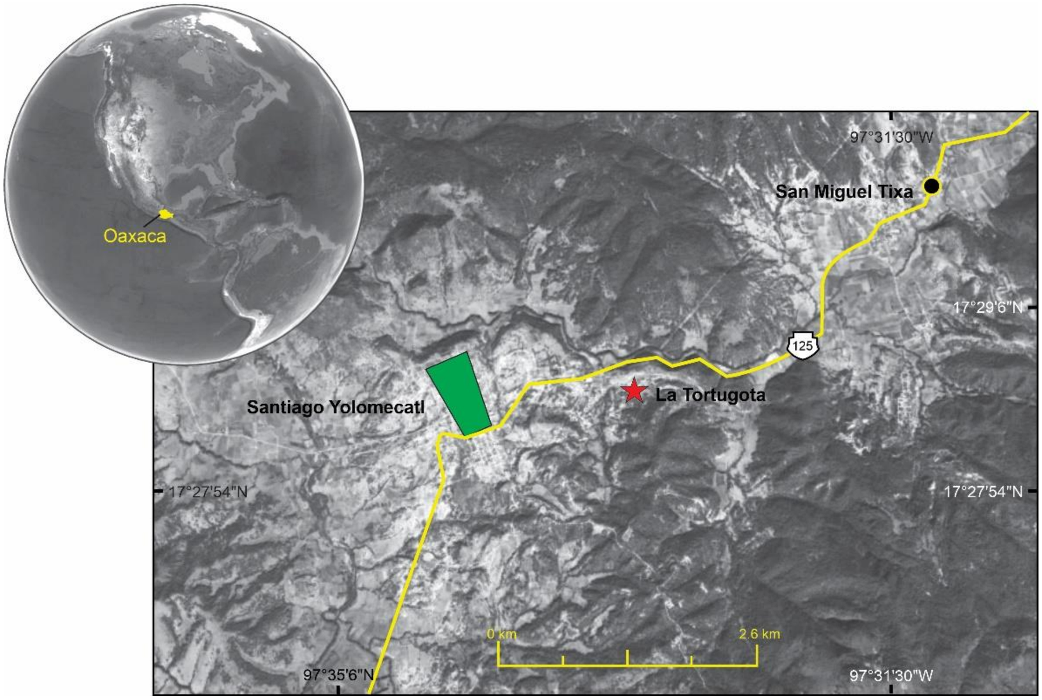

Figure 1. Location of La Tortugota locality, near of Santiago Yolomécatl town, State of Oaxaca, southern of Mexico.

3.4. Material and Methods

3.4.1. Preparation

The specimen UMPE 443 was originally embedded in a reddish silt matrix. The specimen was cleaned using dental needles, and soft bristle brushes. The broken parts were joined with water-proof commercial glue and hardened with cellulose acetate diluted in acetone.

3.4.2. Taxon sampling for comparison

We compared the specimen UMPE 443 with selected Eocene, Oligocene and early-middle Miocene North American testudinid taxa reported in the literature. The validity of the selected taxa and its taxonomic history was discussed by Vlachos (2018). The sample taxa for comparison includes *Hadrianus majusculus* Hay, 1904 from the lower Eocene, San Jose Formation, New Mexico (Hay 1908; Lichtig & Lucas 2015); *Hadrianus corsoni* (Leidy, 1871) from the early–middle Eocene, Grizzly Buttes, Uinta County, Wyoming (Hay 1908);

Oligopherus laticuneus (Cope, 1873), from late Eocene, White River Formation, Weld County, Colorado (Hay 1908; Hutchison 1996); *Floridemys nana* (Hay, 1916) from late Miocene–Pleistocene (precise age unknown), Holder, Citrus County, Florida (Hay 1916); *Stylemys capax* Hay, 1908 from late Oligocene, Grant County, Oregon (Hay 1908); *S. inuscitata* (Hay, 1906) from middle Miocene (Langhian–Serravallian), Deep River Formation, Broadwater County, Montana (Hay 1908; Oelrich 1950); *S. nebrascensis* Leidy, 1951 from early Oligocene, Orellan Formation, White River Group, South Dakota (Hay 1908; Hutchison 1996); "*Testudo" brontops* Marsh, 1890 from the late Eocene, Chadron Formation, Pennington County, South Dakota (Hay 1908; Hutchison 1996); *Hesperotestudo osborniana* (Hay, 1905) from early–middle Miocene (Burdigalian–Serravallian), Pawnee Creek Formation, Logan County, Colorado (Hay 1908; Auffenberg 1974); *Hesperotestudo williamsi* (Auffenberg, 1964) from early Miocene (Burdigalian), Oakville Formation, Grimes County, Texas (Auffenberg 1964); *Gopherus edae* (Hay, 1906) from the early Miocene (Aquitanian), Harrison Formation, Sioux County, Nebraska (Vlachos 2018), and *Gopherus hexagonatus* (Cope, 1893), from the middle Pleistocene, Tule Formation, Rock Creek, Tule Canyon, Briscoe County, Texas (Vlachos 2018).

3.4.3. Phylogenetic analysis

To explore the phylogenetic relationships of the specimen UMPE 443, a total evidence analysis was carried out under three different methods (Implied Weighted Maximum Parsimony, Standard Maximum Parsimony, and Bayesian Inference), using a total evidence data matrix (morphological + molecular) modified from Vlachos and Rabi (2018), with additional information from Vlachos (2018). To this data matrix we added the scoring of UMPE 443 using Mesquite 3.61 (Maddison & Maddison 2019). The scoring of *Paleotestudo canetotiana*, *Pelorochelon soriana*, '*Testudo' antiqua*, and '*Testudo' eocaenica* from Vlachos and Rabi (2018) was updated following Pérez-García et al. (2020) and Vlachos et al. (2020). In total 43 extinct and 27 extant taxa, and 20170 characters (1–170, morphological characters; 171–20170, nuclear and mitochondrial DNA) where used in the Standard Maximum Parsimony and Implied Weighted Maximum Parsimony analysis (see Supplementary data).

3.4.3.1. Implied Weighted Maximum Parsimony. Implied Weighted Maximum Parsimony analysis (IWMP) was carried out in TNT version 5.1 (Goloboff & Catalano 2016) under the New Technology search (*xmult= hits 4 rep 5 drift 20 fuse 6 gfuse 4*), with the Sectorial Search (*sec : xss 3+3-1 gocomb 10 combstart 5 fuse 3 drift 6*), Ratchet (*ratchet : iter 10 numsubs 5*) and Drift (*drift : rfit 0.10 num 150 nogiveup*) options activated. This analysis ran using a concavity of 20 ($k = 20$). The characters 11, 18, 24, 33, 40, 45, 48, 52, 60, 78, 79, 84, 93, 104, 105, 111, 116, 117, 121, 122, 123, 127 and 165 were treated as ordered, the rest were treated as unordered (see Vlachos and Rabi 2018). To get the most parsimonious trees, the phylogenetic uninformative characters were deactivated using the command *xinact*. The designed outgroup taxon was Pleurodira in accordance with Vlachos and Rabi (2018). Statistical supports (Bremer, bootstrap and jackknife support, Consistency Index and Retention Index) were calculated with the command scripts included in TNT.

3.4.3.2. Standard Maximum Parsimony. The Standard Maximum Parsimony analysis ran using the New Technology tree search, following the same parameters and outgroup of the IWMP but considering all characters with equal weight. Statistical supports (Bremer, bootstrap and jackknife support, Consistence Index and Retention Index) were also calculated as in the IWMP analysis above mentioned.

3.4.3.3. Bayesian Inference. For the Bayesian Inference, the molecular data matrix from Guillon et al. (2012) included in Vlachos & Rabi (2018), was modified. This matrix originally contained 20,000 molecular characters from the complete mitochondrial genome and four nuclear genes. The annotate of each gene and its length was allocated after introducing segments of the matrix in Blast®/BlasN suite website (https://blast.ncbi.nlm.nih.gov/Blast.cgi) (Zhang et al. 2000). Then, to confirm their length, each gene was aligned with the corresponding accession gene as downloaded from GenBank® (www.ncbi.nlm.nih.gov/genbank/) (Clark et al. 2016) using the SeaView 5.0.4 (Gouy et al. 2010) interface and the Clustal Omega program (Sievers et al. 2011) for multiple sequence alignment set with the default options. In Mesquite 3.61 (Maddison & Maddison 2019) the molecular sequences were divided into data blocks, the protein coding genes were defined by codon position, and input files for model selection software were generated. Also, sites not assigned to any of the specified data blocks were deleted producing a molecular data set of 19,266 sites. The model selection process was carried out in PartitionFinder2 (Lanfear et al. 2016). The best-fit partitioning scheme and the best model for each molecular subset were selected according to the Bayesian Information Criterion (BIC). The analysis estimated a Maximum-likelihood tree with RaxML v.8 (Stamatakis 2014), reason why the un-assigned sites were removed (see PartitionFinder2 manual) and ran with the *rcluster* algorithm (Lanfear et al. 2014) for large datasets. Settings for the phylogenetic analysis with the molecular blocks were obtained from the best scheme output file.

The morphologic dataset was the same used in the Maximum Parsimony analysis. Both matrices were merged using the Mousepad plain text editor producing a combined matrix of 19,436 characters (see Appendix 5 of Supplementary data). The Bayesian Inference analysis was performed in MrBayes 3.2.7a (Ronquist et al. 2012) for Linux systems and ran for 10,000,000 generations with two parallel runs (20,000,0000 total generations), 3 heated chains and 1 cold chain, discarding 20 percent of the samples from the beginning of the chains. The morphological block was set to use gamma-shaped rate variation (Brusatte & Carr 2016; Díaz-Cruz et al. 2019). The chosen outgroup taxon was the same as in the Parsimony analyses. To optimize the computing time for the phylogenetic analysis, we also used the Beagle library (Ayres et al. 2012). Convergence was assessed in tracer v1.7.1 (Rambaut et al. 2018), and at the end of the analysis we calculated a 50% majority-rule consensus tree.

3.5. Systematic palaeontology

For the suprageneric ranks, we use the categorical clade arrangement, which is independent of categorical rank (PhyloCode 2020, Art. 3.1; Cantino & De Queiroz 2020). The names of turtle clades are based in those proposed by Joyce et al. (2021), who follow the recommendations of the PhyloCode 2020 (Cantino & De Queiroz 2020).

Clade **Testudinata** Klein, 1760 [Joyce et al., 2020a]
Clade **Testudines** Batch, 1788 [Joyce et al., 2020b]
Clade **Cryptodira** Cope, 1868 [Joyce et al., 2020c]
Clade **Testudinoidea** Fitzinger, 1826

Clade **Testuguria** Joyce et al., 2004

Clade **Pan-Testudinidae** Joyce et al., 2004

Clade **Testudinidae** Gray, 1825

gen. nov.

3.5.1. Derivation of name. Pending of assignation.

3.5.2. Diagnosis. As for the species.

sp. nov.

(Figs 2-5)

3.5.3. Holotype. UMPE 443, an almost complete carapace with a relatively good preservation and a poorly preserved plastron.

3.5.4. Diagnosis. UMPE 443 gen. et sp. nov. is referred to Testudinidae because the alternating rectangular and non-rectangular arrangement of neurals; a coincidence between the costo-peripheral suture and the pleuro-marginal sulci; thin medial ends and wide lateral ends of costals, alternating with wide medial ends and thin lateral ends costals; pleural 1 not contacting the nuchal bone, and wide vertebrals, almost equal to pleurals. UMPE 443 gen. et sp. nov. can be differentiated from other members of Testudinidae based on the following combination of morphological characters (autapomorphic characters marked with an asterisk): big size, about of 920 mm; neural formula 4-8-4-8?-6A-6-6-6; marginal 1 overlapping costal 1(*), and "sharp-raised ridges" sulci as to some species of *Chelonoidis*.

3.5.5. Derivation of name. Pending of assignation.

3.5.6. Type locality and horizon. La Tortugota locality, Chilapa Formation, near Yolomécatl town, State of Oaxaca, south Mexico. Early Oligocene, Rupelian (earliest Arikareean [Ar1] NALMA).

The specimen and locality were registered in the Dirección de Registro Público de Monumentos y Zonas Arqueológicos e Históricos of Instituto Nacional de Antropología e Historia (INAH). Universidad del Mar is registered as the legal custodian of the specimen in the Dirección de Registro Público de Monumentos y Zonas Arqueológicos e Históricos of INAH, the national data base of paleontological monuments of the Mexican instance in charge of the preservation and custody of Mexican fossils. Registry number of Universidad del Mar (as a legal custodian) in this database is 3024 P.M.

The exact details of the locality could be provided on request; these data are not published to prevent looting of the fossil site.

3.6. Description and comparison

3.6.1. General shape and preservation of the shell. The specimen UMPE 443 is a tortoise of big size (total length ~920 mm) with a domed shell (Figures 2-5). The nuchal and all the neural series are preserved. In the left side the peripheral 1 and 2, costal 1-3, and 6-8 are partially conserved. In the right side the peripheral 1 and costal 1-4 are conserved, and the costal 5-8 are partially conserved. The sulci between the scales have "sharp-raised ridges", as in some species of *Chelonoidis*.

3.6.2. Nuchal. In UMPE 443 gen. et sp. nov. the nuchal is hexagonal in shape and wider than long, with the anterolateral borders contacting the peripherals 1, while the posterolateral borders contact the costal 1. This morphology is similar to *Hadrianus corsoni*, *Stylemys*, *Hesperotestudo* and *Gopherus*. Only *Floridemys nana* have a nuchal longer than wide (Figure 2).

3.6.3. Neurals. UMPE 443 gen. et sp. nov. possess eight neurals (formula 4-8-4-8?-6A-6-6-6). This is a notorious difference with the Eocene taxa *Hadrianus majusculus* and *Ha. corsoni* who had nine neurals (Vlachos 2018). The neural 1 in UMPE 443 gen. nov., sp. nov. is quadrangular in shape, with all sides almost equal in size, like in *S. capax, S. inuscitata*, *S. nebrascensis*, *Hesperotestudo* and *Gopherus*. In *Hadrianus corsoni*, *Oligopherus laticuneus* and *Floridemys nana* the neural one is hexagonal in shape, with the anterolateral sides longer than posterolateral sides (Hay 1908).

The neural 2 in UMPE 443 gen. et sp. nov. is octagonal, with the anterolateral and posterolateral sides shorter than lateral sides. This morphology is similar to *S. capax*, *Hesperotestudo* and *Gopherus* (Hutchison 1996; Vlachos 2018). Contrary, in *Stylemys* *nebrascensis* and *S. inuscitata*, and in the basal forms *Hadrianus corsoni*, *O. laticuneus* and *F. nana* the neural two is hexagonal in shape with the short sides positioned posterolateraly (Hay 1908).

The neural 3 is quadrangular in shape in UMPE 443 gen. et sp. nov., like in *Ha. corsoni*, *O. laticuneus*, *S. capax*, *Hesperotestudo*, *Gopherus* and *F. nana*. Contrary to *Stylemys nebrascensis* and *S. inuscitata*, where it is hexagonal in shape.

The neural 4 is no clearly visible in UMPE 443 gen. et sp. nov., because this part is slightly damaged (Figure 2). In consequence its form is inferred as octagonal by the configuration of the costal that surrounds it. In *Fl. nana*, "*Testudo*" *brontops*, *Hesperotestudo* and *Gopherus* the neural four is octagonal in shape too (Hay 1908; Hutchison 1996), while in *Ha. corsoni*, *O. laticuneus*, and the *Stylemys* species, the neural 4 is hexagonal.

The neural 5 in UMPE 443 gen. et sp. nov. is hexagonal, like in *Ha. corsoni*, *O. laticuneus*, *F. nana*, *S. capax*, *S. inuscitata*, *S. nebrascensis*, and *G. brevisternus*. In *He. brontops*, *He. osborniana*, *He. williamsi* and *G. edae* the neural five is rectangular in shape.

The neurals six, seven and eight in UMPE 443 gen. et sp. nov. are hexagonal in shape, wider than long, similar to all taxa used here for comparison.

3.6.4. Costals. The costals in UMPE 443 gen. et sp. nov. have an alternating arrangement where the costals 1, 3 and 5 are wider in the medial end than the lateral end, while the costals 2, 4 and 6 are thinner in the medial end than the lateral end. The width of the lateral ends in the costals 2 and 4, is more noticeable than in *Oligopherus*, *Stylemys* and *Hesperotestudo*.

The costal 1 contact the nuchal, neural 1 and 2, and peripherals 1-3. The costal 2 contact medially the neural 2, but the contact with the peripherals is not visible (Figure 3). The costal 3 contact medially the neurals 2-4.

3.6.5. Peripherals. Only the right and left peripheral 1, and the left peripheral 2 are partially preserved. Peripheral 1 reaches the anterolateral border of the nuchal through a strait suture. Posteriorly, the peripheral 1 meets the costal 1. The peripheral 2 is shorter than peripheral 1 and it contacts medially the costal 1. The suture between the peripheral 1 and 2 with the costal 1 is coincident with sulci between pleural 1 and marginal 2.

3.6.6. Suprapygal. Two suprapygals are present. The suprapygal 1 is larger than the suprapygal 2, but due to poor preservation it is not possible to observe if the contact between both suprapygals is straight and perpendicular to the axial plane, or if the first suprapygal embraces a lenticular second one (Figure 4).

3.6.7. Pygal. The pygal is quadrangular in shape and contacts laterally with the peripheral 11. The pygal notch is not present (Figure 4).

3.6.8. Cervical scute. It is only visible the left sulcus of the cervical scute suggesting the presence of the cervical, but its shape and size cannot be deduced (Figure 3).

3.6.9. Vertebral scutes. All five vertebral scutes are preserved (Figure 2). The width of vertebrals is almost equal to that of the pleurals. Vertebral 1 is wider than long. It overlaps the posterior half of the nuchal, the anterior half of neural 1, and the medial side of the costal 1.

The vertebral 2 is almost as wider as long, giving it a semi-square shape. The vertebral 2 overlaps the posterior half of the neural 1 covering the neural 2 entirely, and overlaps the anterior half of the neural 3. Anterolaterally it overlaps the posteromedial side of the costal 1; laterally the medial side of the costal 2, and posterolaterally the anteromedial side of costal 3.

The vertebral 3 is slightly wider than long and overlaps the posterior half of the neural 3, it covers entirely the neural 4, and overlaps the anterior half of the neural 5. Anterolaterally it overlaps the posteromedial side of the costal 3, laterally the medial side of the costal 4, and posterolaterally the anteromedial side of the costal 5.

The vertebral 4 is longer than wide. Its anterior sulcus lies on the anterior half of the fifth neural, and the posterior sulcus lies in the middle part of the neural 8. Anterolaterally it overlaps the posteromedial part of the costal 5, laterally the medial side of the costals 6 and 7, and posterolaterally the anteromedial corner of the costal 8.

The vertebral 5 is not completely visible, but it seems to cover the pygal and suprapygal. Its anterior sulcus lies on the middle part of the neural 8 and anterolaterally overlaps part of the costal 8.

3.6.10. Marginal scutes. Only the right marginals 1 and 2 are visible. The marginal 1 overlaps the anterolateral margin of the nuchal, the medial part of the peripheral 1, and the anterior corner of the costal 1 (Figure 2 and 3). This last morphological character is not present in any other Testudinidae. The marginal 2 do not touch the lateral margin of the nuchal, but it overlaps part of the costals 1 and 2.

3.6.11. Pleural scutes. The sulcus between the marginal 2 and the pleural 1 are coincident with the suture between the peripheral 1and costal 1. The pleural 1 does not contact the nuchal. Its medial sulcus contacts with the vertebrals 1 and 2.

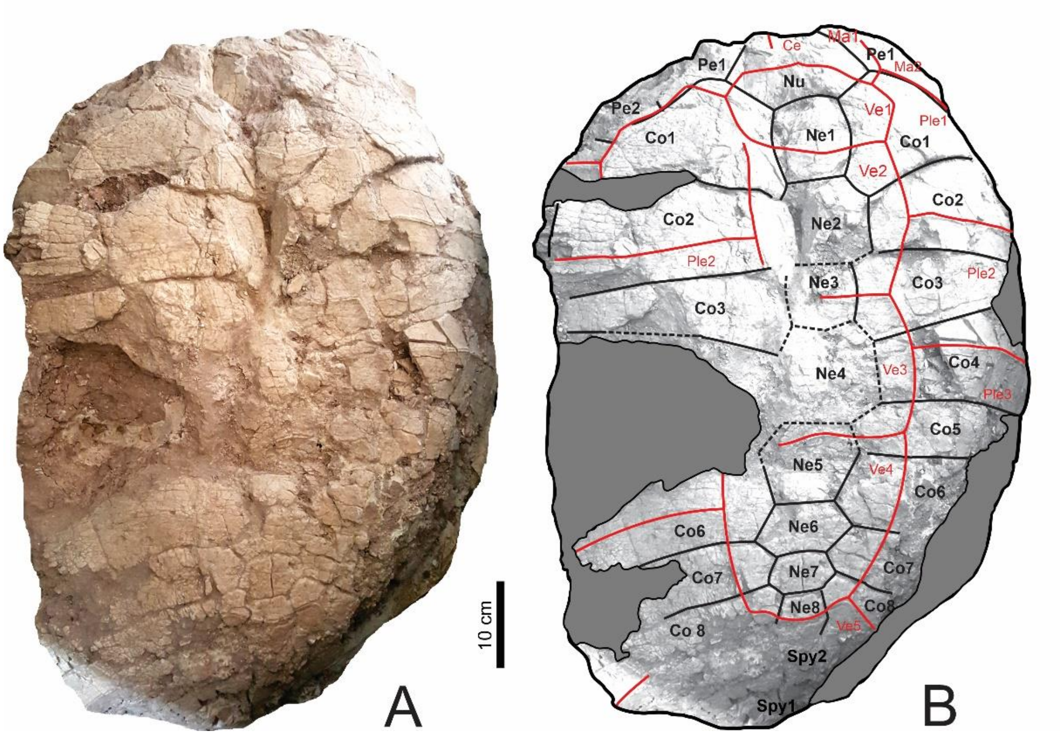

Figure 2. UMPE 443 gen. et sp. nov. (dorsal view) from the early Oligocene of Santiago Yolomécatl, State of Oaxaca. Photograph (A) and schematic draw (B). Abbreviations: Ce, cervical; Co, costal; Ma, marginal; Ne, neural; Nu, nuchal; Pe, peripheral; Ple, pleural; Spy, suprapygal; Ve, vertebral.

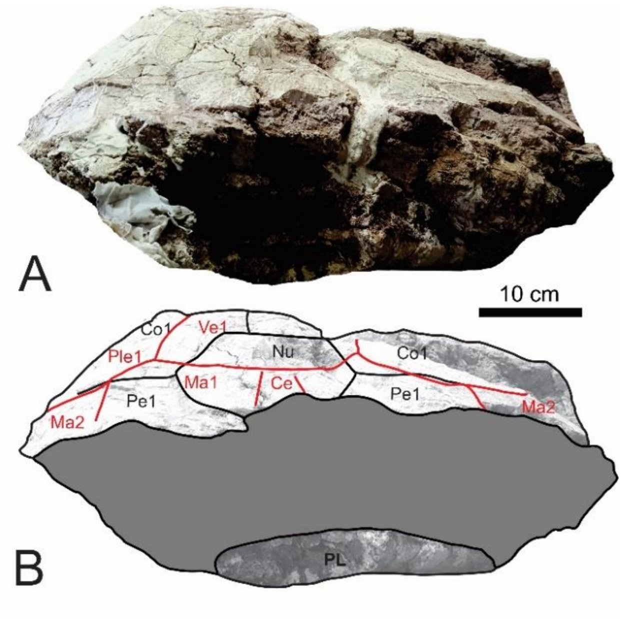

Figure 3. Anterior view of the carapace of UMPE 443 gen. et sp. nov. from the early Oligocene of Santiago Yolomécatl, State of Oaxaca. Photograph (A) and schematic draw (B). Abbreviations: Ce, cervical; Co, costal; Ma, marginal; Pe, peripheral; PL, plastral lip; Ple, pleural; Ve, vertebral.

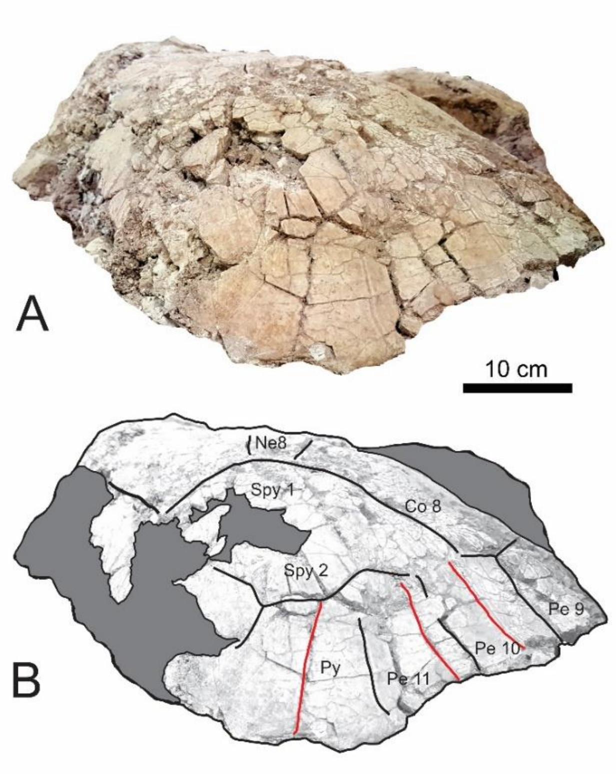

Figure 4. Posterior view of the carapace of UMPE 443 gen. et sp. nov. from the early Oligocene of Santiago Yolomécatl, State of Oaxaca. Photograph (A) and schematic draw (B). Abbreviations: Co, costal; Ne, neural; Pe, peripheral; Py, pygal; Spy, suprapygal.

3.6.12. General shape and preservation of the plastron. The plastron is partially preserved. It is possible to observe the right and left epiplastron, part of the entoplastron, left hyoplastron, left hypoplastron and part of the right xiphiplastron (Figure 5). The scute marks are no visible as consequence of the preservation.

3.6.13. Epiplastra. Only part of the right epiplastron is conserved, but its poor preservation does not allow observing its shape or relationship with the other plastral bones.

3.6.14. Entoplastron. The entoplastron is partially conserved and only the right side is visible. Its general shape is not well appreciated, but presumably it was pentagonal.

3.6.15. Hyoplastra. Almost all the right hyoplastron and part of the left hyoplastron is conserved. The right hyoplastron contacts with the right epiplastron throughout to perpendicular suture, like in others Testudinidae. The contact of the hyoplastron with the hypoplastron is not visible.

3.6.16. Hypoplastra. Just two fragments of the right hypoplastron are preserved. Their poor preservation prevents observing its relationship with other bones.

3.6.17. Xiphiplastra. Only part of the left xiphiplastron is conserved. Its shape and relationships with other bones are not clear.

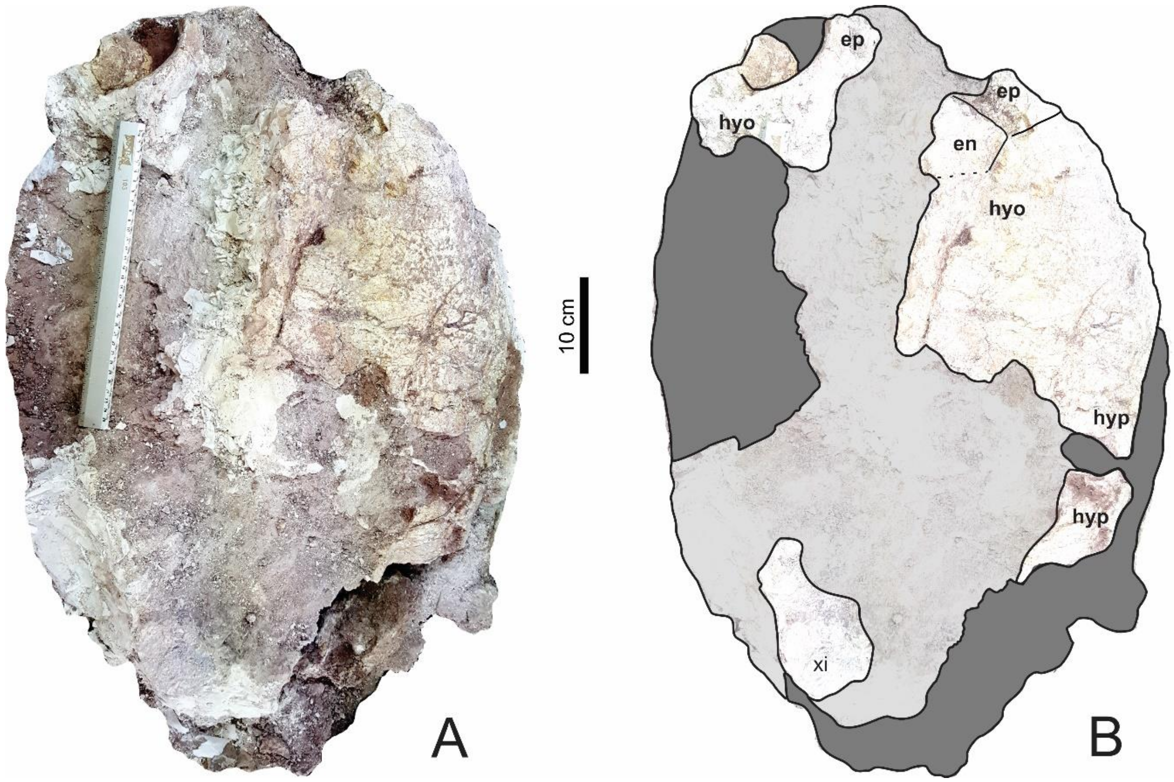

Figure 5. Plastron UMPE 443 gen. et sp. nov. from the early Oligocene of Santiago Yolomécatl, State of Oaxaca. Photograph (A) and schematic draw (B). Abbreviations: Ep, epiplastron; En, entoplastron; Hy, hyoplastron; Hypo, hypoplastron; Xi, xiphiplastron.

3.7. Results

3.7.1. Phylogenetic and character analysis

The Implied Weighted Maximum Parsimony analysis (IWMP) retained three trees with TBR best score of 259.543. The consensus tree has a Tree Length with adjust homoplasy of 13037, Consistency Index (CI) of 0.383, and Retention Index (RI) of 0.338. The topology of the IWMP differ from the topology obtained with the SMP (see supplemental Fig. S1). In general, the IWMP tree is well resolved (Figure 6), although most resolved clades have low support values (boostrap/jacknife group present/contradicted values; Goloboff et al. 2003), which shows a conflict of characters among the different clades included in Pan-Testudinidae. The clade Pan-Testudinidae is supported by six synapomorphies (characters and states in parenthesis): first neural is rectangular in shape (85:1), thin and elongated costal rib head (93:1), the gulars and the entoplastron in contact with the anterior margin (122:1), axillary glands absent (132:1), inguinal glands absent (133:1), and fused trochanter of the femur (155:1). *Fontainechelon cassouleti* (Claude & Tong, 2004) is retrieved as the most basal member of Pan-Testudinidae and its position is consistent with that recovered in Vlachos and Rabi (2018). This position is supported by the following synapomorphies: octagonal third neural (87:3), rectangular fourth neural (88:0), costal rib head far from neural/costal suture (94:1), posterior carapace border posteriorly flared (114:1), the gulars and the entoplastron not in contact (114:1), shape of the femoro-anal sulcus straight or slightly rounded, developed mainly perpendicular to the axial plane (136:1), and medial length of the anals longer than the medial length of femoral (137:1).

The clade *Manouria emys* + *Ma. impressa* is recovered out of Testudinidae, contrary to previous works (e.g. Vlachos & Rabi 2018). This clade is supported by the presence of a protrusion in the nuchal (83:1), vertebrals wider than the pleurals (104:0), lateral portion of the humero-pectoral sulcus relatively straight throughout its width (126:0), and short medial length of pectorals (128:1). The clade *Manouria emys* + *Ma. impressa* has a high boostrap/jacknife GC support (88/99).

Testudinidae is a clade supported by four synapomorphies: twelfth marginal scutes fused in dorsal view (112:1), presence of a well-developed gular protrusion, caused by constriction in the gularo-humeral sulcus (119:1), shape of the dorsal lip of the epiplastra clearly convex (121:1), and short medial length of pectorals (128:1).

The clade *Stylemys capax* + *Ergilemys insolitus* + *Cheirogaster maurini* + *Taraschelon gigas* is recovered as stem clade within Testudinidae. This clade is weakly supported by one synapomorphy: the costo-peripheral suture and the pleuromarginal sulcus are coincident (97:0).

Stylemys inusitata and *St. nebrascensis* are recovered as sister taxa. This clade is supported by three synapomorphies: second neural hexagonal with short sides positioned anteriorly (86:0); third neural hexagonal with short sides positioned anteriorly (87:0), and lateral portion of the humero-pectoral sulcus perpendicular to the axial plane, with convex anteriorly lateral parts (126:2).

UMPE 443 gen. et sp. nov. is recovered as stem member of Testudinidae, supported by the octagonal shape of the fourth neural (88:2), that is shared with *F. nana*, and the species included in *Hesperotestudo* and *Gopherus*. Additionally, in UMPE 443 the pleural 1 is not in contact with the nuchal, the wide vertebrals are almost equal with the pleurals, and the costo-peripheral suture and the pleuromarginal sulcus coincide, morphological characters present in the members of Testudinidae (Vlachos & Raby 2018, Joyce et al. 2021).

UMPE 443 gen. et sp. nov. is the sister group of the clade comprising *Namibchersus namaquensis* plus the *Hesperotestudo* species, which branches sequentially in staggered manner. This clade is weakly supported by one synapomorphy: the major trochanter of the humerus is short, not extending beyond the humeral head (character 152:0). However, this character is only coded for *N. namaquensis* and *He. bermudae*.

The clade conformed by *Impregnochelys pachytestis* + *Gigantochersina ammon* + *Hesperotestudo orthopygia* here is recovered as the more derived stem clade into Testudinidae. This clade is supported by two synapomorphies: the presence of a well-developed gular protrusion, caused by constriction in the gularo-humeral sulcus (character 119:1), and humerals equal to or shorter than gulars (character 124:0).

The *Gopherus*-clade is recovered as monophyletic, although it has lower boostrap/jacknife GC values (14/21). This clade is supported by seven synapomorphies: presence of prefrontal pits (character 5:1), presence of median ridge of the triturating surface of the upper jaw (character 33:1), presence of the lingual border of upper triturating surface joining in premaxillae and forming a well-developed ridge (character 34:1), *processus coronoideus* higher than the dentary (character 60:0), cervical scute wider than long (character 101:1), cervical scute in dorsal view equal or less than 25% of the nuchal length (character 102:1), and median anteroposterior length of humerals equal to or shorter than gulars (character 125:0).

The Testudininae clade is supported by eight synapomorphies: presence of a cusp in the premaxilla–maxilla suture (character 26:1), absence of foramen carotico-pharyngeale (character 45:2), opisthotic expanded seem in posterior view, it contacts basioccipital but not the pterygoid (character 52:1), squamosals not extending beyond the *condylus occipitalis* (character 54:1), contact between surangular and dentary with strongly interdigitated suture (character 59:1), prominent dorsal process on cervical vertebra (character 148:0), length of centralia extensive, preventing the contact of radius and distal carpals (character 156:0), and medial and lateral centrale fused (character 157:0). This clade retrieves two well defined sub-clades, Geochelona and Testudona, according to Joyce et al. (2021).

The Testudona clade is supported by six synapomorphies: the foramen *jugulare posterius* is located in the exoccipital/opisthotic suture (character 53:1), sixth marginal scute not in contact with the third pleural scute (character 109:0), posterior sulcus of the fifth vertebral coincident with the suprapygal-pygal suture (character 111:1), lateral portion of the humero-pectoral sulcus relatively straight throughout its width (character 126:0), inguinal and femoral scutes not in contact (character 131:0), and the angle between the femoral head and the diaphysis of the femur is relatively large (character 154:0). *Malacochersus tornieri* and *Testudo promarginata* are recovered in a polytomy in the basalmost position within Testudona. Additionally, four major sub-clades are recovered within Testudona. The first one includes *Indotestuto forstenii* + *I. elongata* + "*Testudo*" *costaricensis*" + "*Testudo*" *brontops* + "*Testudo*" *kaiseni*. It is supported by four synapomorphies: the posterior sulcus of the fifth vertebral crosses the suprapygal transversely (character 111:2), humero-pectoral sulcus medially wavy in shape (character 125:2), humero-pectoral sulcus coinciding medially with the posterior contact of the entoplastron-hyoplastron (character 127:1), and inguinal and femoral scutes in contact (character 131:1). The second sub-clade comprises *Paleotestudo canetotiana* + "*Testudo*" *antiqua,* and it is supported by one synapomorphy: vertebrals narrower than the pleurals (character 104:2). The third sub-clade includes *Mesochersus orangeous* + *Testudo shensiensis* + *Te. lunellensis* + *Te. oughlamensis,* and it is supported by one synapomorphy: cervical scute short, equal or less than 25% of the nuchal length (character 102:0). Finally, the fourth sub-clade contains *Agrionemys horsfieldii* + *Chersine hermanni* + *Testudo graeca* + *Te. marginata* + *Te. kleinmanni* + *Te. marmorum*. It is supported by two synapomorphies: seven or less neural plates (character 84:2), and humero-pectoral sulcus coinciding medially with the posterior contact of the entoplastron-hyoplastron (character 127:1).

The Geochelona clade is supported by three synapomorphies: dentary hook with medial tooth (character 72:1), nuchal about 1/3 wider than long or as long as wide (character 78:1), and the gulars and the entoplastron not in contact or in contact with the anterior margin (character 122:0/1, polymorphic). Four major sub-clades are recovered into Geochelona. The first clade is integrated by *Floridemys nana* + *Kinixys erosa* + *K. homeana*, and it is supported by six synapomorphies: nuchal markedly longer than wide (character 78:2), first neural hexagonal, with the short sides positioned posteriorly (character 85:0), second neural hexagonal, short sides positioned posteriorly (character 86:1), fifth neural hexagonal (character 89:0), dorsal lip of the epiplastra relatively flat (character 121:1), and the femoro-anal sulcus forms an acute angle (character 136:0). The second clade comprises *Stigmochelys pardalis* + *Titanochelon bolivari* + *Ti. bacharidisi* + *Ti. vitodurana*. This clade is supported by four synapomorphies: presence of a circular or elliptical pit on the ventral side of the premaxillae (character 27:0), *processus pterygoideus externus* situated at the same level with the *foramen palatinus posterious* (character 48:1), the length of *crista supraoccipitalis* extending more than twice the length of the neck of condyles occipitalis (character 57:0), and the angle formed by gularo-humeral sulci greater than 60° (character 123:2). The third clade includes *Geochelone elegans* + *Centrochelys sulcate* + "*Chelonoidis" gringorum* + *Megalochelys atlas*, and it is supported by six synapomorphies: tooth-like tubercles on the median maxillary ridge not present (character 37:0), V-shaped basisphenoid (character 51:1), postero-lateral side of nuchal anteriorly concave (character 77:1), first neural hexagonal with the short sides positioned posteriorly (character 85:0), second neural hexagonal with the short sides positioned posteriorly (character 86:1), and ventral keel on cervical vertebra 8 present in all along the centrum (character 149:0). The fourth clade includes *Chelonoidis chilensis* + *Ch. nigra* + *Ch. carbonaria* + *Ch. denticulata*. The *Chelonoidis*-clade is supported by four synapomorphies: presence of a circular or elliptical pit on the ventral side of the premaxillae (character 27:0), *processus coronoideus* higher than the dentary (character 60:1), presence of dentary hook (character 71:1), and absence of a contact between inguinal and femoral scutes (character 131:0).

After running the 20,000,000 generations of the Bayesian Inference analysis, the average standard deviation of split frequencies was 0.013843 and it reached an Effective Sample Size (ESS) equal to 1,543. The general topology of the molecular consensus tree (Figure 7) is not well resolved and it differs notably from the consensus tree obtained with the IWMP. UMPE 443 gen. et sp. nov is recovered in a large polytomy along with several other taxa.

Stylemys inusitata and *S. nebrascensis* are recovered as sister taxa (posterior probability = 94), while *S. capax* is recovered forming a clade together with *Ergilemys insolitus, Cheirogaster maurini,* and *Taraschelon gigas,* in concordance with their position recovered in the IWMP consensus tree (Figure 6).

“*Testudo” antiqua*, *Te*. *kaiseni* and *Te*. *promarginata* are recovered in a large polytomy, while *Te*. *lunellensis*, *Te*. *oughlamensis*, and *Te*. *shensiensis* are recovered forming a separated clade (posterior probability = 59). On the other hand, *Te*. *graeca*, *Te*. *marginata*, *Te*. *kleinmanni*, and *Te*. *marmorum* formed another clade, supported by a high posterior probability (98).

The Geochelona clade is recovered in part, compared with the IWMP consensus tree. This clade is supported by a low posterior probability (53). Three major sub-clades are recovered into Geochelona. The first clade comprising *Kinixys erosa* and *K*. *homeana*, and it is supported by a high posterior probability (100). The second clade is integrated by *Centrochelys sulcata*, “*Chelonoidis*” *gringorum*, *Geochelone elegans*, and *Megalochelys atlas*, and it is supported by a low posterior probability (59). The last clade is conformed by *Chelonoidis carbonaria*, *Ch. denticulate*, *Ch. chilensis*, and *Ch. nigra*, and it is supported with low posterior probability (77).

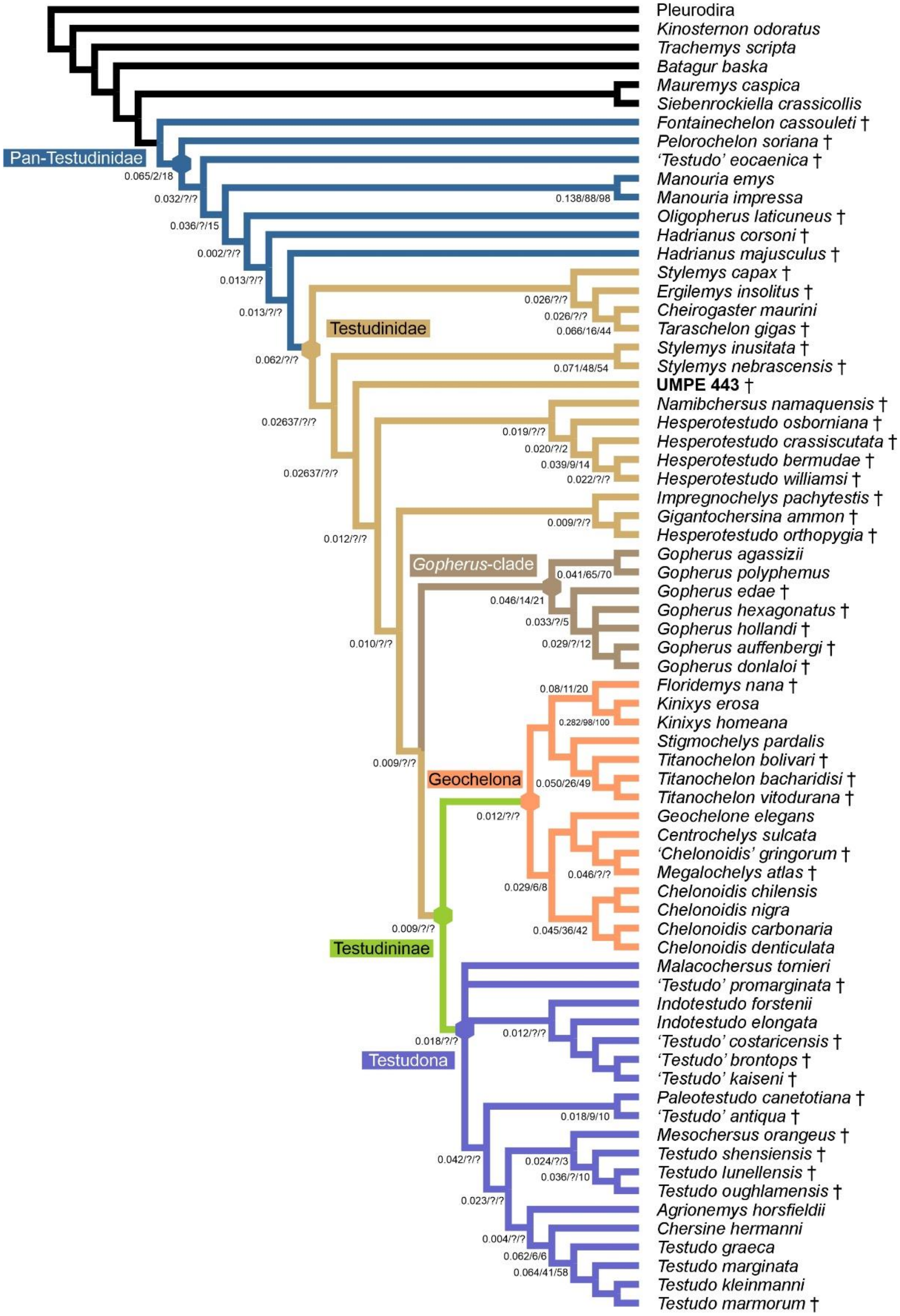

Figure 6. Phylogenetic hypothesis obtained with the Implied Weighted Maximum Parsimony analysis. Consensus tree resulting from the three most parsimonious trees (TL = 13037, CI = 0.383, RI = 0.338), showing the position of UMPE 443 gen. et sp. nov. (in bold). Numbers below the lines indicate Bremer/boostrap/jacknife values. The extinct taxa are indicating with the cross.

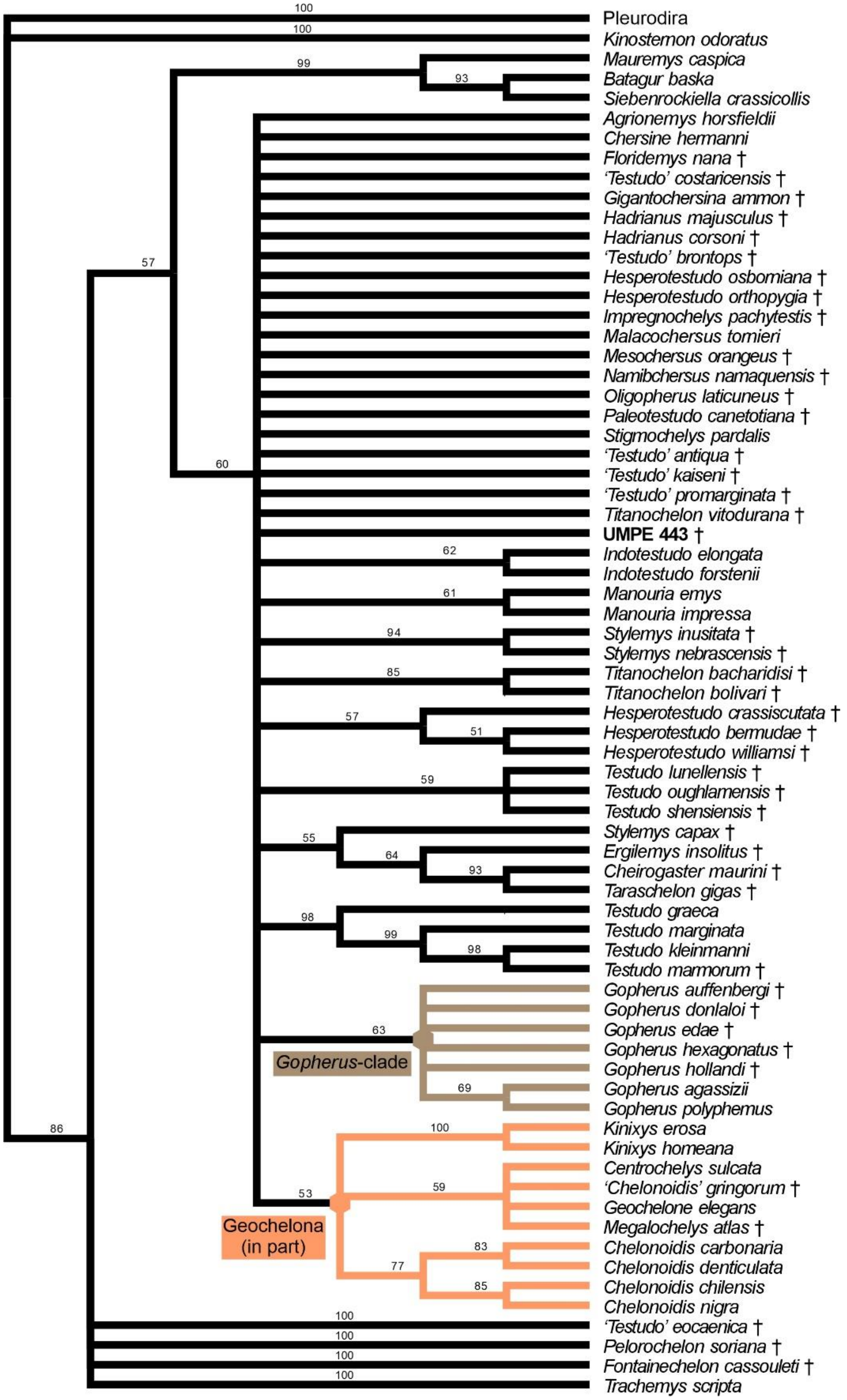

Figure 7. Phylogenetic hypothesis obtained with the Bayesian Inference analysis. Tree resulting from majority rule consensus (>50). Effective Sample Size (ESS) = 1,543. UMPE 443 gen. et sp. nov (in bold) is recovered in a large polytomy. The extinct taxa are indicating with the cross.

3.8. Discussion

3.8.1. Phylogenetic framework

We analyzed the phylogenetic relationships of UMPE 443 gen. et sp. nov. in a global Pan-Testudinidae context using a total evidence (morphological + molecular) phylogenetic analysis, that allowed to confirm their inclusion within the Testudinidae clade. The main differences between the resulting tree of Vlachos and Rabi (2018) and our results may be due to the number of taxa used in each analysis. In our phylogenetic analysis, we used a larger number of taxa within Pan-Testudinidae compared to that in Vlachos and Rabi (2018), because we included a larger sample of North American taxa from the data matrix of Vlachos (2018). We also noticed that the topology of the resulting trees varies according to the type of phylogenetic analysis used. The following phylogenetic discussion is based on the consensus tree resulting from the Implied Weighted Maximum Parsimony analysis carried out in this work, the one with better resolution.

Fontainechelon cassouleti, from the early Eocene (Ypresian) of Saint Papoul, Aude, France has been considered the basal most member of Pan-Testudinidae (Claude & Tong 2004, Pérez-García & Vlachos 2014, Vlachos & Rabi 2018; Pérez-García et al. 2020), although *Hadrianus majusculus*, from early Eocene of New Mexico, USA, has been referred as the oldest taxon in the group (Joyce et al. 2013, Vlachos & Rabi 2018). The phylogenetic position of *Fo. cassouleti* and *Ha. majusculus*, with respect to each other, has been previously discussed. Vlachos (2018) considered that *Ha. majusculus* is more derived than *Fo. cassouleti*, because it has a narrower and longer gular scutes, and "wavy" humero-pectoral sulcus with medial part being convex anteriorly. Contrary, Lichtig et al. (2021) disagree with that assessment because they consider being *Hadrianus* the basal most testudinid, given the absence of the derived traits present in *Fontainechelon*, as the lack of costal wedging and the overlap of the pectoral scutes onto the entoplastron. Nevertheless, our phylogenetic results indicate that *Fontainechelon* is placed lower on the stem than *Hadrianus* since the combination of characters are considered more primitive: octagonal third neural (homoplasic in *Testudo oughlamensis*), rectangular fourth neural (shared with "*Testudo*" *eocaenica* and *Te*. *oughlamensis*), and presence of a medial contact of the seventh and/or eighth costal bones (shared with *Hadrianus corsoni* and "*Testudo*" *antiqua*).

Pelorochelon soriana, “*Testudo*” *eocaenica*, *Oligopherus laticuneus*, *Hadrianus corsoni*, and *Ha*. *majusculus* branch sequentially and confirm their position within Pan-Testudinidae. The position of the clade *Manouria emys* + *Ma*. *impressa* out of Testudinidae is contradictory, because the phylogenetic molecular hypothesis showed that *Manouria* is positioned, together with *Gopherus*, in a stem position within the extant Testudinidae (Guillon *et al*. 2012, Pereira *et al*. 2017). Crumly (1984) mentions that *Manouria* shared primitive characters (e.g. a split supracaudal; gular and femoral scutes with equal mid seam lengths; a broad cervical scute; the first two neurals hexagonal in shape with the short articulation directed posteriorly, and the last five neurals hexagonal in shape with the short articulation directed anteriorly), that could be the reason of their phylogenetic resolution in our analysis. Additionally, the inclusion of *Manouria* within the great data set where most of the OTUs are represented by extinct taxa could influence the obtained resolution.

In the three analyses presented in this work, the *Gopherus*-clade is recovered as monophyletic, consistent with previous morphological and molecular phylogenetic hypotheses (e.g. Guillon et al. 2012, Pereira et al. 2017, Vlachos 2018, Vlachos & Rabi 2018).

Stylemys has been considered a monophyletic taxon in previous phylogenetic hypotheses (e.g. Vlachos 2018). Nevertheless, in our IWMP (Figure 5), only *Stylemys inusitata* and *St*. *nebrascensis* are recovered as sister taxa, while *St*. *capax* is recovered forming a clade with *Ergilemys insolitus*, *Cheirogaster maurini*, and *Taraschelon gigas*. This arrangement is the same as the obtained in the BI consensus tree (Figure 6). This raises the possibility that *St*. *capax* should be refered to a new genus; it differs from *St*. *inusitata* and *St*. *nebrascensis* mainly in the shape of the second and third neural, the coincidence of the costo-peripheral suture with the pleuromarginal sulcus, the shape of the femoro-anal sulcus, and the width of the vertebrals in relation to the pleurals.

Hesperotestudo seems to be monophyletic, except that *He*. *orthopygia* is grouped outside the *Hesperotestudo*-clade, branching together with *Gigantochersina ammon* and *Impregnochelys pachytestis*. In our consensus tree resulting from the BI (Figure 7), *He*. *orthopygia* and *He*. *osborniana* are recovered in a large polytomy, outside the clade formed by *He*. *bermude*, *He*. *crassiscutata*, and *He*. *williamsi*. Therefore, it could be considered that *He*. *orthopygia* and *H*. *osborniana* should be referred to different new genera. Contrarily, in

Vlachos (2018), *He*. *orthopygia* is considered a valid member of *Hesperotestudo*. Both genera, *Stylemys* and *Hesperotestudo* are recovered as basal Geochelona in Vlachos and Rabi (2018), but in our IWMP strict consensus tree they are recovered as basal Testudinidae.

The Neogene European *Titanochelon* genus is recovered as a monophyletic clade, and it is the sister taxon of *Stigmochelys pardalis*. This arrangement is consistent with previous topologies (Vlachos & Rabi 2018; Pérez-García et al. 2020). Similarly, "*Chelonoidis*" *gringorum* (Simpson 1942), from the early Miocene of the Chubut Valley, Patagonia, Argentina, is recovered out of the crown *Chelonoidis*-clade in the three analyses here performed, consistent with the results of Vlachos and Rabi (2018). Although "*Ch*." *gringorum* has been considered part of the crown *Chelonoidis* (de la Fuente 1994; de la Fuente et al. 2018), our results suggests that "*Ch". gringorum* belong to a different new genus.

Testudo is a problematic taxon used as a wastebasket. In our IWMP *Testudo* is recovered as polyphyletic. *Testudo graeca*, *Te*. *marginata*, *Te*. *kleinmanni*, and *Te*. *marmorum* are grouped together with *Agrionemys horsfieldii* and *Chersine hermanni,* similar to previous arrangements (Vlachos & Tsoukala 2016; Vlachos & Rabi 2018). On the contrary, the arrangement of *Te*. *shensiensis*, *Te*. *lunellensis*, and *Te*. *oughlamensis*, together with *Mesochersus orangeus* resulted in a different position with respect to previous works (e.g. Vlachos & Rabi 2018). On the other hand, "*Testudo*" *costaricensis*, "*Te*." *brontops*, and "*Te*." *kaiseni* branch together, in spite it has been proposed that they belong to different genera than *Testudo* (Vlachos & Rabi 2018).

3.8.2. Paleobiogeography

Testudinidae is the most diverse and widely distributed crown-clade of turtles, with 67 extant species (Rhodin et al. 2017). Although the biogeographic history of the clade Pan-Testudinidae is complicated, the fossil record suggests that it possibly originated in Europe or North America, during the earliest Eocene. According to our phylogenetic resolution, *Fo. cassouleti* is the known basal-most member of Pan-Testudinidae. Under this premise, an European origin of Pan-Testudinidae is here supported. During the middle Eocene Pan-Testudinidae spread into North America, with *Hadrianus* entering in the scene. Later, in the late Eocene, Pan-Testudinidae reached Africa, and Asia, diversifying in new taxa included in the Testudinidae clade. The presence of related taxa in North America (*Stylemys nebrascensis*), Asia (*Ergilemys insolitus*), and Europe (*Cheirogaster maurini* and *Taraschelon gigas*) during the late Eocene-early Oligocene, suggest a second radiation, possible from North America. The occurrence of the new Testudinidae taxon in the south of Mexico suggests that this group reached more southern areas during the early Oligocene. The dispersion of the basal members of Testudinidae coincides with the cooling and rapid expansion of Antarctic continental ice-sheets, in a period called Oi-1 Glaciation during the Eocene-Oligocene transition (Zachos et al. 2011), that possible favored the formation of intercontinental land bridges in tropical zones as consequence of the drop in the sea level.

The Miocene was the "golden age" for land tortoises, because the "Tortoise Miocene Explosion" occurred during this period. In the early-middle Miocene, the expansion of Testudinidae in North America and Africa is notorious. In North America, Testudinidae is mainly represented by *Hesperotestudo* spp. and *Gopherus edae* (Hay 1908; Auffenberg 1964, 1974; Vlachos 2018), while in Africa they are represented by *Impregnochelys pachytestis*, *Mesochersus orangeus*, and *Namibchersus namaquensis* (Meylan & Auffenberg 1986; Lapparent de Broin 2003). Testudinidae reached South America in the late Oligocene or the early Miocene. Although the means of arrival of testudinids to South America is not clear, it has been proposed that they derived from Africa by transoceanic drift (de la Fuente et al. 2014). The molecular evidence strongly supports an Afroasiatic origin for the South American taxa (Le et al. 2006; Guillon et al. 2012; Pereira et al. 2017). During the middle Miocene to the Pliocene, *Titanochelon* spread across Europe, becoming the best-represented large testudinid in this continent (Pérez-García & Vlachos 2014; Pérez-García et al. 2017). The higher taxonomic diversity of Testudinidae during the Miocene possibly was favored by the Miocene Climatic Optimum, a warm climate period that was followed by a significant cooling (Zachos et al. 2001).

During the Pliocene and Pleistocene, members of the clades Testudona and Geochelona expanded across Europa, Asia and Africa. In the Pleistocene Geochelona became extinct in North America, but in South America and Africa they become the dominant group. The diversity of Testudinidae decreased considerably worldwide, as consequence of the drastic climatic change occurred in the Late Pleistocene.

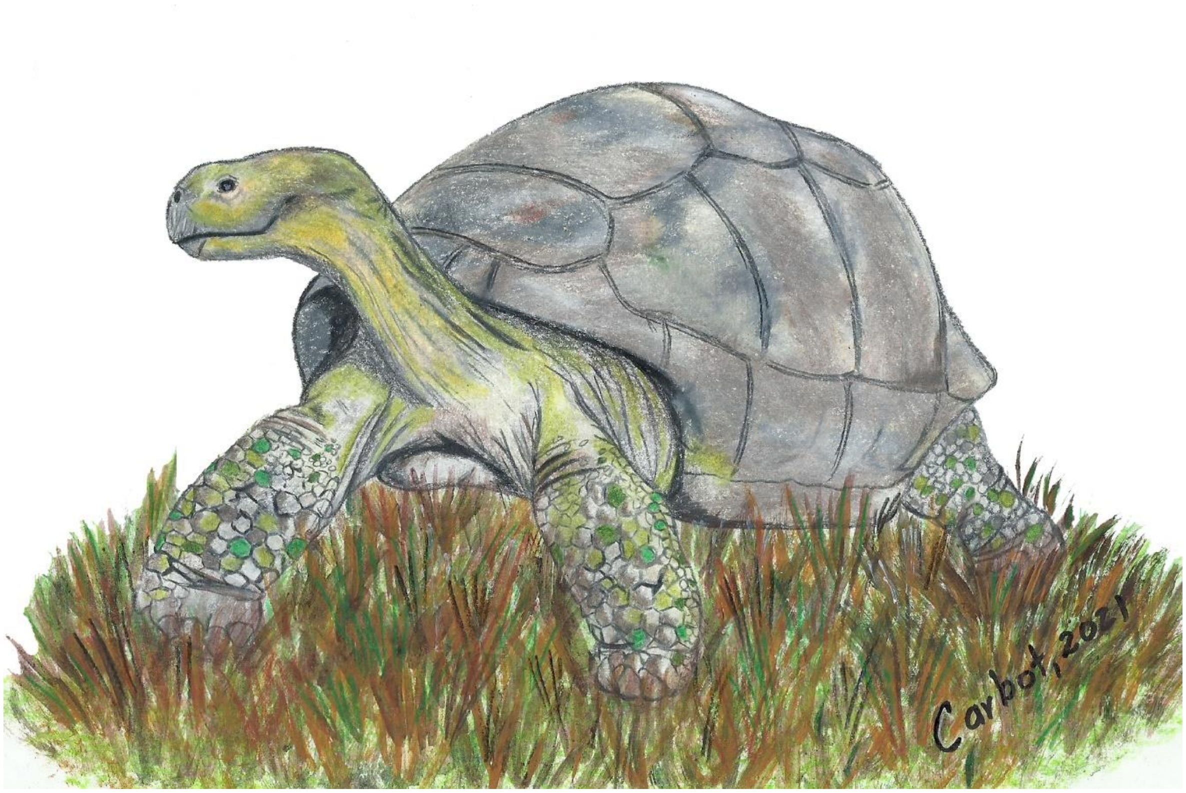

Figure 8. Reconstruction of UMPE 443 gen. et sp. nov. Art by Gerardo Carbot-Chanona.

3.9. Conclusions

The combination of morphological characters, as well as the results obtained by multiple phylogenetic approaches done in this work indicate that UMPE 443 is a new stem taxon within Testudinidae, increasing the geographical distribution and diversity of this clade in North America. This new taxon also represents the first Paleogene tortoise described for Mexico, as well as the oldest Testudinidae known in the country.

Of the three performed analyses, the worst resolution was obtained using the Bayesian Inference because this type of analysis is more sensitive to data consistency. The best phylogenetic resolution was obtained by the Implied Weighted Maximum Parsimony analysis, with results like those obtained by Standard Maximum Parsimony analysis. The difference between the topology of the three phylogenetic analyses shows that the position of several taxa within Testudinidae is sensitive to the phylogenetic method performed, probably by the high homoplasy and polymorphism found in this clade, as well as the great number of missing data in most extinct taxa. Future works including more taxa and better-preserved specimens, may help to better resolve the phylogeny of Pan-Testudinidae.

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CAPÍTULO IV

The first Pan-Carettochelys turtle in the Neogene of the American continent and its paleobiogeographical relevance

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4.1. Abstract

Turtles of the clade Pan-Carettochelys have a broad fossil record, from the Early Cretaceous to the late Miocene in the Old World, and some records in the Paleogene of North America; however, its distribution in the Neogene of the American continent was unknown. Here we describe a new species of Pan-Carettochelys, *Allaeochelys liliae* sp. nov., based on an incomplete single specimen from the Los Pocitos mine, Mazantic Shale (Lower Miocene, Aquitanian), near Simojovel, State of Chiapas, southern Mexico. A midline keel, plastral kinesis, and a single suprapygal, suggest that the new turtle belongs to Pan-Carettochelys, and the loss of plastral scutes includes it in Carettochelyidae. The new fossil is referred to *Allaeochelys* based on the loss of carapacial and plastral scutes and a large plastron. It differs from other *Allaeochelys* by the following unique combination of characters: carapacial ornamentation slightly marked with small and shallow tubercules and pits, xiphiplastron and hypoplastron ornamented with pits and vermicular grooves uniformly distributed in all the bone surface, single suprapygal with general triangular shape but with five contact edges, and costal eight in contact with the peripherals nine and ten. *Allaeochelys liliae* sp. nov., represent the first record of Pan-Carettochelys in the Neogene of the American continent, and it is the first *Allaeochelys* described for the Aquitanian (early Miocene) worldwide.

Key words. *Allaeochelys*, Pan-Carettochelys, Mazantic Shale, Early Miocene, Phylogenetic analysis

4.2. Introduction

Pan-Carettochelys Joyce, Parham, and Gauthier 2004, is defined as the most inclusive clade containing *Carettochelys insculpta* Ramsay 1887, but not *Trionyx triunguis* (Forskål 1775), or any other extant turtle species (Joyce *et al*., 2004a). Pan-Carettochelys comprises the most basal members including the genus *Kizylkumemys* Nessov 1976, from the Early-Late Cretaceous (Aptian-Cenomanian) of central Asia (Uzbekistan), and Carettochelyidae Gill 1889, a clade that ranges from the Paleocene to the Recent (Joyce, 2014). In all Pan-Carettochelys, the shell is formed by an uninterrupted series of seven neurals (except in *C. insculpta*), ten pairs of peripherals, eight pairs of costals, one single suprapygal triangular in shape and the pygal (Joyce, 2014). The plastron is formed by a pair of epiplastra, a large entoplastron triangular in shape, a pair of hyoplastra, a pair of hypoplastra, and a pair of xiphiplastra (Joyce, 2014). The plastron varies in form and size between taxa. In *Kizylkumemys* the plastron is thin, and the xiphiplastra are long and posteriorly acuminate. In *Anosteira*, the plastron is medium-size, while in *Allaeochelys* and *Carettochelys* the plastron is wide and extends along the entire ventral part of the shell (Harrassowitz, 1922; Walther, 1922). The plastral scutes are only present in *Kizylkumemys*.

Pan-Carettochelys have a broad record from the Cretaceous to the late Miocene in Eurasia and Africa, and some records in the Paleogene of North America. In Eurasia there are records from the Early Cretaceous of Laos and Thailand (Lapparent de Broin, 2004; Tong *et al*., 2005; Danilov *et al*., 2017); the Late Cretaceous of France, Mongolia, Uzbekistan, Thailand and Japan (Nessov, 1976; Hirayama and Chitoku, 1994; Hirayama 1998; Vullo *et al*., 2010; Danilov *et al*., 2017); the early Eocene of Belgium, France, Germany, Spain, United Kingdom and Pakistan (Lydekker, 1889a, 1889b; Dollo, 1886; Harrassowitz, 1922; Jiménez Fuentes, 1971; Broin, 1977, 1987; Westgate, 2001; Alonso-Santiago *et al*., 2008); the late Eocene of France, United Kingdom, China, Mongolia and Myanmar (Lydekker, 1889c; Gilmore, 1931; Zangerl, 1947; Cheng, 1961; Broin, 1977; Hutchinson *et al*., 2004; Tong *et al*., 2010); the early and late Oligocene of Germany (Darga *et al*., 1999; Karl, 2002; Karl *et al*., 2006; Karl and Müller, 2008); the early Miocene of Saudi Arabia, Libya and Germany (Lapparent de Broin, 2000; Joyce *et al*., 2004b, Havlik *et al*., 2014). In Africa they are known from the early Miocene of Egypt and the late Miocene of the Democratic Republic of Congo (Thomas *et al*., 1981, Hirayama, 1992), and in Oceania in Papua New Guinea

(Glaessner, 1942). Today, they are represented by the monospecific taxon *Carettochelys insculpta* from northwestern Australia and southern Papua New Guinea (Bonin *et al*., 2006).

In North America Pan-Carettochelys has been reported from the early Eocene of Canada and USA, and the late Eocene of USA (Hay, 1906; Clark, 1932; Clark *et al.*, 1967; Estes and Hutchison, 1980; Hutchison and Storer, 1988; Eaton *et al*., 1999; Weems, 2014). None Pan-Carettochelys have been described southern from eastern Hanover County, Virginia in North América (Weems, 2014). During the Neogene there are no reports of this clade along the American continent. Here we report the first record of a Pan-Carettochelys turtle from the Neogene (Early Miocene-Aquitanian) of the American continent, based in a fossil collected from the State of Chiapas, southern Mexico.

4.3. Geological setting

Simojovel, in the southern Mexican State of Chiapas, is famous for its amber deposits contained in three Cenozoic marine terrigenous units that outcrop in the southern edge of Montañas del Norte (Figure 1). Allison (1967) informally named Simojovel Formation to 884 m thick sequence that crops out northeast of the La Esperanza syncline and southwest of the Simojovel syncline. Later, Frost and Langenheim (1974) proposed the name La Quinta Formation in substitution of Simojovel Formation, and they divided it in three members formed mainly by sandstone, shale, and limestone: Camino Carretero (in the base), Florida Limestone (in the middle) and Finca Carmito (at the top). La Quinta Formation is covered by a sequence of 310 m of dark-gray shales named Mazantic Shale (Allison, 1967), that contains amber in association with benthic foraminifera, corals, echinoids, bivalves, marine gastropods, crabs and shark teeth (Frost and Langenheim, 1974; Gonzalez-Barba *et al.*, 2002; Vega *et al*., 2009; Perrilliat *et al.*, 2010). Overlaying Mazantic Shale is the Balumtum Sandstone, conformed by 760 m of gray sandstone bearing amber, gastropods, bivalves, and crustaceans (Frost and Langenheim 1974; Perrilliat *et al.*, 2010) (see Figure 2).

The specimen here described was recovered from Los Pocitos amber mines, near Simojovel de Allende village, 125 km northwest of Tuxtla Gutiérrez, Chiapas. Los Pocitos mines are located within the Mazantic Shale. This lithographic deposit has been dated as late Oligocene to middle Miocene (Langenheim *et al*., 1966; Tomasini-Ortíz and Martínez-Hernández, 1984; Ferrusquía-Villafranca, 2006; Castañeda-Posadas and Cevallos-Ferriz, 2007; Solorzano-Kraemer, 2007, 2010; Solorzano-Kraemer and Mohrig, 2007). Vega *et al*. (2009) dated the deposit with an absolute age of 23 Ma for the Mazantic Shale based on $^{87}Sr/^{86}Sr$ isotopes of a sample taken from a well-preserved shell of the gastropod *Turbinella maya* from Los Pocitos, placing it in the early Miocene (Aquitanian). A Similar age (22.8 Ma) was obtained by the same radiometric method from the amber deposits in Las Granjas mines that outcrop in the Balumtum Sandstone (Serrano-Sanchez *et al.,* 2015). These results suggest that the radiometric age of ~23 Ma represents an accurate age for the amber deposits. This age is consistent throughout the upper part of La Quinta Formation–Mazantic Shale–Balumtum Sandstone lithographic units.

Figure 1. Location map of Los Pocitos mine, near of Simojovel de Allende town, Simojovel municipality, State of Chiapas, southern Mexico.

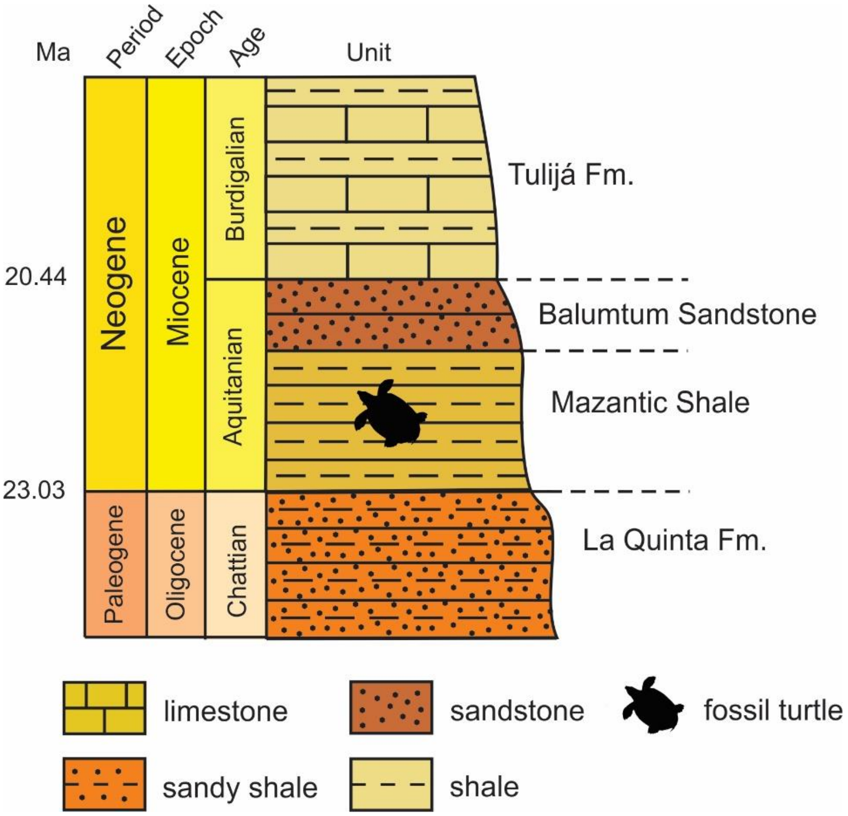

Figure 2. Generalized stratigraphic chart showing the age and geological divisions of the Simojovel area. Modified from Serrano-Sánchez *et al.* (2015).

4.4. Material and methods

4.4.1. Studied material

The turtle was collected by a local miner at Los Pocitos amber mine, in 2004. It preserves the posterior part of carapace with an incomplete plastron, embedded on a dark-gray sandy shale matrix. Latter, the specimen was acquired by Luis Zúñiga Mijangos, who housed it at the Museum of Amber Lilia Mijangos (MALM) in San Cristobal de Las Casas, State of Chiapas, Mexico, with collection number MALM-401. The fossil collection of MALM is formally certified by the Instituto Nacional de Antropología e Historia (INAH), the federal agency that protects the paleontological heritage in Mexico.

4.4.2. Preparation

The specimen was prepared using airscribe, dental needles, and soft bristle brushes to remove rock matrix. It was hardened with Butvar-B90, and the broken parts were joined with water-proof commercial glue.

4.4.3. Comparative materials

The specimen was compared with valid Pan-Carettochelys taxa according to Joyce (2014). It includes the basal species *Kizylkumemys schultzi* Nessov 1976, *K. khoratensis* Tong, Suteethorn, Claude, Buffetaut, Jintasakul 2005, *Anosteira manchuriana* Zangerl 1947; *An. maomingensis* Chow and Liu 1955, *An. mongoliensis* Gilmore 1931, *An. ornata* Leidy 1871; *An. pulchra* (Clark, 1932) and all species within *Allaeochelys* Noulet, 1867. Additionally, we compared it to the extant *Carettochelys insculpta* Ramsay 1887 (see Appendix A). The morphological nomenclature for the bony plates follows Zangerl (1969).

4.4.4 Phylogenetic analysis

To establish the phylogenetic relationships of the new taxa within Pan-Carettochelys, we scored MALM-401 features in a modified dataset (Appendix B) based on Joyce (2007), Havlik *et al*. (2014) and Danilov *et al*. (2017), using Mesquite 3.61 (Maddison and Maddison, 2019). We eliminated character 82 from Joyce (2007) (retaked by Havlik *et al*. [2014]) and Danilov *et al*. [2017]), because it is redundant with the character 81 from the same data matrix; in consequence, we added a new character state (see note in the Appendix C, character 98). A data matrix with 153 morphological characters and 81 taxa was used in the phylogenetic analysis.

We conducted a Maximun Parsimony Analysis in TNT 1.5 (Goloboff *et al*., 2008; Goloboff and Catalano, 2016), considering all characters with equal weight. For analysis we deactivate phylogenetic uninformative characters using the command *xinact*. The characters were treated as unordered. We used the New Technology search option with 100 random seeds, with the Sectorial search, Ratchet, Drift and Tree fusing default options activated. The final tree was obtained by strict consensus. We estimated tree robustness using bootstrap with 1000 replicates (Groups present/Contradicted, GC; Goloboff *et al*. 2003) (Appendix D, Fig.

S2) and we calculated Statistical Support Values (Bremer Index, Consistence Index and Retention Index) with the command scripts included in TNT.

4.4.5. Institutional abbreviations

MALM: Museum of Amber Lilia Mijangos, San Cristóbal de Las Casas, Chiapas, Mexico.

4.5 Results

4.5.1. Systematic paleontology

Testudines Batsch, 1788
Cryptodira Cope, 1868
Trionychoidea Fitzinger, 1826
Pan-Carettochelys Joyce, Parham and Gauthier, 2004
Carettochelyidae Gill, 1889
Carettochelyinae Williams, 1950
Allaeochelys Noulet, 1867
Allaeochelys liliae sp. nov.
Zoobank: urn:lsid:zoobank.org:act:819C03FB-1E74-406C-A11F-A7A913724DA7

4.5.2. Holotype. MALM-401, posterior part of the carapace and partial plastron. Museum of Amber Lilia Mijangos, San Cristóbal de Las Casas, Chiapas, Mexico (Figure 3 and 4).

4.5.3. Etymology. The specific epithet *liliae* is to honor the memory of Mrs. Lilia Mijangos. Her effort has safe a great number of Simojovel fossils. Her interests in scientific research has facilitated many paleontologists to study these fossils.

4.5.4. Type locality and horizon. Los Pocitos mines, municipality of Simojovel de Allende, State of Chiapas, southern Mexico. Mazantic Shale, Lower Miocene (Aquitanian).

4.5.5. Diagnosis. *Allaeochelys liliae* sp. nov. differs from other species of *Allaeochelys* in the following combination of characters: carapacial ornamentation slighty marked with small and shallow tubercules and pits; xiphiplastron and hypoplastron ornamented with pits and vermicular grooves uniformly distributed in all bone surface; single suprapygal with general triangular shape, but with five contact edges, and costal eight in contact with the peripherals nine and ten.

4.6. Description

4.6.1. General aspect of carapace and plastron. The specimen is dark-brown and is embedded in a dark-gray sandy shale matrix. Only the posterior portion of the carapace is preserved, suggesting a drop-like general shape. The carapace preserves part of neural seven, the left and right costals six, seven and eight, the pygal and suprapygal, the right and left peripheral ten, and the left peripheral nine. The carapace has a midline keel from peripheral seven to the pygal bones and there is no evidence of a bridge with the plastron, suggesting that the connection was ligamentous, as in another soft-shell turtles (Figure 3). The plastron preserves both xiphiplastra and the left hypoplastron and lacks plastral fontanels. The surface of the carapace and plastron are ornamented with smooth pits and grooves. There is no evidence of scute sulci neither in the carapace nor the plastron (Figure 4).

4.6.2. Neurals. Only neural seven is preserved. It is semi-rectangular and longer than width. The lateral side contacts costal six, but posteriorly barely touches costal seven. The surface of the neural is almost smooth with no evident ornamentation.

4.6.3. Costals. Costal bones six, seven and eight are preserved. All costal bones are completely ossified showing no lateral fontanels. Costal six is longer than width, slightly curved posteriorly, and medially it contacts neural seven. Costal seven is longer and more curved than costal six and laterally it reaches peripheral seven. Costal eight is posteriorly curved contacting the suprapygal and distally the peripherals nine and ten. Both costals seven and eight are in contact medially. All costal bones are ornamented with slighty marked grooves and slight irregular bumps.

4.6.4. Peripherals. Only the anterior part of the left peripherals nine and ten, and proximal part of the right peripheral ten are preserved. Peripheral nine contacts costal seven, but their shape cannot be defined. Peripheral ten is rectangular in shape. Lateral side of the peripheral contacts costal eight and the pygal, while the anteromedial side contacts the suprapygal. The surface of both conserved peripherals is sculpted with small pits.

4.6.5. Suprapygal. There is only one suprapygal with a general triangular shape, but with five edges. Anterolaterally it contacts costal eight, posterolaterally peripherals ten, and posteriorly the pygal.

4.6.6. Pygal. The pygal is incomplete and only preserves de anterior part, which contacts the suprapygal with a straight suture. The general shape cannot be established.

4.6.7. Hypoplastron. The specimen preserves a nearly complete left hypoplastron and a portion of the right hypoplastron. In the left hypoplastron the "wing" is missing. The bone surface is ornamented with small and shallow pits and tubercles, more abundant in the distal portion.

4.6.8. Xiphiplastron. Both xiphiplastra are preserved. The xiphiplastron is semitriangular, longer than wide, narrowing posteriorly. The left xiphiplastron contacts the left hypoplastron with a straight suture, condition not seen in the right xiphiplastron because the bone is displaced to the right from the original position. There is a clear evidence of a hinge indicating that was some degree of plastral kinesis between these two bones. Both xiphiplastra are ornamented with pits and vermicular grooves uniformly distributed in all their bone surface.

4.6. Discussion

4.6.1. Taxonomic assessment and comparation

Following Joyce (2014), the specimen MALM-401 can be referred to Pan-Carettochelys by the following synapomorphies: presence of a midline keel, plastral kinesis and a single suprapygal; it can be referred to Carettochelyinae by the loss of plastral scutes and is referred to *Allaeochelys* by the loss of vertebral scutes and a large-size plastron.

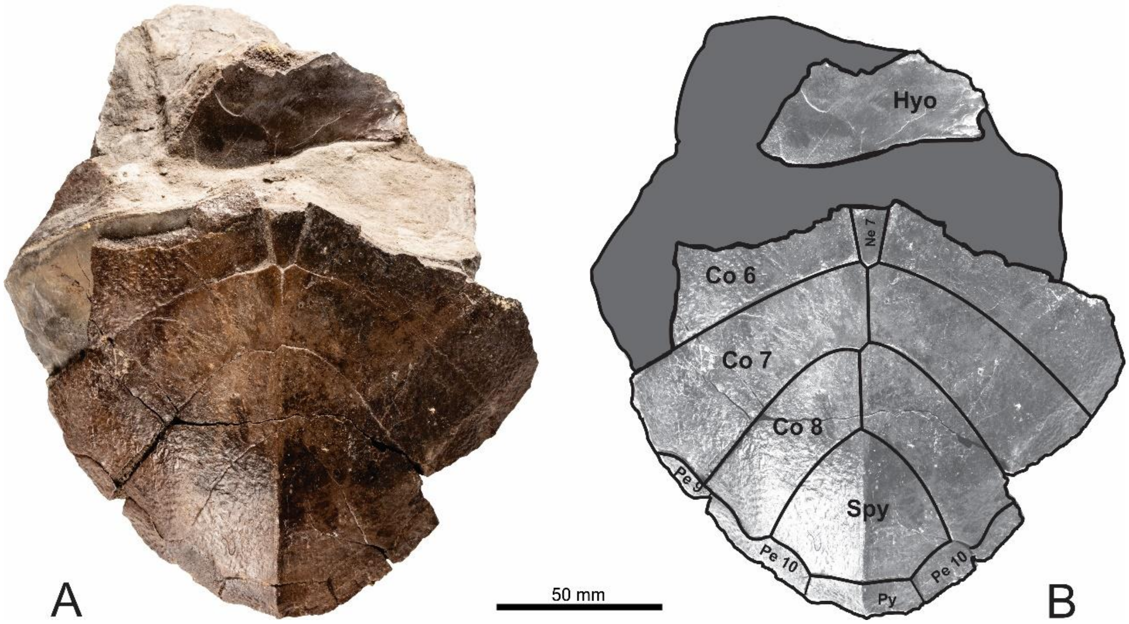

Figure 3. MALM-401, holotype of *Allaeochelys liliae* sp. nov. (dorsal view) from the early Miocene of Simojovel, State of Chiapas. Photograph (A) and schematic draw (B). Abbreviations: Co, costal; Hyo, hyoplastron; Ne, neural; Pe, peripheral; Py, pygal; Spy, suprapygal.

Allaeochelys liliae sp. nov. is considered a new species of *Allaeochelys* because of a unique combination of characters compared to previously described species of the genus. *Allaeochelys liliae* sp. nov. differs from the Eocene species *Al. delheidi* (Dollo 1886), *Al. crassesculpta* (Harrassowitz 1922) and *Al. parayrei* Noulet 1867 in the contact of the last neural. While in the new species the neural seven contacts the suture between the costals six and seven, in *Al. delheidi*, *Al. crassesculpta* and *Al. parayrei* the neural seven reaches the middle part of the costal seven (Figure 5). Similarly, *Al. liliae* sp. nov. shows differences with *Al. delheidi* and *Al. crassesculpta* in the contact of the posterior costals and peripherals. In *Al. liliae* sp. nov. costal eight contact peripherals nine and ten, and costal seven contact peripherals nine, contrary to *Al. delheidi* in which costal eight only contact peripheral ten, and costal seven contact peripheral nine and barely peripheral ten (Figure 5B). In *Al. crassesculpta* costal eight contact peripheral nine, and costal seven contact peripheral eight (Figure 5C).

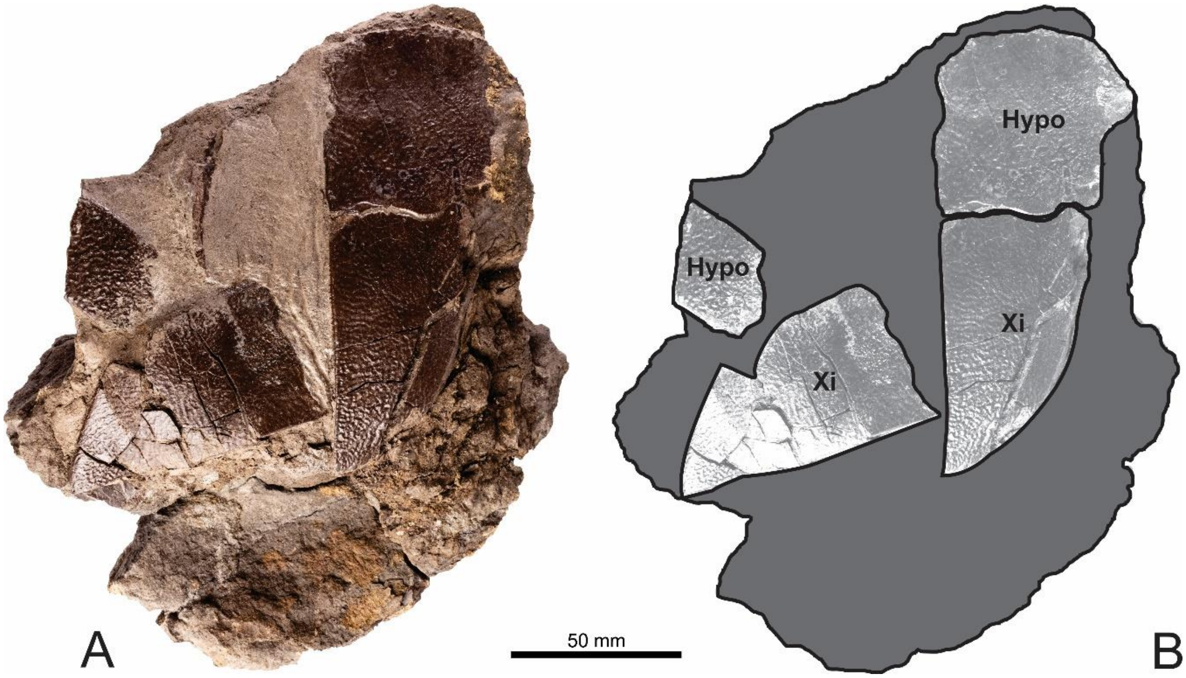

Figure 4. MALM-401, holotype of *Allaeochelys liliae* sp. nov. (ventral view) from the early Miocene of Simojovel, State of Chiapas. Photograph (A) and schematic draw (B). Abbreviations: Hypo, hypoplastron; Xi, xiphiplastron.

Also, in *Allaeochelys liliae* sp. nov. the suprapygal have five contact sides, similar to that of *Al*. *delheidi* (Alonso-Santiago et al., 2008: fig. 6), differing to the middle Eocene *Al. magnifica* (Hutchison, Holroyd and Ciochon 2004), and the late Eocene *Al*. *parayrei* that have a triangular suprapygal, with three contact sides (Figure 5D and E). Additionally, the new species is considerably smaller than *Al. magnifica*, reaching about 1000 mm (Hutchison *et al*., 2004) compared to the 350 mm estimated for *Al. liliae* sp. nov.

Allaeochelys liliae sp. nov. has slighty marked carapacial ornamentations, with small and shallow tubercules and pits. Shell ornamentation differs from remaining *Allaeochelys* species. In the early Eocene *Al. lingnanica* Young and Chow 1962 the carapacial sculpturing consists on elongated anteroposterior ridges more prominent along the costals toward the neurals (Joyce, 2014). In the early Eocene *Al. rouzilhacensis* Lapparent de Broin 2018, carapace ornamentations are less pronounced, fine, with parasagittal pleural margins interrupted, tight, with punctuations in low relief (Godinot *et al*., 2018). In *Al. liliae* sp. nov. the hypoplastron and xiphiplastron are completely sculpted, differing from the late Eocene *Al. parayrei* where the xiphiplastron is smooth and the hypoplastra exhibit ornamentations conformed by vermicular grooves only in their lateral “wings”. Contrary to the middle Miocene *Al. libyca* Havlik, Joyce and Böhme 2014, with hypoplastron ornamentations radially developed, more distinct along the bridge and worn along the main body of the element (Havlik *et al*., 2014), in the new species, ornamentations are uniformly distributed in all the bone surface, showing no difference between the ornamentation of the bridge area and the rest of the bone surface. Also, the new species differs to the early Eocene *Al. crassesculpta* (Harrassowitz 1922) and the extant species *Carettochelys insculpta* Ramsay 1887 in which the ornamentation grooves in the hypoplastron and xiphiplastron are radially distributed from the center to the sides of the bone, and not uniformally distributed along the bone surface as are in the new species.

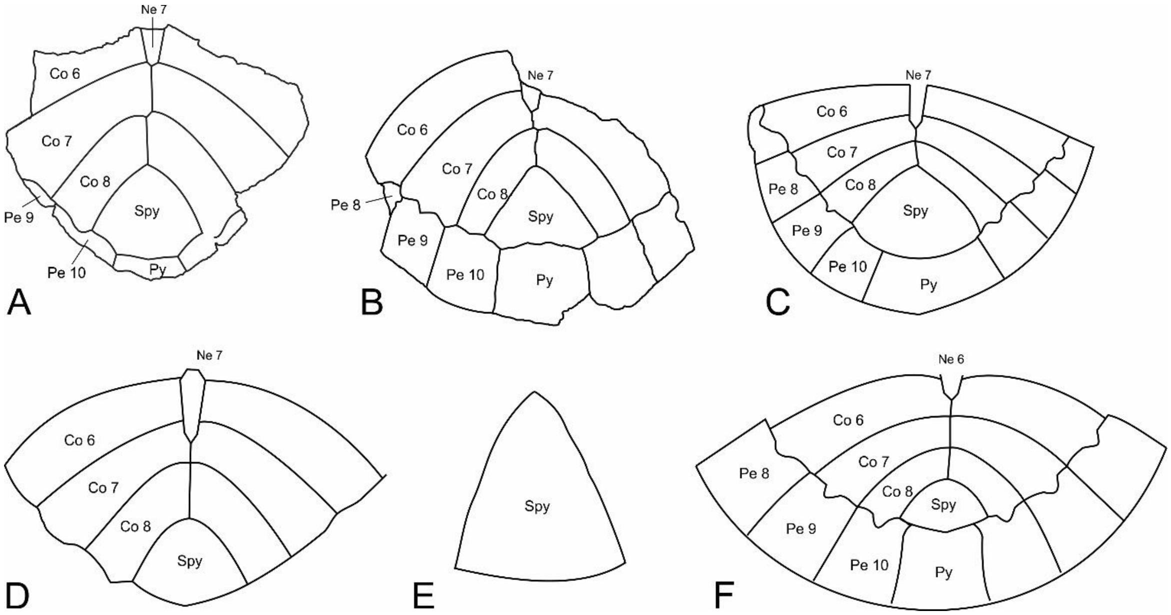

Figure 5. Schematic draw of the posterior part of the carapace of *Allaeochelys* selected species plus Carettochelys. A) *Allaeochelys liliae* sp. nov. (holotype MALM-401); B) *Al. delheidi* (based on specimen STUS 14.132; Alonso-Santiago *et al*., 2008); C) *Al. crassesculpta* (Harrassowitz 1922); D) *Al. parayrei* (based on the specimen MHNT-PAL-2010-0-115); E) *Al. magnifica* (illustration of the suprapygal based on the reconstruction by Hutchison *et al*., 2004, fig. 5); F) *Carettochelys insculpta* (based on the specimen 4800 of the Peter C. H. Pritchard Collection). Not to scale. Abbreviations: Co, costal; Ne, neural; Pe, peripheral; Py, pygal; Spy, suprapygal.

4.6.2. Phylogenetic analysis

In our Maximum Parsimony analyses, the strict consensus tree shows *Allaeochelys liliae* sp. nov. grouped within Pan-Carettochelys, Carettochelyidae and Carettochelyinae in unresolved polytomies. The analysis recovered four Most Parsimonious Trees (MPTs). The general topology of Pan-Carettochelys in the strict consensus tree (Figure 6) is similar to that presented by Joyce (2014, fig. 3), Havlik *et al*. (2014, fig. 1) and Danilov *et al*. (2017, fig. 5B), with the difference that *Kizylkumemys khoratensis* was placed out of Pan-Carettochelys, together with *Sandownia* Meylan, Moody, Walker and Chapman 2000, and *Peltochelys* Dollo 1884, possibly because material on these species is very fragmentary. In Havlik *et al*. (2014) and Joyce (2014), *Anosteira maomingensis* resulted as the sister taxon of Carettochelyinae, while in our analysis all *Anosteira* species branched together in an unresolved clade here treated as Anosteirinae, according to Nessov (1976), that excludes *K. khoratensis*. *Allaeochelys liliae* sp. nov. is recovered in a polytomy with all *Allaeochelys* species together with *Carettochelys insculpta*, forming the clade Carettochelyinae. This arrangement does not differ from those obtained by Joyce (2014), Havlik *et al*. (2014) and Danilov *et al*. (2017).

The disparity in the available morphological data per taxon was the major source for the weak resolution of the Maximum Parsimony analyses. For example, of all known *Allaeochelys*, only *Al. crassesculpta* is based in cranial and postcranial anatomy, including carapace, plastron and appendicular skeleton (Harrassowitz, 1922), *Al. libyca* and *Al. rouzilhacensis* are known by their skull, and the description of remaining species are based on incomplete carapace or/and plastral elements.

The complete results of the Maximum Parsimony Analysis can be consulted in Appendix D (https://www.sciencedirect.com/science/article/abs/pii/S0895981120304685).

4.6.3. Character analysis

In our analysis (Figure 6), Trionychia Humel 1929, is supported by five unambiguous synapomorphies: premaxillae fused (character 24[1]), foramen pre-palatinum absent (character 25[2]), vomer–pterygoid contact in palatal view absent (character 29[1]), ten pairs of peripherals presents (character 73[1]), and posterior cervicals with strongly developed ventral keels absents (character 120[1]). Pan-Carettochelys is supported by eight unambiguous synapomorphies: fossa behind articular process of quadrate absent (character

18[1]), pterygoid-pterygoid suture between foramen *posterius canalis caroticus interni* and basisphenoid present (character 45[1]), foramen *nervi trigemini* divided into two parts by prootic (character 63[1]), ventral processes of nuchal paired (character 69[1]), anterior margin of pygal greatly thickened and with visceral groove (character 79[1]), carapace with single midline keel (character 80[1]), absence of sulcus between vertebrals 3 and 4 (character 89[1]), and plastral kinesis because the scute sulci coincide with hyoplastral–epiplastral contact (character 94[1]). Our character distribution differs from previous phylogenetic studies where 11 synapomorphies (Joyce, 2014; Havlik *et al*. 2014) or one synapomorphy (Danilov *et al*., 2017) were recovered defining the Pan-Carettochelys clade.

The clade Carettochelyidae (Anosteirinae + Carettochelyinae) is supported by two unambiguous synapomorphies: *antrum postoticum* deep (character 61[1]), and plastral scutes absent (character 106[1]). ACCTRAN optimization added two ambiguous synapomorphies: vertebral 1 partly or completely divided along the midline (characters 86[1]*, and additional vertebral scute between vertebrals 2 and 3 (characters 91[2])*. In the analysis by Danilov *et al*. (2017), Carettochelyidae is supported by two unambiguous synapomorphies, i) *antrum postoticum* deep, also recovered in our analysis (here character 61[1]) and ii) additional vertebral scute between vertebrals 2 and 2, fused with vertebrals 3+4 (here character 91[3]). The additional vertebral scute is present in *Anosteira* (Danilov *et al*., 2017), but absent in *Allaeochelys* and *Carettochelys*.

Anosteirinae (*Anosteira* spp.) is supported by two unambiguous synapomorphies: an additional vertebral scute between vertebrals 2 and 3 fused with vertebrals 3+4 (character 91[3]), and posterior plastral lobe reduced (characters 105[1]). Under the DELTRAN optimization one ambiguous synapomorphies is added: sulcus between cervical and/or marginal and vertebral I absent (characters 87[1])*.

Carettochelyinae (*Allaeochelys* + *Carettochelys*) is supported by four unambiguous synapomorphies: quadratojugal–maxilla contact present (character 17[1]), large fossa behind articular process of quadrate (character 18[2]), foramen *posterius canalis caroticus interni* distant from the posterior border of basisphenoid on the ventral surface of the skull within pterygoids (character 62[2]), and all carapacial scutes absent (character 66[2]). Under ACCTRAN optimization one ambiguous synapomorphies is added: wide posterior plastral lobe (character 105[0]*), and under DELTRAN optimization two additional ambiguous synapomorphies support the clade: elongate flippers manus (character 150[2])*, and two manual claws (character 153[3])*.

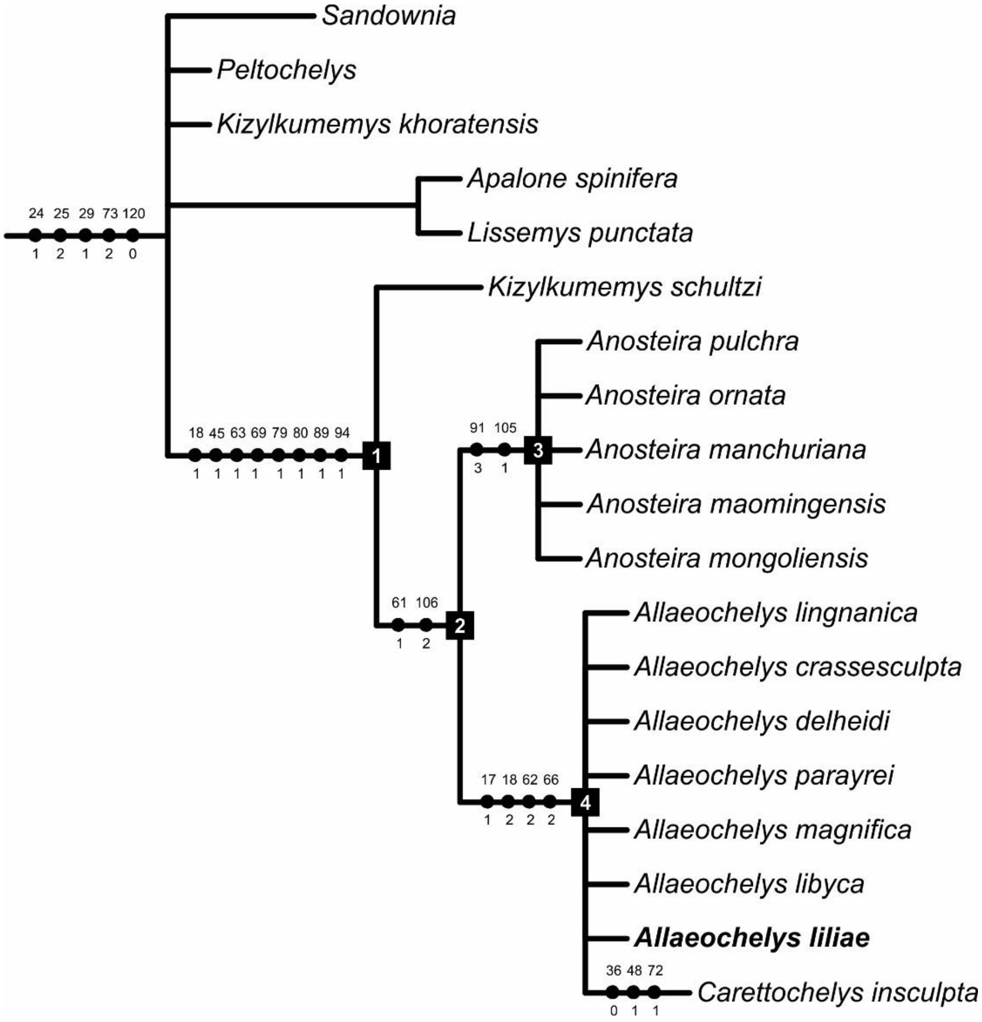

Figure 6. Phylogenetic hypothesis resulted when including *Allaeochelys liliae* sp. nov. Simplified consensus tree of four MPTs (CI = 0.461, RI = 0.807) resulting from the Maximum Parsimony Analysis showing the position of *Allaeochelys liliae* sp. nov. (in bold). Only unambiguous characters are shown. Numbers in the nodes indicate the Clades: 1, Pan-Carettochelys; 2, Carettochelyidae; 3, Anosteirinae; 4, Carettochelyinae.

4.6.4. Paleobiological aspects

The holotype specimen of *Allaeochelys liliae* sp. nov. was an adult female. The carapace and plastron are completely ossified, with no evidence of fontanels between the costals and peripherals bones, expected in juvenile turtle specimens (Suzuki, 2006), and the suture between the hypoplastron and xiphiplastron is almost straight as expected in female *Allaeochelys*, as indicated by Joyce *et al*. (2012) for *Al. crassesculpta*. The straight hypoplastron/xiphiplastron suture allows plastral kinesis, which is useful in oviposition (Joyce *et al*., 2012).

The extant species *Carettochelys insculpta* inhabits rivers, billabongs, estuarine reaches and river deltas in Papua New Guinea and Australia (Bonin *et al*., 2006). Local people of the Purari region mentioned that the hatchling turtles feed on vegetation and fruits of mangroves (Georges *et al*., 2008). A mangrove estuarine habitat has been proposed for the Simojovel area during the early Miocene (Langenheim *et al*., 1966; Serrano-Sánchez *et al*., 2015; Huys *et al*., 2016) and it is possible that *Allaeochelys liliae* sp. nov. preferred this type of habitat, as in *C. insculpta*. This agree with the discovery of Eocene *Allaeochelys* and Miocene fragmentary carettochelyine specimens in marine, near-shore, or deltaic sediments (Joyce, 2014).

4.6.5. Paleobiogeography

Kizylkumemys schultzi from the early Cenomanian of Uzbekistan (Figure 6; Nessov, 1976) and *Kizylkumemys khoratensis* from the Early Cretaceous of Thailand (Tong *et al*., 2005) has been considered the oldest members of Pan-Carettochelys (Havlik *et al*., 2014; Joyce, 2014; Danilov *et al*., 2017). Additional ancient records of Pan-Carettochelys come from the Late Cretaceous of France, Mongolia, and Japan (Hirayama and Chitoku, 1994; Hirayama 1998; Vullo *et al*., 2010). The Euro-Asiatic origin hypothesis for the clade is consistent with the fossil record.

Similarly, the genus *Anosteira* has been recorded from the late Paleocene to the late Eocene of Asia and North America (Hutchison and Storer, 1998; Hutchinson *et al.*, 2004; Tong *et al*., 2010; Joyce, 2014). Based on its current fossil record, the genus *Anosteira* was restricted in the northern hemisphere of the Earth during the Paleogene. Its sister taxa *Allaeochelys* extends also throughout the Paleogene, but with a broader geographic distribution in Eurasia. The oldest member of the genus is *Al. lignanica* from the Paleocene deposits in Guangdong, China (Young and Chow, 1962; Tang and Zhou, 1965) supporting an Asiatic origin of the genus. The presence of *Al. delheidi*, *Al. crassesculpta*, and *Al. parayrei* in the Eocene of Europe, suggests that the genus *Allaeochelys* reached this continent by the late Paleocene or early Eocene and then it diversified. During the late Eocene or Oligocene *Allaeochelys* extended its distribution range outside Eurasia to Africa and North America (Figure 7).

The presence of *Allaeochelys* in North America is better explained by dispersion from the Old World. Unfortunately, the unresolved resolution of *Allaeochelys* members in our phylogenetic analysis does not allow us to know which lineage is the closest to *Al. liliae*, and infer whether the genus spread to North America from Europe, Asia or Africa. *Allaeochelys liliae* shares the triangular pygal with five contacts with *Al. delheidi* from the early Eocene of Europe, and it is possible that *Al. liliae* was closer to *Al. delheidi* than to any other *Allaeochelys*. Under this hypothesis, it is highly probable that once European *Allaeochelys* crossed to North America via the Greenland bridge during the global warming of the Paleocene–Eocene Thermal Maximum. This hypothesis agrees with the dispersal of several mammal taxa from Europe to North America during a key event called the Mammalian Dispersal Event, during the Paleogene-Eocene boundary. During this time there was a well-represented faunal correlation in the NALMA Wa-0 of the Tienen Formation of Dormaal, Belgium and the Bighorn Basin, Wyoming, that includes the equiodes *Sifrihippus*, the artiodactyl *Diacodexis*, the hyaenodontid *Hypsodus*, the amphilemurid *Macrocranium* and the primate *Teilhardina* (Smith *et al*., 2006; Hooker, 2015).

The presence of one fragmentary specimen referred as *Allaeochelys* sp. from the Piney Point Formation (late Lutetian-early Bartonian, middle Eocene) in Pamunkey River, eastern Hanover County, Virginia, USA (Weems, 2014), provide support for the idea that *Allaeochelys* has a pre-Neogene presence in North America. The new species *Allaeochelys liliae* sp. nov. extends the time and spatial distribution of the genus *Allaeochelys* into the Miocene and far south into northern middle América.

If the sister species of *Al. liliae* sp. nov. is an African taxon, a second hypothesis would include a trans-Atlantic dispersion to North America from North Africa or southwestern Europe during the late Oligocene or early Miocene. The arrival of Old-World terrestrial taxa (*e.g*. platyrrhine primates and caviomorph rodents) to America has been traditionally explained by a trans-Atlantic dispersion during the Oligocene-Miocene interval (Hoffstetter, 1972; Martin, 1994; Poux *et al*., 2006; Seiffert *et al*., 2020). This hypothesis suggests that during the earliest Oligocene there was an eustatic drop in the sea level (Miller *et al*., 2008) favoring the dispersal of terrestrial vertebrates. Although the distance between the two landmasses during the Oligocene-Miocene was still large, the colonization could have occurred by rafting, aided by equatorial paleocurrents (Godinot, 2020). A rafting hypothesis is presented by Peris *et al*. (2015) to explain the presence of African beetles of the subfamily Platypodinae in the Miocene Mexican and Dominican amber.

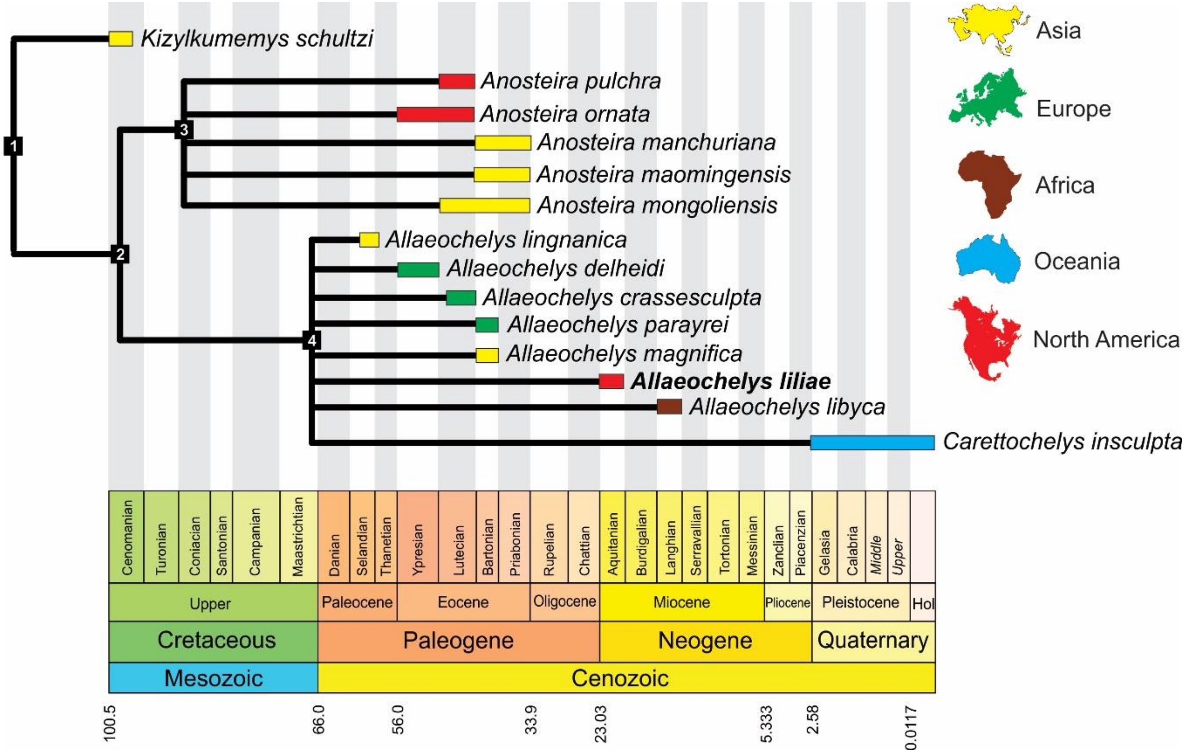

Figure 7. Simplified cladogram of the Pan-Carettochelys showing the temporal and geographical distribution of the members of this clade.

4.8. Conclusions

The morphological characters included in the description of *Allaeochelys liliae* sp. nov. and the phylogenetic analysis presented in this work, support its inclusion as a new species into the Carettochelyidae, increasing the diversity and geographical distribution of this clade.

Allaeochelys liliae sp. nov. differs from the rest of the species of the genus *Allaeochelys*, mainly in the sculpturing of the carapace and plastron, and some shell structure features.

Allaeochelys liliae sp. nov. is biogeographically important because it expands the geographical range of the genus to the south, into State of Chiapas, Mexico, and represents the only known species of the Pan-Carettochelys in the Aquitanian age (early Miocene) worldwide, and the first Neogene record of the clade in the American continent. The distribution of the genus *Allaeochelys* in the American continent (a very common turtle in the Paleogene and Neogene of Eurasia and Africa), can be better explained by dispersion from Europe to North America via the Greenland bridge during the global warming at the Paleocene–Eocene Thermal Maximum, or in second term by trans-Atlantic dispersion from Africa or southern Europe during the eustatic drop in the sea level in the earliest Oligocene.

The Simojovel area represents the only known early Miocene fossil deposit with continental organisms in Mexico. This locality is better known because of the amber and their biological inclusions. Prior to this work, only two continental vertebrates were formally described for the Simojovel area, the protoceratid *Paratoceras tedfordi* Webb, Beatty and Poinar 2003 (Webb *et al*., 2003), and the tayassuid *Simojovelhyus pocitosense* Ferrusquía-Villafranca 2006 (Ferrusquía-Villafranca, 2006; Prothero *et al*., 2013). *Allaeochelys liliae* sp. nov. is the third continental vertebrate formally described from this area, and contribute to the knowledge of middle-American faunas.

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de Chiapas, México, a través de la microfotografia digital). Finally, we thanks to the three assigned reviewers for the comments that helped to improve this manuscript.

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CAPÍTULO V

5.1. Discusión general

Diversos estudios con vertebrados fósiles del sur y sureste de México, soportan la hipótesis de que esta región ha sido un punto geográfico clave, donde se han suscitado procesos de especiación. Estos estudios se han centrado principalmente en vertebrados marinos del Jurásico tardío de Oaxaca (*e.g.* Brito *et al*., 2017; López-Conde *et al*., 2017; Barrientos-Lara *et al*., 2018;) y Cretácico tardío de Chiapas (*e.g.* Alvarado-Ortega y Than-Marchese, 2012; 2013; Díaz-Cruz *et al*., 2016, 2019, 2020; Cantalice *et al*., 2021).

Aunque existen innumerables evidencias fósiles de vertebrados terrestres provenientes de yacimientos del Paleógeno y Neógeno en diversas localidades del sur y sureste de México, estos han sido poco estudiados desde un enfoque filogenético y biogeográfico, especialmente los Testudines.

Pocos grupos de Testudines están presentes en el Paleógeno de América del Norte. Uno de ellos es Testudinidae, un clado de tortugas de hábitos terrestres que tiene una amplia distribución espacial y temporal (Ernst y Barbour, 1989). Se tienen las hipótesis de que este clado entró en América del Norte vía Beringia, durante los periodos cálidos del Paleoceno tardío (Vlachos, 2018), o posiblemente por el puente de Groenlandia que unió Europa del este con América del Norte. La diversidad de Pan-Testudinidae durante el Eoceno es relativamente baja. En América del Norte solo están presentes *Hadrianus majusculus* en el Eoceno temprano y *Hadrianus corsoni* en el Eoceno medio (Hay, 1908; Lichtig y Lucas, 2015). Para el Eoceno tardío se tienen documentados los taxones *Oligopherus laticuneus* y "*Testudo*" *brontops* (Hay, 1908; Hutchison, 1996), mientras que para el Oligoceno temprano se conocen *Stylemys nebrascensis* y *St. capax* (Hay, 1908; Vlachos, 2018). Aunque la diversidad de Pan-Testudinidae sigue siendo baja en el Oligoceno temprano, la presencia del nuevo taxon de Oaxaca descrito en esta tesis, sugiere que un miembro basal de este clado alcanzó el sur de México durante el Eoceno tardío u Oligoceno temprano, en donde se diversificó en nuevos taxones. El enfriamiento ocurrido durante la transición Eoceno-Oligoceno (Zachos *et al*., 2011), pudo favorecer la expansión de pastizales y zonas semiáridas, beneficiando así la dispersión de Pan-Testudinidae hacia el sur de América del Norte. Existe evidencia de que estas tortugas toleran temperaturas frías (Moll y Brown 2017), por lo que las condiciones ambientales templadas del Eoceno-Oligoceno no debieron ser un impedimento.

En el cladograma presentado en la Figura 6, del Capítulo 3 de este trabajo, UMPE 443 gen. et sp. nov. se ubica en una posición más basal que *Hesperotestudo* y *Gopherus*, dos géneros que tienen un amplío registro fósil en localidades que abarcan edades desde el Mioceno hasta el Pleistoceno en el centro-sur de los Estados Unidos de América (Hay, 1908; Auffenberg, 1974; Van Devender *et al*., 1976; Wall y Maddox, 1998; Biewer *et al*., 2016; Vitek *et al.*, 2017; Vlachos, 2018) y centro y noroeste de México (Mooser, 1972; Moodie y Van Devender 1979; Reynoso y Montellano-Ballesteros, 2004; Carbot-Chanona *et al*., 2020a). Esto sugiere que posiblemente el nuevo taxon de Oaxaca, o un taxón cercano a él, sea el antecesor de estos dos géneros, los cuales, posteriormente radiarían desde el sur de México hasta latitudes más norteñas. La mayor diversidad de especies actuales de *Gopherus* en el norte de México, con relación a la presente en Estados Unidos (Rhodin *et al*., 2017), apoya esta hipótesis.

Ferrari *et al*. (1999) mencionan que la actividad tecto-volcánica que afectó México durante el Paleógeno y Neógeno, comenzó durante el Oligoceno, evolucionando en episodios alternados durante el Mioceno. Esta actividad tecto-volcánica dio pie a la formación de la Faja Volcánica Transmexicana (FVTM) hacia el Mioceno medio, que originó una barrera fisiográfica que dividió el norte y el sur de México. La FVTM parece haber sido el factor principal para frenar la expansión de Testudinidae hacia el sur después del Oligoceno, tal como lo sugiere la ausencia de registros fósiles de este clado en la parte más sureña del país en sedimentos del Mioceno, Plioceno y Pleistoceno (Carbot-Chanona *et al.*, 2020a; ver Capítulo 2 de esta tesis). Durante el Mioceno temprano a medio se tiene documentado un ligero incremento de la temperatura global, lo que seguramente provocó climas más húmedos (Zachos *et al*., 2001; Zhang *et al*., 2013). Justamente es durante el Mioceno que se expanden y diversifican en América del Norte las familias dulceacuícolas Kinosternidae, Geoemydidae, Emydidae y Trionychidae, no obstante, Testudinidae parece haber sido afectado, ya que su diversidad se redujo drásticamente (Vlachos, 2018).

Carettochelyidae es otro clado dulceacuícola que tuvo una amplia distribución durante el intervalo Eoceno-Mioceno, principalmente en Europa, Asia y parte de África (Joyce, 2014), pero en América del Norte está pobremente representado en algunas localidades del

Eoceno temprano de Canadá y Eoceno temprano y tardío de Estados Unidos de América (Hay, 1906; Clark, 1932; Clark *et al*., 1967; Estes y Hutchison, 1980; Hutchison y Storer, 1988; Eaton *et al*., 1999; Zonneveld *et al*.; 2000; Weems, 2014).

El ejemplar proveniente de la localidad Los Pocitos (Mioceno más temprano, Aquitaniano), en Simojovel de Allende, estudiado en este trabajo, arrojó como resultado la descripción de una nueva especie, *Allaeochelys liliae* (Carbot-Chanona *et al*., 2020b; ver Capítulo 4 de esta tesis), que evidencia que durante el Mioceno más temprano (23-22 millones de años atrás), se estaban suscitando procesos de especiación del clado Carettochelyidae en el sur de América del Norte. Adicionalmente, la presencia de *Allaeochelys liliae* en Chiapas documenta el primer registro del clado Carettochelyidae para el Neógeno en todo el continente americano, además de ser la primera especie descrita para el Mioceno más temprano en todo el mundo.

Hutchison (1998) plantea la hipótesis de que las tortugas caretoquélidas emigraron de Asia hacia América del Norte durante el Eoceno temprano, posiblemente a través de Europa (Godinot y Lapparent de Broin, 2003). Sin embargo, Joyce (2014), basado en la distribución conocida del género *Anosteira* propone que Carettochelyidae se dispersó desde Asia a través del puente terrestre Beringia. La presencia de *Allaeochelys liliae* en la parte sur de América del Norte resalta la importancia paleobiogeográfica que tuvo esta región durante el Neógeno. Dos nuevas hipótesis se plantearon para tratar de explicar la presencia de tortugas caretoquélidas en el continente americano. La primera plantea que, posiblemente, un miembro del género *Allaeochelys* cruzó desde Europa hacia América del Norte vía el Puente de Groenlandia formado durante el calentamiento global del Máximo Térmico en el límite Paleoceno-Eoceno; esta hipótesis se apoya en que en ese tiempo ocurrió la dispersión de varios taxones de mamíferos desde Europa a América del Norte durante un evento clave llamado Evento de Dispersión de Mamíferos (Smith *et al*., 2006; Hooker, 2015). La segunda hipótesis plantea la llegada de un miembro de *Allaeochelys* por dispersión transatlántica hacia América del Norte desde el norte de África o el suroeste de Europa durante el Oligoceno tardío o el Mioceno temprano.

La importancia filogenética y paleobiogeográfica de los Testudines provenientes de localidades del Paleógeno y Neógeno del sur de México, ha quedado de manifiesto a través de esta tesis. Por tal motivo, es necesario continuar con estudios que incluyan más ejemplares, además de otros grupos, como crocodiliformes y lepidosauromorfos, con el fin de entender de manera integral el papel que jugó esta parte de México en la evolución y dispersión de los diversos grupos de vertebrados terrestres.

5.2. Conclusiones generales

El estudio de los ejemplares del Oligoceno de Oaxaca y del Mioceno de Chiapas, descritos en este trabajo, permitió establecer sus relaciones filogenéticas y paleobiogeográficas, cubriendo de esta manera el objetivo general planteado.

La descripción morfológica detallada de ambos ejemplares, así como su comparación con taxones previamente conocidos, demostró que ambos especímenes representan entidades taxonómicas nuevas, que ameritaron erigir un nuevo género y especie de Testudinidae (ejemplar UMPE 443) y una nueva especie (*Allaeochelys liliae*). Asimismo, la inclusión de estos ejemplares en análisis cladísticos, permitió establecer hipótesis sobre su posición filogenética. UMPE 443 gen. et sp. nov. fue recuperado como un miembro basal del clado Testudinidae. Por su parte, aunque la posición filogenética de *Allaeochelys liliae* no fue completamente resuelta, permitió establecer que se trataba de una especie nueva dentro del clado Carettochelyidae perteneciente al género *Allaeochelys*.

La presencia de UMPE 443 gen. et sp. nov. y *Al. liliae* en Oaxaca y Chiapas, respectivamente, soporta la hipótesis de la importancia que tuvo el sur de México en la diversificación y dispersión de los Testudines durante el Oligoceno-Mioceno.

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APÉNDICES

Se enlistan los apéndices que corresponden al material suplementario referido en los Capítulos 3 y 4. Los archivos pueden consultarse en la versión electrónica de esta tesis.

Material suplementario del Capítulo 3: A new large Testudinidae tortoise from the early Oligocene (Arikareean NALMA) of Oaxaca, southern Mexico and its phylogenetic position within Pan-Testudinidae.

Appendix 1. Morphological character list.

Appendix 2. Total evidence data matrix in .txt file.

Appendix 3. Total evidence data matrix in TNT file used in the Implied Weighted Maximum Parsimony analysis.

Appendix 4. Total evidence data matrix in TNT file used in the Standard Maximum Parsimony.

Appendix 5. Merged total evidence matrix in nexus file for Bayesian Inference.

Appendix 6. Molecular matrix with empty columns in nexus file.

Appendix 7. Molecular matrix with no-assigned columns in nexus file.

Figure S1. Standard Maximum Parsimony consensus tree.

Figure S2. Trace plot for the log posterior probabilities of the analysis showing convergence.

Material suplementario del Capítulo 4. The first Pan-Carettochelys turtle in the Neogene of the American continent and its paleobiogeographical relevance.

Appendix A. Description of the select taxa for comparison

Appendix B. Data matrix in TNT format

Appendix C. List of morphological characters

Appendix D. Additional resulting trees