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Late Miocene turtles from Southern Costa Rica

Tortugas del Mioceno Tardío del sur de Costa Rica

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ABSTRACT: Recent vertebrate fossil collections in southern Costa Rica have uncovered fragmentary remains of five fossil turtle taxa. These remains were recovered from deltaic sedimentary deposits of the Upper Miocene San Gerardo unit, which unconformably overlies the Early–Middle Miocene Térraba Formation. Most of these remains belong to the highly aquatic living turtle genera *Dermatemys* and *Apalone*. Other taxa, which are less frequently found, include *Bairdemys* and *Pseudemys*, as well as the extinct terrestrial tortoise *Hesperotestudo*. Except for the marine-tolerant *Bairdemys*, all genera exhibit North American affinities, suggesting that this assemblage likely predates the formation of the Central American land bridge and the subsequent biotic interchange with South America.
Keywords: Central America; Costa Rica; fossil turtles; *Apalone*; *Bairdemys*; *Dermatemys*; *Hesperotestudo*; *Pseudemys*.

RESUMEN: Recientes descubrimientos fósiles en el sur de Costa Rica han revelado restos fragmentarios pertenecientes a cinco taxones de tortugas fósiles. Estos especímenes fueron recuperados de depósitos sedimentarios deltaicos asignados a la unidad San Gerardo del Mioceno Tardío, la cual yace en discordancia sobre la Formación Térraba del Mioceno Temprano–Medio. La mayoría de los restos corresponden a

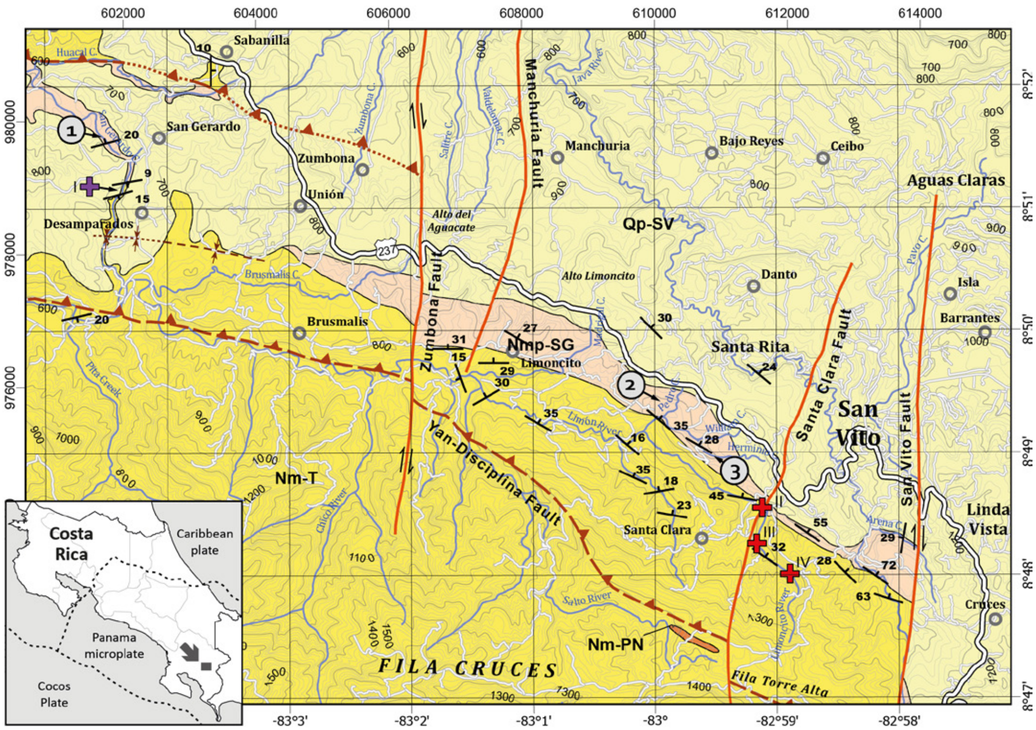
los géneros actuales altamente acuáticos *Dermatemys* y *Apalone*. Además, se han identificado otros taxones, como *Bairdemys* y *Pseudemys*, junto con la extinta tortuga terrestre *Hesperotestudo*, aunque estos últimos se encuentran con menor frecuencia. Exceptuando a *Bairdemys*, un género tolerante a ambientes marinos, todos los demás taxones muestran afinidades norteamericanas. Esto sugiere que este conjunto fósil probablemente precede la formación del puente terrestre centroamericano y el consecuente intercambio biótico con Sudamérica.
Palabras clave: América Central; Costa Rica; tortugas fósiles; *Apalone*; *Bairdemys*; *Dermatemys*; *Hesperotestudo*; *Pseudemys*.

Introduction

The first fossil vertebrates from Costa Rica were discovered and described in the early 20th century (Alfaro, 1911; Alvarado, 1986, 1988). Over the past three decades, significant progress has been made in the understanding of Costa Rican vertebrate paleontology, surpassing the knowledge accumulated during the previous century (Lucas, 2014). These developments are largely credited to the contributions of local geologists and vertebrate paleontologists such as Eduardo Vega, César Laurito, and Ana Valerio.

A wide variety of vertebrate fossils have been documented across Costa Rica, particularly in San Gerardo, including bony fish, cartilaginous fish (sharks and rays), crocodilians (*Crocodylus*, *Gavialosuchus* [=*Thecacampsa*]), cetaceans (*Eurhinodelphis*, *Goniodelphis*, *Orycterocetus*, *Hadrodelphis*), proboscideans (*Gomphotherium*), giant sloths (*Sibotherium*, *Zacatzontli*), pampatheres (*Scirrotherium*), horses (*Protohippus*, *Calippus¸ Dinohippus*), camels (*Hemiauchenia*), and peccaries (*Protherohyus*, *Prosthennops*) (Laurito & Valerio, 2005, 2008a, 2008b, 2010, 2012a, 2012b, 2013, 2016; Mead et al., 2006; Valerio & Laurito, 2008, 2012, 2014, 2020; Lucas & Alvarado, 2010; Valerio, 2010; Rincón et al., 2020; Valerio et al., 2022). Among these taxa, fossil turtles are particularly well-represented in the country, with pieces attributed to the new species *Rhinoclemmys nicoyana*, found in the Nacaome River of the Nicoya peninsula (Acuña & Laurito, 1996), and the genus *Apalone*, found in San Gerardo (Laurito et al., 2005). Additionally, the species *Geochelone costarricensis*, initially described as the new species *Testudo costarricensis* and said to be found in the "Oligo-Miocene" or "Eocene" deposits of Peralta (Segura, 1944), was based on a fossil apparently found outside of Costa Rica (Coto & Acuña, 1986; Lichtig et al., 2018).

This study provides new data on the diversity of turtles and tortoises from the Upper Miocene (Hemphillian) San Gerardo unit in southern Costa Rica (Fig. 1). The turtle fossils, collected as loose specimens (“float”), were primarily found in association with Hemphillian mammal fossils, although some associated specimens of mammals may postdate this age. The turtle fossil assemblage includes five taxa, collected by Amado Vargas, Cristian Vargas and Joe Rojas. Most specimens belong to the aquatic genera *Dermatemys* and *Apalone*. Additional taxa include *Bairdemys*, *Pseudemys*, and *Hesperotestudo*. These finds represent a significant addition to the Central American fossil record of turtles and suggest that the Panamanian seaway, which separated Central America from northern South America, remained open until after the late Miocene.



#	Fossils	Method	Ma	Series	Stage	NALMA / Plank. zone
I	Vertebrate	Biostratigraphy		Mio-Pliocene	Tortonian-Zanclean	Hemphillian (Hh1-Hh4)
I	Oyster	$^{87}Sr/^{86}Sr$ dating	5.8	Miocene	Messinian (terminal)	Hemphillian (Hh3)
II	Plankt. foram.	Biostratigraphy		Miocene	Langhian (basal)	M6
III	Plankt. foram.	Biostratigraphy		Miocene	Langhian (basal)	M6
IV	Plankt. foram.	Biostratigraphy		Miocene	Burdigalian (top)-Langhian (basal)	M5a-M6

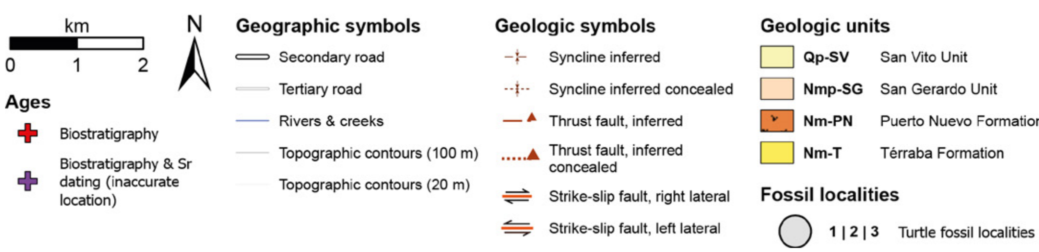


Fig. 1: Geologic and geographic setting of the study area in southern Costa Rica. Turtle fossil sites discussed herein include: (1) San Gerardo Creek, (2) Pedro Creek, and (3) Herminio Creek. Abbreviations used in the figure and table: C. = Creek; Plankt. foram. = planktonic foraminifera; Plank. zone = planktonic foraminifera biozones. Age estimates are drawn from the following sources: Site I (unnamed creek southwest of San Gerardo) is based on Laurito & Valerio (2010, 2012a, 2012b, 2016), Valerio (2010), Valerio & Laurito (2012, 2014, 2020), Rincón et al. (2020), and Valerio et al. (2022). Field evidence suggests that the published location of these ages may be imprecise and instead corresponds to Lower Miocene strata of the Térraba Formation. Sites II–IV correspond to an upstream segment of the Limoncito River, south of San Vito, with age data originally reported by Yuan (1984). These age interpretations were revised using the time scale by Wade et al. (2011) along with two online databases: *Cenozoic Planktonic Foraminifera* (https://www.mikrotax.org/) and the *World Register of Marine Species* (WoRMS) (https://www.marinespecies.org/). Updated acrozone ranges were calculated using MicroStratiRange, a free tool developed by the Institute for Research in Stratigraphy at the University of Caldas (https://microstratirange-iies.site/). Coordinates are displayed using both the national CRTM05 grid (top and left margins) and the international WGS84 system (bottom and right margins).

Geological timescale

The ages of vertebrate fossils from Costa Rica are based on the North American Land-Mammal "Ages" (NALMAs) and follow the Late Cenozoic epochs. This framework follows Tedford et al. (2004) for the Miocene and Bell et al. (2004) for the Pliocene to Pleistocene. The Pleistocene is redefined in this context, with its base set at approximately 2.6 Ma. The NALMAs relevance to Costa Rica's vertebrate fossil record are as follows: (1) Hemphillian: Late Miocene–Early Pliocene (9.0–4.7 Ma); (2) Blancan: Early Pliocene–Early Pleistocene (4.7–1.8 Ma); (3) Irvingtonian: Early-Middle Pleistocene (1.8–0.2 Ma); and (4) Rancholabrean: Middle-Late Pleistocene (200,000–10,000 years) (Fig. 2).

Institutional Abbreviations

The following institutional abbreviations are used in this paper: UCR = University of Costa Rica, San Pedro, Costa Rica. ECG = Escuela Centroamericana de Geología.

Geological context and stratigraphy

Geological context

The fossils analyzed in this study were collected in the southernmost section of the Fila Costeña, near San Vito town, Costa Rica (Fig. 1). The Fila Costeña is a fold-and-thrust belt formed in a forearc setting, where the Farallon tectonic plate (now the Cocos Plate) was subducted beneath the Caribbean Plate (Fisher et al., 2004; Kolarsky et al., 1995; Morell et al., 2008, 2013, 2019; Sitchler et al., 2007; among others).

The stratigraphic sequence of the Fila Costeña begins with the calcareous Eocene strata of the Fila de Cal Formation, which hypothetically rests atop the Cretaceous–Paleocene mafic basement (Chesnel & Rodríguez, 2021; Mann, 1995; Terry, 1956;). Above these strata lie the Oligocene Térraba Formation and its members—Palmar Sur-Coobó, Río Claro, and Corredor—consisting of siliciclastic and calcareous deposits (Godínez, 2024; E. Rodríguez, 2020; Yuan, 1984). The Early to early-Middle Miocene Térraba Formation, which constitutes much of the range, occurs as overthrust units in older faults and as detachment layers in younger faults. In the southernmost Fila Costeña, deposits from the Upper Miocene to Pliocene (?) strata overlying the Térraba Formation are here identified as the San Gerardo unit. This unit, previously described as the Río Boquilla unit or grouped within the Curré Formation, remains poorly defined. Above the San Gerardo unit lies the San Vito volcano-sedimentary deposits, which unconformably overlie the older formations. These deposits are characterized by meter-sized lava blocks and regolithic soils enriched with amphiboles. Unstable weathered zones are dominated by clay-rich landslide deposits, while rivers and streams cutting through the San Gerardo unit frequently expose fossil-bearing alluvium.

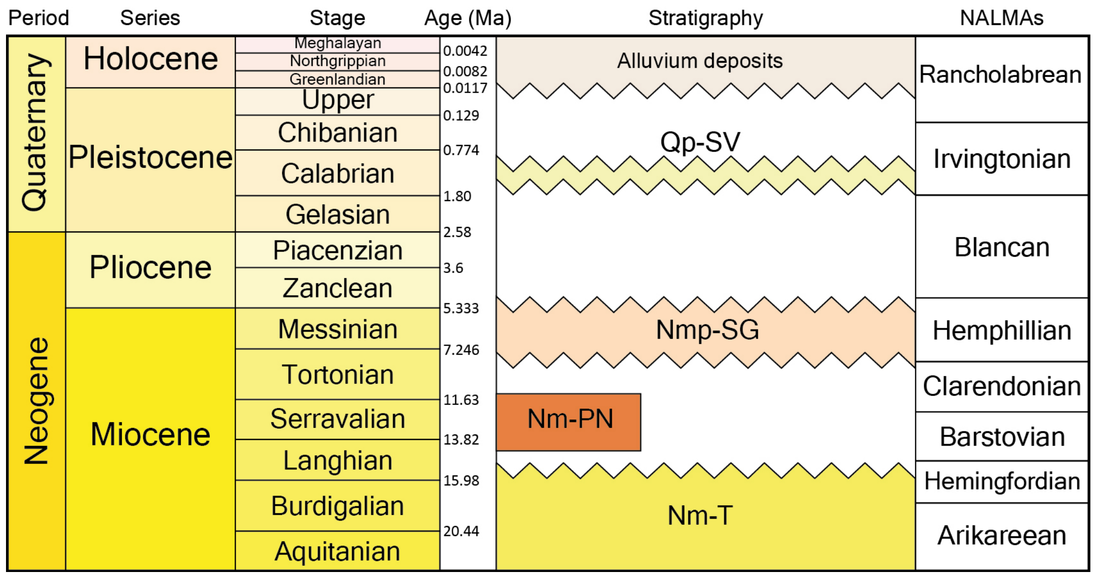


Fig. 2: Diagram showing the correlation between the geologic timescale, the regional stratigraphic framework of the San Vito area, and North American Land-Mammal Ages (NALMAs). Most turtle fossil finds are linked to Holocene alluvial deposits, although they are primarily associated with the Hemphillian-age San Gerardo unit (Nmp-SG). Additional stratigraphic units include: Qp-SV = Pleistocene San Vito unit; Nm-PN = Miocene Puerto Nuevo Formation; and Nm-T = Miocene Térraba Formation.

Stratigraphy

The Térraba Formation was initially described as a succession of principally fine-grained turbiditic Oligocene to Lower Miocene strata exposed along the Térraba River between Palmar and Lagarto (Dengo, 1962a; Henningsen, 1965, 1966). Over time, the Térraba Formation has been divided into the Zapote and Lagarto units, principally based on lithologic differences and stratigraphic superposition (Mora, 1979). Recent studies have confirmed the ages of the unit, revealing an Oligocene to Aquitanian–Burdigalian age, with occasional Langhian markers (E. Rodríguez, 2020; Yuan, 1984). However, some authors refer to similar-aged deposits as belonging to the Curré Formation (Aguilar et al., 2010; Godínez, 2024).

The Curré Formation was introduced to differentiate the Térraba Formation from a series of sandstone and conglomerate also exposed along the Térraba River, beneath the conglomerates of Paso Real (first mentioned as Paso Real Formation), between the hamlets of Curré and La Escuadra (Dengo, 1962a). The Curré Formation was originally correlated with the Middle to Late Miocene–Pliocene Gatún Formation of Panama (Dengo, 1962a; Henningsen, 1965, 1966; Mora, 1979), mainly based on the recognition of mollusks assemblages from the Concepción and Curré rivers (Lohmann, 1934; Mora, 1979).

The San Gerardo unit is introduced in this study to avoid confusion with the Curré Formation. Previously, it was considered equivalent to the informal Río Boquilla unit (Laurito & Valerio, 2005), initially described by students of UCR's *Campaña Geológica* field course as a subunit of the Pliocene-Pleistocene Paso Real volcanic rocks of Dengo (1962) (Alán, 1998; Arias, 1998; Carillo, 1998; Garita, 1998; Murillo, 1998; Ramírez, 1998; Ramos, 1998; A. Rodríguez, 1998). This designation was later abandoned in favor of the Curré Formation (Laurito & Valerio, 2008a; Laurito et al., 2005), largely due to perceived chronological similarities. Indeed, fossil evidence from the San Gerardo unit indicates a Hemphillian LMA, corresponding to the Late Miocene (Laurito & Valerio, 2010, 2012a, 2013, 2012b, 2016; Valerio, 2010; Valerio & Laurito, 2012, 2014, 2020; Rincón et al., 2020; Valerio et al., 2022). Following previous descriptions, both units represent shallow marine to transitional continental deposits. However, the San Gerardo unit is distinguished by its highly fossiliferous layers, containing vertebrate fossils such as gomphotheres, megalonychids, equids, turtles, and selachians, among others (Laurito & Valerio, 2005, 2008, 2010, 2016; Valerio & Laurito, 2014, 2020, among others). It also presents abundant charcoal trunks, scarce mollusks and rare microforaminifers. Moreover, geological mapping of the fossil-bearing region reveals the presence of an angular unconformity (Fig. 1; western sector) or a paraconformity (Fig. 1; eastern sector) between the underlying Térraba Formation and the San Gerardo unit, a stratigraphic configuration not observed between the Térraba and Curré formations.

The volcanic-sedimentary deposits near San Vito have been described by various broad terms, such as "andesitic breccia" (Tournon, 1984), "Talamanca volcanics" (Drummond et al., 1995), and "andesitic breccia in a tuff matrix" (Tournon & Alvarado, 1997). These deposits were later grouped under the name San Vito Unit, characterized as a composite unit comprising interdigitated layers of diverse origins, including lava flows, volcanic domes, volcanic debris avalanches, fluvial sediments (including debris flows), and ash layers. The unit predominantly consists of basaltic andesites to dacites, typically rich in amphibole, with minor occurrences of olivine-bearing basalts (Arroyo, 2001). Around San Vito, these deposits have been dated to between 1.7 and 1.07 Ma (Alvarado & Gans, 2012; Tournon & Alvarado, 1997).

Fossil turtle localities

Fossil turtle fragments were collected from three localities within the San Gerardo unit near San Vito (Fig. 1). Fossils numbered CF 66##, CF 67## and CF 69## are stored in the San Vito branch of the paleontological collection of the Central American School of Geology (Escuela Centroamericana de Geología – ECG). Specimens with the code CF JRC pertain to the private collection of Joe Rojas.

The most fossiliferous site is an unnamed creek, a tributary of the Limoncito River southwest of San Vito. Locally, this site is referred to as Pedro Creek, a name given by residents and amateur paleontologists. The second locality, also an unnamed tributary of the Limoncito River, is referred to as Herminio Creek by the same people. The third site is an unnamed stream here designated as San Gerardo Creek, a tributary of Huacal Creek, situated west of the village of San Gerardo, a well-documented fossiliferous area.

Fossil turtle taxonomy

Class REPTILIA Laurent, 1768
Order TESTUDINES Linnaeus, 1758
Suborder CRYPTODIRA Cope, 1868
Superfamily KINOSTERNOIDEA Joyce, Parham, and Gauthier, 2004
Family DERMATEMATIDAE Gray, 1879
Genus *Dermatemys* Gray, 1847
Dermatemys sp. indet.

Material: Pedro Creek – Neural elements (CF 6713, CF 6715, CF 6716, CF 6717A, CF 6717C, CF 6739, CF JRC 1), costal elements (CF 6718, CF 6724, CF 6737, CF JRC 2), peripheral element (CF 6919, CF 6721, CF 6722, CF 6723, CF 6726, CF 6727, CF 6728, CF 6729, CF 6731, CF 6731A, CF 6740), plastral elements (CF 6738, CF 6741, CF 6742, CF 6743, CF 6744, CF JRC 4). Herminio Creek – Five carapace fragments (CF 6617). San Gerardo Creek – Costal fragments (CF 6629) (Fig. 3).

Description: The shell elements are thick, dense and exhibit a smooth external surface.

Discussion: Modern *Dermatemys mawii* populations (hickatees) inhabit riverine marshlands along the Caribbean coastal regions of southern Mexico, Guatemala, Belize, and possibly Honduras. Notably, they have not been historically recorded in Costa Rica. These turtles are herbivorous, aquatic, and they do not exhibit basking behavior.

Paleogeographic and biostratigraphic distribution: The discovery of *Dermatemys* remains in Upper Miocene deposits of Costa Rica suggests a much wider distribution during prehistoric times compared to their current range. These fossils represent the most abundant turtle taxon recovered from Costa Rican fossil beds to date.

Superfamily TESTUDINOIDEA Fitzinger, 1826
Family EMYDIDAE Rafinesque, 1815
Genus *Pseudemys* Gray, 1856
Pseudemys sp. indet.

Material: Pedro Creek – Nuchal element (CF 6743A), neural element (CF 6714) (Fig. 4A-B).

Description: The thin carapace elements of emydids have crinkled, snake-like patterns etched onto their external surfaces, with occasional traces of costal grooves. While the surficial textures of *Pseudemys* and *Trachemys* are quite similar, *Pseudemys* can be distinguished by its square-shaped nuchal scute pattern (Figure 5A), in contrast to the narrow and elongate nuchal scute typical of *Trachemys*.

Discussion: Modern *Trachemys* species (*T. emolli* and *T. venusta*) inhabit riverine marshlands in Costa Rica, but the genus *Pseudemys* is absent from the country today. Fossil evidence suggests that *Pseudemys* was present in Costa Rica during the late Miocene but has since been replaced by *Trachemys*.

Paleogeographic and biostratigraphic distribution: Today, the Rio Grande cooter (*Pseudemys gorzugi*) is found in northern Mexico and the southern United States. Pond sliders (*Trachemys scripta s.l.*) share a similar distribution but range much farther south, reaching northern Argentina. The Miocene

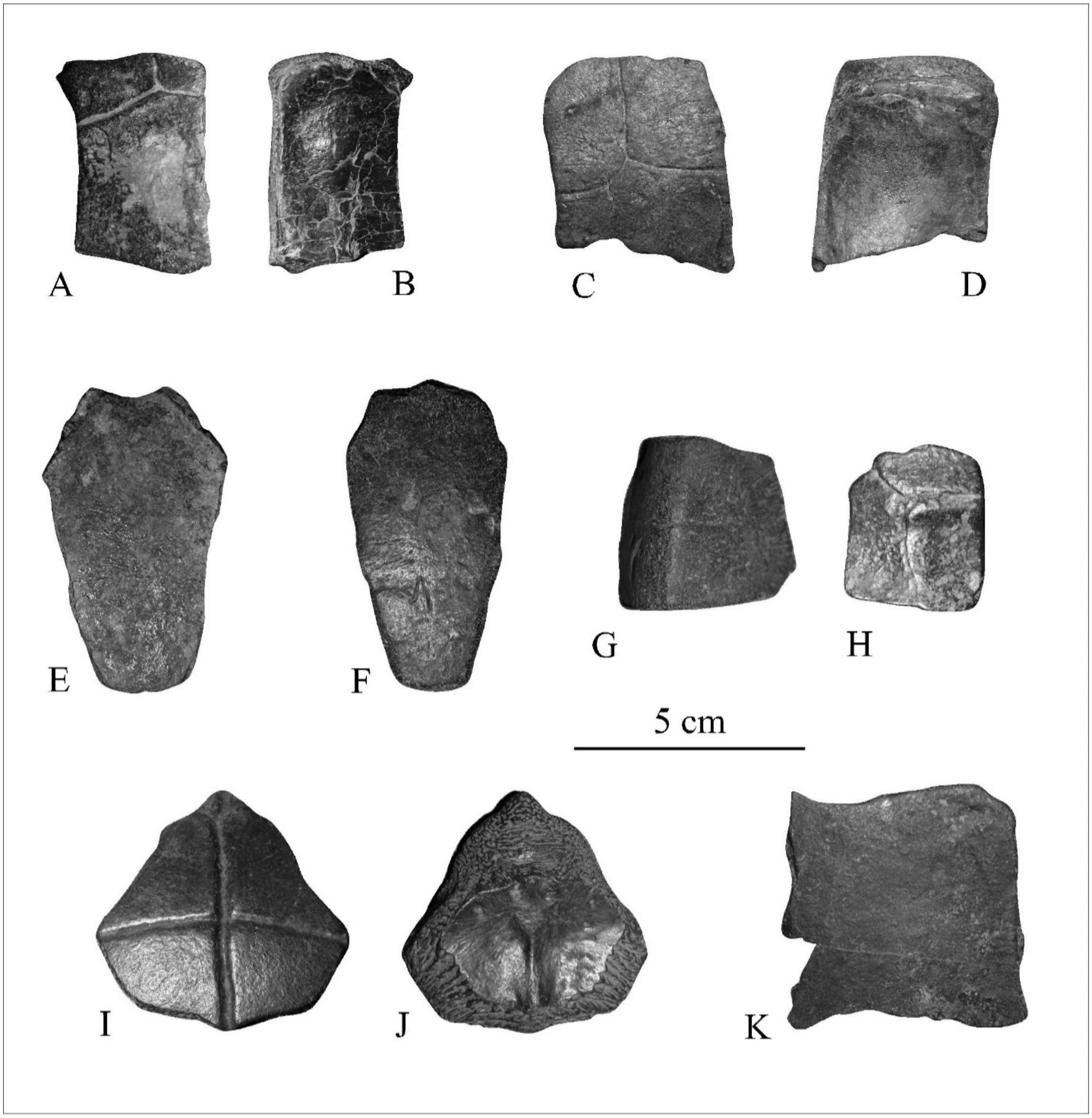


Fig. 3: Images of carapace elements of *Dermatemys* sp. A-B) Costal element in external and internal views (CF JRC 2). C-D) Costal element in external and internal views (CF 6724). E) Anterior neural element in external view (CF 6717A). F) Central neural element in external view (CF 8592). G) Left lateral peripheral element in dorsal view (CF 6726). H) Posterior peripheral element in dorsal view (CF 6629). I-J) Entoplastron in external and internal views (CF 6617). K) Right epiplastron fragment in external view (CF 6743).

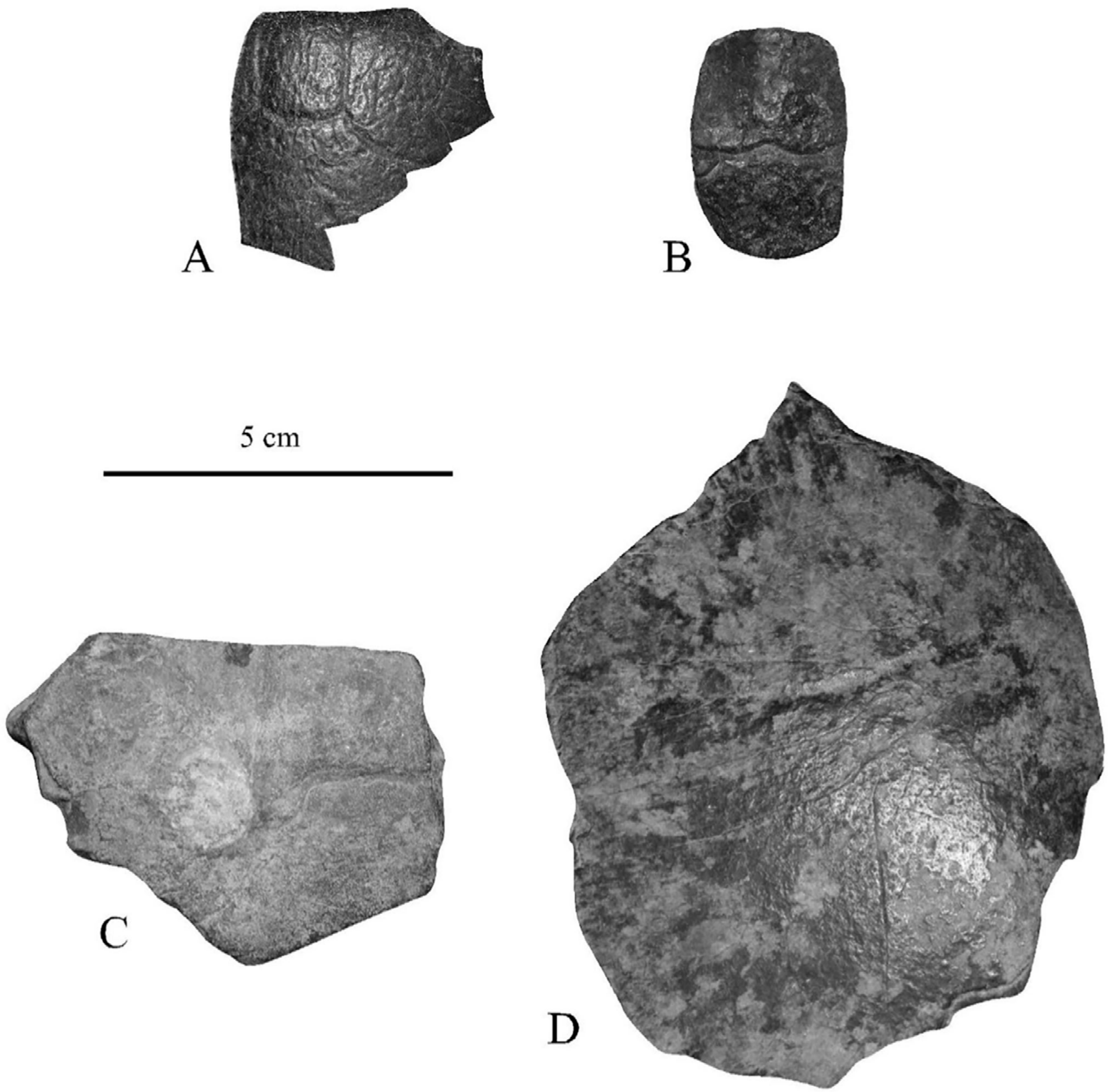


Fig. 4: Images of carapace elements of *Pseudemys* and *Hesperotestudo*. A) Nuchal element of *Pseudemys* sp. in external view (CF 6743A). B) Neural element probably of *Pseudemys* sp. in external view (CF 6714). C) Costal fragment of *Hesperotestudo* sp. with stump of spine in external view (CF 6735). D) Entoplastron of *Hesperotestudo* sp. in external view (CF 6730).

occurrence of *Pseudemys* in Costa Rica suggests a historical southward extension of its range well beyond its modern southern limits. The disappearance of *Pseudemys* from Costa Rica and its replacement by *Trachemys* remains an unresolved biogeographic question.

Family TESTUDINIDAE Batsch, 1788
Genus *Hesperotestudo* Williams, 1950
Hesperotestudo sp. indet.

Material: Pedro Creek – Costal element (CF 6735, CF JRC 3), entoplastron (CF 6730) (Fig. 4C-D).

Description: Shell elements are large but relatively thin, with smooth external surfaces and visible costal grooves. Some costal elements feature prominent spiky knobs on their external surfaces.

Discussion: *Hesperotestudo* was widespread across North America during the Neogene but went extinct near the end of the Pleistocene, likely due to predation by early Native Americans. Although a large tortoise species (*Testudo costarricensis*) was historically attributed to Costa Rica (Segura, 1944), it was later proven that the type specimen originated from North America and was misattributed (Lichtig et al., 2018). The material described here confirms the presence of *Hesperotestudo* in Costa Rica during the Late Miocene. However, the fragmentary nature of the fossils precludes precise species-level identification.

Paleogeographic and biostratigraphic distribution: *Hesperotestudo* exhibited adaptability to a range of environments and was likely a highly mobile species. Its large size differentiates it from modern tortoises like *Gopherus*, which are significantly smaller.

Superfamily TRIONYCHIA Hummel, 1929
Family TRIONYCHIDAE Gray, 1825
Genus *Apalone* Rafinesque, 1832
Apalone sp. indet.

Material: Pedro Creek – neural element (CF 6704), costal element (CR 6731), plastral elements (CF 6705, CF 6706). San Gerardo Creek – plastral fragment (CF JRC 5) (Fig. 5A-E).

Description: Shell elements are thick, with external surfaces characterized by strong wrinkling or papillation.

Discussion: In North America, all extant trionychid turtles belong to the genus *Apalone* (Bonin et al., 2006; Meylan, 1987). Modern softshell turtles (*Apalone spinifera*) are restricted to riverine marshlands in northern Mexico; however, during the Late Miocene, they were also present in Costa Rica (Laurito et al., 2005 and references therein). Earlier records of trionychid turtles from Panama, dating back to the Early Miocene (Cadena et al., 2012), and from northwestern Venezuela in the Late Miocene (Head et al., 2006; Sánchez-Villagra et al., 2004; Wood & Patterson, 1973), suggest a broader prehistoric distribution. Furthermore, abundant trionychid remains in Paleocene and Eocene shallow marine deposits in Virginia and Maryland, USA (Weems, 2014) indicate that some species were likely tolerant of saline water environments. This tolerance may have facilitated their spread into South America even before the closure of the Central American land bridge (Cadena et al., 2012). Today, trionychids are fast swimmers and actively hunt fish.

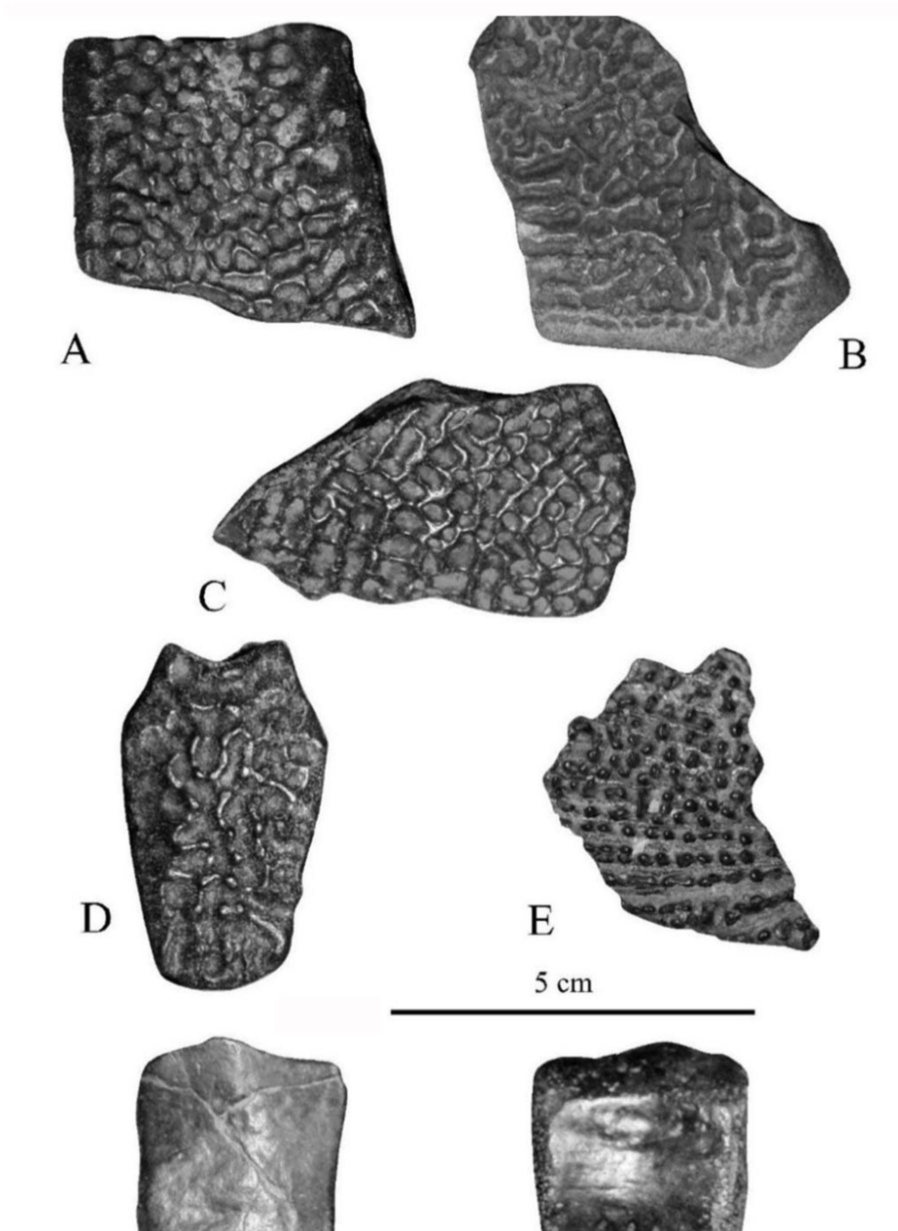


Fig. 5: Images of carapace elements of *Apalone* and *Bairdemys*. A-C) Coastal fragments of *Apalone* sp. in external view (CF 6703). D) Neural element of *Apalone* sp. in external view (CF 6704). E) Plastral element of *Apalone* sp. in external view (CF 6706). F, G) Peripheral element of *Bairdemys* sp. in dorsal and ventral views (CF 6629).

Paleogeographic and biostratigraphic distribution: The Miocene occurrences of *Apalone* in Costa Rica suggest a much broader prehistoric distribution compared to the present day. This taxon is the second most frequently found turtle species in beds collected during this study.

Suborder PLEURODIRA Cope, 1865
Family PODOCNEMIDIDAE Cope, 1868
Genus *Bairdemys* Gaffney and Wood, 2002
Bairdemys sp. indet.

Material: San Gerardo Creek – peripheral element (CF 6629) (Fig. 5F-G).

Description: The shell elements are thin with smooth external surfaces, except for grooves along the scutal boundaries.

Discussion: Podocnemid turtles have been identified at the familial level in late Oligocene and Early Miocene beds in Panama (Cadena et al., 2012), although no attempts were made at generic or species identification at that time. More recent podocnemid remains from the Middle Miocene Alajuela Formation in Panama have been assigned to *Bairdemys* (Bourque, 2022). Podocnemid turtles are primarily known from South America, but *Bairdemys* has also been recorded from several near-coastal marine localities in the Caribbean region (Gaffney & Wood, 2002) and along the eastern coast of North America (Weems, 2023; Weems & George, 2013; Weems & Knight, 2013). It is likely that the remains described from Panama and the specimen from Costa Rica belong to this genus. *Bairdemys* is thought to have been adapted to living and hunting in marine environments (Ferreira et al., 2015), which likely explains its broader distribution beyond South America during the middle part of the Cenozoic Era, unlike other podocnemid turtles.

Paleogeographic and biostratigraphic distribution: The discovery of *Bairdemys* in the Miocene strata of Central America is consistent with its adaptation to marine environments, which enabled it to spread into the region before a land route between South America and Costa Rica had been established.

Biogeography

The modern nonmarine turtle fauna of Costa Rica comprises nine species that belong to four genera. One genus, *Rhinoclemmys*, is clearly of South American origin and includes three living species (*R. funerea*, *R. annulata*, and *R. pulcherrima*) together with one Pleistocene fossil species (*R. nicoyana*) (Acuña & Laurito, 1996). The other three genera, found in Costa Rica today, appear to have North American origins and include *Kinosternon* (*K. angustipons*, *K. leucostomum*, and *K. scorpioides*), *Trachemys* (*T. emolli* and *T. venusta*), and a snapping turtle, *Chelydra* (*C. acutirostris*).

In contrast, the Late Miocene fauna discussed in this study reveals the presence of five turtle taxa in Costa Rica: *Dermatemys* sp., *Apalone* sp., *Bairdemys* sp., *Pseudemys* sp., and *Hesperotestudo* sp. Four of these taxa (*Apalone*, *Dermatemys*, *Hesperotestudo* and *Pseudemys*) have North American origins, while only *Bairdemys* originated from South America. Notably, *Bairdemys* had adapted to the marine environment, which likely facilitated its appearance north of the Panama Seaway during the Late Miocene, predating the arrival of other South American turtles in Central America. All these Late Miocene turtles apparently lived in a rainforest habitat that had local clearings, very similar to the landscape that still exists today in Costa Rica (Pérez Crespo et al., 2018).

Conversely, the only North American turtle known to have ventured south of the Panama Seaway during the Miocene is *Apalone*. This genus, known for its tolerance to marine environments (e.g., Weems, 2014; in the Paleocene Aquia Formation of Maryland and Virginia), could have traversed narrow saltwater barriers. This highlights that during the Late Miocene, land turtles faced significant limitations in crossing the Panama Seaway, with only saltwater-tolerant species being able to overcome this barrier. The appearance of the first South American ground sloth (*Sibotherium*) and pampathere (*Scirrotherium*) in Costa Rica during the Late Miocene (Rincón et al., 2020) likely correlates with the narrowing of the Panama Seaway during this period.

The biogeographic history of land animals during the Late Miocene and Pliocene provides further context. The earliest South American land mammals to reach North America were large edentates, crossing the Panama Seaway during the Late Miocene (Rincón et al., 2020). However, the mid-Pliocene marks the sudden appearance of diverse small mammals from South America in southeastern North America (e.g., Charleston, South Carolina; Albright et al., 2019). This coincides with the disappearance of the giant shark *Carcharocles* from the shallow marine fossil record in North America. These concurrent events suggest that the seaway connection between the Caribbean and the Pacific had significantly contracted by the mid-Pliocene, or closed entirely. Collectively, these findings indicate that while the Panama Seaway began to narrow in the Late Miocene, its complete closure occurred around the middle of the Pliocene.

Conclusions

The text supports the following conclusions:

1. In the San Vito area of southern Costa Rica, fossils of five turtle taxa have been recovered from deltaic sedimentary deposits of the Upper Miocene San Gerardo unit, which overlies the Aquitanian to Langhian Térraba Formation either unconformably or paraconformably.
2. Most of the turtle fossils correspond to the highly aquatic and still extant genera *Dermatemys* and *Apalone*.
3. Less common taxa include *Bairdemys*, *Pseudemys*, and the extinct terrestrial tortoise *Hesperotestudo*.
4. Except for the marine-tolerant *Bairdemys*, all identified genera exhibit clear North American affinities.
5. Consequently, these turtle fossils likely predate the full emergence of the Central American land bridge and the resulting biotic interchange with South America.

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