



# EARLY TO MIDDLE MIOCENE TURTLES FROM THE NORTHERNMOST TIP OF SOUTH AMERICA: GIANT TESTUDINIDS, CHELIDS, AND PODOCNEMIDIDS FROM THE CASTILLETES FORMATION, COLOMBIA

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**Abstract.** Here we describe the northernmost South American record of fossil turtles from the late early Miocene to early middle Miocene of the Castilletes Formation, on the Alta Guajira Peninsula, Cocinetas basin, Colombia. Turtles in the lower segment of the Castilletes Formation (c. 16.33 Ma) are pleurodires or side-necked turtles belonging to *Chelus colombiana* Wood, *Chelus* sp., and Podocnemididae *incertae sedis*, and cryptodires or hidden-necked turtles attributed to *Chelonoidis* sp., all of them characterized by the large size of their shells, 1 meter or more total length. The middle segment of the formation (c. 14 Ma) contains specimens of Podocnemididae *incertae sedis* and *Chelonoidis* sp. The turtle fauna from Castilletes share taxa with faunas from La Venta (middle-late Miocene of Colombia), Urumaco, and Western Amazonia (late Miocene from Venezuela, Brazil, and Peru); all of these records indicate a wider geographical distribution for podocnemidids, chelids, and testudinids of tropical South America during the early to middle Miocene. The large size of the fossils described here also confirms that gigantism was characteristic of South American tropical turtles during the early Miocene, a trend that lasted at least from the Paleocene to the Pliocene in different lineages.

**Key words.** Turtles. Testudinidae. Chelidae. Podocnemididae. Miocene. Colombia.

**Resumen.** TORTUGAS DEL MIOCENO TEMPRANO A MEDIO EN EL EXTREMO MÁS SEPTENTRIONAL DE SURAMERICA; TESTUDÍNIDOS GIGANTES, QUÉLIDOS, Y PODOCNEMÍDIDOS DE LA FORMACIÓN CASTILLETES, COLOMBIA. En este artículo describimos el registro fósil de tortugas de la parte tardía del Mioceno temprano a la parte temprana del Mioceno medio en el extremo más septentrional de Suramérica, en la Península de la Alta Guajira, Cuenca de Cocinetas, Colombia. Las tortugas del segmento más inferior de la Formación Castilletes (c. 16.33 Ma) pertenecen a pleurodiras o tortugas que retraen el cuello en forma lateral que incluyen a: *Chelus colombiana* Wood, *Chelus* sp., y Podocnemididae *incertae sedis*, y las cryptodiras o tortugas que retraen el cuello en forma vertical, atribuidas al género *Chelonoidis* sp. Todas estas tortugas están caracterizadas por el gran tamaño de sus caparazones de 1 metro de longitud o más. En el segmento medio de la Formación (c. 14 Ma) solo se encontraron Podocnemididae *incertae sedis* y *Chelonoidis* sp. La fauna de tortugas de la Formación Castilletes comparte taxones con la fauna de La Venta (Mioceno medio de Colombia), y con la faunas de Urumaco y el Oeste Amazónico (Mioceno tardío de Venezuela, Brasil y Perú), indicando una distribución geográfica más extensa de los podocnemídeos, quélidos, y testudínidos de la parte tropical de Suramérica durante el Mioceno temprano a medio. El gran tamaño de los fósiles descritos aquí confirma que el gigantismo fue una característica de las tortugas tropicales de América del Sur también durante el Mioceno temprano, una tendencia que duró al menos desde el Paleoceno hasta el Plioceno en diferentes linajes.

**Palabras clave.** Tortugas. Testudinidae. Chelidae. Podocnemididae. Miocene. Colombia.

DURING the late early Miocene to the early late Miocene (Burdigalian to Tortonian, c. 17 to 10 Ma) northwestern South America was already at tropical latitudes (0 to 12° N), in close proximity to the Central American volcanic arc but still separated by the Central American Seaway (Montes *et al.*, 2012: fig. 10b). The paleohabitats in this part of the continent were mainly controlled by the occurrence of a major riverine system (Pebas wetland system) that ran towards the northeast, ending at the Caribbean Sea. By the late Miocene to Pliocene this system had branched extensively,

to form the systems of the present-day Magdalena, Maracaibo, Orinoco, and Amazonas rivers (Hoorn *et al.*, 2010: fig 1c). The faunistic composition of the Miocene tropical South American habitats is known from six localities: (1) La Venta, Upper Magdalena River Basin of Colombia (Kay *et al.*, 1997); (2) Urumaco, Estado de Falcón, Venezuela (Sánchez-Villagra and Scheyer, 2010 and references therein); and four localities from southwestern Amazonia, Peru-Brazil: (3) Fitzcarrald local fauna from Peru, (Antoine *et al.*, 2006, 2007; Negri *et al.*, 2010; Goillot *et al.*, 2011); (4) Napo lo-

cality from Peru (Pujos *et al.*, 2009); (5) Alto Juruá locality from Brazil (Goillot *et al.*, 2011) and (6) Madre de Dios (MD-67) from Brazil (Antoine *et al.*, 2013: fig. 4 for location of the six localities).

Of the above localities, La Venta is the only one with fossil turtles from the middle-late Miocene (all others are late Miocene–Pliocene in age), including freshwater pleurodires belonging to the Podocnemididae and Chelidae clades and cryptodires of the Testudinae clade, summarized as follows: the chelid *Chelus colombiana* Wood, 1976; the podocnemidids “*Podocnemis*” *medemi* Wood, 1997, “*Podocnemis*” *pritchardi* Wood, 1997; cf. *Podocnemis* Wagler 1830; and the testudinids *Chelonoidis hesterni* Auffenberg, 1971 and *Chelonoidis* sp. from the Villa vieja and La Victoria Formations (c. 13 to 12 Ma) (Auffenberg, 1971; Wood, 1997). The early Miocene record of fossil turtles in tropical South America is restricted to *Chelus colombiana* and undescribed podocnemidids from the Barzalosa Formation, Cundinamarca, Colombia (Cadena *et al.*, 2008).

Recently, field expeditions led by the Smithsonian Tropical Research Institute discovered a new Miocene fossiliferous

region at the northernmost tip of South America, Alta Guajira Peninsula, Cocinetas basin, Colombia (Fig. 1.1– 2). Most of the outcrops in this region belong to the Castilletes Formation (Renz, 1960; Rollins, 1965), a formation that was recently redefined by Moreno *et al.* (in press) (Fig. 1.3). The Castilletes Formation is composed principally of marly limestones, claystones, calcareous and non-calcareous sandstones, and conglomerates. The age of the Castilletes Formation was recently obtained by radiometric strontium ( $Sr^{27}/Sr^{26}$ ) dating, which indicated a range of c. 17.3 to 14.5 Ma (late early Miocene to early middle Miocene) (Moreno *et al.*, in press).

Here we describe the turtles from the Castilletes Formation, which were found in six different stratigraphical horizons, spanning the lower and middle segments of the formation. We also discuss their paleobiogeographical implications and their relevance to understanding body size trends in Cenozoic South American turtles.

**Institutional abbreviations.** MUN, Museo de la Universidad del Norte, Barranquilla, Colombia, the repository of the specimens. STRI-dbid, Smithsonian Tropical Research Institute,

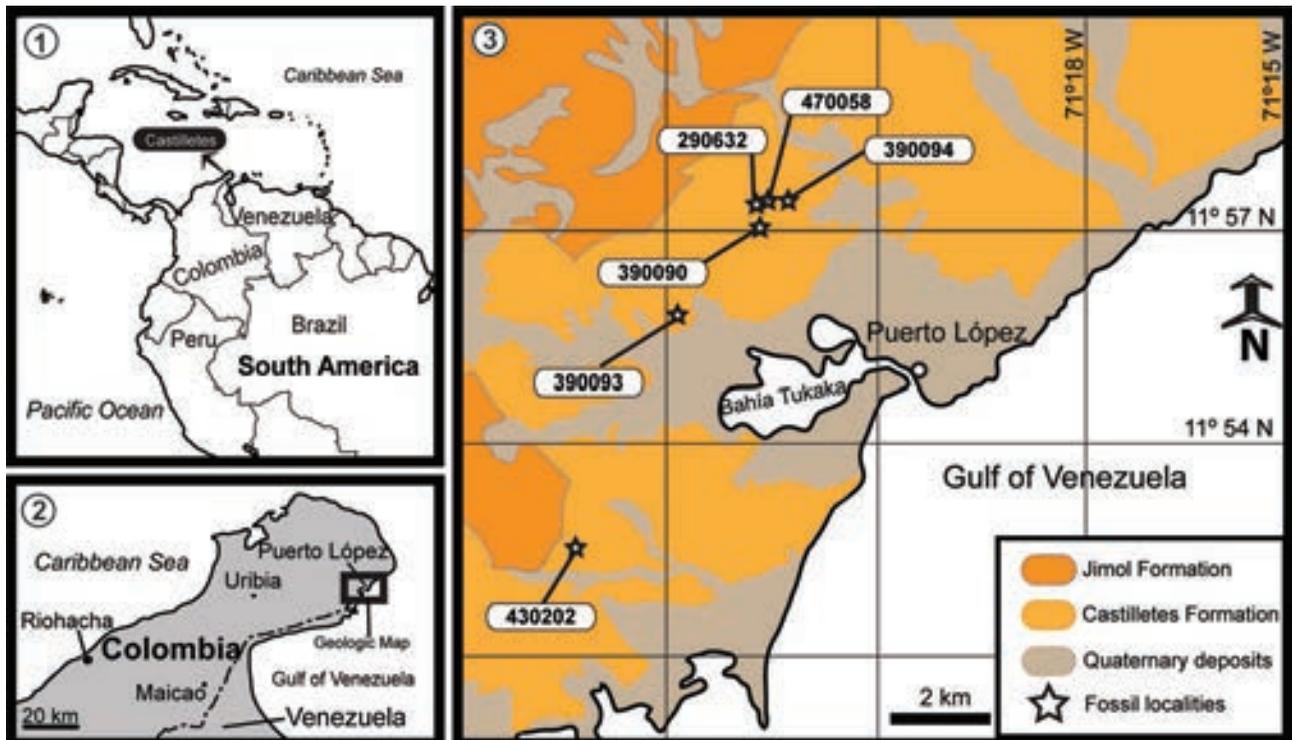


Figure 1.1, Map showing Castilletes region at the northernmost tip of South America, Colombia; 2, map of the Guajira Peninsula, Colombia, and the area of study, delimited by the black square outline; 3, geologic map of the Castilletes region, showing the six fossil localities where the turtles described in this study were found. Redrawn from Moreno *et al.* (in press).

Geological sample collection; Balboa, Ancon, Panama. Web access to this database is available at <http://biogeodb.stri.si.edu>.

**FOSSIL LOCALITIES**

The fossil turtles described here come from six different fossiliferous horizons (localities) belonging to two sections of the Castilletes Formation (Patajau Valley Lat-430103 and Long-170514 ) (Fig. 2). The stratigraphically lowest localities have STRI-dbid identification numbers of 290632 (Patajau West) (11°51'23" N; -71°21'55"W); 470058 (As-trapolletes) (11°57'2" N; -71°19'25" W); 390094 (Beautiful Bone) (11°56'47" N; -71°19'31" W); and 390090 (La Tienda) (11°55'33" N; -71°21'33" W). Fossil turtles from these localities are found in claystones and occasionally in conglomeratic sandstones with abundant freshwater mollusks,

mammals, fishes, and crocodiles. Also from the lower segment, but slightly higher stratigraphically in the Castilletes Formation, is locality 430202 (Kaitamana-Sand Dollars) (11°51'24" N; -71°21'55" W), where turtle fragments are found in siltstones along with abundant brackish mollusks and occasional shark teeth. The uppermost locality of the Castilletes Formation with fossil turtles is 390093 (Jimo-lletes) (11°54'32.0394" N; -71°20'24.36" W); fossils here are found in poorly consolidated and highly oxidized sandstone, imparting a particular orange-brownish color to the bones. Fossils are housed at the collections of the Museo de la Universidad del Norte, Barranquilla, Colombia (MUN), Museo José Royo y Gómez, Bogotá, Colombia and there is online access through the Smithsonian Tropical Research Institute, Geological sample collection (STRI-dbid), Balboa, Ancon, Panama. Web access to this database is available at <http://biogeodb.stri.si.edu>.

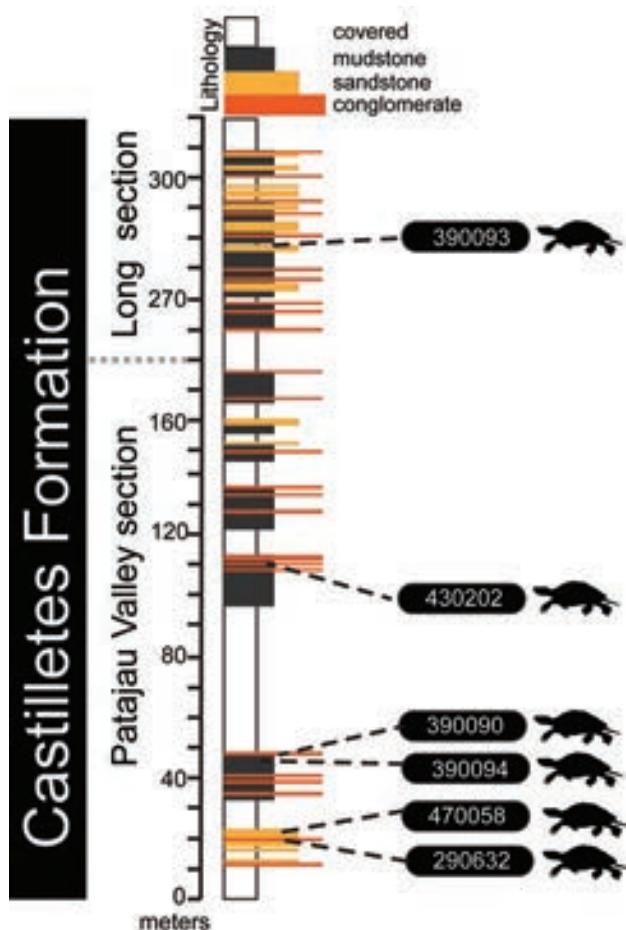


Figure 2. Stratigraphic column for the three segments of the Castilletes Formation showing the six different localities-horizons with fossil turtles. Redrawn from Moreno *et al.* (in press).

**SYSTEMATIC PALEONTOLOGY**

- TESTUDINES Batsch, 1788
- PLEURODIRA Cope, 1874
- PELOMEDUSOIDES Cope, 1868
- PODOCNEMIDIDAE Cope, 1868

*Incertae sedis*

Figures 3.1–3.28 and 4.1–4.27

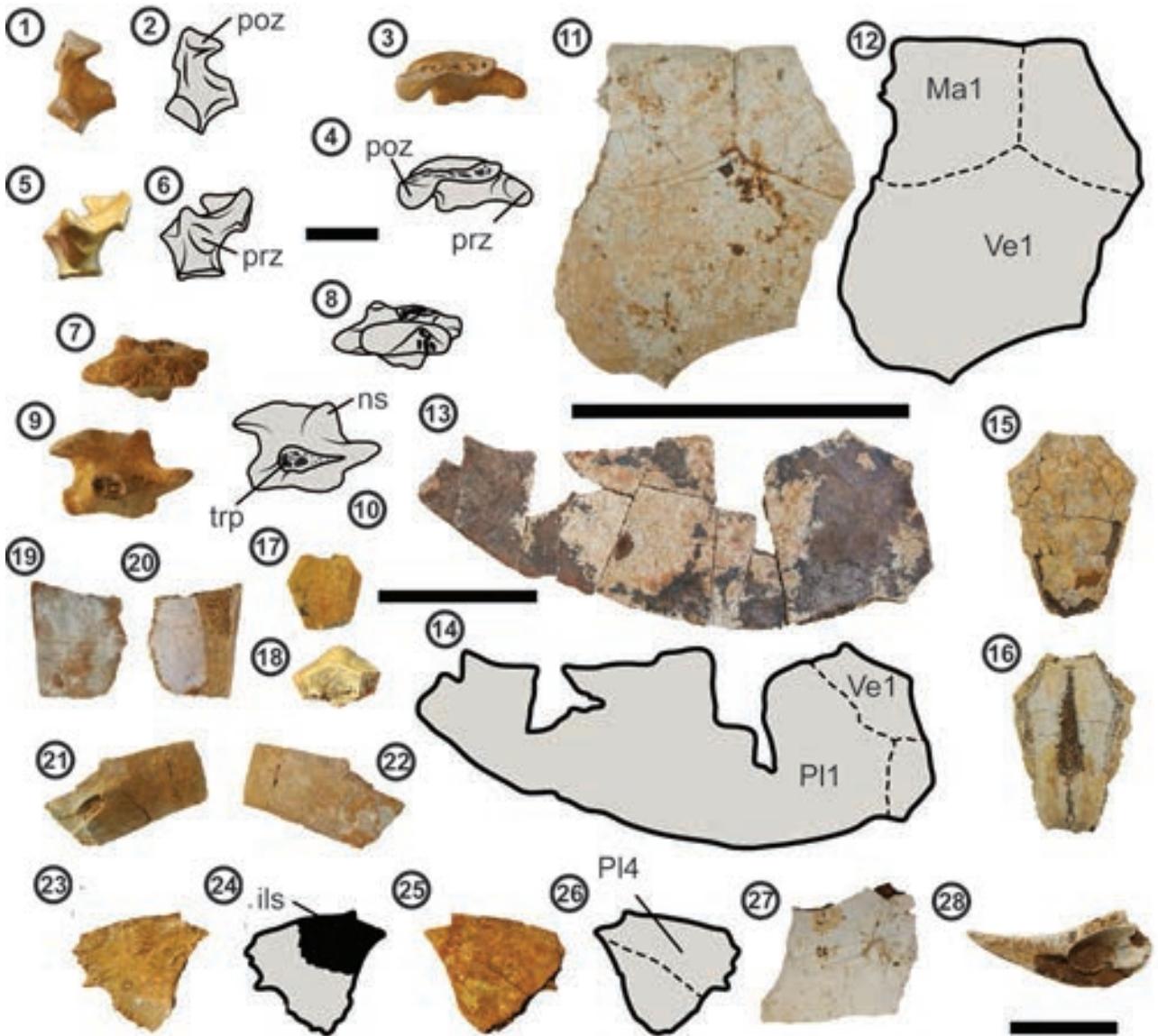
**Referred material.** MUN-STRI-dbid 37423, 37443, 37444, 37445, 37446, 37448, 37449, 37450, 37451, 37452, 37453, 37454, 37455, 37456, 37457, 37458, 37459, 37460, 37461.

**Occurrences and age.** MUN-STRI-dbid 37423 comes from locality 430202. MUN-STRI-dbid 37443, 37450, and 37451 come from locality 390093. MUN-STRI-dbid 37449 from locality 390090, MUN-STRI-dbid 37452 from locality 290632, MUN-STRI-dbid 37444, 37446, 37447, and 37456 from locality 390094, and the remaining referenced specimens from locality 470058 (Fig. 2). The age range from the lowest to the uppermost locality is from the early Miocene to middle Miocene (17.3–14.5 Ma) (Moreno *et al.*, in press).

**Descriptions and remarks.** MUN-STRI-dbid 37443 (Fig. 3.1–10) right upper portion of cervical vertebrae 3? or 4?. The pre- and postzygapophyses are widely separated, a characteristic shared by all pleurodire (Lapparent de Broin *et al.*,

2007). The preserved right postzygapophysis is placed very medially, indicating the possible presence of cervical vertebrae forming a collerette as in *Podocnemis* spp. (Lapparent de Broin, 2000). The suture between the centrum and the

upper body of the vertebra is located more ventrally and not at the transverse process level as in other pelomedusoids. The prezygapophysis is long and dorsolaterally projected, as in the cervical vertebrae of all other podocnemidids. The



**Figure 3.** Carapace and neck bones belonging to *Podocnemididae incertae sedis* from the Castilletes Formation; 1–9, MUN-STRI-dbid 37443, right upper portion of cervical vertebra 3? or 4?; 1, 2, posterior view; 3, 4, dorsal view; 5, 6, anterior view; 7, 8, ventral view; 9, 10, right lateral view; 11, 12, MUN-STRI-dbid 37444, nuchal bone in dorsal view; 13, 14, MUN-STRI-dbid 37445, left costal 1; 15, 16, MUN-STRI-dbid 37446, neural 3; 15, dorsal view; 16, ventral view; 17, 18, MUN-STRI-dbid 37448, neural 4?; 17, dorsal view; 18, posterior view; 19, 20, MUN-STRI-dbid 37449, left peripheral 6?; 19, dorsal view; 20, ventral view; 21, 22, MUN-STRI-dbid 37450, right costal 5; 21, ventral view, showing the inguinal scar; 22, dorsal view; 23–26, MUN-STRI-dbid 37451, right costal 8; 23, 24, ventral view; 25, 26, dorsal view; 27, 28, MUN-STRI-dbid 37447, left peripheral 7?; 27, dorsal view; 28, anterior view. Scale bar= 2 cm (below 4) applies to figures 1–9. Scale bar= 15 cm (right of 11) applies to figures 11–12. Scale bar= 10 cm (below 13) applies to figures 13–16. Scale bar= 5 cm (above 28) applies to figures 17–28. Abbreviations: ils, iliac scar; Ma, marginal scute; ns, neural spine; Pl, pleural scute; poz, postzygapophysis; prz, prezygapophysis; trp, transversal process; Ve, vertebral scute. Dotted lines represent sulci. Black shapes represent scars.

dorsal crest is very high anteriorly, forming an almost straight line with the postzygapophysis in lateral view (Figs. 3.9–10); in this aspect it differs from most of the extant podocnemidids, which exhibit this condition only in cervical 2.

MUN-STRI-dbid 37444 (Fig. 3.11–12) is an almost complete nuchal bone, missing only the rightmost posterolateral portion. The cervical scute is absent as in all other pelomedusoids (Lapparent de Broin, 2000), allowing a medial contact between both marginals 1. With a maximum length of 14.3 cm and width of 8.3 cm as preserved, this nuchal suggests a very large shell with an estimated total length between 100 and 120 cm. The dorsal surface is smooth without any particular sculpturing pattern, as is the most common condition in podocnemidids; this is also shared by all other shell elements described in the following paragraphs.

MUN-STRI-dbid 37445 (Fig. 3.13–14) is a very large left costal 1, missing most of its anterolateral margin. The sulcus between vertebral 1 and 2, as well as the one between these two scutes and pleural 1, is visible and similar in shape to that of other pelomedusoids. A contact between neural 2 and costal 1 is indicated by the tapering posteromedial margin. The large size of this costal 1 also indicates a large shell, longer than 100 cm, and corresponding to a different individual than MUN-STRI-dbid 37444. Three meters away from the large costal 1 a neural 3 (MUN-STRI-dbid 37446, Fig. 3.15–16) was found, indicating that both might belong to the same individual. The elongated hexagonal shape and the presence of a sulcus between vertebral scutes suggest that it corresponds to neural 3.

MUN-STRI-dbid 37448 (Fig. 3.17–18) is a neural bone, probably neural 4?; it lacks a sulcus between vertebrae and has a short, hexagonal shape. On the dorsal surface it has a medial knob, which is also present in most of the species of *Podocnemis*, principally in *Podocnemis sextuberculata* Cornalia, 1849, where it is strongly protuberant in neurals 3 and 4 (pers. observation).

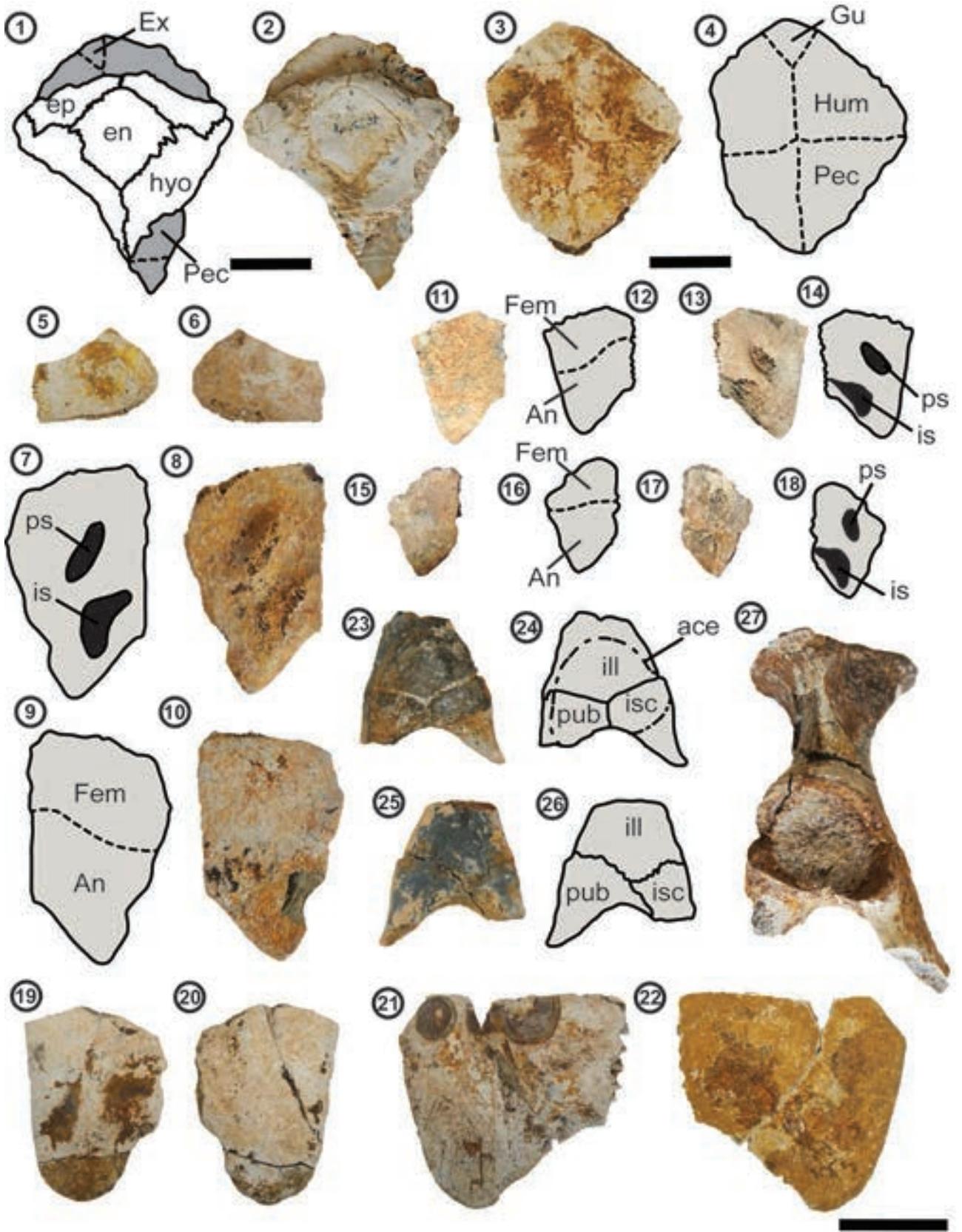
Other carapace elements attributed here to podocnemidids are the following: MUN-STRI-dbid 37449 (Fig. 3.19–20) corresponds to a left peripheral bone from the bridge region, with a visible sulcus between pleural and marginals, indicating that pleural scutes reached the medial portion of peripherals as in most podocnemidids. MUN-STRI-dbid

37450 (Fig. 3.21–22) is a right costal 5, with a very strong and long inguinal scar restricted to this costal on ventral view as in all other podocnemidids. MUN-STRI-dbid 37451 (Fig. 3.23–24) is a right costal 8 from a juvenile specimen, with the sulcus between pleural 4 and vertebral 5 on the dorsal surface and the iliac scar on the ventral surface. The iliac scar continues onto the most posteromedial margin of costal 7, a condition also found in *Podocnemis* spp. and other podocnemidids (pers. observation). MUN-STRI-dbid 37447 (Fig. 3.25–26) is a left peripheral from the posterior end of the bridge region, probably 7?, indicating a relatively high dome shape of the carapace.

Plastron elements and pelvic elements are also attributed here to Podocnemididae *incertae sedis*; these are as follows: MUN-STRI-dbid 37452 (Fig. 4.1–2) corresponds to a portion of an anterior plastral lobe dorsally exposed, missing the most anterolateral margins of both epiplastra and posterior portions of both hyoplastra. The entoplastron is diamond-shaped, and although the anterior portion of the left epiplastron is missing, the impression of the sulcus between the extragular and the gular scute is preserved on the surface of the rock matrix, indicating that extragulars were small and restricted to the epiplastron as in other podocnemidids except *Erymnochelys madagascariensis* Baur, 1888, which exhibits a different pattern of gular-extragular scutes (Lapparent de Broin, 2000). An impression of the pectoro-abdominal sulcus of the right hyoplastron is also preserved on the rock matrix, indicating a long pectoral scute as in other podocnemidids and in contrast to the short pectoral of bothremyidids (Cadena *et al.*, 2012a).

MUN-STRI-dbid 37453 (Fig. 4.3–4) represents an isolated entoplastron, with a gular scute reaching the most anterior corner of this bone, and a humero-pectoral sulcus crossing at the center level of this bone as is most podocnemidids, except in *Peltocephalus dumerilianus* Schweigger, 1812, and some specimens of *Podocnemis erythrocephala* Spix, 1824 and *P. lewyana* Duméril, 1852 (see Cadena *et al.*, 2012b: p. 325), where the sulcus is positioned more posteriorly.

MUN-STRI-dbid 37455 (Fig. 4.5–6) is a left mesoplastron. On the ventral surface there is no evidence of a pectoro-abdominal sulcus crossing it, at least not reaching the central portion of the bone, as in most podocnemidids (see Cadena *et al.*, 2010: p. 376).



Xiphiplastra of podocnemidids are one of the most abundant plastral elements found in the Castilletes Formation; they exhibit a variety of shapes in the anal notch, from narrow V to wide U-shaped, and represent specimens at different ontogenetic stages, indicating that the pattern of pubic and ischiac scars is conservative in shape and relative size proportions through ontogeny. MUN-STRI-dbid 37454 (Fig. 4.7–10) is a left xiphiplastron from a juvenile specimen, with a V-shaped anal notch, oval elongated pubic scar, triangular ischiac scar positioned very close to the anal notch, and a femoro-anal sulcus visible on the ventral surface and located at the midline on the xiphiplastron; in all these features it resembles the condition seen in all other podocnemidids. MUN-STRI-dbid 37461 (Fig. 4.11–14) and MUN-STRI-dbid 37459 (Fig. 4.15–18) represent right xiphiplastra from hatchlings to very juvenile turtles, with shells probably not larger than 15 to 20 cm. MUN-STRI-dbid 37456 (Fig. 4.19–20) and MUN-STRI-dbid 37457 (Fig. 4.21–22) represent right and left xiphiplastra respectively, of two juvenile to adult individuals, the former showing a U-shaped anal notch.

Pelvic girdles are represented by two specimens: MUN-STRI-dbid 37460 (Fig. 4.23–26) corresponds to a left acetabulum capsule and the most proximal end of the ischium, pubis, and ilium, with a clearly visible sutural contact between these three bones at the acetabulum capsule. MUN-STRI-dbid 37458 (Fig. 4.27) is a complete articulated right pelvic girdle, from a large individual, resembling in shape and sutural contacts the pelvis of podocnemidids (see Cadena *et al.*, 2012c: fig. 9.13).

TESTUDINES Batsch, 1788

PLEURODIRA Cope, 1874

CHELIDAE Gray, 1825

*Chelus* Duméril, 1806

*Chelus colombiana* Wood, 1976a *sensu* Cadena *et al.*, 2008

Figure 5.1–5.5

**Referred material.** MUN-STRI-dbid 37471, 37463.

**Occurrences and age.** Both specimens, attributed here to *Chelus colombiana*, come from locality 470058. Early Miocene (c. 17.3–15.30 Ma) (Moreno *et al.*, in press) (Fig. 2).

**Descriptions and remarks.** MUN-STRI-dbid 37471 (Fig. 5.1–4) is a right xiphiplastron missing the posterior tip; MUN-STRI-dbid 37463 (Fig. 5.5) corresponds also to a right xiphiplastron missing its medial and most posterior portions. Both xiphiplastra share a pubic scar broader posteriorly with an anterior margin exhibiting a notch, diagnostic of this species (Cadena *et al.*, 2008). Although the posterior tips are missing in the two xiphiplastra, it is evident that they were wider and thicker than the tips of *Chelus lewisi* Wood, 1976 and *Chelus fimbriata* (Schneider 1783), the other two known species of *Chelus*. Both xiphiplastra are also large in size, indicating turtles that could have reached 100 cm or more.

*Chelus* Duméril, 1806

*Chelus* sp.

Figure 5.6–5.31

**Referred material.** MUN-STRI-dbid 37462, 37464, 37465, 37466, 37467, 37468, 37469, 37470, 37472, and 37473.

**Occurrences and age.** All specimens come from locality 470058, except MUN-STRI-dbid 37484, which comes from locality 290632 (Fig. 2). Early Miocene (c. 17.3–15.30 Ma) (Moreno *et al.*, in press).

**Descriptions and remarks.** As for the podocnemidids des-

**Figure 4.** Plastron and pelvis bones belonging to Podocnemididae *incertae sedis* from the Castilletes Formation; **1, 2**, MUN-STRI-dbid 37452, partial anterior plastral lobe in dorsal view; **3, 4**, MUN-STRI-dbid 37453, entoplastron in dorsal view; **5, 6**, MUN-STRI-dbid 37455, left mesoplastron; **5**, dorsal view; **6**, ventral view; **7–10**, MUN-STRI-dbid 37454, left xiphiplastron; **7, 8**, dorsal view; **9, 10**, ventral view; **11–14**, MUN-STRI-dbid 37461, right xiphiplastron; **11, 12**, ventral view; **13, 14**, dorsal view; **15–18**, MUN-STRI-dbid 37459, right xiphiplastron; **15, 16**, ventral view; **17, 18**, dorsal view; **19, 20**, MUN-STRI-dbid 37456, left xiphiplastron; **19**, dorsal view; **20**, ventral view; **21, 22**, MUN-STRI-dbid 37457, left xiphiplastron; **21**, dorsal view; **22**, ventral view; **23–26**, MUN-STRI-dbid 37460, left partial pelvic girdle; **23, 24**, left lateral view; **25, 26**, right lateral view; **27**, MUN-STRI-dbid 37458, right pelvic girdle. Scale bar= 5 cm (left of **1**) applies to figures 1, 2. Scale bar= 2 cm (left of **3**) applies to figures **3, 4**. Scale bar= 5 cm (left of **27**) applies to figures **5–27**. Abbreviations: **ace**, acetabulum capsule; **An**, anal scute; **en**, entoplastron; **ep**, epiplastron; **Ex**, extragular scute; **Fem**, femoral scute; **Gu**, gular scute; **um**, humeral scute; **hyo**, hyoplastron; **ill**, ilium; **isc**, ischium; **is**, ischiac scar; **Pec**, pectoral scute; **ps**, pubis scar; **pub**, pubis. Dotted lines represent sulci. Dark gray represents rock. Light gray represents bone. Black shapes represent scars.

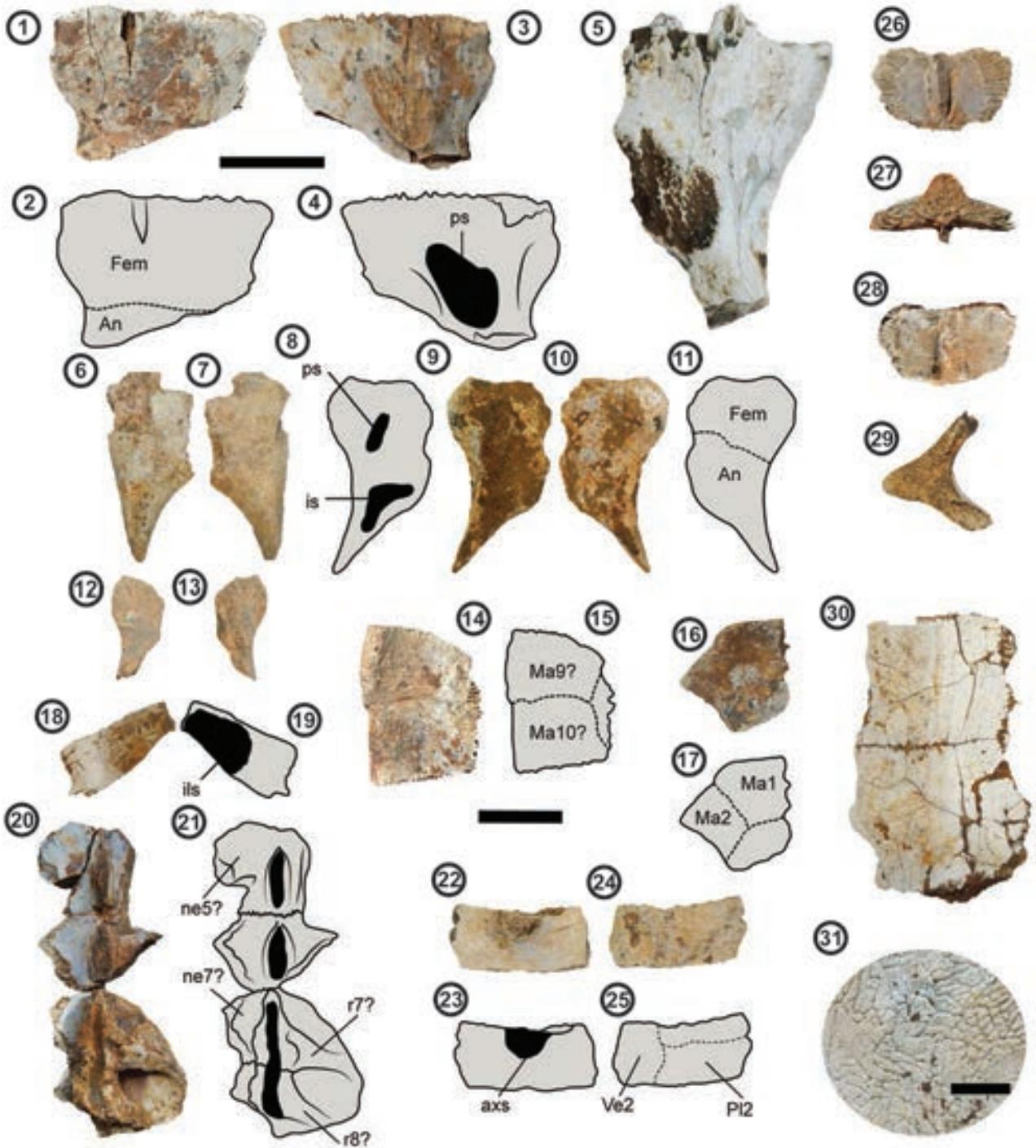


Figure 5. 1–5, *Chelus colombiana*; 1–5; 6–31, *Chelus* sp. 6–31; 1–4, MUN-STRI-dbid 37471, partial right xiphiplastron; 1, 2, ventral view; 3, 4, dorsal view; 5, MUN-STRI-dbid 37463, partial right xiphiplastron in dorsal view. 6–31, *Chelus* sp.; 6, 7, MUN-STRI-dbid 37484, left xiphiplastron; 6 dorsal view; 7 ventral view; 8–11, MUN-STRI-dbid 37464, left xiphiplastron; 8, 9, dorsal view; 10, 11, ventral view; 12, 13, MUN-STRI-dbid 37472, right xiphiplastron; 12, ventral view; 13, dorsal view; 14, 15, MUN-STRI-dbid 37469, left peripheral 9? or 10? in dorsal view; 16, 17, MUN-STRI-dbid 37462, left peripheral 1 in dorsal view; 18, 19, MUN-STRI-dbid 37467, right costal 7 in ventral view; 20, 21, MUN-STRI-dbid 37465, partial carapace including neurals 5 to 7 and portion of the left costal 7 and 8 in ventral view; 22–25, MUN-STRI-dbid 37468, right costal 2; 22, 23, ventral view; 24, 25, dorsal view; 26–28, MUN-STRI-dbid 37470, neural 6? or 7?; 26, ventral view; 27, posterior view; 28, dorsal view; 29, MUN-STRI-dbid 37466, left peripheral from the bridge level; 30–31, MUN-STRI-dbid 37473, peripherals 7? and 8? articulated in ventral view; 31, dorsal sculpturing of the shell, showing dichotomizing lines and micropitted bone surface. Scale bar = 5 cm (below of 1) applies to figures 1–5. Scale bar = 5 cm (left of 18) applies to figures 3–30. Scale bar = 1 cm (inside 31). Abbreviations: An, anal scute; axs, axillary scar; Fem, femoral scute; is, ischiac scar; Ma, marginal scute; ne, neural bone; Pl, pleural scute; r, thoracic rib; Ve, vertebral scute. Dotted lines represent sulci. Light gray represents bone. Black shapes represent scars.

cribed above, xiphiplastra are the most abundant plastral element of *Chelus* found in the Castilletes Formation, and they represent specimens at different ontogenetic stages. All xiphiplastra described in this section have an elongate oval pubic scar, a triangular ischiac scar bordering the anal notch, and a posterior tip long, narrow, and thinner than in *Chelus colombiana*. In all features these xiphiplastra are similar to those from *Ch. lewisi* from the late Miocene of Urumaco (Venezuela) and the extant *Ch. fimbriata* from the Orinoco and Amazonia basins (Wood, 1976a; pers. observation); however, considering the geographical proximity of Castilletes to Urumaco, it is plausible that these specimens belong to *Ch. lewisi*. MUN-STRI-dbid 37484 (Fig. 5.6–7) is a left xiphiplastron from a juvenile-adult individual, based on the size and strong pelvic elements scars. MUN-STRI-dbid 37464 (Fig. 5.8–11) corresponds to a left xiphiplastron of an adult specimen; MUN-STRI-dbid 37472 (Fig. 5.12–13) represents a right xiphiplastron from a hatchling *Chelus* turtle.

Carapace bones include the following: MUN-STRI-dbid 37469 (Fig. 5.14–15) is a left peripheral from the posterior margin of the carapace, probably 9 or 10, with the characteristic lateral notch at the contact between marginals exhibited by all *Chelus* species. MUN-STRI-dbid 37462 (Fig. 5.16–17) is a left peripheral 1, with a visible sulcus between marginals 1, 2, and pleural 1 in dorsal view. MUN-STRI-dbid 37467 (Fig. 5.18–19) corresponds to a right costal 7 with a large iliac scar on the ventral surface that indicates its continuation onto costal 8. MUN-STRI-dbid 37465 (Fig. 5.20–21) represents the most articulated specimen of *Chelus* found so far from the Castilletes Formation, including three neurals (5 to 7) and a portion of left costals 7 and 8 exhibiting the ribs at the end of the costovertebral tunnel. MUN-STRI-dbid 37468 (Fig. 5.22–25) is a right costal 2, with the sulcus between pleurals 1 and 2 on the dorsal surface, and the most posterior portion of the axillary scar on the ventral surface, a possible autapomorphy of *Ch. colombiana* (Cadena *et al.*, 2008); however, considering that the condition is unknown for *Ch. lewisi*, we attribute this costal to the genus level only while we await the description of a new complete specimen of *Ch. lewisi* (R. Sanchéz pers. communication). MUN-STRI-dbid 37470 (Fig. 5.26–28) corresponds to an isolated neural bone, probably 6 or 7, with the characteristic dorsal knob of *Chelus*.

MUN-STRI-dbid 37466 (Fig. 5.29) is a left peripheral from the bridge level, indicating a high dome shell and a short lateral peripheral extension. MUN-STRI-dbid 37473 (Fig. 5.30–31) represents two articulated large right peripheral bones from the posterior portion of the carapace, just after the bridge, probably 7 and 8; these peripherals suggest a very large specimen, with an estimated total carapace length of 100 cm or more; both dorsal and ventral surfaces exhibit the characteristic sculpturing pattern of *Chelus* with long lines that dichotomize, forming squares and a micro-pitted bone surface (Fig. 5.31).

TESTUDINES Batsch, 1788

CRYPTODIRA Cope, 1868

TESTUDINIDAE Gray, 1825

*CHELONOIDIS* Fitzinger, 1835

*Chelonoidis* sp.

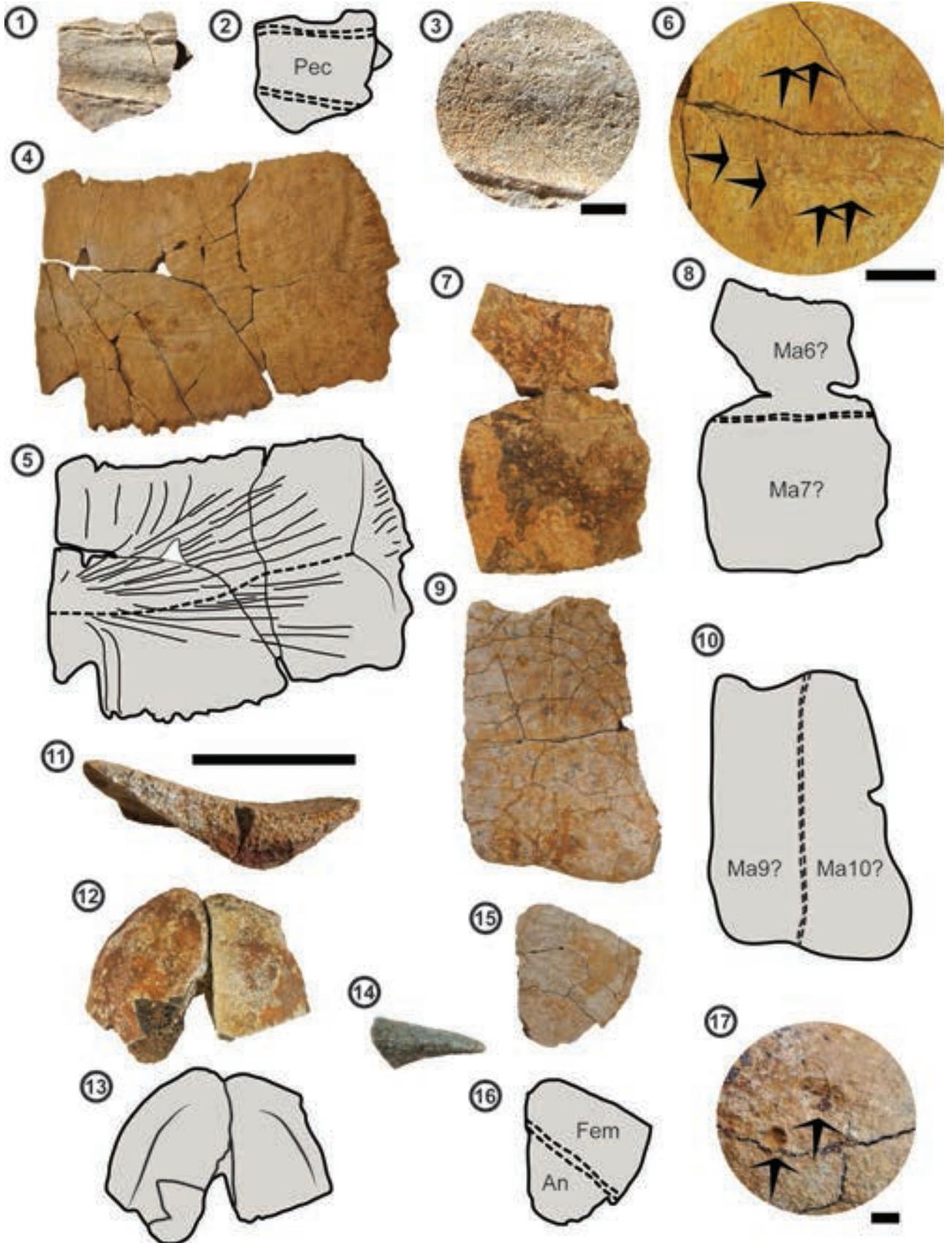
Figure 6.1–6.17

**Referred material.** MUN-STRI-dbid 37475, 37476, 37477, 37478, 37479, 37480, 37481, and 37483.

**Occurrences and age.** MUN-STRI-dbid 37480 and 37481 come from locality 390093. All other specimens referred here come from locality 390094. Early Miocene to middle Miocene (c. 17.3–14.5 Ma) (Moreno *et al.*, in press).

**Descriptions and remarks.** Tortoises are the third group of turtles from the Castilletes Formation, and although all the material collected so far is still too fragmentary to reach a species-level identification, it is possible that at least two different taxa inhabited this region during the middle Miocene. The first is represented by tortoises with shells ranging from 20 to 40 cm long (MUN-STRI-dbid 37475 and 37476) and the second by giant shells longer than 80 cm (MUN-STRI-dbid 37477, 37478, 37479, 37480, 37481). It may be also possible that the differences in size correspond to different ontogenetic stages of the same taxon.

MUN-STRI-dbid 37475 (Fig. 6.1–3) is the medial portion of the left hyoplastron. On the dorsal surface the sulci between humeral and pectoral scutes and between pectoral and abdominal scutes are visible, having the characteristic testudinid sulcus shape, similar to a canal with high lateral walls and a fine and highly dense vermiculation of the bone surface without long dichotomized lines (Fig. 6.3), shared



also by the other specimens described here and assigned to *Chelonoidis*. The pattern of sulci indicates that the pectoral scute was very narrow as is the most common condition in testudinids.

MUN-STRI-dbid 37481 (Fig. 6.4–6) represents a very large costal bone, probably 2 or 4, which though exhibiting the sculpturing pattern described above, also has a distinctive pattern of radial lines originating at the medial/central region of the costal, not seen in other extant or fossil *Chelonoidis*. On the ventral surface, the bone exhibits an unusual pattern of growth, marked by regions with bone fibers oriented almost parallel to the axis of the carapace midline, interrupted by narrower stripe-like regions with fibers oriented perpendicular to the axis of the carapace midline (Fig. 6.6); it is unclear whether this unique bone pattern is restricted only to the most external layer of the internal cortex or extends to the cancellous bone tissue. This pattern could be also a consequence of an anomaly or pathology in the bone growth. However, validation of this hypothesis will be only possible with the discovery of more numerous and complete specimens.

MUN-STRI-dbid 37480 (Fig. 6.7–8) is a left peripheral bone from the posterior margin of the carapace, probably 6 or 7. On the dorsal surface, the sulcus between marginals is visible and exhibits the canal-like shape mentioned before. The maximum thickness in lateral view is 4.1 cm. MUN-STRI-dbid 37477 (Fig. 6.9–11) also represents a left peripheral of a giant tortoise, but in this case from the posterior margin of the carapace, probably 9? or 10?. On the dorsal surface the sulcus between the marginals is projected onto the costals, indicating that pleural scutes are restricted to costals as in *Chelonoidis* and most other testudinids (Claude and Tong, 2004).

MUN-STRI-dbid 37478 (Fig. 6.12–13) corresponds to

both epiplastra bones. Although no sulci are preserved in dorsal or ventral view, the shape, the weak medial sutural contact between the two bones, and their great thickness are extremely similar to the epiplastra of *Chelonoidis* sp. indet, Creutzberg specimen from La Venta fauna, Colombia, figured in Wood (1997: fig. 9.7). MUN-STRI-dbid 37479 (Fig. 6.14) is a large claw, almost 7 cm long, similar in size and shape to the claws of extant *Chelonoidis* from the Galápagos Islands, Ecuador. MUN-STRI-dbid 37476 (Fig. 6.15–16) represents a left xiphiplastron from a juvenile specimen, having a wide femoro-anal sulcus in dorsal view, and indicating a very small anal scute as in other *Chelonoidis* and most testudinids. MUN-STRI-dbid 37483 (Fig. 6.17) is a right peripheral bone, from the posterior margin of the carapace, exhibiting attack marks, probably of crocodiles, which are also an important component of the fossil faunas from the Castilletes Formation (Moreno-Bernal *et al.*, 2012).

## DISCUSSION

### *Turtle assemblages, stratigraphy, and taphonomy*

Fossil turtle remains are found in the lower and middle segments of the Castilletes Formation. The lower segment (the first 60 m of Patajau Valley - 430103 section) is the most prolific for fossil vertebrates and for turtles in particular, with an assemblage of podocnemidids probably belonging to *Podocnemis* or a closely related genus, chelids (*Chelus colombiana* and *Chelus* sp.), and tortoises attributed here to *Chelonoidis* indeterminate species, a taxon of giant turtles very similar to *Chelonoidis* sp. from the La Venta Fauna (Wood, 1997), including also a potential second taxon or alternatively juvenile representatives of the first one. These fossils are found in rocks deposited in lacustrine to small riverine systems with less marine influence than apparent for the middle segment (Moreno *et al.*, in press).

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**Figure 6.** *Chelonoidis* sp. from the Castilletes Formation; 1–3, MUN-STRI-dbid 37475, medial portion of left hyoplastron, showing a very narrow pectoral scute; 1, 2, ventral view; 3, ventral sculpturing of the hyoplastron, showing the sulcus shape similar to a canal with high lateral walls and a fine and highly dense vermiculation of the bone surface; 4–6, MUN-STRI-dbid 37481, left costal 2? or 4?; 4, 5, dorsal view; 6, ventral view, bone surface exhibiting two orientations of growth, almost perpendicular to each other, indicated by arrows; 7, 8, MUN-STRI-dbid 37480, left peripheral 6? or 7? in dorsal view; 9–11, MUN-STRI-dbid 37477, left peripheral 9? or 10?; 9, 10, dorsal view; 11, anterior view; 12, 13, MUN-STRI-dbid 37478, left and right epiplastra in dorsal view; 14, MUN-STRI-dbid 37479, claw in left lateral view; 15, 16, MUN-STRI-dbid 37476, left xiphiplastron in ventral view; 17, MUN-STRI-dbid 37483, bite marks in a right peripheral bone, indicated by arrows. Scale bar= 10 cm (above of 11) applies to all figures except to 3, 6, and 17, which have a scale bar= 1 cm located at their bottom right side, respectively. Abbreviations: **An**, anal scute; **Fem**, femoral scute; **Ma**, marginal scute; **Pec**, pectoral scute. Dotted lines represent sulci. Light gray represents bone.

Disarticulation of the fossil turtles from the lower segment is high, but much less than the material from the middle segment of the formation, as is true also for fragmentation; in most of the bones, from 70 to 100% of the total area of the bone is preserved. Bioerosion is common, especially on bones that tend to be flatter, as, for example, plastron elements (Fig. 4.21). Bite marks also are very common (Fig. 6.17), indicating possible attacks by crocodiles. In the lower segment we infer a shorter exposure time of the skeletons to environmental conditions before burial, and also little to almost no transport, something that is supported by the occurrence of specimens of different sizes for the same taxon; a long transport distance before burial would have resulted in sorting of bone elements, for example, xiphiplastra, which is the most abundant plastral bone in this segment. This fossil assemblage suggests that the animals lived nearby or in the environments suggested by the rocks in which they were found.

Somewhat higher up in the lower segment of the Castilletes Formation (80–120 m, in the Patajau Valley – 430103 section) only podocnemidid turtles were found, in rocks deposited in estuarine-brackish environments with a marked marine influence (Moreno *et al.*, in press). Fossil remains are highly fragmented disarticulated bones. In most cases, only 20–40% of the total area of the bone is preserved, and many show some amount of bioerosion, principally by oysters attached to the external surface. These findings suggest a long time of exposure before final burial, similar to the pattern obtained in simulations with extant turtle skeletons in semiaquatic-terrestrial conditions (Brand *et al.*, 2003). The high degree of fragmentation suggests that transport was also considerable for some of these fossils and that the turtles did not necessarily inhabit the sedimentary environment where their fossils were found.

The third turtle assemblage, in the middle segment of

the Castilletes Formation (250–300 m at the Long – 170514 section), is composed of podocnemidids, as indicated by one cervical vertebra (Fig. 3.1), and giant *Chelonoidis* tortoises. In contrast to the record in the lower segment, *Chelus* turtles are absent. The depositional environment of the middle segment of the Castilletes Formation is reconstructed as more fluvial (Moreno *et al.*, in press). Disarticulation of turtle skeletons is high for this segment – all bones (peripheral, costals, and cervical) are found isolated. However, fragmentation and bioerosion are very low compared to the material in the lower segment of the formation. Turtles from this segment probably lived very close to or in the environment of deposition suggested by the rocks where they were found.

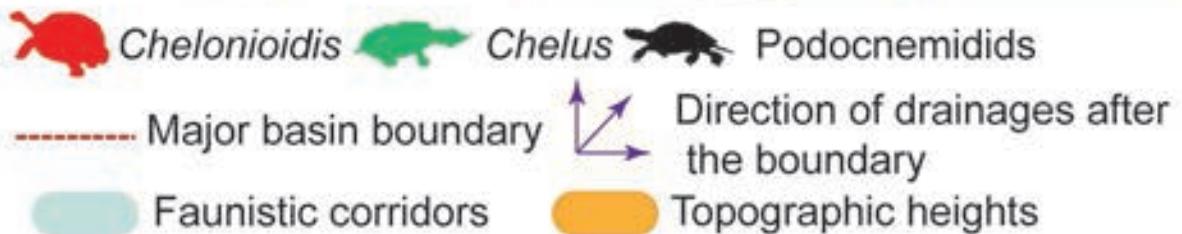
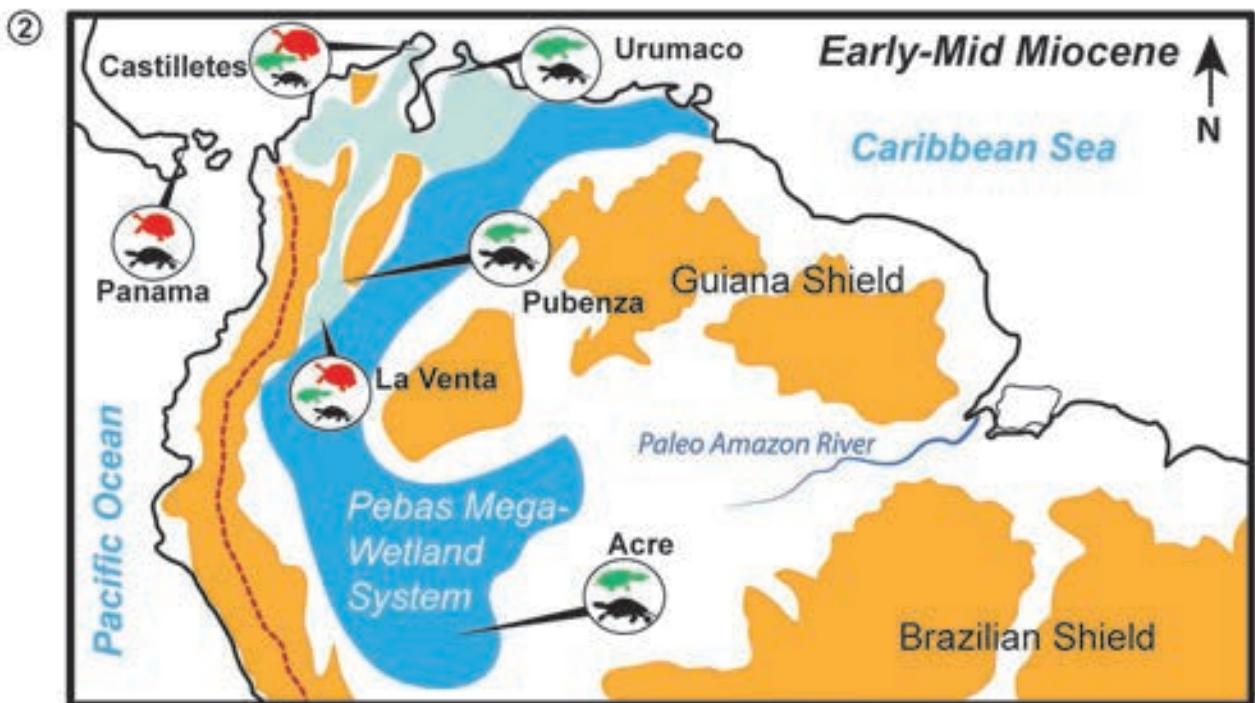
### ***Paleobiogeography***

The Castilletes turtle fauna shares two taxa with the middle Miocene La Venta Fauna (*Chelus colombiana* and *Chelonoidis* sp.), and one taxon with the late Miocene of the Urumaco and Western Amazonia areas. It is identified here as *Chelus* sp., but may possibly belong in *Ch. lewisi*. Podocnemidids are also shared by all four regions, La Venta, Urumaco, Amazonia, and Castilletes. These records indicate a wider past geographical distribution for these taxa/clades compared to the current distribution of their close relatives. The genus *Chelus* is now restricted to the Amazon, Orinoco, Esequibo, and Oyapoque riverine systems (Pritchard, 2008). *Chelonoidis* and podocnemidids are presently absent in the Guajira Peninsula of Colombia and Urumaco in Venezuela, and their current distributions are geographically segregated by cordilleras and major current drainages (Restrepo and Páez, 2013) (Fig. 7).

At least two hypotheses can be proposed to explain the early to middle Miocene geographical distribution of turtles in tropical South America. The first is based on the existence

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**Figure 7. 7.1**, Present-day major riverine systems and distribution of *Chelonoidis*, *Chelus*, and podocnemidid turtles in northern South America. The northern Andean cordillera (major basin boundary) separates the drainages of the rivers in two main groups. On the left (west) side of the Andes, rivers run in a north-northwest direction, including the Magdalena, Cauca, Sinu, Rancheria, Atrato, and all other minor Pacific systems. On the right (east) side, rivers run in a north-northeast direction, including the Maracaibo, coastal Caribbean Venezuela rivers, Orinoco, and Amazon. *Chelus* is absent in riverine systems on the west side; **7.2**, paleogeographical map of northern South America during the middle Miocene (redrawn from Antoine *et al.*, 2013). Miocene localities with records of *Chelonoidis*, *Chelus*, and podocnemidid turtles are also plotted, showing a wider northwestern South American distribution for all three of these turtle lineages, possibly favored by the Pebas Mega-Wetland system and potential corridors between the emerging Eastern cordillera of Colombia and the Maracaibo and Rancheria basins.



of the Pebas wetland system during the middle Miocene (Hoorn *et al.*, 2010), which could have served as a route for the dispersion of taxa facilitated by the connectivity between major and minor drainages, even with potential interruptions to this system due to the increasing uplifting of the Eastern Cordillera of Colombia (Horton *et al.*, 2010a; Horton *et al.*, 2010b; Ochoa *et al.*, 2012). Alternatively, the geographical distribution of tropical South American turtles during the Miocene can be explained as a relict of an extensive distribution reached during the Eocene or Oligocene and modified subsequently by the uplifting of the Andes and the changes in the pattern of the main river systems.

The Eocene and Oligocene epochs, however, still represent a large gap in the fossil record of tropical South American lower vertebrates, a gap that should be the focus of attention of future expeditions in this region, in order not only to test biogeographical hypotheses such as the ones proposed here, but also to explore the effects of climatic events including the Eocene-Oligocene transition, which had profound effects on vertebrates in temperate zones (Prothero and Emry, 1996; Hooker *et al.*, 2004).

### **Body-size trend implications**

Podocnemidids, chelids, and testudinids from the Castilletes Formation exhibit a very large body size. In the case of podocnemidids the carapace may have reached 1.5 m in length. Large body-size in tropical South American turtles has been documented for the late Miocene–Pliocene, with *Stupendemys geographicus* Wood, 1976b and *Caninemys tridentata* Meylan *et al.*, 2009; for the middle–late Miocene, with the *Chelonoidis* and podocnemidids from La Venta; and more recently for the middle–late Paleocene, with podocnemidids from the Cerrejón coal mine in Colombia (Cadena *et al.*, 2012b). The Castilletes turtles confirm that turtles from tropical South America exhibited a very large body size during the early Miocene too, independently from lineages and ecological preferences (terrestrial and freshwater). The Cenozoic trend toward large body-size in tropical South American turtles was acquired after the K-Pg boundary and lasted at least until the Pliocene (see Cadena *et al.*, 2012b for a discussion on the potential causes or triggers of this trend).

The age range of the Castilletes Formation (early to middle Miocene) makes it an ideal section to understand the

possible effects of one of the most remarkable Neogene climatic events, known as the Mid-Miocene Climatic Optimum (MMCO, 17–15 Ma) (Flower and Kennett, 1994; Krapp, 2012 and references therein). Migrations and extinctions, particularly of thermophilic ectothermic vertebrates (lizards, crocodiles, and some turtles), have been documented in Central Europe as a result of the MMCO event (Böhme, 2003). Unfortunately, the upper segment of the Castilletes Formation, which probably corresponds to the time just after the MMCO event, lacks fossil vertebrates so far, preventing a precise comparison of body-size of turtles from before, during, and after this event. However, it is clear from the late Miocene related taxa (in particular *Chelus*) found in other localities geographically close to Castilletes (for example Urumaco), that a large body-size was maintained without major changes. Apparently the MMCO did not have any significant effects either on the Cenozoic body-size trend exhibited by tropical South American turtles or on their diversity.

### **CONCLUSIONS**

The fossil turtles from the Castilletes Formation described here represent the northernmost record of *Chelus colombiana* and *Chelus* spp. in South America, showing also a more extensive paleodistribution of testudinids, and confirming once again the very extensive Miocene geographical distribution of podocnemidids. Testudinids referred here as *Chelonoidis* sp., are the earliest record of this group of tortoises in Colombia and northernmost tropical South America.

Chelids and podocnemidids from Castilletes were larger than any of their extant representatives, supporting the persistence during the early Miocene of the large body-size trend developed by pleurodires during the Paleocene (Cadena *et al.*, 2012b).

Specimens of *Chelonoidis* sp. from the Castilletes Formation were also larger than their extant continental representatives and similar in size to the extant *Chelonoidis* tortoises from the Galapagos Islands.

The Castilletes Formation has an enormous potential for more and better discoveries that could contribute to understand not only the evolution and paleobiogeography of South American tropical turtles, but also to explore the effects of climatic and geological events on them.

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