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THE FOSSIL RECORD OF TURTLES IN COLOMBIA; A REVIEW OF THE DISCOVERIES, RESEARCH AND FUTURE CHALLENGES

El registro fósil de las tortugas en Colombia; una revisión de los descubrimientos, investigaciones y futuros desafíos

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ABSTRACT
This is a review article on the fossil record of turtles in Colombia that includes: the early Cretaceous turtles from Zapatoca and Villa de Leyva localities; the giant turtles from the Paleocene Cerrejón and Calenturitas Coal Mines; the early Miocene, earliest record of *Chelus* from Pubenza, Cundinamarca; the early to late Miocene large podocnemids, chelids and testudinids from Castilletes, Alta Guajira and La Venta; and the small late Pleistocene kinosternids from Pubenza, Cundinamarca. I also discuss here the current gaps in the fossil record of tropical South American turtles, as well as the ongoing research and future projects to be developed in order to understand better the evolutionary history of Colombian turtles.

Keywords: Colombia, Cryptodires, paleontology, Pleurodires, Testudines.

RESUMEN
En este artículo resumo el registro fósil de tortugas de Colombia, incluyendo las tortugas del Cretácico temprano de Zapatoca y Villa de Leyva, las tortugas gigantes del Paleoceno en las minas de carbón de El Cerrejón y Calenturitas, el registro más antiguo de *Chelus*, proveniente del Mioceno temprano de Pubenza (Cundinamarca), los grandes podocnémidos, chélidos, y testudínidos del Mioceno temprano a tardío de Castilletes en la Alta Guajira y La Venta, y los pequeños kinostérnidos del Pleistoceno tardío de Pubenza, Cundinamarca. En este artículo discuto también los actuales intervalos para los cuales no se conocen registro fósil de tortugas en la parte tropical de Suramérica, así como también las investigaciones que se están desarrollando actualmente, c también los futuros proyectos a desarrollar con el fin de entender mejor la historia evolutiva de las tortugas en Colombia.

Palabras clave: Colombia, Cryptodiras, paleontología, Pleurodiras, Testudines.

INTRODUCTION
Turtles are one of the most abundant fossil vertebrates in Mesozoic (~250–66 Ma) and Cenozoic (~66Ma–to present) rock sequences around the world (Paleobiology data base, fossilworks.org). This is due principally to: 1) the large number of bones that constitute their shell (~56), increasing the chances of preservation (in most of the cases disarticulated); 2) their wide spectrum of habitat adaptations, including freshwater, marine, and terrestrial environments, and also their wide latitudinal and geographical distribution (Turtle Taxonomy Working Group, 2011). Colombia is not an exception to this global pattern of abundant fossil record of turtles, as I show in this review paper on the fossil record and research done in

the last decade (Fig. 1), which includes also the most recent discoveries not included in Cadena (2012). I also discuss the future challenges in order to understand better the origin and evolutionary history of extant tropical South American turtles biodiversity and distribution.

MESOZOIC FOSSIL TURTLES FROM COLOMBIA

At present, the Mesozoic fossil record of turtles from Colombia is only known for the Early Cretaceous (~145–100 Ma). The late Valanginian (~130 Ma) stem-pleurodiran *Notoemys zapatocaensis* (Cadena and Gaffney, 2005), from the shallow marine rock sequences belonging to the Rosablanca Formation, Zapatoca, Santander (Fig. 1, locality 1), is not only the oldest fossil turtle so far known from Colombia, but also the oldest in northern South America. Represented by two nearly complete articulated shells and some other fragmentary material (Fig. 2A), *N. zapatocaensis* is a key fossil to understand the evolution of the turtle shell, principally the plastron, and evinces the oldest evidence of sexual dimorphism in the fossil record of turtles (Cadena *et al*., 2012a). Other fossil turtles from Zapatoca include the potentially oldest record for Podocnemidoidea (one of the most diverse lineages of the pleurodiran crown) (Cadena, 2011a) and fragmentary shells belonging to eucryptodirans (which includes crown-Cryptodira and other lineages) (Cadena, 2011b).

The second Colombian locality with early Cretaceous fossil turtles is Villa de Leyva, Bóyaca (Fig. 1, locality 2). Fossils in this locality are found in rocks from the Paja Formation, Barremian-Aptian (~125 Ma). A first publication describing a mandible and a cranial mold fragment from an eucryptodiran turtle was presented by de la Fuente and Goñi (1983). Years later, a nearly complete skull was partially described and attributed to the family Protostegidae by Smith (1989). For the last 12 years the Colombian Foundation of Geobiology (*Fundación Colombiana de Geobiología*) has been collecting several nearly complete skeletons, some of them corresponding to a new protostegid species, with implications for the evolution of the different radiations of turtles adapted to marine life (Cadena E., personal communication).

CENOZOIC FOSSIL TURTLES FROM COLOMBIA

Paleogene (65–23 Ma)

For decades the faunistic composition of northernmost South America just after the Cretaceous-Paleogene event (K-Pg event) that triggered the extinction of (non-avian) dinosaurs and other vertebrates and invertebrates was completely unknown. However, this changed when in 2004 geologists and paleontologists of the Smithsonian Tropical Research Institute (STRI) and Cerrejón Coal Mine discovered what is thus far the most complete and diverse middle-late Paleocene (~59 Ma) tropical South American fauna and flora. Fossils found at the Cerrejón Formation, Cerrejón Coal Mine, Guajira (Fig. 1, locality 3) include fossil leaves, seeds, fruits and a diverse record of pollen and spores (Jaramillo *et al*., 2007; Herrera *et al*., 2008; Doria *et al*., 2008; Wing *et al*., 2009). Fossil vertebrates from Cerrejón include *Titanoboa cerrejonensis* (the largest snake ever known) (Head *et al*., 2009), three species of crocodiles (Hastings *et al*., 2010; Hastings *et al*., 2011) and five different taxa of turtles including: 1) the podocnemid *Cerrejonemys wayuunaiki* (sister taxa of the extant genus *Podocnemis*) (Cadena *et al*., 2010); 2) the podocnemid *Carbonemys cofrinii*, which with a skull length of 23 cm represents the largest Paleogene turtle ever found (Fig.2B-C), 3) a potential shell of this species, referred as Pelomedusoides incertae sedis Taxon A, with a length of 170 cm (Cadena *et al*., 2012a); 4) a small turtle characterized by the complete absence of neural bones referred as Pelomedusoides incertate sedis Taxon B (Cadena *et al*., 2012b) (Fig. 2D); and the bothremydid *Puentemys mushaisaensis* (Fig.2E-H) with its extremely circular shell (Cadena *et al*., 2012c). Cerrejón turtles show that few million of years after the K-Pg event, tropical South American environments were diverse with some of the extant lineages already inhabiting this region and developing a very large body-sizes.

Recently, a new fossil turtle belonging to Pelomedusoides incertae sedis (Fig. 2I), potentially a bothremydid related to *Puentemys mushaisaensis,* was found at the late Paleocene-early Eocene (~56 Ma) rocks of Los Cuervos Formation, Calenturitas Coal Mine, Cesar (Fig. 1, locality 4) (Cadena and Schweitzer, 2014). Preservation of bone cells (osteocytes) (Fig. 2J) and blood vessels (Fig. 2K) was detected in this fossil, indicating that even in tropical environments long term preservation of soft tissues and cells is possible, depending on mechanisms that are still under study. Also from the late Paleocene, fragmentary material of turtles has been found at Nemocon, Cundinamarca (Fig. 1, locality 5), and at the Doña Juana dump, Bogotá (Fig. 1, locality 6), in rocks of the Bogotá Formation; this material is currently under study by the author of this paper in collaboration with the Florida Museum of Natural History.

Turtle fragmentary and undescribed material, mostly missing or lost from museum collections have been reported for the upper Eocene and Oligocene of Colombia (Stirton, 1953; Hoffstetter, 1970). These reports include turtle remains from the upper Eocene, Mugrosa Formation, at Tama (Santander); lower Oligocene, turtle remains from the Tuné Formation (Gualanday group), Chaparral, Tolima and Honda Group from Coyaima, Tolima. Recently, I had the opportunity of revisit the upper Eocene locality at the middle Magdalena Valley, Mugrosa Formation, however until present not turtle material has been recovered.

Neogene (23–2.5 Ma)

The early Miocene (~23–16 Ma) is represented by turtles from Pubenza, Tocaima, Cundinamarca (Fig. 1, locality 7). In this locality, the fossils are found in rocks of the Barzalosa

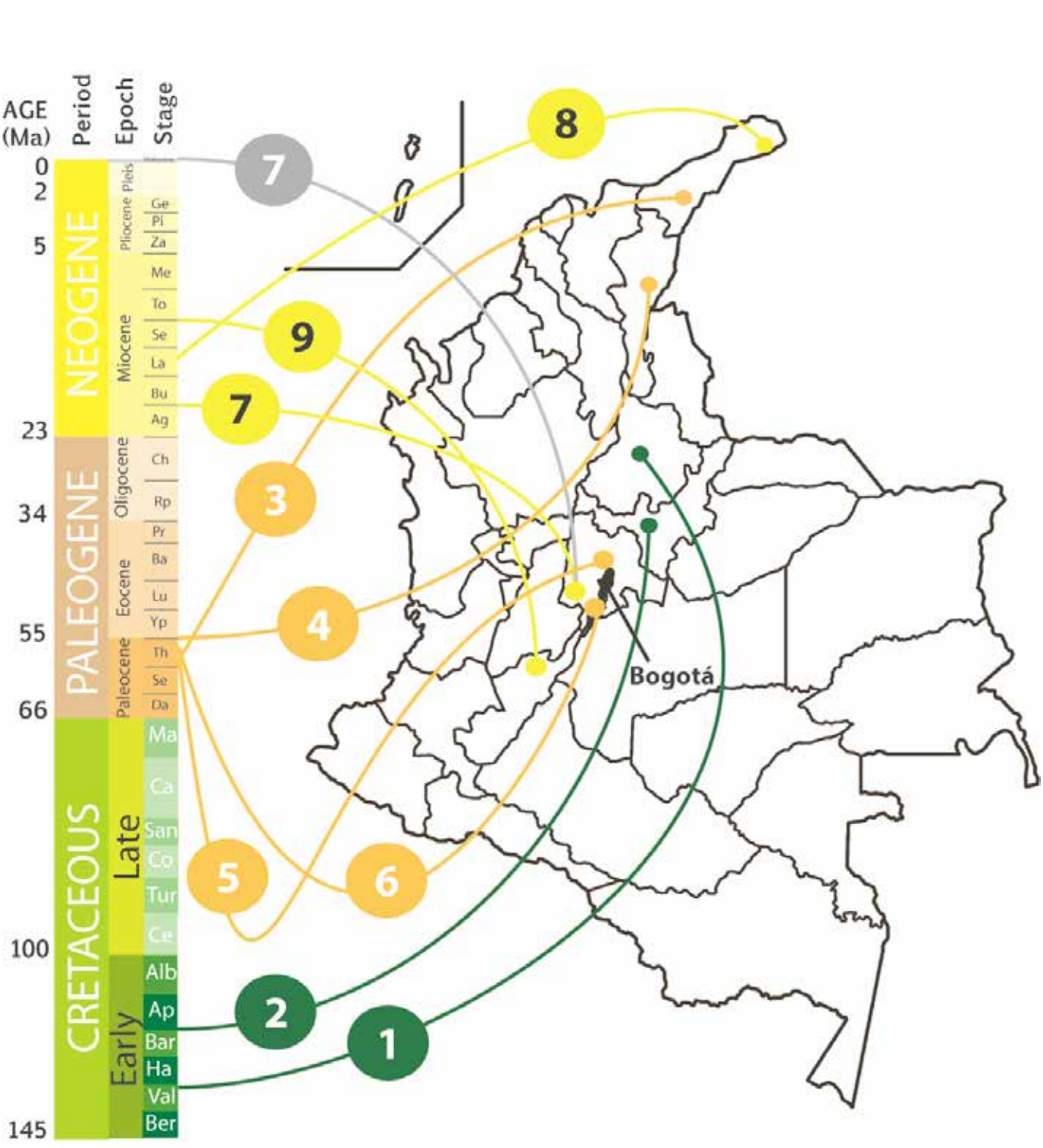

Figure 1. Map of Colombia showing the nine different localities where fossil turtles have been found so far and their position in the geological time scale. Locality 1. Zapatoca, Santander, early Cretaceous (Valanginian); locality 2. Villa de Leyva, Bóyac, early Cretaceous (Barremian-Aptian); locality 3. Cerrejón Coal Mine, Guajira, middle-late Paleocene; locality 4. Calenturitas Coal Mine, César, Paleocene-Eocene; locality 5. Nemocón, Cundinamarca, late Paleocene; locality 6. Doña Juana Dump, Bogotá D.C, late Paleocene; locality 7. Pubenza, Tocaima, Cundinamarca, early Miocene and late Pleistocene; locality 8. Castilletes, Guajira, early to late Miocene; locality 9. La Venta, Villavieja, Huila, middle to late Miocene.

Formation, deposited in fluvio-lacustrine environments. Fossil material from this locality includes the earliest indisputable record of the genus *Chelus*, *C. colombiana* Wood 1976, and some unpublished fragments of podocnemids (Cadena *et al*., 2008).

In the last three years a new locality of fossil vertebrates has been explored in detail by the Smithsonian Tropical Research Institute and other Colombian and foreign institutions. The new locality is at the northernmost tip of Colombia, near the Colombian-Venezuelan border, in Puerto López, Guajira (Fig. 1, locality 8). Fossils here are found in fluvial to marine transitional environments of the Castilletes Formation and span an age range from the late early Miocene (~17 Ma) to the late Miocene (~10 Ma) (Moreno F. personal communication). Turtles of the Castilletes Formation include very large podocnemids (~130 cm shell length), large *Chelus* (~90 cm shell length), and the earliest record of tortoises (testudinids), probably related to *Chelonoidis*, in tropical South America. These fossils have implications for understanding the response of tropical vertebrates to climatic events (particularly warmings) and to the geographical and geological events during the middle Miocene in northern South America (Cadena E. personal communication).

One of the most famous paleontological areas in Colombia is La Venta, in the Tatacoa desert, Huila (Fig. 1, locality 9). Fossils in this area are found in rocks deposited in fluvio-lacustrine environments of the Villavieja and La Victoria formations, from the middle to late Miocene (~13–12 Ma). The record of turtles includes: the chelid *Chelus colombiana*; the podocnemids "*Podocnemis*" *medemi*, "*Podocnemis*" *pritchardi*; cf. *Podocnemis*; and the testudinids *Chelonoidis hesterna* and *Chelonoidis* sp. (Auffenberg, 1971; Sánchez-Villagra, 1993; Wood, 1997), new photographs of this specimen were recently presented in Sánchez-Villagra and Scheyer (2010), however the specimen is still undescribed in detail. A revision of the podocnemid material from La Venta is needed, considering that most of the diagnostic characteristics used by Wood (1997) have been recently reevaluated or considered very homoplastic among different lineages of turtles (Gaffney *et al*., 2011; Cadena *et al*., 2012a). There is only one report of Pliocene turtle remains in Colombia, from the Savana Formation, near El Carmen de Bolivar and also near Corozal (Sucre) (Porta, 1961), however the material is missing from collections and never was described or figured.

Quaternary (2.5 Ma –to present)

The youngest locality with fossil turtles in Colombia is also at Pubenza, Tocaima, Cundinamarca (Fig. 1, locality 7). From Quaternary lacustrine deposits of the late Pleistocene (~16,500 years), turtles in this locality are found associated with mastodons and belong to the kinosternid genus *Kinosternon* sp. (Cadena *et al*., 2007). Kinosternidae is a group of cryptodires that reached South America via the Isthmus of Panama probably in Plio-Pleistocene times.

CHALLENGES AND ONGOING RESEARCH

In the following paragraphs I discuss some of the unresolved questions and existent gaps in the fossil record of Colombian turtles and formulate suggestions for potential future projects and research in this field. The first big, unresolved question is the timing and geographic origin of turtles in northern most South America: whether they dispersed from the southern part of the continent, where late Triassic and Jurassic turtles have been found (de la Fuente *et al*., 2014), or alternatively from Laurasia (North America-Eurasia) where the earliest known turtles evolved (Li *et al*., 2008; Joyce *et al*., 2014). Only the discovery of Triassic and Jurassic vertebrate assemblages in tropical South America could reject or support any of these two hypotheses; or, even more unexpectedly, support the origin of turtles in this particular region of the supercontinent Pangaea. Thick rock sequences of Triassic-Jurassic rocks deposited in fluvial environments are common in the eastern cordillera and other regions of Colombia (Julivert 1968), most of which have never been explored for fossil vertebrates, creating a promising framework for future fieldworks and fascinating discoveries.

The Late Cretaceous (~100–66 Ma) is the first major gap in the fossil record of northern most South American turtles. Thus, we do not know which lineages inhabited this part of the continent just before the K-Pg event and if they were more closely related to the Early Cretaceous lineages found in Zapatoca and Villa de Leyva or instead to the Paleogene turtles from Cerrejón. Late Cretaceous sequences are abundant in the Magdalena river basin principally at the upper and middle valleys (Julivert, 1968). Exploration the search for Late Cretaceous fossil turtles has been recently conducted near the hydroelectric dam of Hidrosogamoso in Santander in cooperation with the Colombian Geological Survey, Isagen, and STRI; unfortunately no fossil turtles have been found so far in this region.

The second major gap in the fossil record of tropical South American turtles corresponds to the Eocene and Oligocene epochs (~56–23 Ma). Fossils from this time period could clarify not only the persistence of Paleocene lineages in this region, but also shed light on the past geographical distribution of certain lineages, principally podocnemids and chelids, as well as the arrival of testudinids, and also the response of tropical turtles to the global cooling event of the Eocene-Oligocene transition (Liu *et al*., 2008). Eocene and Oligocene rocks are also abundant at the Magdalena river basin and at the Bogotá highland plateau (Julivert, 1968).

The last major gap in the fossil record of Colombian turtles corresponds to the Pliocene (~5–2.5 Ma). This epoch is of particular interest because it is when the Great American Biotic Interchange (GABI) took place (Marshall, 1979; Woodburne 2010, and references therein), including the possible dispersal of kinosternidids and emydids turtles from North-Central America to South America. Recently, as result of expeditions to the Alta Guajira of Colombia headed

by STRI, a new lithostratigraphic unit has been revealed. It is currently being defined and has preliminary radiometric ages between 5 and 3 Ma; its fossil record includes mammals, crocodiles, fish, and turtles, which are currently under study. Other minor gaps exist within the periods and epochs from which the aforementioned fossils are known, and although not described in detail here, they should also form part of future fieldwork goals. Closing these gaps will contribute our knowledge of the evolutionary history of South American turtles and especially of how their extant geographical distribution and diversity was reached. The fossil record will also help us to understand the possible response of tropical turtles to the coming decades of climate and ecosystems changes.

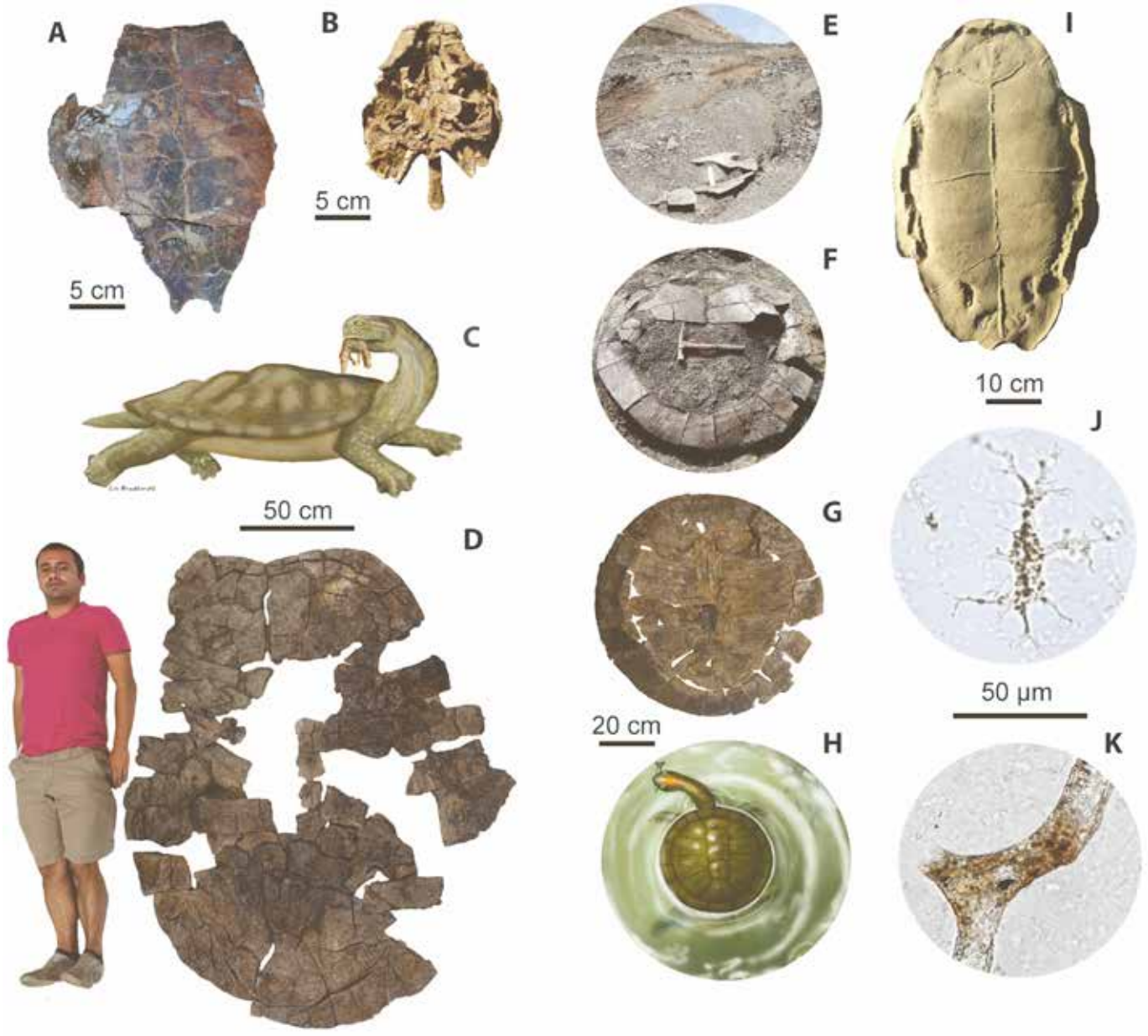

Figure 2. Fossil turtles from Colombia. A. Paratype of *Notoemys zapatocaensis* described in Cadena *et al*., (2012a), plastron in ventral view. B. Skull of the holotype of *Carbonemys cofrinii* described in Cadena *et al*., (2012b), skull in ventral view. C. Reconstruction of *Carbonemus cofrinii* done by Liz Bradford. D. Pelomedusoides incertae sedis Taxon A, from Cerrejón, potentially the shell of *Carbonemys cofrinii,* carapace in dorsal view. E-H. *Puentemys mushaisaensis* from Cerrejón, described in Cadena *et al*., (2012c). E. Discovering of the holotype of *P. mushaisaensis* in a claystone layer of Cerrejón Formation. F. Holotype shell in situ after five days of removing the rock surrounding. G. Ventral view of the carapace after preparation. H. Reconstruction of *Puentemys mushaisaensis* done by Liz Bradford. I. Ventral view of the plastron of Pelomedusoides incertae sedis, potentially a bothremydid from Calenturitas coal mine described in Cadena and Schweitzer (2014). J-K. Isolated osteocyte and blood vessel from Pelomedusoides incertae sedis from Calenturitas coal mine, scale bar for both figures.

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