

An Early Cretaceous *Sphenophyllum* or a hatchling turtle?

Héctor D. Palma-Castro, Diego A. Cómbita-Romero, Edwin-Alberto Cadena,
Mónica R. Carvalho, and Fabiany Herrera

ABSTRACT

Correctly identifying fossil specimens from parautochthonous deposits where marine and terrestrial organisms co-occur can be challenging due to the abundance of rare and obscure specimens with unclear morphologies. In this study, we reviewed fossils from the Lower Cretaceous La Paja Formation (Ricaurte Alto, Villa de Leyva, Colombia) that were originally described as the plant “*Sphenophyllum colombianum*” based on an apparent resemblance to the upper Paleozoic genus. We determined that the type specimen corresponds to the carapace of a hatchling turtle. In addition, a second specimen of “*S. colombianum*” although less well-preserved, also exhibits similar features of a hatchling turtle. The two fossil specimens are significant as they represent the first report of hatchling marine turtles from the Aptian of northwestern South America and provide evidence of the exceptional preservation of the Marine Reptile Lagerstätte of Ricaurte Alto.

Héctor D. Palma-Castro. Departamento de Biología and Grupo de investigación en Paleobiología e Historia Natural, Universidad Nacional de Colombia, Carrera 30 No. 45-03 Bogotá, Colombia and Museo Paleontológico de Villa de Leyva, Universidad Nacional de Colombia, Km 1.5 Vía Arcabuco Villa de Leyva, Colombia. Corresponding author. hdpalmac@unal.edu.co

Diego A. Cómbita-Romero. Departamento de Geociencias and Grupo de investigación en Paleobiología e Historia Natural, Universidad Nacional de Colombia, Carrera 30 No. 45-03 Bogotá, Colombia and Museo Paleontológico de Villa de Leyva, Universidad Nacional de Colombia, Km 1.5 Vía Arcabuco Villa de Leyva, Colombia. dacombitar@unal.edu.co

Edwin-Alberto Cadena. Facultad de Ciencias Naturales and Grupo de Investigación Paleontología Neotropical Tradicional y Molecular (PaleoNeo), Universidad del Rosario, Bogotá, 111221, Colombia and Smithsonian Tropical Research Institute, Box 0843–03092, Balboa, Ancon, Panama, Republic of Panama and Field Museum of Natural History, Chicago, Illinois–, 60605, U.S.A. edwin.cadena@urosario.edu.co

Mónica R. Carvalho. Museum of Paleontology and Department of Earth and Environmental Sciences, University of Michigan, Ann Arbor, Michigan 48109, USA. marvalho@umich.edu

Fabiany Herrera. Earth Sciences, Negaunee Integrative Research Center, Field Museum of Natural History, Chicago, Illinois 60605, USA. fherrera@fieldmuseum.org

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INTRODUCTION

According to the most recent list published by the International Union of Geological Sciences (IUGS), only two Geological Heritage Sites have been recognized in Colombia (IUGS, 2022): the Nevado del Ruiz Quaternary Volcanic Complex and the Marine Reptile Lagerstätte from the Lower Cretaceous of the Ricaurte Alto. The Ricaurte Alto is a coastal and shallow marine sequence comprising approximately 1.9 km of sedimentary rocks from the Upper Valanginian to the Albian. It is divided into four formations (Ritoque Formation, La Paja Formation, San Gil Inferior Formation, and San Gil Superior Formation) as described by Etayo-Serna (1968).

Within the Ricaurte Alto sequence, La Paja Formation has yielded an enormous quantity and diversity of exceptionally preserved Hauterivian to Aptian fossils (~132 to ~113 Ma; Etayo-Serna, 1968). These fossils include a large number of marine reptiles, such as plesiosaurs (Welles, 1962; Páramo-Fonseca et al., 2019), pliosaurs (Páramo-Fonseca et al., 2016, 2018; Gómez-Pérez and Noè, 2017; Noè and Gómez-Pérez, 2022;), ichthyosaurs (Páramo-Fonseca, 1997; Maxwell et al., 2016; Páramo-Fonseca et al., 2020; Cortés et al., 2021), turtles (Cadena, 2015; Cadena and Parham, 2015; Cadena et al., 2019), crocodylomorphs (Cortés et al., 2019), and dinosaurs (Carballido et al., 2015; Cortés et al., 2023). Marine invertebrates are also widespread in the sedimentary sequence, particularly ammonoids (Etayo-Serna, 1968, 1979; Patarroyo, 2000, 2020) and orithopsid crabs (Luque et al., 2020).

Plant remains are sporadically found in calcareous concretions and shale beds of La Paja Formation. These plants likely reflect elements of the coastal vegetation that were capable of withstanding transportation. Over 50 plant taxa have been described (Huertas, 1967, 1970a, 1976, 2003; van Waveren et al., 2002; Moreno et al., 2007), however, most of their descriptions and affinities require a systematic review (Palma, 2020). In his last work, Huertas (2003) described abundant cast-mold and permineralized remains of stems, branches, leaves, and reproductive structures of gymnosperm affinity. Most plants appear to be related to Araucariaceae, Cupressaceae, and Bennettitales (van Waveren et al., 2002). Among these plants, a presumed sphenophyte species, "*Sphenophyllum colombianum*" (Huertas, 2003) (Figure 1A), was also described from La Paja Formation, far extending the temporal and stratigraphic range known for this Paleozoic genus. *Sphenophyllum* is an extinct plant found worldwide, ranging from the Late Devonian to the Permian and exhibiting a large morphological diversity during the Carboniferous (Taylor et al., 2009; de Felice et al., 2019; Huang et al., 2022; Rischbieter et al., 2022). Well-identified leaves of *Sphenophyllum* (Figure 1B-C) are borne in whorls and typically show wedge-shaped forms with veins radiating from the leaf base (Taylor et al., 2009). The unexpected discovery of a species of *Sphenophyllum* in the La Paja Formation represents a conundrum: either this Paleozoic genus extended into the Early Cretaceous or the affinity of "*S. colombianum*" is incorrect.

Here, we re-examined the material described as "*Sphenophyllum colombianum*" by Huertas (2003) and additional material found in the Huertas' collection related to the same species. Our reevaluation shows that the specimens described as "*S. colombianum*" are unequivocal carapaces of hatchling turtles.

MATERIAL AND METHODS

The "type" specimen of "*Sphenophyllum colombianum*" described by Huertas is an open and slightly eroded calcareous concretion (Figure 2A-D). A second specimen with similar characteristics, labeled as a "Cotypus" was also analyzed (Figure 2E). Both specimens are housed in the paleontological collections of the Department of Geosciences at the Universidad Nacional de Colombia (UNDG). The "type" specimen (MONQ-602) was obtained from Monquirá, near the "Estación del Kronosaurio" in Villa de Leyva (~5°38'13" N, ~73°33'33" W), while the second specimen (LLC-65) was collected from La Catalina Hill, located on the border between the towns of Villa de Leyva and Sutamarchán (~5°38'2" N, ~73°34'40" W).

The fossils were photographed using a Canon EOS R camera with MP-E 65mm f/2.8 1-5x and TS-E 50mm f/2.8L Macro lenses attached to a StackShot system at the Universidad Nacional de Colombia, Bogota. The digital images were merged using Helicon Focus software.

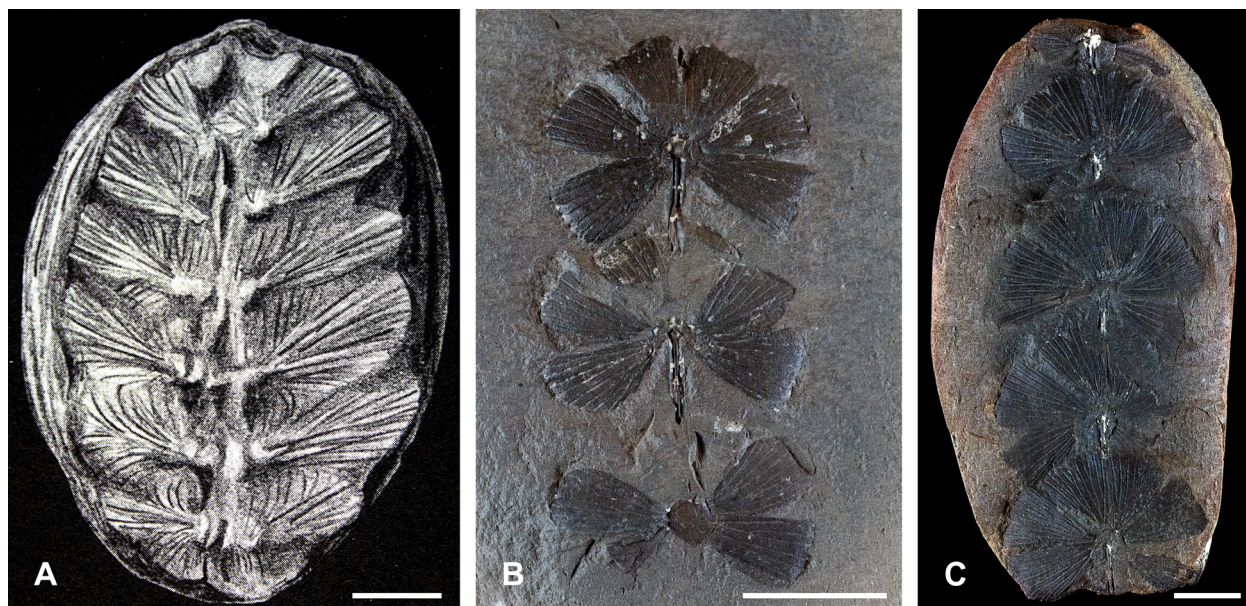


FIGURE 1. A. Reconstruction of “*Sphenophyllum colombianum*” (MONQ-602) from Huertas (2003). Note the apparent wedge-shaped structures that resemble leaves borne in whorls and having veins that radiate from their attachment point. B, C. *Sphenophyllum emarginatum* from the Paleozoic Mazon Creek Flora (IL, USA) for comparison (PP-16865, PP-58015). Scale bars equal 1 cm.

The fossils were compared with specimens of extant marine turtles, including *Eretmochelys imbricata* MTKD-8295 (Senckenberg Museum, Dresden), *Caretta caretta* AMNH-129869 (American Museum of Natural History, New York), and *Lepidochelys olivacea* QM-J85545 (Queensland Museum, Brisbane). Specimens of *Sphenophyllum emarginatum* (PP-16865 and PP-58015) from the Mazon Creek flora, Carbondale Formation (Pennsylvanian) were photographed at the Field Museum (Chicago, USA) for comparison.

RESULTS

Upon close examination, the specimens of “*Sphenophyllum colombianum*” do not represent a fossil plant but rather the remains of carapaces of hatchling marine turtles. The specimen MONQ-602 (Figure 2A-D) corresponds to a partially preserved, small carapace (~6.1 cm long) in ventral view, missing all the peripherals, the anteromedial portion of the nuchal, the suprapygal 2, and the pygal. It preserves at least seven neural bones, seven costal bones, suprapygal 1, and the most posterior portion of the nuchal (Figure 2A-B). The sutural contact between these bones is serrated (Figure 2C-D), however, many of the neural and costal sutural contacts can only be inferred, especially those involving the posterior neurals after neural 4 (Figure 2B). The rib head that articulates with the missing thoracic vertebrae are also visible and well

defined. The bone surface is characterized by an irregular pitted texture and radial bone growth patterns, which Huertas (2003) described as leaf venation (Figure 2B, D). MONQ-602 also shows part of the fontanelles between lateral portion of costals and the missing peripherals, and an oval-shaped space between the nuchal and the left costal 1 that resembles the post-nuchal fontanel (Figure 2B).

The specimen LLC-65 (Figure 2E) corresponds to the impression of a poorly ossified carapace (~5 cm long) in ventral view, which does not show a clear bone texture or growth pattern. However, the rough impressions of the neurals, costals (rounded due to the poor preservation), and the scars for the insertion of thoracic vertebrae into the neurals are discernable.

DISCUSSION

Misidentified Fossil Plants from Colombia

The re-examination of “*Sphenophyllum colombianum*” indicates that this species is invalid as it was based on misinterpreted skeletal remains of marine turtles. The hypothesized occurrence of *Sphenophyllum* in the Early Cretaceous of Colombia would have implied that the genus survived beyond the Permian in northwest Gondwana. However, the new evidence presented here cannot uphold this interpretation. Other incorrectly identi-

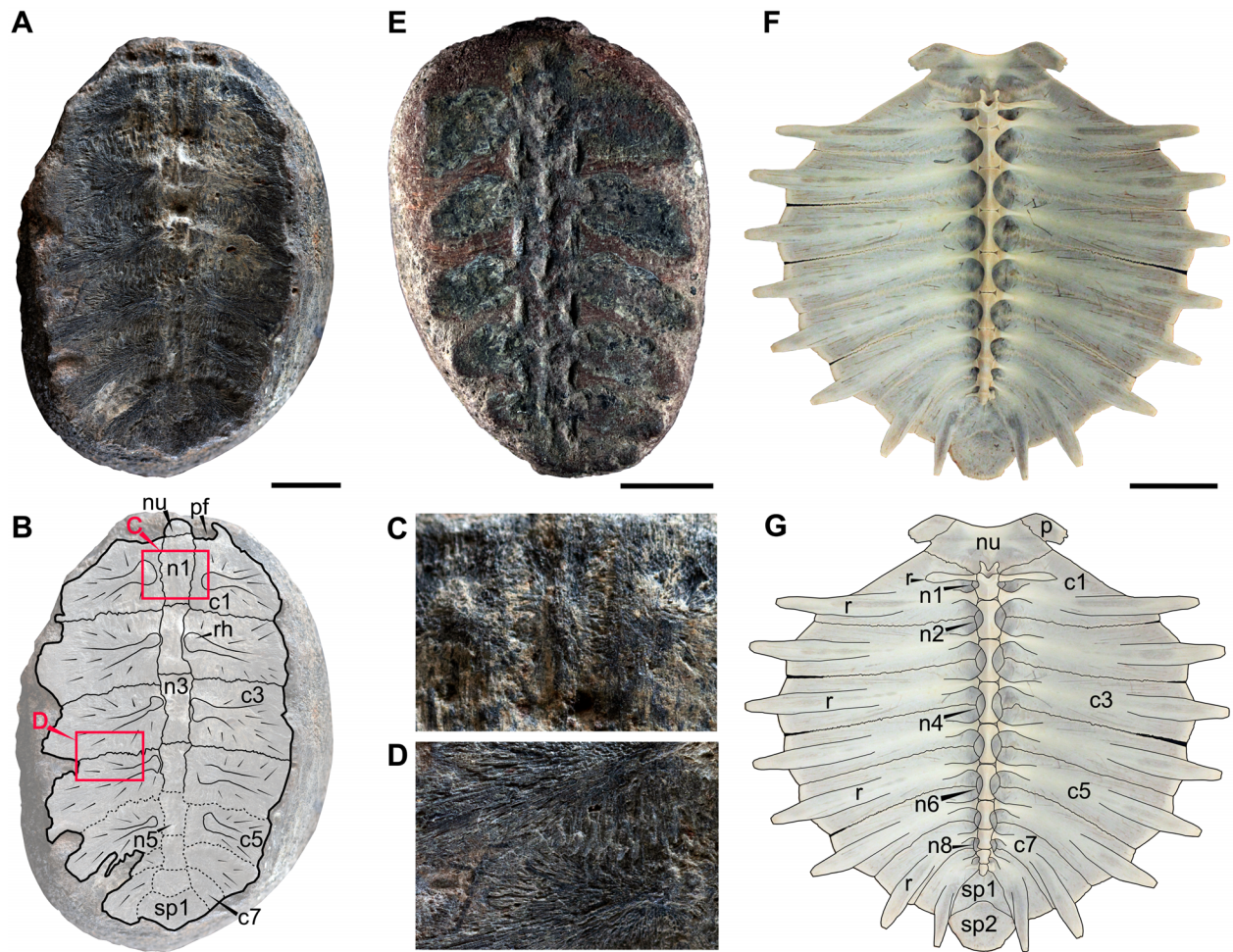


FIGURE 2. *Pan-chelonioides* indet. turtles (A, B, C, D, E) and extant turtle carapace in ventral view (F, G). A. Partially preserved carapace in ventral view (MONQ-602). B. Outline of MONQ-602 specimen indicating the preserved bones and texture. C. Close-up of the serrated sutural contact between neural 1 and costals 1, see red rectangle in B for reference. D. Close-up of the bone growth showing radial pattern and sutures between left costal 3 and 4, see red rectangle in B for location. E. Partially preserved carapace in ventral view showing probable scars from the insertion of thoracic vertebrae into the neurals (LLC-65). F. Extant *Lepidochelys olivacea* showing the complete bone morphology of the carapace in ventral view (QM-J85545). G. Same from F showing outline of diagnostic bones and sutures. Abbreviations: c, costal bone; n, neural bone; nu, nuchal bone; pf, post-nuchal fontanel; p, peripheral bone; r, rib; rh, rib head; sp, suprapygals bone. Scale bars equal 1 cm (A, B, C, D, E), 9 cm (F, G).

fied fossil plants from Villa de Leyva include the cocoa plant "*Theobroma fossilium*" Berry (1929), which is actually the jaw fragment of a marine reptile (Brown, 1946; Huertas, 1971). Seeds of "*Musa ensetiformis*" Berry (1925) from Bogotá, later transferred to *Ensete ensetiformis* (Berry) Jain (1965), turned out to be modern seeds of *E. ventricosum* (Manchester and Kress, 1993). Similarly, a presumed Cretaceous fruit of Musaceae (Huertas and van der Hammen, 1953; Huertas, 1970b) was, in fact, a banana-shaped sedimentary concretion found in Cundinamarca (Manchester and Kress, 1993). All these misidentified fossils that are historically attached to the paleobotanical literature sup-

port the re-examination of other critical fossils that Huertas (2003) described from the La Paja Formation.

Age of the Fossils

The age of these fossils is re-interpreted based on previous and new geological data. Huertas (2003) considered the fossils as Barremian in age. However, this is highly unlikely because the ages near the "Estación del Kronosaurio" and the outcrop from the La Catalina Hill are late Aptian or Aptian based on ammonoids (Etayo-Serna, 1968; Acosta et al., 1979; Forero and Sarmiento L., 1985; Noè and Gómez-Pérez, 2022; Benavides-Cabra et

al., 2023). Therefore, MONQ-602 and LLC-65 turtle specimens are now interpreted as late Aptian or Aptian in age.

Taxonomic Identification of the Fossils

MONQ-602 and LLC-65 specimens from La Paja Formation resemble hatchlings and juveniles of both extant and extinct marine turtles in many aspects, including a relatively poor ossification, highly serrated sutural contacts between bones, and the presence of fontanelles (Reisz and Head, 2008). We can exclude the possibility that they belong to pleurodirans (side-necked turtles) due to the lack of evidence of an iliac scar on the posterior costal bones, which suggests that the illium was not fused to the carapace. The iliac scar is present in hatchling/juvenile pleurodirans, like *Puentemys mushaisaensis* from the Paleocene of Colombia (Cadena et al., 2012). In addition, the continuous series of neurals reaching the suprapygal 1 exclude them from being pan-pelomedusoids.

Overall, the skeletal and morphological characteristics preserved in both fossil specimens match those exhibited by the carapace's ventral surface of extant marine turtles, such as those seen in *Lepidochelys olivacea* (Figure 2F-G). However, MONQ-602 shows fewer neurals and costals than expected for a turtle of this size, seven instead of the expected eight. It is possible that a very small neural 8 and narrow costals 8 with weak sutural contact may exist in the specimen but are not discernible due to poor preservation of this posterior region. Another hypothesis is that the structure that we interpret as the nuchal, could correspond to the posterior portion of neural 1. However, this hypothesis seems to be invalid, as what we attribute as neural 1 is restricted to the first pair of costals, as seen in other pan-chelonioids and the *Lepidochelys olivacea* specimen shown in Figure 2G.

Giving the co-occurrence of the two specimens re-examined here and other mature turtles in La Paja Formation, it is plausible to suggest that the specimens correspond to hatchlings of the protostegid *Desmatochelys padillai* Cadena and Parham (2015). *D. padillai* is a marine fossil turtle abundant in La Paja Formation, and nearly complete specimens of adults have been found (Cadena and Parham, 2015). However, in the absence of fully preserved skeletons including skulls, we refrain from establishing a detailed systematic paleontology, and for now, the fossils should be considered as *Pan-Chelonioidea* indet. turtles.

Until now, only a few Cretaceous marine pan-chelonioid hatchlings and juvenile specimens have been described from the early Campanian of USA (Zangerl, 1953; Matzke, 2007; Gentry, 2018), and late Middle Cenomanian of Lebanon (Tong et al., 2006). The MONQ-602 specimen shows intercostal contacts, distinguishing it from other protostegid hatchlings such as *Rhinochelys nammourensis* (Tong et al., 2006). However, other hatchling turtles outside *Pan-Chelonioidea* also lack intercostal contacts, as observed in the pelomedusoid *Araripemys barretoii* (Oliveira and Kellner, 2017). This indicates that this characteristic cannot be used as diagnostic or exclusive of hatchling protostegids.

Ontogenetic Stage Determination

Aside from species-specific ontogenetic distinctions, two common co-occurring characteristics can help in identifying hatchling turtles in the fossil record: (i) skeletal immaturity, characterized by reduced ossification and the presence of large fontanelles, and (ii) small size (Lindgren et al., 2017). By examining the correlation between body size and age in extant turtles (Chaloupka and Zug, 1997; Zug et al., 2002), we can hypothesize estimates of the ontogenetic stage of the MONQ-602 and LLC-65 specimens.

Extant marine turtle hatchlings typically grow to have a curved carapace length (CCL) of 4 to 6 cm within their first year. On average, after this initial year, hatchlings transition into the juvenile stage in which their lengths increase beyond 17 cm. Adulthood is reached at around 14 years of age, when straight carapace length (SCL) measurement exceeds 40 cm (Snover et al., 2007; Avens et al., 2009; Avens et al., 2012; Avens et al., 2021; Turner-Tomaszewicz et al., 2022; Baldi et al., 2023) (Table 1). The specimen MONQ-602 is ~6.1 cm long and LLC-65 is ~5 cm long. Based on these measurements and the growth patterns observed on living turtles, the La Paja specimens were likely in the hatchling/post-hatchling stage, implying that they were probably between 0-1 years old at the moment of death. However, it is important to point out that the size of marine turtles is affected by various factors, and not all living marine turtles exhibit the same growth patterns or reach the same sizes in adulthood. For instance, *Dermochelys coriacea* grows faster and reaches a larger size than all other living marine turtles. Similarly, protostegid turtles show a consistent evolutionary trend towards larger size. Recently, Wilson (2023) demonstrated that the osteohistology of *Protostega gigas* closely resembles that of *D. coriacea*, sug-

TABLE 1. Curved carapace length in centimeters across different ontogenetic stages in extant marine turtles, including MONQ-602 and LLC-65 fossil specimens.

Taxon	Hatchling/post-hatchling (0-1 years old)	Juveniles (1-14 years old)	Adults (>15 years old)	Reference
<i>Natator depressus</i>	6-17.0	17.6-36.6	60-90	Turner-Tomaszewicz et al., 2022
<i>Chelonia mydas</i>	4.6-20.0	20-40	40-96	Avens et al., 2012
<i>Dermochelys coriasea</i>	6	16-27	122-171	Avens et al., 2009
<i>Eretmochelys imbricata</i>	4-23.0	23-30	50-60	Avens et al., 2021
<i>Caretta caretta</i>	<25	25-40	>40	Baldi et al., 2023
<i>Ledpidochelys kempfi</i>	4.2-23.0	23-60	60-70	Snover et al., 2007
MONQ-602	6.1			This study
LLC-65	5			This study

gesting that both species share a rapid early ontogenetic growth, while *Desmatochelys lowi* (an Early Cretaceous protostegid) (Elliott et al., 1997) lacks the same quick growth patterns, leading to the conclusion that this strategy likely evolved within the protostegid lineage and is not an ancestral trait of the clade. The presence of Valanginian large protostegid shells and limb bones provides evidence that this turtle lineage rapidly evolved large body size during the Early Cretaceous (Cadena and Combata-Romero, 2023).

In addition to their size, the skeletal immaturity observed in MONQ-602 and LLC-65 specimens is discernible. The ontogenetic stage is comparable to that of extant turtle hatchlings, such as four weeks old *Chelonia mydas*, as documented by Zug et al. (2002). The presence of large fontanelles and very low carapace thickness due to poor dermal ossification supports the interpretation that these fossil specimens represent hatchlings. The specimen MONQ-602 has strong and well-developed intercostal sutural contacts, different from other smaller fossil hatchling carapaces, like the protostegid *Rhinochelys nammourensis* (Tong et al., 2006) and the pelomedusoid *Araripemys barretoii* (Oliveira and Kellner, 2017). This suggests that MONQ-602 probably died in a post-hatchling stage when its carapace was slightly more developed than that of specimen LLC-65.

Taphonomic Insights

Although La Paja Formation hatchling turtles slightly differ in size (specimen MONQ-602 is somewhat larger than LLC-65), both fossils exhibit similar modes of preservation. Most of the outer bones of the carapace, including the anteromedial portion of the nuchal, all peripherals, suprapygals 2, and pygal are missing. This suggests that these elements, along with cranial and limb bones, were

lost prior to burial and subsequent fossil diagenesis through concretion formation. In addition, both concretions show no evidence of marginal breaks, only moderate abrasion, which excludes the possibility that the peripheral bone elements were lost during a later erosional event. Furthermore, there is no evidence of anatomical displacement between the preserved bone elements (neurals, costals, and suprapygals 1) in both specimens, indicating minimal disarticulation. Considering studies of extant turtle disarticulation (Brand et al., 2003), the preservation of the Paja hatchlings suggests that the burial was likely rapid, occurring a few weeks after death.

CONCLUSIONS

The fossils described originally as “*Sphenophyllum colombianum*” by Huertas, from the La Paja Formation in Colombia, have now been identified as hatchling marine turtles belonging to *Pan-Chelonioidea* indet. This discovery represents the first report of hatchlings turtle carapaces from northwestern South America. MONQ-602 specimen is a new example of the outstanding record of turtles from the Ricaurte Alto Lagerstätte that now includes eggs, hatchlings, and completely articulated adults. Further preparation and potential micro-CT scanning of specimen MONQ-602 will likely allow the identification of the dorsal surface of the carapace and explore if other bone remains were also preserved in the concretion. This work aims to promote future collaborative work between different paleontological disciplines, such as paleobotany and vertebrate paleontology, to prevent taxonomical misidentifications, especially when dealing with fossils that are partially complete or pose specific identification challenges.

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