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A new conifer record from the late Aptian of La Paja Formation from Veléz, Santander (Colombia)

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ABSTRACT. A new plant assemblage from the La Paja Formation at the Los Guayabos section of Vélez, Santander (Central Colombia) is described here. Based on ammonite biostratigraphy, the age of the flora is estimated as late Aptian. The plant remains, found alongside vertebrate and invertebrate fossils, consist exclusively of conifers, including *Cupressinocladus*, *Brachyphyllum*, *Podozamites*, and putative reproductive structures. The apparent absence of ferns and putative angiosperms distinguishes the Vélez location from other La Paja localities and Early Cretaceous floras of Colombia. The plant and associated faunal features suggest deposition in a low-energy marine environment.

KEYWORDS: Early Cretaceous, La Paja Formation, palaeobotany, conifers, taphonomy

INTRODUCTION

The plant record from the Early Cretaceous of Colombia (north-western Gondwana) primarily consists of a combination of conifers, ferns, cycads, bennettitales and angiosperms (Lemoigne, 1984; Pons, 1988; Huertas, 2003; Monje-Dussán et al., 2016). These floras (Fig. 1A) have been mainly recovered along the Eastern Cordillera, including the Upper Magdalena Valley (Moreno-Sanchez, 1994; Monje-Dussán et al., 2016), Quetame, Gachetá and Villavicencio floras (Royo y Gómez, 1945; Pons, 1988). Outside the Eastern Cordillera, exceptions include the San Félix and Valle Alto floras from the Central Cordillera (Lemoigne, 1984) (Fig. 1A). The Early Cretaceous floras from Colombia belong to the Palaeoequatorial sub-provinces proposed by Vakhrameev (1991) and McLoughlin (2001), showing mainly cosmopolitan taxa.

The La Paja Formation is the most extensively collected stratigraphic unit for Early Cretaceous macrofloras in Colombia, primarily in the Ricaurte Alto province (Villa de Leyva, Santa Sofía, Sáchica and Sutamarchán municipalities) (Van Waveren et al., 2002; Huertas, 2003; Moreno-Sánchez et al., 2007). Previous studies, primarily by Huertas (1967, 1970, 1976, 2003), revealed a high abundance of conifers and a lower occurrence of cycads, bennettitales,

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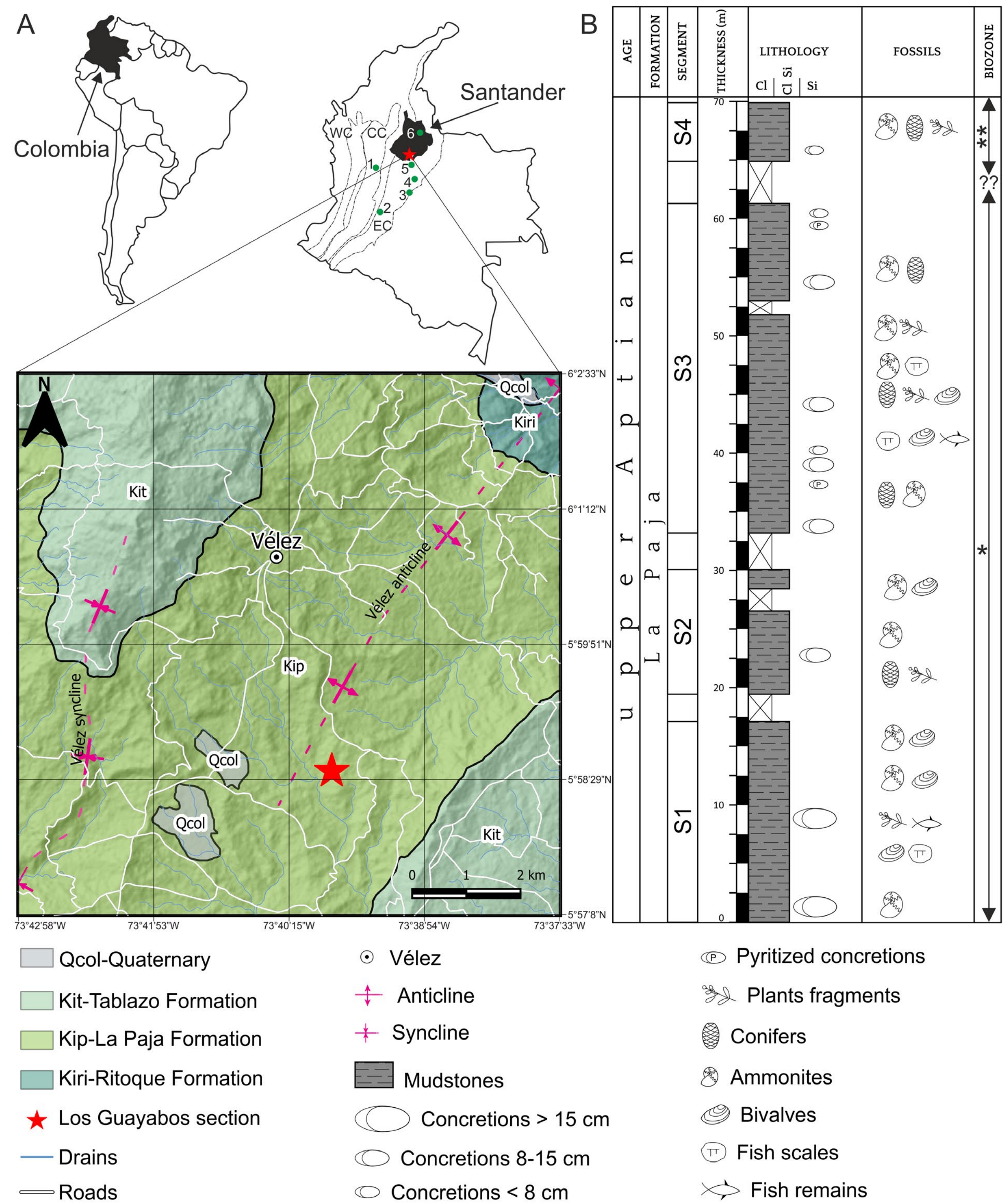

Figure 1. Geographical and geological location of the studied section. **A**. Geological map of the Vélez region (Santander, Colombia) showing the location of the Los Guayabos section (map taken and redrawn from Mendoza et al. (2009). WC – West Cordillera, CC – Central Cordillera, EC – East Cordillera; 1. San Félix and Valle Alto floras, 2. Upper Magdalena Valley floras, 3. Gachetá and Villavicencio floras, 4. Quetame locality, 5. The Ricaurte Alto province, 6. Middle Magdalena Valley area, red star = Los Guayabos section; **B**. Stratigraphic column at Los Guayabos section. The asterisks * and ** refer to Etayo-Serna (1979) biozones: **Dufrenoyia sanctorum – Stoyanowiceras treffryanus*, ***Parahoplites* (?) *hubachi – Acanthohoplites* (?) *leptoceratiforme*

ferns, and putative angiosperms (Van Waveren et al., 2002; Huertas, 2003). The La Paja fossils are usually found in concretions that likely formed within the upper tidal and supra-tidal zones, indicating the presence of a shallow epicontinental sea in the north-western corner of Gondwana (Montoya Arenas, 2019). The exact age of the flora from the Ricaurte Alto province remains uncertain; however, Huertas (2003) stated that the macroflora and ammonoid association could provide an excellent opportunity to construct a "Palaeobotanical stratigraphic column" that could reveal changes in the flora over time (Huertas, 2003). This hypothesis has yet to be tested.

Here, we present new plant specimens of the La Paja Formation from a recently discovered site in the Los Guayabos section of Vélez, Santander Department (Fig. 1A). At this location, the stratigraphic relationship between the plant fossils and ammonoids is more precisely defined than at any other La Paja locality. Our study shows that the flora of the Los Guayabos section is of late Aptian age. Preliminary taphonomic analyses also reveal that the flora was deposited in a low-energy environment, characterized by minimal transport and anoxic conditions that facilitated the preservation of the plant specimens.

GEOLOGICAL BACKGROUND

The La Paja Formation is a heterochronous geological unit, in the Middle Magdalena Valley (Fig. 1A), it ranges from the lower Barremian to the lower Albian (Montoya Arenas, 2019), whereas in the Ricaurte Alto province of the Eastern Cordillera (Fig. 1A), it spans from the Hauterivian to the upper Aptian (Etayo-Serna, 1968, 1979; Patarroyo, 2000). The La Paja Formation was first described by O.C. Wheeler (Morales et al., 1958) at the Middle Magdalena Valley in the La Paja Creek. This unit consists of shales and slightly calcareous black shales with fine lamination, tubular limestones, concretions, and septarian nodules (Morales et al., 1958). In its type locality, at the La Paja Creek, the unit shows a sharp, concordant contact with the underlying Rosa Blanca Formation, while the contact with the overlying Tablazo Formation appears gradational (Morales et al., 1958).

In the Ricaurte Alto province, the La Paja Formation was initially divided into three segments (Etayo-Serna, 1968), which were later reclassified as members (Forero and Sarmiento, 1985). The lower member, "Lutitas negras inferiores", corresponds to Hauterivian strata and is characterized by black mudstones interspersed with sporadic sandstones (Etayo-Serna, 1968). The middle member, "Arcillolitas abigarradas", ranges from the lower Barremian to the upper Aptian and is the most fossiliferous of the members; it consists of pink, grey and black mudstones with limestone concretions (Etayo-Serna, 1968; Forero and Sarmiento, 1985). The uppermost member, "Arcillolitas con nódulos huecos" corresponds to upper Aptian beds and is characterized by grey claystone and small ellipsoidal nodules (Etayo-Serna, 1968). Limited stratigraphic work has been done in the La Paja Formation in the Vélez region. In this locality (Fig. 1A), the lower contact is with the Ritoque Formation (Patarroyo, 2008; Mendoza et al., 2009), whereas the upper contact is with the Tablazo Formation (Ulloa and Rodríguez, 1979; Mendoza et al., 2009).

MATERIAL AND METHODS

STRATIGRAPHIC SECTION AND MATERIALS

The new stratigraphic section was described along a dirt road near the village of Vélez, Santander (5°58′44.2″N, 73°39′42.3″W) (Fig. 1). The outcrops were small, located on both sides of the road. The stratigraphic section was measured using Jacobs' staff (1.5 m) and a compass, following the methodology described by Compton (1985). The collected plant fossils (25 samples) consist of vegetative shoots, leaves, and cones. These fossils are preserved as impressions in mudstones and are more or less three-dimensional within concretions. In addition, ammonoids, bivalves and fish remains were collected to characterize the fossil assemblage of the studied section. The ammonoids were identified by CDB-C based on the taxonomy proposed by Etayo-Serna (1979) and on direct comparisons with the specimens described by this author, which are currently housed at the Museo Geológico Nacional José Royo y Gómez, Bogotá, Colombia. We then used the identified ammonoids as biostratigraphic indicators based on the ammonoid biozones proposed by Etayo-Serna (1979) for Central Colombia.

Specimens labeled with MPVL are housed at the Palaeontological Museum of Villa de Leyva, affiliated with the Universidad Nacional de Colombia, Villa de Leyva, Colombia. Acronyms CB, JB, and HP are collection field numbers. The specimen LP210416-1 is housed at the Palaeontological Collections of the Geosciences Department at the Universidad Nacional de Colombia, Bogotá, Colombia (UNDG).

FOSSIL PREPARATION AND IMAGING

The plant specimens required minimal preparation due to the soft matrix in which the fossils are preserved. Covering sediment was removed with needles; fragile specimens were consolidated with Paraloid B-72 resin. Ammonites were extracted with an Air-scribe ME-9100 at the Palaeontological Museum of Villa de Leyva. Ammonites and bivalves were coated with ammonium chloride using the process for whitening fossils described by Feldmann (1989) at MPVL. Light photographs were taken with a digital Canon EOS Rebel 6 DSLR camera with 18–55 mm lenses at MPVL, the digital photographs were stacked using Helicon Focus software 8.0.4 (Helicon Soft Ltd, Kharkiv, Ukraine). One plant fossil specimen embedded in a concretion was µCT scanned at the CTEES facility, University of Michigan, Ann Arbor, United States, using a Nikon XT H 225ST system with a Perkin Elmer 1620 X-ray detector panel and a tungsten reflection target. The scan used a 155 kV micro-focus tube at 155 kV and 165 µA at 500 m exposure timing, using a 0.5 mm Cu filter. Resolution of voxel x=y=z= 0.056575 µm with 3141 projection images was achieved. The µCT volume of the specimen was visualized using Avizo Software 3D 2024. (Thermo Fisher Scientific, Waltham, MA, USA). The µCT data have been deposited in the Field Museum's database and are available upon request.

RESULTS

LOS GUAYABOS STRATIGRAPHIC SECTION

The stratigraphic section (Fig. 1B) spans ~70 metres of monotonous lithology, consisting of black, grey, and yellowish non-calcareous mudstones with sporadic calcareous and pyritized concretions. Approximately 17% (12 metres) of the section is covered by vegetation and minor landslides. However, we divided the 70-metre section into four informally named segments, based on the recovered Palaeontological material and other sedimentological features (e.g. concretions, pyrite concentration) (Fig. 1B).

Segment 1 (S1) is ~17.11 m thick and is characterized by black and yellowish mudstones with planar lamination and calcareous concretions measuring between 20 and 25 cm. The fossils recovered from this segment include flattened and three-dimensionally preserved ammonoids, thin-shell bivalves, fish vertebrae and isolated fish scales. Segment 2 (S2) is ~8.74 m thick and consists of black mudstones with parallel lamination and abundant impressions of ammonoids, thin-shell bivalves, small oysters, as well as a few conifer shoots and leaves (Fig. 2F–H). Concretions are scarce, and pyrite is present on the impressions.

Segment 3 (S3) is ~26.92 m thick and is composed of black mudstones with pyritized concretions, which are smaller (8–15 cm) compared to those in S1. This segment has a high diversity and abundance of fossils, including conifer shoots, leaves, ammonoids, ammonoid aptychi, bivalves, and partially articulated fish remains (Fig. 2A, I). The fourth and final segment (S4) is ~5 m thick, composed of grey mudstones with planar lamination and contains conifer branches, leaves, flattened ammonoids, ammonoid aptychi, and thin-shell bivalves (Fig. 2C, D, J–L).

Stratigraphic range of the Los Guayabos section (La Paja Formation)

Ammonoid specimens were recovered across the different segments of the Los Guayabos section, although the poor preservation of some specimens hindered their taxonomic identification. From S1, we identified two three-dimensionally preserved ammonoid specimens (Fig. 2E) as *Riedelites* (?) *quebradanegra* Etayo-Serna 1979 (HP200919-01a; HP200919-01b). This taxon is included by Etayo-Serna (1979) in the biozone of *Dufrenoyia sanctorum – Stoyanowiceras treffryanus*. From S2, we identified four flattened ammonoid specimens (Fig. 2F–H), three as *Juandurhamiceras* sp. Etayo-Serna 1979 (JB220103-2-01; JB220103-2-10a JB220103-2-10b), and one as *Stoyanowiceras* sp. Etayo-Serna 1979 (HP141121-26a). These taxa are included by Etayo-Serna (1979) in the biozone of *Dufrenoyia sanctorum – Stoyanowiceras treffryanus*. From S3, we identified an external mold of an ammonoid specimen (Fig. 2I) as *Cheloniceras* (*Epicheloniceras*) *camachoi* Etayo-Serna 1979 (HP210919-01). According to Etayo-Serna (1979), this taxon belongs to the biozone of *Dufrenoyia sanctorum – Stoyanowiceras treffryanus*. From S4, we identified three flattened ammonoid specimens (Fig. 2J–L), two of them as *Parahoplites* Anthula 1899 (CB130719-02-06a; CB130719-02-03) and one as *Parahoplites* (?) *triston* Etayo-Serna 1979 (CB130719-02-03); representing the biozone of *Parahoplites* (?) *hubachi – Acanthohoplites* (?) *leptoceratiforme*. According to Etayo-Serna (1979), the biozones *Dufrenoyia sanctorum – Stoyanowiceras treffryanus* and *Parahoplites* (?) *hubachi – Acanthohoplites* (?) *leptoceratiforme* indicate the upper Aptian in Colombia, with the latter being younger.

Based on the identified ammonoids and associated biozones, we interpret that the biostratigraphic age of the Los Guayabos section is upper Aptian. This stratigraphic range allows for a correlation of the Los Guayabos section with two members of the Ricaurte Alto

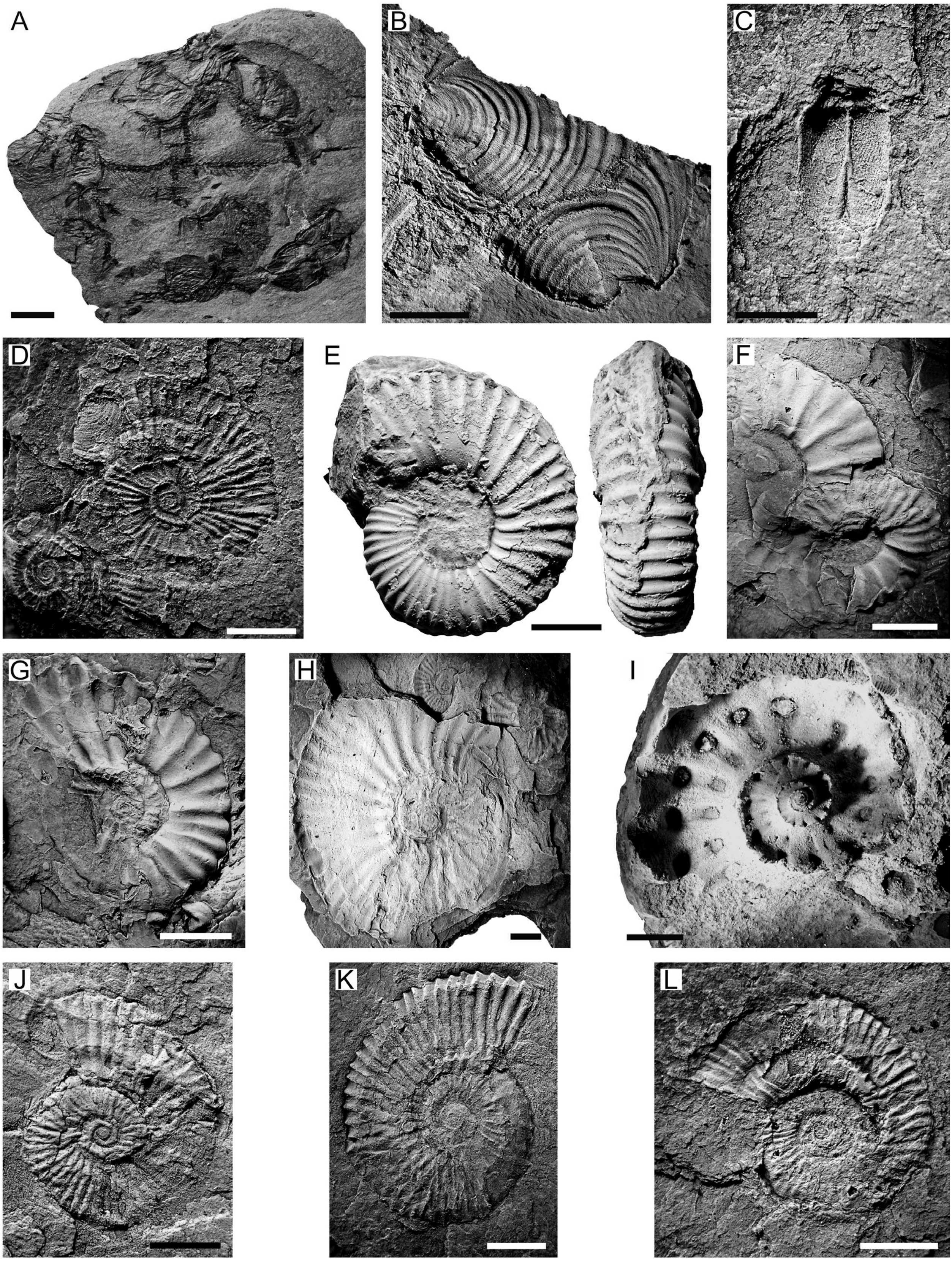

Figure 2. Invertebrate and vertebrate fossils collected in the Los Guayabos section. **A**. Articulated fish vertebrae and skull bones; **B**. Thin shell bivalves; **C**. Isolated aptychus; **D**. Parahoplitinae ammonite with aptychus inside the body chamber; **E**. *Riedelites* (?) *quebradanegra* in lateral and ventral views, HP200919-01a; **F**, **G**. *Juandurhamiceras* sp. in lateral views, **F**. JB220103-2-10b, **G**. JB220103-2-10a; **H**. *Stoyanowiceras* sp. in lateral view, HP141121-26a; **I**. *Cheloniceras* (*Epicheloniceras*) *camachoi* external mold in lateral view, HP210919-01; **J**, **K**. *Parahoplites* sp. in lateral views, **J**. CB130719-02-06a, **K**. HP170721-01-1; **L**. *Parahoplites* (?) *triston* in lateral view, CB130719-02-03. Scale bars = 1 cm in A, B, F, G–I; 0.5 cm in C–E, J–L

province: segment E of the "Arcillolitas abigarradas" and "Arcillolitas con nódulos huecos" members of the La Paja Formation in the Ricaurte Alto province (Etayo-Serna, 1968). Also, the Los Guayabos fossil fauna correlates with segments III, IV and the base of segment V of the type locality of the La Paja Formation (Montoya Arenas, 2019).

Taphonomic remarks

The dominant facies present in the Vélez section correspond to planar laminated black mudstones containing thin-shell bivalves, isolated fish scales and bones, flattened ammonoids, ammonoid aptychi, and fragmentary plants. Fossil concretions preserve ammonoids and plants in nearly three-dimensional form (Figs 2–6). No significant biological or physical disturbance was observed in the stratigraphic section, with the exception of a small dislocation in one articulated conifer branch (Fig. 3A, arrow). The ammonoid aptychi are relatively well-preserved (Fig. 2C), with some specimens found closely associated with their respective ammonoid individuals, even preserved within the body chamber (Fig. 2D, J, L). In most cases, the aptychi occur as isolated specimens but are rarely preserved in situ, either closing the aperture or within the body chamber of ammonoids (Tanabe et al., 2015). The taphonomic observations of the fossil fauna and plants suggest low-energy settling velocities and marginal water flow rates on the palaeo-seafloor (Spicer, 1989). In particular, the preservation of the aptychi in these beds, along with the presence of abundant articulated fish specimens (Fig. 2A), further suggest relatively rapid sediment coverage (Briggs, 2003). In a few specimens, we also observe pyrite covering the surface of fish, bivalves and ammonoids. The presence of pyrite is common in rocks from the La Paja Formation, and it has been determined to result from the breakdown of organic matter by bacterial reduction under anoxic conditions (Gaona-Narvaez et al., 2013; Farrell, 2014; Montoya Arenas, 2019).

The majority of the plant fossils (20 specimens out of 25) are impressions found within finely laminated mudstones, whereas only five plants were found as molds in concretions. Most of the collected specimens are fragmentary, but some shoots with secondary order branching are preserved. No cuticles were preserved in any of the collected specimens. The presence of both fragmentary and partially articulated material may be related to the distance from the source areas and varying periods of transport and flotation (Greenwood, 1991; Spicer, 1991). The coastal deposition of the La Paja Formation, along with the preservation features, indicates that the plant remains from the Los Guayabos section correspond to an allochthonous assemblage.

SYSTEMATIC PALAEONTOLOGY

Cupressinocladus Seward (1919)

Cupressinocladus sp.

Figs 3, 4, 5A–D

S p e c i m e n s. Twelve specimens. MPVL (HP141121-38, HP170721-01-01, HP170721-01-39, HP210919-01, HP210919-03, HP210919-07, HP210919-12, HP210919-1R, JB160421-2R, JB220103-1-4-64, JB220103-1-4-69); UNDG (LP210416-1)

D e s c r i p t i o n. The specimens consist of branched leafy shoots. The penultimate shoots vary in length from 0.5 to 15 cm and in width from 0.4 to 0.8 cm (Figs 3, 4). The ultimate shoots exhibit an opposite arrangement (Figs 3, 4) and range in length from 0.4 to 3.5 cm and in width from 0.4 to 0.8 cm (Figs 3, 4A–D). The spacing between the ultimate shoots varies from 0.5 to 1.4 cm, with the angle of insertion of the penultimate shoots measuring from 45° to 60°.

The leaves are scale-like, decussately arranged, adpressed, abaxially keeled and slightly imbricated (Figs 3B, 4C–D, 5A–D). In some specimens, the leaf apex is slightly falcate (Fig. 5D). In transverse section, the leaves have rhomboidal outlines (Figs 3B, 5A–D). Individual leaves are 0.25 to 0.45 cm long and 0.15 to 0.25 cm wide, length/width ratio 1.5 to 2. Distal leaves are smaller than those near the base (Figs 3A, B, D, 4, 5D). The visible portion of the adpressed leaf base accounts for approximately one-half to one-third of the total leaf length (Fig. 5A–C, arrows). Leaves have an entire margin. The leaf insertion angle is ~45° to 55° (Figs 3, 5A–D).

R e m a r k s. The genus *Cupressinocladus* was proposed by Seward (1919) to classify vegetative shoots of conifers that resemble extant

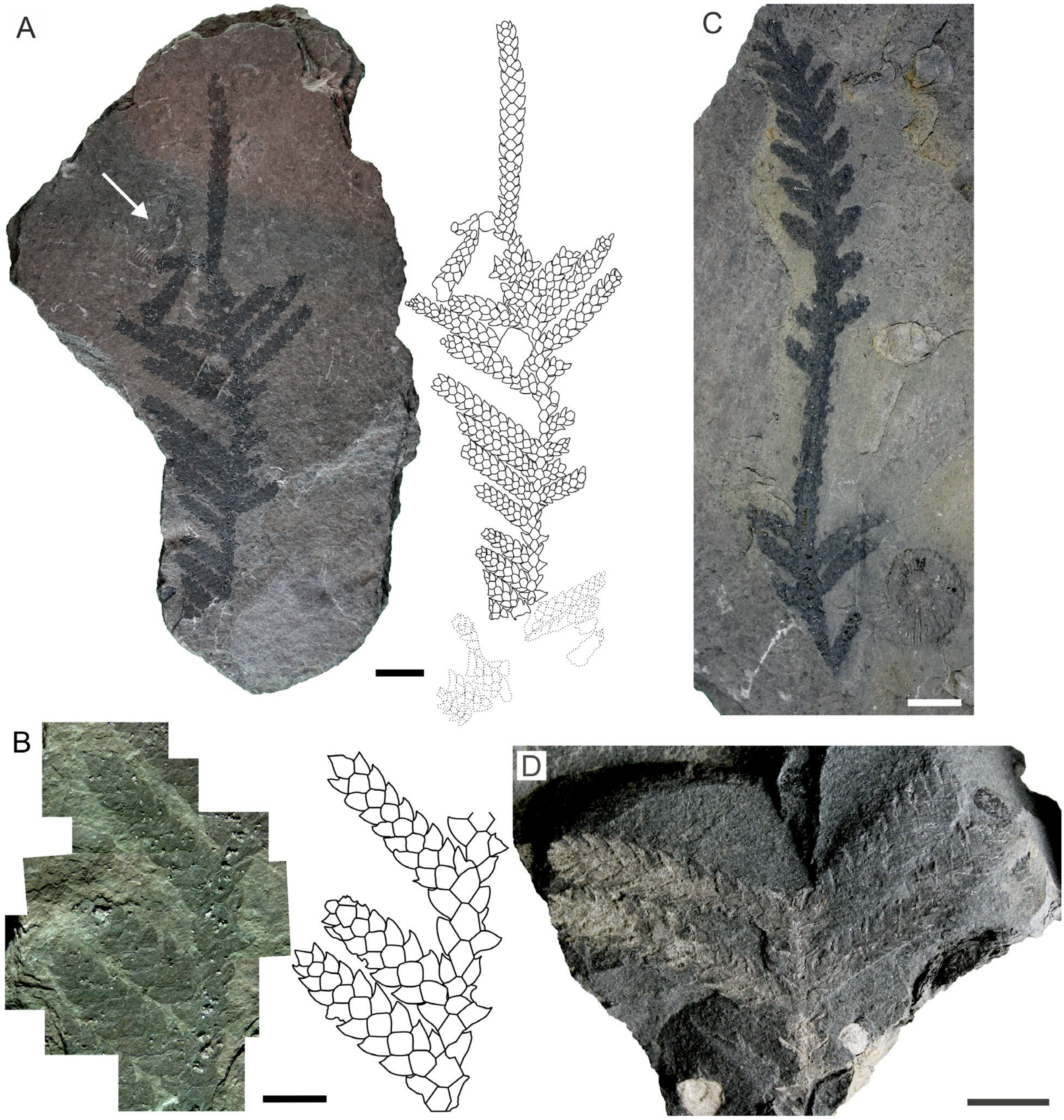

Figure 3. *Cupressinocladus* sp. Leafy shoot specimens with two levels of ramification, preserved in mudstones, associated with ammonoids and bivalves. **A**. LP210416-1 with schematic interpretation, arrow indicating an ultimate branch dislocated; **B**. Composite photo, detail of A, branch organization with schematic interpretation; **C**. HP170721-01-01; **D**. HP210919-03. Scale bars = 1 cm

taxa, characterized by their branched habit and decussately arranged leaves. This genus is frequently used when sterile shoots lack reproductive structures (seed or pollen cones) or when cuticular features are absent (Seward, 1919; Watson and Alvin, 1999). Fossil remains attributed to *Cupressinocladus* have been identified in Jurassic and Cretaceous strata (Harris, 1976a, b) and are hypothesized to belong to the families Araucariaceae, Cupressaceae, Podocarpaceae, or Cheirolepidiaceae. In South America, this genus has been reported from the Early Cretaceous, mainly from impressions or compressions without cuticular characters (Pons, 1988; Moreno-Sánchez, 1994; Martínez et al., 2020). It is also worth mentioning that leafy shoots with this morphology are similar to genera such as *Hirmeriella* and *Glenrosa*, but these genera preserve cuticular and other anatomical characters (Watson and Fisher, 1984; Clement-Westerhof and Van Konijnenburg-van Cittert, 1991; Srinivasan, 1992; Guignard et al., 1998). *Moriconia* is also similar (Bosma and Van Konijnenburg-van

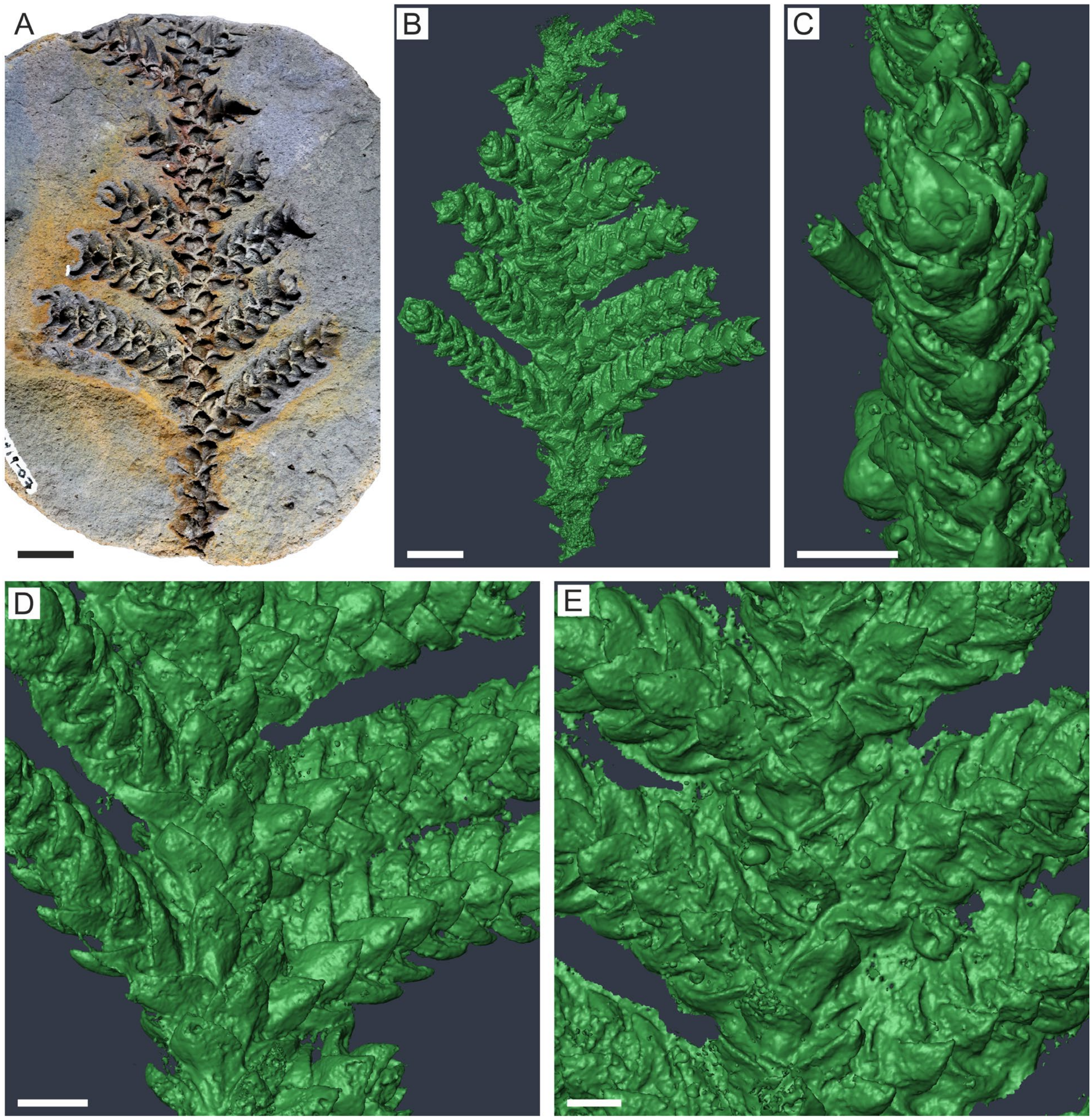

Figure 4. *Cupressinocladus* sp. Light photography and 3D reconstruction of a leafy shoot, specimen HP210919-07. **A**. Leafy shoot impression; **B**. Micro CT-scan 3D reconstruction of the branch; **C**, **D**. Close-ups and details of B. Scale bars = 1 cm in A, B; 0.5 cm in C–E

Cittert, 2014). However, the Los Guayabos branched leafy shoots have all axes covered with leaves, unlike *Moriconia* (Bosma and Van Konijnenburg-van Cittert, 2014).

The *Cupressinocladus* specimens from the Los Guayabos section exhibit both similarities and differences with six other conifer branch taxa from the Early Cretaceous of Colombia. These include four species classified within *Cupressinocladus* (*C. lepidophyllus* Lemoigne, *C. sutamarchensis* Van Waveren, Van Konijnenburg-van Cittert, Van der Burgh and Dilcher (Huertas), *C. pompeckji* Pons and *C. hoedemaekeri* Van Waveren, Van Konijnenburg-van Cittert, Van der Burgh and Dilcher) and two species of *Thuites* (*T. puicher* Huertas and *T. frequens* Huertas), which may also be assignable to *Cupressinocladus* (Palma-Castro, 2024). *Cupressinocladus lepidophyllus*, *C. pompeckji* *C. sutamarchensis*, and *T. frequens* share the scale-like leaf morphology with Los Guayabos specimens (Huertas, 1967, 2003; Lemoigne, 1984; Pons, 1988; Van Waveren et al., 2002). In contrast, the leaves of *C. hoedemaekeri* and *T. puicher* appear hexagonal in outline (Van Waveren et al., 2002; Huertas, 2003).

Leaf size in the Los Guayabos *Cupressinocladus* is comparable to that of *C. lepidophyllus*, *C. pompeckji*, *C. hoedemaekeri*, *T. frequens* and *T. puicher* (Huertas, 1967, 2003; Lemoigne, 1984; Pons, 1988; Van Waveren et al., 2002). In contrast, *C. sutamarchensis* exhibits larger leaves, measuring 0.8 cm in length and 0.5 cm in width, compared to the smaller Los Guayabos leaves, which range from 0.25 to 0.45 cm in length and from 0.15 to 0.25 cm in width (Huertas, 1967; Van Waveren et al., 2002).

The primary differences among these taxa lie in the angle of insertion of the penultimate shoots and the leaf insertion angle. These variations may reflect intraspecific factors, such as ontogeny or positional variation within the tree, or could be attributed to taphonomic processes. The observed differences prevent the assignment of *Cupressinocladus* specimens from the Los Guayabos section to any previously established species. Also, the proposal to erect a new species is not supported, as the material is fragmentary, and a new name would only add confusion to a group of fossils with already unclear affinities. A comprehensive revision of this genus is necessary to enhance our understanding of this foliage type during the Early Cretaceous in northern South America.

Brachyphyllum Brongniart 1828

Brachyphyllum sp.

Fig. 5E

Specimen. One specimen. MPVL (HP170721-02-03).

Description. The specimen consists of an unbranched leafy shoot. Ultimate shoot measures 4.2 cm long and 0.6 cm wide, bears scale-like leaves arranged spirally (Fig. 5E). Individual leaves are 0.32 to 0.44 cm long and 0.13 to 0.23 cm wide, with a length/width ratio of 1.9 to 2.4 (Fig. 5E). Leaves adpressed, imbricated with the visible portion of the adpressed leaf base less than two-thirds of the total leaf length (Fig. 5E). Leaf margin is entire, and the apex is acute (Fig. 5E).

Remarks. The distinguishing characters of this sterile shoot are the scale-like leaf shape, adpressed leaves, and spiral arrangement. These characters support its classification within *Brachyphyllum* (see Harris, 1979), and the absence of cuticle and lack of association with reproductive organs support the use of *Brachyphyllum* as a fossil genus. This genus had a wide geographical and temporal distribution during the Mesozoic (Batista et al., 2021). Some specimens with preserved cuticles have been associated mainly with the Araucariaceae and Cheirolepidaceae (Van der Ham and Van Konijnenburg-van Cittert, 2003; Du et al., 2013; Batista et al., 2021), but similar morphologies also occur in the Cupressaceae and Podocarpaceae (Van der Ham and Van Konijnenburg-van Cittert, 2003; Du et al., 2013).

In Colombia, a few vegetative shoots have been assigned to *Brachyphyllum* (i.e. Huertas, 1970, 2003; Van Waveren et al., 2002; Monje-Dussán et al., 2016). The noteworthy difference between *Brachyphyllum* sp. from the Los Guayabos section and previously described sterile foliage from the La Paja Formation is the shape of the leaves. Shoots of *B. leivanum* Huertas present leaves with a rounded apex and a prominent abaxial keel (Huertas, 1970, 2003). In shoots of *B. winklerprinsii* Van Waveren, Van Konijnenburg-van Cittert, Van der Burgh and Dilcher, the leaves present a falcate apex and the length/width ratio is 1.3, in contrast to the 1.9 to 2.4 length/width ratio in *Brachyphyllum* sp. (Van Waveren et al., 2002). The Vélez specimen cannot be assigned to any previously established species based on the present characters, and since the material is fragmented, it does not justify the designation as a new species.

Podozamites Braun 1843

cf. ***Podozamites*** sp.

Fig. 5F–J

Specimens. Eight specimens. MPVL (HP170721-01-27, HP170721-04-05, HP210919-2R, JB220103-2-11, JB220103-1-4-62, HP141121-03, HP141121-22, HP141121-31d).

Description. The material consists of incomplete and fragmentary impressions of isolated strap-shaped leaves with parallel venation, with 8 to 12 veins (Fig. 5F–J). The veins run from the base (Fig. 5H) to the apex, where they converge (Fig. 5F, H). A complete leaf measures 6 cm long and 0.8 cm wide (Fig. 5H). The other leaves are fragmented and just preserve parts of the middle area (Fig. 5F, G, I, J). The symmetry is not visible due to the highly fragmented material. The base is truncated and slightly constricted, and the apex is straight and obtuse (Fig. 5H).

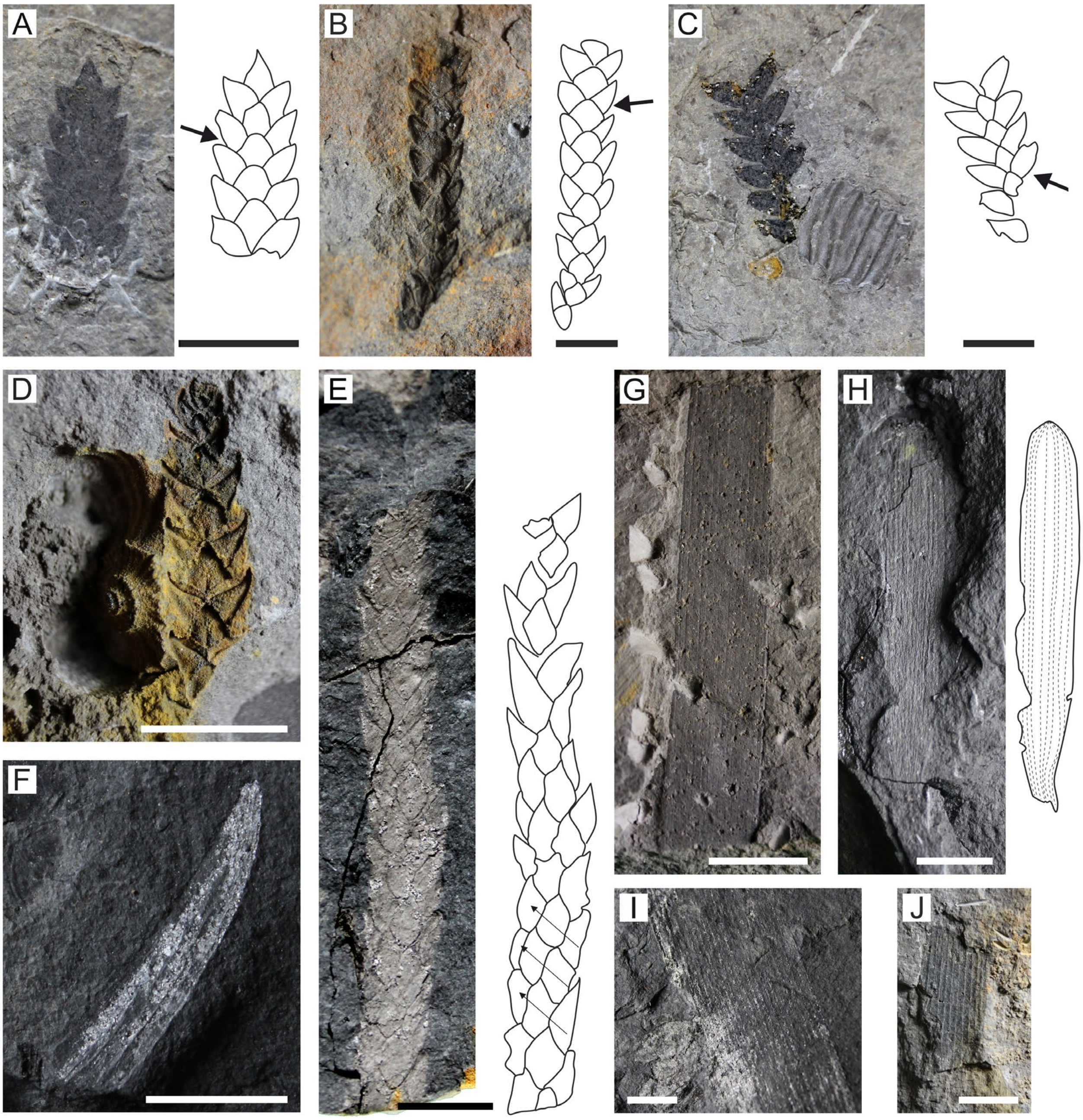

Figure 5. **A–D**. *Cupressinocladus* sp. isolated leafy shoots, **A**. MPVL-HP170721-01-39 with schematic interpretation, arrow indicating the free part of the leaf, **B**. MPVL-HP210919-12 with schematic interpretation, arrow indicating the free part of the leaf, **C**. MPVL-HP170721-01-01 with schematic interpretation, arrow indicating the free part of the leaf, **D**. MPVL-HP210919-01; **E**. *Brachyphyllum* sp. MPVL-HP170721-02-03 with schematic interpretation, arrows indicating the spiral arrangement of the leafy shoot; **F–J**. cf. *Podozamites* sp., **F**. MPVL-HP210919-2R, **G**. MPVL-JB220103-1-4-62, **H**. MPVL-JB220103-2-11 with schematic interpretation, **I**. MPVL-HP170721-04-05, **J**. MPVL-HP170721-01-27. Scale bars = 0.5 cm in A–C, I, J; 1 cm in D–G

Remarks. Specimens referred to as *Podozamites* are a common genus in the La Paja Formation (Huertas, 1967, 2003; Van Waveren et al., 2002) and in other Early Cretaceous floras from Colombia (Berry, 1945; Royo y Gómez, 1945; Lemoigne, 1984; Pons, 1988; Moreno-Sánchez, 1994) and South America (Kunzmann et al., 2004; Martínez et al., 2020) and Antarctica (Cantrill and Falcon-Lang, 2001). The parallel venation and the strap-shaped leaves are the main characteristics of this taxon.

The absence of cuticles and the fragmentary condition of the specimens preclude a specific taxonomic assignment. Strap-shaped leaves with parallel venation, without cuticles or other diagnostic characters, are not restricted to conifers. This plant fossil may belong to the families such as Araucariaceae, Podozamitaceae and Pseudotorelliaceae (Harris, 1979; Meyen, 1987; Van Konijnenburg-van Cittert and Morgans, 1999; Shi et al., 2018).

Putative reproductive structure 1

Fig. 6A

S p e c i m e n. One specimen. MPVL (HP210919-08).

D e s c r i p t i o n. Incomplete seed cone impression, flattened, with an oval shape. The cone is 8 cm long and 7.5 cm wide (Fig. 6A). The base is concave and truncated; the apex is not preserved (Fig. 6A). The impressions of the bract/scale complexes are 0.5 cm wide and 0.5 cm high, with hexagonal or rhomboidal outline (Fig. 6A). The bract/scale complexes impressions are spirally arranged with no visible imbrication. The impression of the umbo is circular and is placed in the centre of the apophysis (Fig. 6A).

R e m a r k s. This impression resembles a conifer cone, mainly the overall shape, the hexagonal arrangement of the bract/scale complexes, and the lack of imbrication between the external part of the bract/scale complexes. It is difficult to assess a specific affinity since it is just an impression without diagnostic characters.

Putative reproductive structure 2

Fig. 6B

S p e c i m e n. One specimen. MPVL (JB160421-1R).

D e s c r i p t i o n. Incomplete seed cone impression, with a sub-spherical shape, measures 4 cm in length and 3.5 cm in width (Fig. 6B). The external impressions of the bract/scale complexes are rhomboidal, 1.4 cm wide and 0.9 cm high, and are spirally arranged (Fig. 6B). The impression of the umbo is circular and is in the center of the bracts (Fig. 6B). The fossil impression is poorly preserved, and no further characters are visible.

R e m a r k s. This fossil impression lacks internal features. However, the few observable characters resemble a conifer cone. Similar to Putative reproductive structure 1. It is difficult to assess a specific affinity.

DISCUSSION

COMPARISON WITH OTHER EARLY CRETACEOUS FLORAS

The fossil flora presented here in the Los Guayabos section at Vélez, Santander is composed of conifers, similar to the Ricaurte Alto province (Van Waveren et al., 2002; Huertas, 2003). However, the number of taxa and specimens appears much lower at Vélez. This significant difference between localities can be

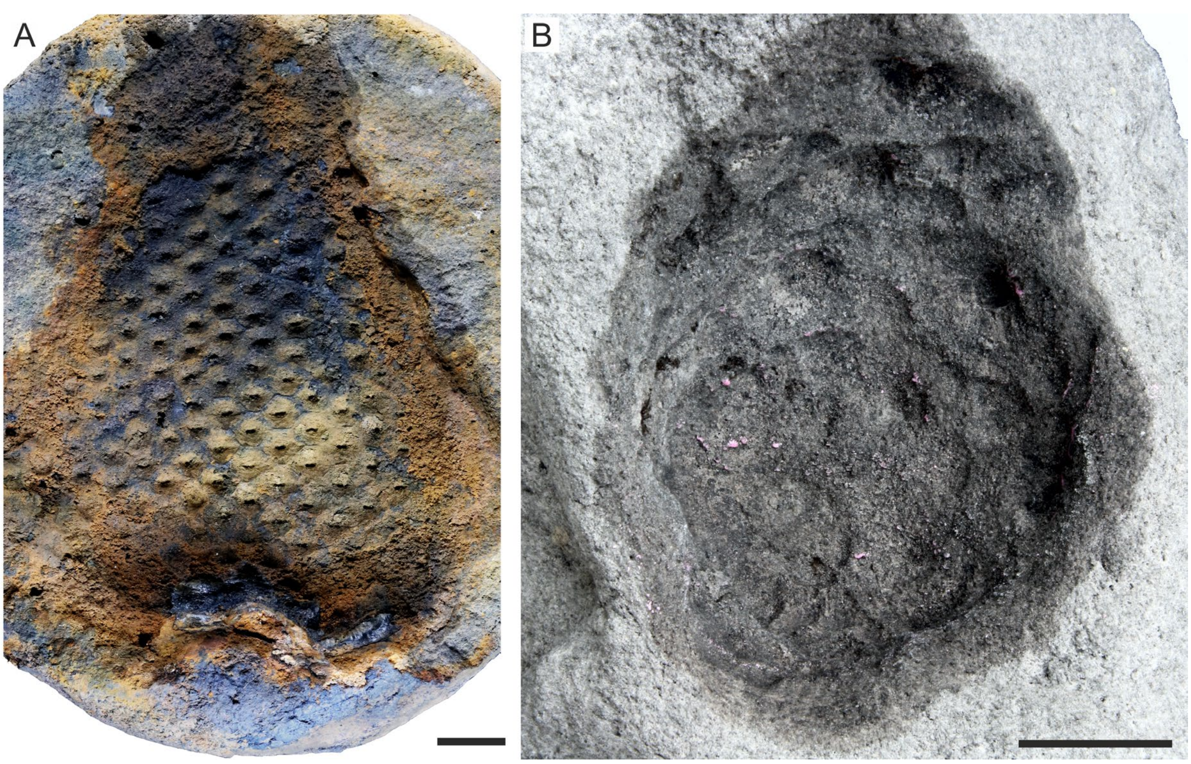

Figure 6. Putative reproductive structures. **A**. Putative reproductive structure 1, MPVL-HP210919-08; **B**. Putative reproductive structure 2, MPVL-JB160421-1R. Scale bars = 1 cm

attributed to over 60 years of historical exploration and today's climatic regime differences. The Ricaurte Alto province has a drier climate and less vegetation, providing easier access to suitable outcrops and facilitating more extensive palaeontological explorations.

Genera, such as *Cupressinocladus*, *Brachyphyllum* and *Podozamites* were common during the Early Cretaceous of northern South America (Berry, 1937, 1945; Lemoigne, 1984; Pons, 1988; Moreno-Sánchez, 1994; Van Waveren et al., 2002; Huertas, 2003; Monje-Dussán et al., 2016), but their reproductive organs are scarce (Van Waveren et al., 2002; Huertas, 2003; Monje-Dussán et al., 2016). Besides the reproductive organs from La Paja Formation flora at the Ricaurte Alto province (Van Waveren et al., 2002; Huertas, 2003), Monje-Dussán et al. (2016) described an ovuliferous complex with affinities to the family Araucariaceae from the late Albian of the Upper Magdalena Valley (Alpujarra, Tolima). The main difference between the macroflora from the Los Guayabos section and other Early Cretaceous floras from Colombia is the apparent absence of ferns and angiosperms (Berry, 1937, 1945; Lemoigne, 1984; Pons, 1988; Moreno-Sánchez, 1994; Monje-Dussán et al., 2016).

A distinct regional macrofloral composition pattern across the sub-provinces proposed for the Early Cretaceous of South America (Vakhrameev, 1991; McLoughlin, 2001) is characterized by multiple conifer families (e.g. Araucariaceae, Podocarpaceae and Cheirolepidiaceae), Bennettitales, and ferns (e.g. Dipteridaceae, Gleicheniaceae, Osmundaceae, Schizaeaceae, Matoniaceae) (McLoughlin, 2001). Genera such as *Cupressinocladus*, *Brachyphyllum* and *Podozamites* are present in both the palaeoequatorial and Patagonia–Palmer floras sub-provinces (McLoughlin, 2001; Martínez et al., 2020; Batista et al., 2021). The fossil taxa found in the Los Guayabos section represent an assemblage of both sub-provinces from the Early Cretaceous. Beyond the taxonomic composition, the biostratigraphic significance of the new material deserves attention. Although the material described here is fragmentary, it provides critical biostratigraphic information by narrowing the age of the Los Guayabos section to the late Aptian, supported by invertebrate correlations. This refinement is significant, as precise age assignments are often lacking in Colombian Early Cretaceous floras. While detailed taxonomic comparisons with other contemporaneous floras remain limited by preservation quality, the age constraint will facilitate more robust palaeofloristic and palaeoenvironmental comparisons at both regional and global scales.

CONCLUSION

The new macrofloral remains from the La Paja Formation in the Los Guayabos section consist of conifers (*Cupressinocladus*, *Brachyphyllum* and *Podozamites*) and putative reproductive structures. This flora shows similarities with those found in other localities of the La Paja Formation in the Ricaurte Alto province.

This is the first locality from the La Paja Formation in which the macroflora is placed in a biostratigraphical and lithological context. Until now, the flora from this unit was broadly considered Barremian-Aptian; however, in the Los Guayabos section, the age is constrained to the late Aptian.

The preservational features of the plant fossils from the Los Guayabos section indicate an allochthonous assemblage. The presence of articulated fish remains and ammonoid aptychi inside or near the body chamber suggests a low-energy depositional marine environment. The occurrence of pyrite is indicative of anoxic bottom conditions, which likely enhanced preservation and increased the potential for fossilization.

The new findings are significant because they provide one of the few macrofloral assemblages from the La Paja Formation associated with a well-constrained stratigraphic framework. Although the material is fragmentary, its late Aptian age assignment offers a critical reference point for comparisons with other contemporaneous South American floras, refining regional palaeoecological and palaeobiogeographical interpretations.

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ADDITIONAL INFORMATION

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