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PALAEONTOLOGY

Stratigraphic distribution of marine vertebrates from the Arcillolitas abigarradas Member (Paja Formation) of the Villa de Leiva – Sáchica - Sutamarchán region, Boyacá, Colombia

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ABSTRACT

The Villa de Leiva – Sáchica - Sutamarchán region is the most prolific locality for Early Cretaceous marine vertebrates in Colombia and one of the richest in these vertebrates in the world. All of these vertebrates come from beds of the Barremian-Aptian Arcillolitas abigarradas Member of the Paja Formation. Although many of the specimens have already been taxonomically studied, no publications have discussed their stratigraphic position and distribution within the Barremian-Aptian interval. Herein, we provide, for the first time, detailed stratigraphic information for the majority of the Barremian-Aptian marine vertebrates of the Villa de Leiva – Sáchica - Sutamarchán region reported so far. Based on 10 stratigraphic sections described in the several specimens finding sites, together with biostratigraphic information associated with specimens of imprecise geographical origin, we determined the stratigraphic provenance of 26 marine vertebrate specimens. We also refined the stratigraphic provenance of some specimens including the holotypes of *Muiscasaurus catheti*, *"Kyhytysuka" sachicarum,* and *Protolamna ricaurtei* whose stratigraphic origin was not previously specified beyond the Arcillolitas abigarradas Member. The data obtained allowed us to identify four vertebrate assemblages representing coeval faunas within the Barremian-Aptian interval, two from the Barremian and two from the upper Aptian.

Keywords: Stratigraphic distribution; marine vertebrates; Barremian-Aptian; Lower Cretaceous; Paja Formation.

Distribución estratigráfica de vertebrados Marinos del miembro Arcillolitas abigarradas (Formación Paja) de la región de Villa de Leiva - Sáchica - Sutamarchán, Boyacá, Colombia

RESUMEN

La región de Villa de Leiva - Sáchica - Sutamarchán es la localidad más prolífica en vertebrados marinos del Cretácico Temprano en Colombia y una de las más ricas en estos vertebrados en el mundo. Todos estos vertebrados provienen de las capas del Miembro Arcillolitas abigarradas del Barremiano-Aptiano de la Formación Paja. Aunque muchos de los especímenes ya han sido estudiados taxonómicamente, ninguna publicación ha discutido su posición y distribución estratigráfica dentro del intervalo Barremiano-Aptiano. En este trabajo proporcionamos, por primera vez, información detallada sobre la procedencia estratigráfica de la mayoría de los vertebrados marinos del Barremiano-Aptiano de la región de Villa de Leiva - Sáchica - Sutamarchán reportados hasta ahora. Con base en 10 secciones estratigráficas descritas en los sitios de hallazgo de diversos especímenes, junto con la información bioestratigráfica asociada a los especímenes con origen geográfico impreciso, nosotros determinamos la procedencia estratigráfica de 26 especímenes de vertebrados marinos. También afinamos la procedencia estratigráfica de algunos ejemplares, entre ellos los holotipos de *Muiscasaurus catheti*, "*Kyhytysuka*" *sachicarum* y *Protolamna ricaurtei* cuya procedencia estratigráfica no estaba previamente precisada más allá del Miembro Arcillolitas abigarradas. La información obtenida permitió identificar cuatro conjuntos de vertebrados que representan faunas coetáneas dentro del intervalo Barremiano-Aptiano, dos del Barremiano y dos del Aptiano superior.

Palabras Clave: Distribución estratigráfica; vertebrados marinos; Barremiano-Aptiano; Cretácico Inferior; Formación Paja;

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1. Introduction

In the localities of Villa de Leiva, Sáchica, and Sutamarchán, abundant marine vertebrate fossils have been found, all of which come from the Arcillolitas abigarradas Member of the Paja Formation of Barremian-Aptian in age (Cadena, 2015; Cadena and Parham, 2015; Cadena *et al.*, 2019; Carrillo-Briceño *et al.*, 2019; Cortés and Páramo-Fonseca, 2018; Cortés *et al.*, 2019; 2021; Gómez-Pérez and Noè, 2017; Maxwell *et al.*, 2016; 2019; Noè and Gómez-Pérez, 2022; Páramo-Fonseca, 2015; Páramo-Fonseca *et al*., 2016; 2018; 2019a; 2019b; 2021; 2023; Schultze and Stöhr, 1996), This material includes mainly marine reptiles (plesiosaurs, ichthyosaurs, turtles, and a crocodylomorph) and some fishes.

The published plesiosaurs were identified as the elasmosaurids *Callawayasaurus colombiensis* (Welles, 1962) and *Leivanectes bernardoi* Páramo-Fonseca *et al.*, 2019a from specimens found in Villa de Leiva (Goñi and Gasparini, 1983; Páramo-Fonseca *et al.*, 2019a; Welles, 1962) and the pliosaurids *Acostasaurus pavachoquensis* Gómez-Pérez and Noè 2017 represented by a specimen found in Sutamarchán (Gómez-Pérez and Noè, 2017), *Stenorhynchosaurus munozi* Páramo-Fonseca *et al.*, 2016 represented by specimens found in Sáchica, Sutamarchán and Villa de Leiva (Páramo-Fonseca *et al.*, 2016; 2019b; 2023), *Sachicasaurus vitae* Páramo-Fonseca *et al.*, 2018 represented by a specimen found in Sáchica (Páramo-Fonseca *et al.*, 2018), and *"Monquirasaurus" boyacensis* (Hampe, 1992) represented by a specimen found in Villa de Leiva (Hampe, 1992; Noè and Gómez-Pérez, 2022). This last species was initially described as *Kronosaurus boyacensis* by Hampe (1992) and recently Noè and Gómez-Pérez (2022) proposed the genus *"Monquirasaurus"* to include this species. Here we use the name within quotes because we consider that the attribution of this species to a new genus is not fully supported. The published ichthyosaurs were identified as the opthalmosaurids *Muiscasaurus catheti* Maxwell *et al.*, 2016 represented by specimens found in Villa de Leiva and Sáchica (Maxwell *et al.*, 2016; Páramo-Fonseca *et al.*, 2021); *Platypterygius* sp. represented by a specimen found in Villa de Leiva (Cortés and Páramo-Fonseca, 2018), and *"Kyhytysuka" sachicarum* (Páramo-Fonseca, 1997) represented by specimens found in Villa de Leiva (Cortés *et al.*, 2021; Maxwell *et al.*, 2019; Páramo-Fonseca, 1997). This last species was originally referred to the genus *Platypterygius* by Páramo-Fonseca (1997) and recently Cortés *et al.* (2021) referred the species to a new genus *"Kyhytysuka"*. Here we use the name within quotes because we consider that the attribution of this species to a new genus is not fully supported. The published turtles were identified as *Leivachelys cipadi* Cadena, 2015 and *Desmatochellys padillai* Cadena and Parham, 2015, from specimens found in Villa de Leiva (Cadena, 2015; Cadena and Parham, 2015; Cadena *et al.*, 2019; De la Fuente and Goñi, 1983). A crocodylomorph specimen found in Villa de Leiva was identified as an indeterminate Teleosauroid (Cortés *et al.*, 2019). Among the fishes there have been reports of a bony fish identified as *Vinctifer* sp. Jordan 1919 from Sáchica (Schultze and Stöhr, 1996) and the lamniform shark *Protolamna ricaurtei* Carrillo-Briceño *et al.*, 2019 from Villa de Leiva.

Although there are many studies on the marine vertebrates from the Arcillolitas abigarradas Member, there has never been an attempt to refine their stratigraphic occurrences. This lack of refinement can be attributed to several challenges, including the presence of geologic faults and folds, the lateral variations of the facies and thickness of the different stratigraphic intervals (Etayo-Serna, 1968a), and the discontinuity of the outcrops due to vegetation and soil coverage. This contribution aims to establish the stratigraphic distribution of many of the marine vertebrate specimens that have been found in the Arcillolitas abigarrradas Member in the Villa de Leiva - Sáchica - Sutamarchán region. We hope that the results obtained here serve as a stratigraphic framework for future studies on the Barremian-Aptian marine paleofauna of this region.

2. Material and methods

A large number of marine vertebrate specimens (at least more than 50 specimens) have been discovered in the Arcillolitas abigarradas Member in the Villa de Leiva - Sáchica - Sutamarchán region. However, we did not include all the specimens in this study due to a lack of essential information on some of them, which did not allow us to determine their stratigraphic position. We selected the specimens based on the availability of reliable geographic, stratigraphic, and biostratigraphic data. We excluded those specimens for which none of these data are known, or if the available information was deemed unreliable or insufficient. Following these selection criteria, we included a total of 26 specimens which comprise several elasmosaurid and pliosaurid plesiosaurs, some ophthalmosaurid ichthyosaurs, one turtle, one crocodylomorph, two sharks, and one actinopterygian fish (see table 1).

We describe stratigraphic sections to determine the stratigraphic provenance of the specimens from which only the geographic provenance was known. We described eight stratigraphic sections in localities where one or more of the selected specimens were collected (see Fig. 1). We followed the stratigraphy of the Arcillolitas abigarradas Member described by Etayo-Serna (1968a) in Villa de Leiva as a reference to correlate our stratigraphic columns and, focused on correlating the stratigraphic provenance of the selected specimens with the stratigraphic segments established by this author. Using the ammonoid biozones established for Colombia (Bürgl, 1956a; Etayo-Serna, 1979; Patarroyo, 2000; Patarroyo, 2020) we correlated the specimens in which accurate information on their geographical origin is unknown but associated ammonoids were found.

We measured the stratigraphic sections using Jacob's staff (1.5 m) and compass following the methodology described by Compton (1985). We draw them at a scale of 1:100. For the lithologic description, we followed the rock classification scheme presented by Nichols (2009), the subdivisions of layer thickness of Campbell (1967), the bioturbation index proposed by Taylor and Goldring (1993), and the fissility categories proposed by Potter *et al.* (1980, table 1.3). We used the Munsell (2009) color table to establish the color of the rocks in fresh samples. Finally, we digitized the obtained stratigraphic columns with the open-access program Inkscape 1.2. The full-scale digitized columns can be accessed in Supplemental Data 1.

We collected in-situ ammonoids and prepared them mechanically using a ME-9100 air scribe. We (CDB-C) identified the ammonoids based on the works of Bürgl (1956a), Etayo-Serna (1979), Kakabadze and Hoedemaeker (2004), and Wright (1996). The identification of these ammonoids can be accessed in Supplemental Data 2. We correlated the described stratigraphic columns to the ammonite biozones proposed by Patarroyo (2000) for the Barremian and by Etayo-Serna (1979) for the Aptian. In this way, we defined the biostratigraphic origin of some vertebrate specimens whose stratigraphic provenance within the Arcillolitas abigarradas Member had not been previously specified.

In 2014 one of us (MPR-C) described an unpublished stratigraphic section of the complete Arcillolitas abigarradas Member in Sáchica to correlate the stratigraphic origin of two of the here selected specimens. Here, we provide the stratigraphic column and the description of the stratigraphic section. This section was described in the Vereda Arrayán Alto, a locality characterized by extensive covered areas, in which the few outcrops are small, abandoned artisanal gypsum mining sites and a small creek. As the outcrops in the locality were non-continuous, the different described parts of the stratigraphic sections were connected using the polygonal method. We (MPR-C) described this stratigraphic section at a 1:200 scale using Jacob's staff (1.5 m) and Abney clinometer following the methodology described by Etayo-Serna (1985). We (MPR-C) determined the thickness of the layers following the subdivisions of layer thickness of Campbell (1967) and established the lithology of the strata following the rock classification scheme presented by Folk (1980). We (MPR-C) described the sedimentary structures and collected fossils following the parameters established by Etayo-Serna (1985) and defined the color of the rocks in fresh samples using the color table TGL 34329 Gesteinsfarben (1979). We (MPR-C) digitized the stratigraphic column in three segments using AutoCAD 2014. The full-scale digitized column of this section can be accessed in Supplemental Data 3. Dr. Fernando Etayo-Serna identified the ammonoids collected from this section and provided their age following the Barremian biozones proposed by Bürgl (1956a, b) and the Aptian biozones proposed by Etayo-Serna (1979). The identification of these ammonoids can be accessed in the Supplemental Data 3.

A published stratigraphic column of the Arcillolitas abigarradas Member described on the road from Sáchica to Samacá (Schultze and Stohr,1996) provided us the stratigraphic provenance of one of the selected specimens. We correlated the part of this section that includes the specimen stratigraphic provenance with the sections described here. Moreover, we correlated the Aptian ammonoids identified by Schultze and Stohr (1996) from their described section, to the ammonoid biozones of Etayo-Serna (1979).

As a whole, we correlated ten stratigraphic columns, taking as a reference the Stratigraphic section of the Arcillolitas abigarradas Member of Etayo-Serna (1968a) and the ammonoid biostratigraphic schemes of Patarroyo (2000), Bürgl (1956a) and Etayo-Serna (1979). In the text figures, we provide a generalized version of these stratigraphic columns. Through a graphical correlation of the stratigraphic and biostratigraphic provenance of the specimens, we obtained a precise stratigraphic distribution of marine vertebrate specimens within the Barremian-Aptian interval of the Arcillolitas abigarradas Member of the Paja Formation.

Institutional abbreviations: CB, **MP**, **MPR**, **UNDG**, acronyms used in sample numbers from paletontological collections of the Departamento de Geociencias, Universidad Nacional de Colombia, Bogotá, Colombia; **CFSTA**, Colección Fundación Santa Teresa de Avila, Villa de Leiva, Colombia; **CIP**, Centro de Investigaciones Paleontológicas, Villa de Leiva, Colombia; **DON**, **MP**, **RA**, **VL**, acronyms used in sample numbers from the paleontogical collection of the Servicio Geológico Colombiano, Bogotá, Colombia; **FCG-CBP**, Fundación Colombiana de Geobiología, now Centro de Investigaciones Paleontológicas, Villa de Leiva, Colombia; **MB**, Museum für Naturkunde Berlin, Berlin, Germany; **MJACM**, Museo Junta de Acción Comunal vereda Monquira, Villa de Leiva, Colombia; **MPVL**, Museo Paleontológico de Villa de Leyva; Universidad Nacional de Colombia, Villa de Leiva, Colombia; **UCMP**, University of California Museum of Paleontology, California, USA.

Table 1. Selected specimens by taxonomic group. The last column shows the number assigned to each specimen in figures 1-5

Taxonomic group	Specimen	Taxon	Reference	Material	Nº in figures
Elasmosauridae	FCG-CBP-3	Elasmosauridae	unpublished	Anterior part of an articulated skeleton	1
Elasmosauridae	FCG-CBP-22 (holotype)	*Leivanectes bernardoi*	Páramo-Fonseca *et al.*, 2019a	Anterior fragment of a skull	2
Elasmosauridae	UCMP 38349 (holotype)	*Callawayasaurus colombiensis*	Welles, 1962	Nearly complete skeleton	3
Elasmosauridae	UCMP 125328; IGMp174997	*Callawayasaurus colombiensis*	Welles, 1962	Nearly complete skeleton	4
Pliosauridae	CFSTA 2-1	Pliosauridae	unpublished	Incomplete skull	5
Pliosauridae	FCG-CBP-4	Pliosauridae	unpublished	Nearly complete skeleton	6
Pliosauridae	MPVL-MP110210-1	Pliosauridae	unpublished	Posterior half of a skeleton	7
Pliosauridae	MJACM 1 (holotype)	*"Monquirasaurus" boyacensis*	Hampe, 1992; Noè and Gómez-Pérez (2022)	Nearly complete skeleton	8
Pliosauridae	MP111209-1 (holotype)	*Sachicasaurus vitae*	Páramo-Fonseca *et al.*, 2018	Nearly complete skeleton	9
Pliosauridae	VL17052004-1 (holotype)	*Stenorhynchosaurus munozi*	Páramo-Fonseca *et al.*, 2016	Nearly complete skeleton	10
Pliosauridae	MP050310-1	*Stenorhynchosaurus munozi*	Páramo-Fonseca *et al.*, 2019b	Skull and first cervical vertebrae	11
Pliosauridae	MPVL-667	*Stenorhynchosaurus munozi*	Páramo-Fonseca *et al.*, 2023	anterior end of the snout	12
Pliosauridae	UN-DGR-1000 (holotype)	*Acostasaurus pavachoquensis*	Gómez-Pérez and Noè (2017)	Skull and postcranial elements	13
Ophthalmosauridae	FCG-CBP-8	Ophthalmosauridae	unpublished	Skull	14
Ophthalmosauridae	FCG-CBP-18	Ophthalmosauridae	unpublished	Skull	15
Ophthalmosauridae	FCG-CBP-28	Ophthalmosauridae	unpublished	Skull	16
Ophthalmosauridae	DON-19671 (holotype)	*"Kyhytysuka" sachicarum*	Páramo-Fonseca, 1997; Cortés *et al.*, 2021	Skull	17
Ophthalmosauridae	CIP-GA-01042014	*"Kyhytysuka" sachicarum*	Maxwell *et al.*, 2019	Nearly complete skeleton	18
Ophthalmosauridae	FCG-CBP-74 (holotype)	*Muiscasaurus catheti*	Maxwell *et al.*, 2016	Skull and axial skeleton	19
Ophthalmosauridae	FCG-CBP-16	*Muiscasaurus catheti*	Páramo-Fonseca *et al.*, 2021	Skull and axial skeleton	20
Ophthalmosauridae	FCG-CBP-87	*Platypterygius* sp.	Cortés and Páramo-Fonseca, 2018	Forelimb	21
Teleosauroidea	CIP-0001	Teleosauroidea indet.	Córtes *et al.*, 2019	Vertebrae and ventral and dorsal osteoderms	22
Testudines	CFSTA090318	Testudines	unpublished	Incomplete skeleton	23
Lamniforme	CFSTA090318	Lamniforme	unpublished	Teeth and axial skeleton	24
Lamniforme	FCG-CBP-93 (holotype)	*Protolamna ricaurtei*	Carrillo-Briceño *et al.*, 2019	Teeth	25
Osteoichthyes	MB f. 3500	*Vinctifer* sp.	Schulzte and Stöhr, 1996	Postcranial axial fragment	26

Stratigraphic context

The Paja Formation was defined by Morales *et al.* (1958) based on an unpublished description by O. C. Wheeler on the north side of the Quebrada La Paja, Betulia, Santander. In this region, the Paja Formation overlies the Rosa Blanca Formation and underlies the Tablazo Formation (Morales *et al.*, 1958). Recently Montoya Arenas (2019) described the Paja Formation in the type section and used the name initially utilized by Wheeler "La Paja" Formation. Here we employ the name Paja Formation which was used by Etayo-Serna (1968a) in his stratigraphic description of the Villa de Leiva region and later coined by many authors (Cadena and Parham, 2015; Cadena *et al.*, 2019; Carrillo-Briceño *et al.*, 2019; Cortés *et al.*, 2019; Hoedemaeker, 2004; Noè and Gómez-Pérez, 2020; 2022; Patarroyo, 2000; 2020; among many others).

The Paja Formation was described and mapped in the Villa de Leiva region by Etayo-Serna (1968a), who determined the age of the rocks based on ammonoids. According to this author, in this region, the Paja Formation overlies the Ritoque Formation and underlies the Lower San Gil Formation, and it ranges from the Hauterivian to the upper Aptian. Etayo-Serna (1968a) identified three lithostratigraphic assemblages that he named from base to top: Lutitas negras inferiores (Hauterivian), Arcillolitas abigarradas (lower Barremian to upper Aptian), and Arcillolitas con nódulos huecos (upper Aptian). While Etayo-Serna (1968a) did not use the term "member" to refer to the divisions of the Paja Formation in the original description, Forero and Sarmiento (1985) employed this term, and subsequently, numerous publications adopted the term "member" to designate the divisions proposed by Etayo-Serna (1968a) for the Paja Formation in the Villa de Leiva region (Cortes *et al.*, 2019; Gómez-Pérez and Noè, 2017; Páramo-Fonseca *et al.*, 2016; Páramo-Fonseca *et al.*, 2018; Páramo-Fonseca *et al.*, 2019a; b). In this work, we focus on the Arcillolitas abigarradas Member as described by Etayo-Serna (1968a), since it is within these rocks that the marine vertebrate specimens of the Paja Formation have been found.

The Arcillolitas abigarradas Member was described by Etayo-Serna (1968a) as gray, pink, yellow, and sometimes black claystones, intercalated with some levels of calcite, marls, and gypsum and says that the latter sometimes appears, filling cracks. The whole succession presents abundant ellipsoidal concretions of various sizes, morphologies, and ammonoid content (Etayo-Serna, 1968a). This author subdivided the Arcillolitas abigarradas Member into five segments from base to top (A-E) which he describes as follows: Segment A (56 m), consisting of pink claystones (black when fresh), with hard levels of slightly calcareous clayey sandstones that present fibrous calcite, with septarians and spherical or elliptical calcareous concretions up to 50 cm in diameter covered by clay and sometimes by gypsum; Segment B (1.60 m), composed of a layer of very compact clayey limestone with lenses of sandy clay that stands out as a cornice for its competence, usually underlaid by accumulations of gypsum and with poorly preserved fossils and concretions; Segment C (86 m), comprising gray claystones with some hard marly layers overlaid by 1 cm thick gypsum layers; Segment D (102 m), composed of gray to brown claystones interstratified with gypsum and interbedded with 8 prominent hard calcareous levels, abundant oxidized elliptical concretions throughout the segment, and in the top a white clayey layer with compressed ammonites covered by gypsum; and Segment E (235 m), composed of gray, yellow, pink, and sometimes black claystones intercalated with calcareous-clay layers, with ellipsoidal calcareous concretions throughout the segment which contain small fossils.

Forero and Sarmiento (1985) conducted a facial analysis of the Arcillolitas abigarradas Member of the Paja Formation in the Villa de Leiva region and subdivided the member into five segments. The correspondence between the segments proposed by Forero and Sarmiento (1985) and those described by Etayo-Serna (1968a) can be seen in figure 2 of Forero and Sarmiento (1985). Based on their analysis, Forero and Sarmiento (1985) concluded that the deposition of the Arcillolitas abigarradas Member occurred in intertidal and low supramareal environments of a saline tidal plain protected from the influence of the open sea.

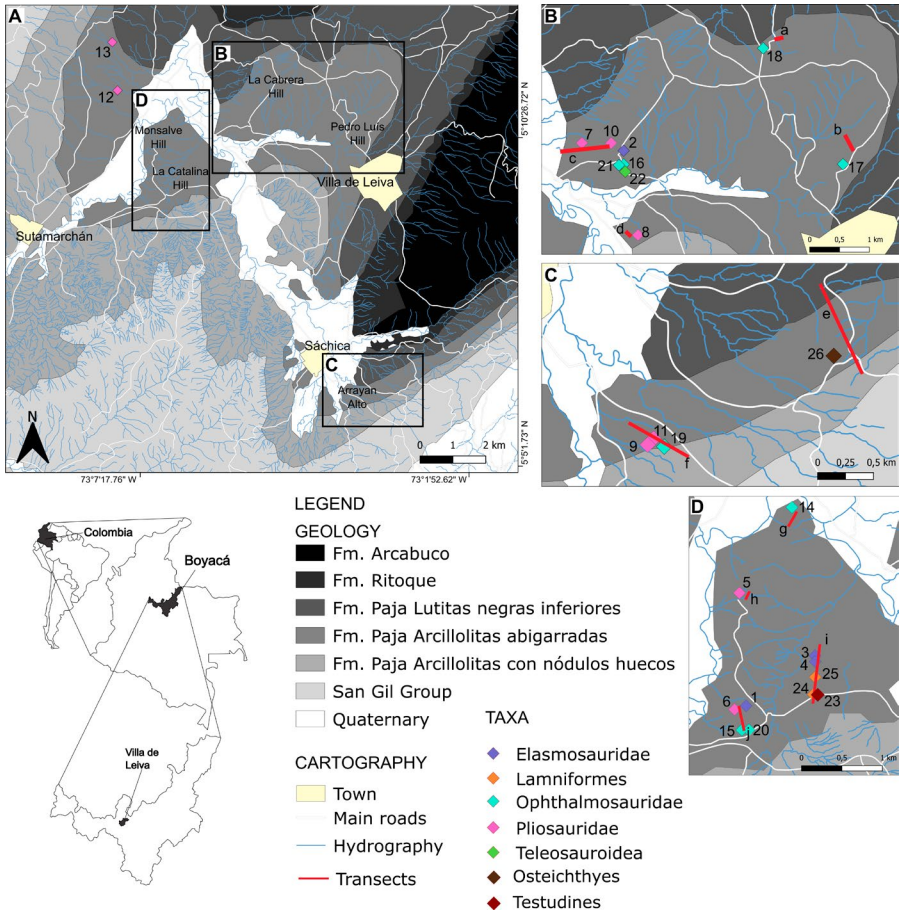

Figure 1. Geographic and stratigraphic provenance of the marine vertebrate specimens and location of the stratigraphic sections included in this study. A, General geological map of the Villa de Leiva – Sáchica - Sutamarchán region (modified from Etayo- Serna, 1968a), cartographic base: Instituto Geográfico Agustín Codazzi. B-D close-ups of the geological map showing the location of the vertebrate finding sites (indicated with numbers; see table 1) and the stratigraphic sections (indicated with lowercase letters). a, El Roble; b, Pedro Luis; c, La Cabrera; d, El Fósil; e, Loma Blanca; f, Arrayán Alto; g, Monsalve-1; h, Monsalve-2; i, Catalina; j, Monsalve-3.

3. Results

Stratigraphic sections from Sáchica

ARRAYÁN ALTO SECTION

In 2013, one of the authors (MEP-F) excavated two specimens of pliosaurids (MP050310-1 and MP111209-1) at the Arrayán Alto locality, southeast of Sáchica, Boyacá (Páramo-Fonseca *et al*., 2018; 2019b), which were found 108 topographic meters from each other. Both specimens were collected from the Arcillolitas abigarradas Member of the Paja Formation. To establish the accurate stratigraphic position of the two pliosaurids, in 2014, a stratigraphic section of the Arcillolitas abigarradas Member was described in the finding sector. The stratigraphic column was constructed from sections outcropping in the discovery locality between the coordinates N 5º34'23.4''; W73º31'56.8'' and N 5º34'14.0''; W73º31'40.2'' (Fig. 1). In this part of the article and the Supplemental Data 3, we provide all the information collected in that work. We give the stratigraphic description of the Arrayán Alto section with the stratigraphic provenance of the two pliosaurids and the results of the collected ammonoid identification. Based on this described section, it is here also established the previously unknown stratigraphic provenance of the ichthyosaur specimen CIP-FCG-CBP-73, which also came from the Arrayán Alto sector (Maxwell *et al.*, 2016).

Description

The Arcillolitas abigarradas Member in the Arrayán Alto Sector comprises 380.47 m violet claystones, calcareous claystones, and limestones, with abundant gypsum and concretions containing fossils. In addition, sporadic discontinuous layers of white claystone, forming lenses, were observed. The described section was divided into three segments, having as criteria the content of calcareous intercalations, the presence of gypsum, and the predominance of some lithologies (Ramos-Clavijo, 2015) (Fig. 2A) (see Supplemental Data 3).

Segment I. This segment overlaps the Lower Lutitas negras inferiores Member of Etayo-Serna (1968a) and has a thickness of 96.56m. Its dominant characteristics are the presence of septarian at the base, the frequent intercalations of calcareous layers, and the gradual increase in gypsum content towards the top. The predominant rocks in segment I are light violet non-calcareous claystones with undulating lamination, representing 60.8% of the segment thickness. It contains 26 hard layers of dark brown purplish limestone representing 13.5% of the segment thickness. The average thickness of these layers is 0.5 m. These layers usually present fibrous calcite crusts on their top. Among the claystones, calcareous concretions of up to 60 cm in diameter can be observed. These concretions are covered by iron oxides and sometimes by a coat of gypsum that takes the shape of the concretion. Ammonites are usually found within the concretions. From the middle of the segment, the gypsum appears sporadically as veins of 2 mm to 2 cm parallel to the stratification or cutting it and increases towards the top but remains scarce. At 34.19 m from the base, one of the calcareous layers stands out by containing algal mats, which appear as a gray calcareous rock with undulating parallel lamination. This level is correlated with segment B of Etayo-Serna (1968a) by its greater thickness and its lithology (168 cm) (Fig. 2A and Supplemental Data 3). Ammonoids collected from basal beds of segment I of the Arrayán Alto section were identified as *Nicklesia pulchella* (D'Orbigny, 1840) (MPR-300914-5) and *Karsteniceras beyrichi* (Karsten, 1858) (MPR-300914-6) (see Supplemental Data 3, fig. 11-12) that indicate the "*Nicklesia* biozone" of the lower Barremian (sensu Bürgl, 1956a). From the top of the segment, *Heinzia* cf. *veleziensis* Hyatt, 1903 was identified (MPR-140414-2) (see Supplemental Data 3, fig. 3), which indicates the middle Barremian (sensu Bürgl, 1956a) or lower upper Barremian (sensu Patarroyo, 2000; 2020). In this way, segment I can be correlated with segments A, B, and part of segment C of Etayo-Serna (1968a) (Fig. 2A).

Segment II. The thickness of this segment is 168.67m. Its dominant characteristics are the abundance of gypsum in non-calcareous clay layers, the decrease in the number of calcareous layers, the presence of fibrous calcite on the top and the base of some limestone layers, and the scarce invertebrate fossils within the concretions. The predominant rocks in segment II are non-calcareous claystones of light violet color with undulating lamination and abundant gypsum veins, representing 63.9% of the thickness of the segment. Two layers of white claystone are located at the base of the segment. The segment contains 15 hard layers of dark brown purplish limestone representing 4.1% of the thickness of the segment. These layers have fibrous calcite up to 10 cm thick on the top. A bed of algal mat is found at 129.8m from the base of the segment. The gypsum veins are more common in outcrops, they occur parallel to the lamination or cutting it, and it also occurs in macroscopic crystals. Progressive oxidation from the outside to the inside is observed in some concretions, as mentioned by Etayo-Serna (1968a) in his segment D. Only in this segment calcareous concretions with sulfur inside associated with the white claystone layers (iron oxide concretions) are found (Supplemental Data 3).

The pliosaurid specimens MP050310-1 and MP111209-1 were found in a non-calcareous claystone layer 3 m thick, located at 106,5 m from the base of segment II. Although most of this segment is not highly fossiliferous, some ammonites can be found within the concretions, mainly at the top of the segment. An ammonoid from the base of the segment was identified as *Heinzia* cf. *veleziensis* (MPR140414-5) (see Supplemental Data 3, fig. 5), indicating the middle Barremian (sensu Bürgl, 1956a) or lower upper Barremian (sensu Patarroyo, 2000; 2020). Ammonoids collected from the middle of the segment were identified as *Pulchellia* sp. Uhlig, 1883 (MPR-150414-3) (see Supplemental Data 3, fig. 5), *Subpulchellia* sp. Hyatt, 1903 (MPR-150414-4, MP110414-5, MP110414-11) (see Supplemental Data 3, fig. 1-2, 6), and *Acanthoptychoceras*? Manolov, 1962 (MPR150414-6) (see Supplemental Data 3, fig. 7), which indicates the middle Barremian (sensu Bürgl, 1956a) or lower upper Barremian (sensu Patarroyo, 2000; 2020). From the top of the segment, a fossiliferous concretion (MPR 170414-7) contained gastropods (*Chenopus* (*Tessarolax*) *evolutior* Jaworski, 1938; bivalves (*Crassatella aequalis* Gerhardt, 1897 and ammonoids identified as *Dufrenoyia sanctorum* Bürgl, 1956b, *Acanthohoplites bigouretiforme* Etayo-Serna, 1979, and *Acanthohoplites pulcher* Riedel, 1938 (see Supplemental Data 3, fig. 10). Other ammonoids collected from the top of the segment were identified as *Paracrioceras* sp. Spath, 1924 (MPR170414-5) (see Supplemental Data 3, fig. 8) and a juvenile specimen of *Cheloniceras* sp. Hyatt, 1903 (MPR-170414-6) (see Supplemental Data 3, fig. 9). The ammonoid assemblage from the top of segment II indicates the upper Aptian *Dufrenoyia sanctorum* - *Stoyanowiceras treffryanus* biozone of (Etayo-Serna, 1979) (Fig. 2A).

The fossil content, as well as lithologic features such as the low fossiliferous content in the concretions, the decrease of calcareous layers towards the top of the segment, and the morphology of the concretions, allows correlating the segment II with part of segment C, the segment D and probably the most basal portion of segment E of Etayo-Serna (1968a) (Fig. 2A).

Segment III. This segment is overlaid by the Arcillolitas con nódulos huecos Member of Etayo-Serna (1968a). The boundary with the upper member was interpreted as where hollow nodules begin to appear within the lithology. The thickness of segment III is 115.24m. It is characterized by the presence of algal mats at the base; the increase in the number and thickness of calcareous claystone layers; the decrease in gypsum content from the base to the top of the segment; and the abundant fossils in concretions. The predominant rocks in this segment are light violet non-calcareous claystone with undulating lamination, representing 48.4% of the thickness of the segment. There are shale packages of purple, pink and orange colors whose partitioning is very fine. The concretions of these packages are clayey and ash-shaped and sometimes contain external molds of ammonoids. The segment contains eight hard levels of dark brown purplish limestone representing 3.6% of the thickness of the segment. The average thickness of these layers is 0.5 m. From the middle of the segment, the gypsum becomes scarce until its complete disappearance at the top of the segment. Round and elliptical calcareous concretions of up to 35 cm maximum diameter with iron oxides on the outside predominate within all the concretions. Ammonites, bivalves, and fish remains are usually found within the concretions (see Supplemental Data 3). Among the ammonoids collected in this segment were identified: *Epicheloniceras pardoi* Etayo-Serna, 1979 (MPR-031014-20), *Gargasiceras pulcher* (Riedel, 1938) (MPR-031014-6), *Epicheloniceras* cf. *camachoi* Etayo-Serna, 1979 (MPR-031014-6), *Dufrenoyia sanctorum* (MPR-031014-4), *Acanthohoplites eleganteante* Etayo-Serna, 1979 (MPR-021014-8) and *Acanthohoplites odiosus* Etayo-Serna, 1979 (MPR-021014-2; MPR-021014-8) (see Supplemental Data 3, fig. 13-15, 17, 20). This ammonoid assemblage indicates the upper Aptian *Dufrenoyia sanctorum* - *Stoyanowiceras treffryanus* biozone (Etayo-Serna, 1979). The described lithologic features and the identified ammonoid genera allow us to confidently correlate segment III with segment E of Etayo-Serna (1968a) (Fig. 2A).

Stratigraphic position of the pliosaurid specimens MP 050310-1 and MP111209-1

The pliosaurid specimens MP050310-1 and MP111209-1 were found in two different geographic sites of the Arrayán Alto sector. They were found 108 m from each other and separated by overgrown terrain, so their precise stratigraphic position could not be defined by direct measurement. Both specimens came from the described Segment II and were found in a layer of non-calcareous purplish claystone having calcareous concretions with scarce ammonoids, iron oxides on their inside, and a gypsum coating on their outside (see Supplemental Data 3). The position of the pliosaurids MP050310-1 and MP111209-1 in the stratigraphic column, together with that of the identified ammonites, restrict the stratigraphic provenance of the pliosaurids to the uppermost part of segment C, near the boundary with segment D of Etayo-Serna (1968a) (Fig 2A).

The accurate stratigraphic position of the two pliosaurid specimens was determined by taking as reference a 0.18 m thick bed of limestone with iron oxides and pyrites, which underlies the pliosaurids bearing bed. This guide layer was seen in outcrops and found in trenches made in the excavation sites. The marking bed is distinguished in the field because it overlies a level with concretions between 15 to 28 cm in diameter, with elongated and rounded shapes. Petrographic analyses of this guide layer, done from samples collected in both pliosaurid excavation sites, showed that the rock corresponds to a sparitic limestone, with the presence of 200 micron euhedral micas and pyrite. No sedimentary structures or microfossils were observed. A second reference limestone layer, lower than the guide one, was also analyzed to corroborate the stratigraphic origin of both pliosaurids. The petrographic analyses of this layer were done from samples collected in the MP111209-1 finding site and an intermediate place between the two pliosaurid finding sites. The results showed a sparitic limestone lithology with presence of micas. The difference found with the first guide layer was the smaller size of carbonates and pyrites.

MP050310-1 (*Stenorhynchosaurus munozi*) was found 0,48 m above the guide layer (109.2 m from the base of segment II), whereas MP111209-1 (*Sachicasaurus vitae*) was found 2.09 m above the guide layer (110.8 m from the base the segment II). Based on these observations, we determine that the two specimens were extracted from the same stratigraphic layer but separated from each other by 1.06 m of rocks (see Supplemental Data 1). With these results, we conclude that *St. munozi* and *Sa. vitae* were contemporaneous species, but the individuals to which the remains belonged did not coexist, and the deposition of their remains was not coeval.

Stratigraphic provenance of the ichthyosaur specimen CIP-FCG-CBP-73

The holotype of the ichthyosaur *Muiscasaurus catheti* (specimen CIP-FCG-CBP-73) was described in 2016 by Maxwell *et al.* (2016). However, the stratigraphic provenance of the specimen had not been specified until now. Based on the geographic coordinates given by Maxwell *et al.* (2016), we recently visited the finding site and collected an ammonoid, which was identified by one of the authors (CDB-C) as *Cheloniceras (Epicheloniceras) carlosacostai* Etayo-Serna 1979 (MP101022-1) (see Supplemental Data 2, Fig. 4E). The genus *Cheloniceras* is included by Etayo-Serna (1979) in the biozone of *Dufrenoyia sanctorum* - *Stoyanowiceras treffryanus*, which according to this author, indicates the upper Aptian in Colombia. Moreover, the finding site corresponds to one of the GPS points taken in 2014 during the description of the Arrayán Alto section, where some ammonoids were collected. Therefore, we establish that the specimen comes from the upper part of segment II of the here described section, more precisely from the meter 147 from the base of the section (Fig. 2A). The identified ammonoids corroborate the upper Aptian *Dufrenoyia sanctorum* - *Stoyanowiceras treffryanus* biozone of Etayo-Serna (1979). As discussed in previous paragraphs, segment II of the section is equivalent to part of segment C, segment D, and probably the lowermost portion of segment E of Etayo-Serna (1968a). Therefore, we conclude that the specimen CIP-FCG-CBP-73 probably comes from the basal part of segment E of Etayo-Serna (1968a) (Fig. 2A).

LOMA BLANCA SECTION

Schultze and Stohr (1996) described the section of the Loma Blanca hill that outcrops in the road from Sáchica to Samacá (Fig. 1). They described the entire Arcillolitas abigarradas Member and the Arcillolitas con nódulos huecos Member of Etayo-Serna (1968a) and indicated the stratigraphic provenance of the specimen MB f. 3500 (*Vinctifer* sp.) in meter 353.05 of their section. They found various ammonoids in the levels below and above the level from which MB f. 3500 was collected. They identify the ammonoids as *Cheloniceras (Epicheloniceras)* ex gr. *martini* D'Orbigny, 1841, *Cheloniceras* (*Epicheloniceras*) ex gr. *cornuelianum* D'Orbigny, 1841, *Gargasiceras* cf. *interiectum* Riedel, 1938, *Dufrenoyia sanctorum*, *Toxoceratoides* (*Colomboceratoides*) *renzoni* Etayo-Serna, 1979 (see Schultze and Stohr, 1996). Following Etayo-Serna (1979), these ammonoids indicate the biozone *Dufrenoyia sanctorum* - *Stoyanowiceras treffryanus* that represents the upper Aptian in Colombia. To correlate the stratigraphic section of MB f. 3500 provided by Schultze and Stohr (1996) with the segments of Etayo-Serna (1968a), we used the limit of the Arcillolitas abigarradas Member with the Arcillolitas con nódulos huecos Member as a correlative point. We establish that MB f. 3500 came from the upper half of segment E of Etayo-Serna (1968a) (Fig. 2B).

Stratigraphic sections from Villa de Leiva

LA CABRERA SECTION

This section was described in the La Cabrera hill, west of Villa de Leiva town, outcropping between coordinates N 5º38'59.1"; W73º33'07.9" and N 5º39'01.7"; W73º33'43.3" (Fig. 1). In this section the stratigraphic provenance of the published pliosaurid *Stenorhynchosaurus munozi* specimen VL17052004-1 and the unpublished (currently under study) pliosaurid specimen MPVL-MP110210-1 are provided.

In their description of the specimen VL17052004-1 Páramo-Fonseca *et al.* (2016) indicated that the provenance of this specimen corresponds to the segment C of Etayo-Serna (1968a), and the ammonoids collected below the specimen and within the specimen skull correspond to the *Gerhardtia provincialis* D'Orbigny, 1850 subzone of the *Gerhardtia sartousiana* D'Orbigny, 1841 biozone of Reboulet *et al.* (2014) of the lower upper Barremian (see Páramo-Fonseca *et al.*, 2016). This biozone is correlated by Patarroyo (2020, fig. 7) with his *Gerhardtia veleziensis* biozone, representing the lower part of the upper Barremian in Colombia. The stratigraphic section of La Cabrera was described to specify the stratigraphic provenance of the specimen VL17052004-1 within the segment C of Etayo-Serna (1968a) and to locate the stratigraphic origin of specimen MPVL-MP110210-1 on the base of its geographical provenance.

This section comprises 94 meters of claystones, interspersed with occasional layers of calcareous claystone, siltstone, and regular competent layers of silty limestone. Concretions were found in different intervals of the section (meters 1-11, 28-34, 60-69, 81-94). The concretions at the base of the section are large (diameter> 40 cm). Additionally, at meters 8-9 a level with septarian was found. At meters 15-16 of the described section, a very competent 1.1 m thick silty limestone is found, which forms a ledge on the ground. In the upper part of the section (meter 59 onwards), more competent limestone levels stand out, which form steps in the direction of the counter slope and form resistant floors on their structural planes. These layers of silty limestone usually have fibrous calcite on their top (see Supplemental Data 1).

Specimen MPVL-MP110210-1 comes from the beds of the first two meters of the measured section, and specimen VL17052004-1 comes from a layer of clay corresponding to meter 94 of the described section (Fig. 3A and Supplemental Data 1). The presence of septarian and concretions with diameters greater than 40 cm in the first 12 meters allows us to correlate this part of the section with segment A of Etayo-Serna (1968a). In this section, the thick layer of silty limestone (meters 15-16) is correlated with segment B of Etayo-Serna (1968a) based on the similarity of its lithology and its expression in the terrain. In the described section, above meter 16, we found a lithology similar to that described by Etayo-Serna (1968a) for his segment C, so meters 16 to 94 of the described section are correlated with segment C of Etayo-Serna (1968a). At meter 81, a pair of ammonoid specimens identified as *Pulchellia* sp. (CB160121-4 and 5) were found (see Supplemental Data 2, Fig. 9A-B). This genus is included within the upper lower Barremian *Pulchellia galeata* biozone by Patarroyo (2000). With the exposed data, we correlate the stratigraphic position of the specimen MPVL-MP110210-1 with the lower part of Segment A and that of the specimen VL17052004-1 with the upper part of Segment C of Etayo-Serna (1968a) (Fig. 3A).

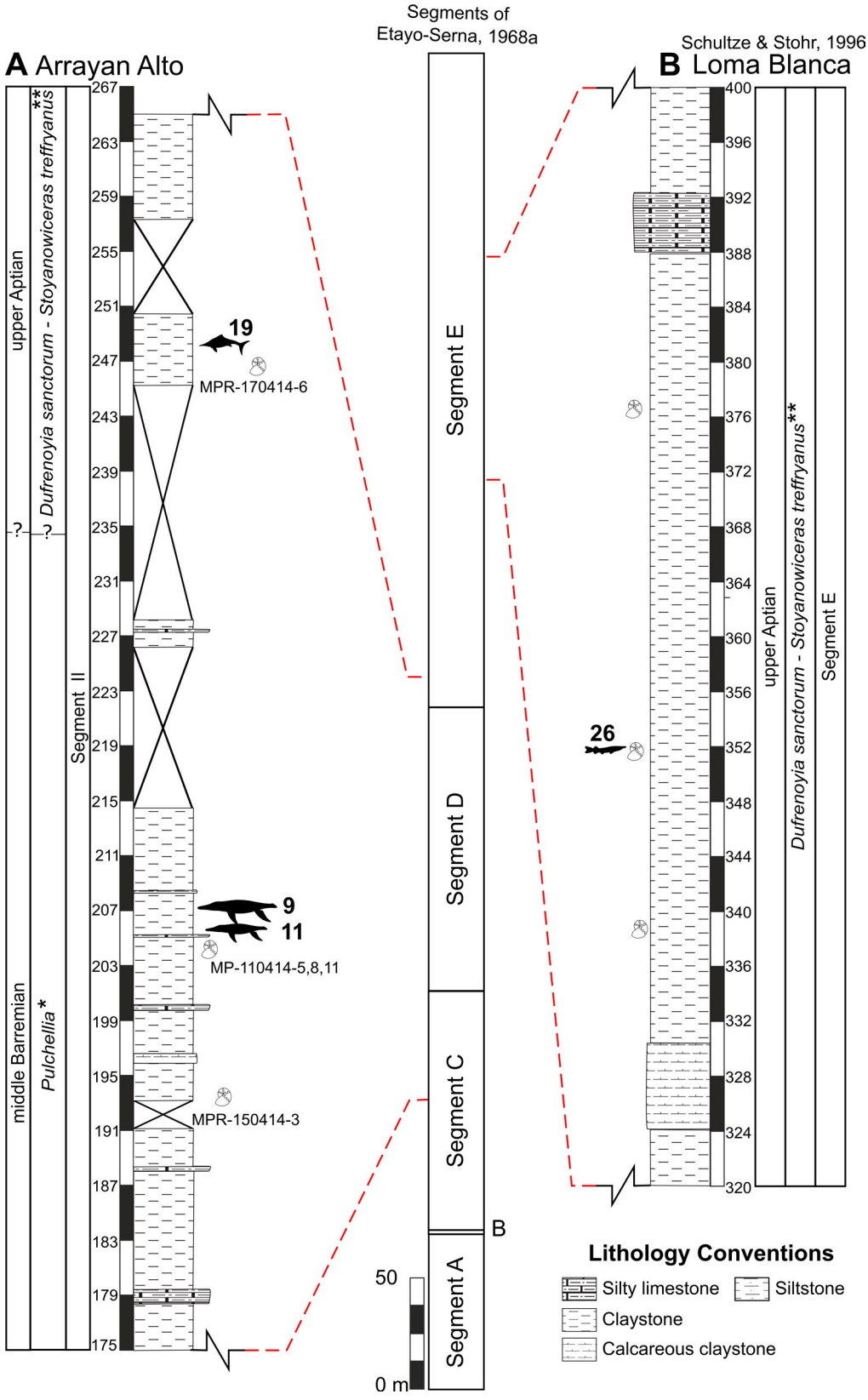

Figure 2. Generalized stratigraphic columns from two localities of Sáchica, correlated with the segments stated by Etayo-Serna (1968a) within the Arcillolitas abigarradas Member. A, Arrayán Alto section (portion bearing marine vertebrates); B, Loma Blanca section (modified from Schulzte and Stohr, 1996). *, Barremian ammonoid biozones of Bürgl, 1956a; **, Aptian ammonoid bionozes of Etayo-Serna, 1979. The information associated with the number accompanying the marine vertebrate silhouettes can be consulted in Table 1.

PEDRO LUIS SECTION

According to Páramo-Fonseca (1997), the ichthyosaur specimen DON-19671, holotype of "*Kyhytysuka*" *sachicarum*, came from a detached concretion found in the Pedro Luis Hill, north of Villa de Leiva town. We visited the finding site and described the stratigraphic section outcropping at the locality, between coordinates N 5º39'07.0"; W73º31'33.3" and N 5º39'0.17"; W73º32'08.4" (Fig. 1). In the described section we locate the approximate stratigraphic origin of this specimen.

This section comprises 23 meters of grayish claystones, interspersed with sporadic layers of calcareous claystone, silt, and competent layers of silty limestone. As in the La Cabrera section, the silty limestones form steps toward the counter slope. The concretions are small in size (diameter <10 cm) and are rare in the entire described section, they are only present in some intervals (meters 2-3, 4-5, 17-19, 20-22) (see Supplemental Data 1).

The presence of several competent layers of silty limestone within a thick succession of grayish claystones, altogether with the size and scarcity of the concretions, allows for correlating the described section with the Segment C of Etayo-Serna (1968a). Within the concretions found in the layers of meters 8-9, we collected specimens of the ammonoids *Heinzia* sp. Sayn, 1891 (CB050222-1) and *Gerhardtia* sp. Hyatt, 1903 (CB050222-2 and CB060222-2) (see Supplemental Data 2, Fig. 10C; 11B-C), and in concretions of the meters 20-22, we collected the ammonoid *Colchidites* sp. Djanélidzé (1926) (MP061121-5) (see Supplemental Data 2, Fig. 8B). Patarroyo (2000; 2020) includes the genera *Heinzia* and *Gerhardtia* in his lower upper Barremian biozone *Gerhardtia veleziensis* and the genus *Colchidites* in his upermost Barremian biozone *Colchidites breistrofferi*. As the beds of the Pedro Luis Hill provided upper Barremian ammonoids, we conclude that the specimen DON-19671 comes from the upper Barremian (sensu Patarroyo, 2000; 2020) of the segment C of Etayo-Serna (1968a) (Fig. 3B).

EL ROBLE SECTION

This section was described in the El Roble locality, north of Villa de Leiva town, outcropping between coordinates N 5º40'04.0"; W73º32'11.1" and N 5º40'01.0"; W73º32'08.4" (Fig. 1). In this locality the published ichthyosaur specimen CIP-GA-01042014 referred to *"Kyhytysuka" sachicarum* was found (Córtes *et al*., 2021; Maxwell *et al.*, 2019). In their description of this specimen, Maxwell *et al.* (2019) provided the geographic coordinates of the finding site but do not provide details on the stratigraphic origin of the specimen. However, based on an ammonite referred to *Colchidites* sp., these authors indicate the ichthyosaur "is uppermost Barremian in age" (here understood as collected from the uppermost Barremian). Therefore, to correlate the stratigraphic provenance of the specimen CIP-GA-01042014 with the segments of Etayo-Serna (1968a), we visited the finding site and described a stratigraphic section.

The stratigraphic section comprises 21.5 meters of calcareous claystones and siliciclastic claystones, interspersed with sporadic layers of siltstone and competent layers of silty limestone. As in La Cabrera and Pedro Luis's sections, the silty limestones form steps toward the counter slope. The concretions are medium in size (diameter ~10 – 25 cm) and are only found in intervals 8-9 meters and 17-18 meters. Gypsum is scarce, and only appears forming lenses in the first three meters (see Supplemental Data 1).

The ichthyosaur CIP-GA-01042014 comes from a calcareous clay layer corresponding to meter 17 of the described section (Fig. 3C and Supplemental Data 1). The presence of competent silty limestones and the low content of concretions allows for correlating this section with part of the segment C of Etayo-Serna (1968a). In the layers of meters 8-9 and meter 16, ammonoids referred to *Heinzia* (CB160722-1B, 4, 12) and *Gerhardtia* (CB070222-2) were collected (see Supplemental Data 2, Fig. 10A-B, D; 11A). These taxa are included by Patarroyo (2000; 2020) in his lower upper Barremian *Gerhardtia veleziensis* biozone. However, one meter above (meter 17), at the same level from where the ichthyosaur CIP-GA-01042014 comes from, an ammonoid identified as *Colchidites* sp. (CB070222-1) was found (see Supplemental Data 2, Fig. 8A); this genus is included by Patarroyo (2000) in his uppermost Barremian *Colchidites breistrofferi* biozone. According to this, the stratigraphic position of the ichthyosaur CIP-GA-01042014 is here located in the upper part of the segment C of Etayo-Serna (1968a) (Fig. 3C).

MONSALVE-1 SECTION

This section was described in the Monsalve hill, west of Villa de Leiva town, outcropping between coordinates N 5º39'07.2"; W73º34'47.3" and N 5º39'02.7"; W73º34'49.9" (Fig. 1). In this section, the stratigraphic provenance of the unpublished (currently under study) ophthalmosaurid ichthyosaur specimen FCG-CBP-8 was located on the base of its geographic provenance.

The described section consists of 24 meters of claystones interspersed with sporadic layers of calcareous claystone and frequent competent layers of silty limestone. Abundant gypsum lenses are found in the lower part of the section (up to meter 11) but disappear in the upper part of the section. There are calcareous concretions in almost the entire section; these are common in meters 5 to 10 and from meters 14 to 24. The concretions are 10 to 20 cm in diameter. There is an increase in the size of the concretions (diameter> 30 cm to 50 cm) from meter 14 to meter 18; then, they decrease in size again (diameter <20 cm). At the top of the section, there is a thick layer (~ 1 m) of silty limestone that stands out on the ground as a cornice and is overlaid by a layer of fibrous calcite approximately 10 cm thick (see Supplemental Data 1).

The FCG-CBP-8 specimen comes from the stratigraphic interval between meters 6 to 7 of the described section (Fig 4A and Supplemental Data 1). The thick layer of silty limestone observed in this section at meter 24 is correlated with segment B of Etayo-Serna (1968a) based on the similarity of its lithology and its expression in the terrain. Furthermore, the presence of concretions of 50 cm in diameter below meter 24 (meters 18-24) suggests that the first 23 meters of the section correlate to segment A of Etayo-Serna (1968a). Therefore, it can be concluded that the FCG-CBP-8 specimen comes from the rocks of segment A of the Etayo-Serna (1968a) (Fig. 4A). Some ammonoids were collected at meter 8 (1 m above the ichthyosaur specimen) and were identified as *Pedioceras* sp. Gerhardt (1897) (CB140121-3,5,7) and *Acrioceras julivertii* Etayo-Serna, 1968b (CB140121-8) (see Supplemental Data 2, Fig. 2A-C; 3). This last taxon was included by Patarroyo (2000) in the *Nicklesia pulchella* biozone, which according to this author, represents the lower part of the lower Barremian in Colombia. The FCG-CBP-8 specimen is, therefore, correlated with the *Nicklesia pulchella* biozone of Patarroyo (2000) (Fig. 4A).

MONSALVE-2 SECTION

This section was described in the Monsalve hill, west of Villa de Leiva town, outcropping between coordinates N 5º38'33.8"; W73º35'12.0" and N 5º38'35.9"; W73º35'11.0" (Fig. 1). In this stratigraphic section, we located the stratigraphic provenance of the unpublished pliosaurid specimen CFSTA 2-1 (currently in prep. by CDB-C and MEP-F), based on the geographic location of its discovery site.

This section comprises 18 meters of claystones interspersed with four layers of competent silty limestone. The base of the section (~ 2 m) is characterized by whitish claystones with flattened ammonoids covered by gypsum. Small (<5 cm) clayey nodules are found at the base of the section, but ascending stratigraphically, these nodules disappear, and medium to small calcareous concretions (diameter <15 cm) appear (see Supplemental Data 1).

Based on the geographic origin of the specimen CFSTA 2-1, it was established that it was extracted from levels corresponding to meters 14-16 of the described section (Fig. 4B and Supplemental Data 1). According to Etayo-Serna (1968a), at the top of his segment D, there is a level of white claystones with flattened ammonoids covered by gypsum. Due to the presence of a level with these features at the base of the described section, it was determined that the section Monsalve-2 corresponds to the top of segment D and the base of segment E of Etayo-Serna (1968a) (Fig.4B). In this stratigraphic section, one ammonoid specimen from meter 6 was collected. This specimen was identified as *Cheloniceras* (*Epicheloniceras*) *carlosacostai* (CB150121-2) (see Supplemental Data 2, Fig. 4D). This species is included by Etayo-Serna (1979) in the biozone of *Dufrenoyia sanctorum – Stoyanowiceras treffryanus*, which according to this author, indicates an upper Aptian in Colombia. In conclusion, the stratigraphic provenance of the CFSTA 2-1 specimen is located in the basal portion of segment E of Etayo-Serna (1979) (Fig. 4B).

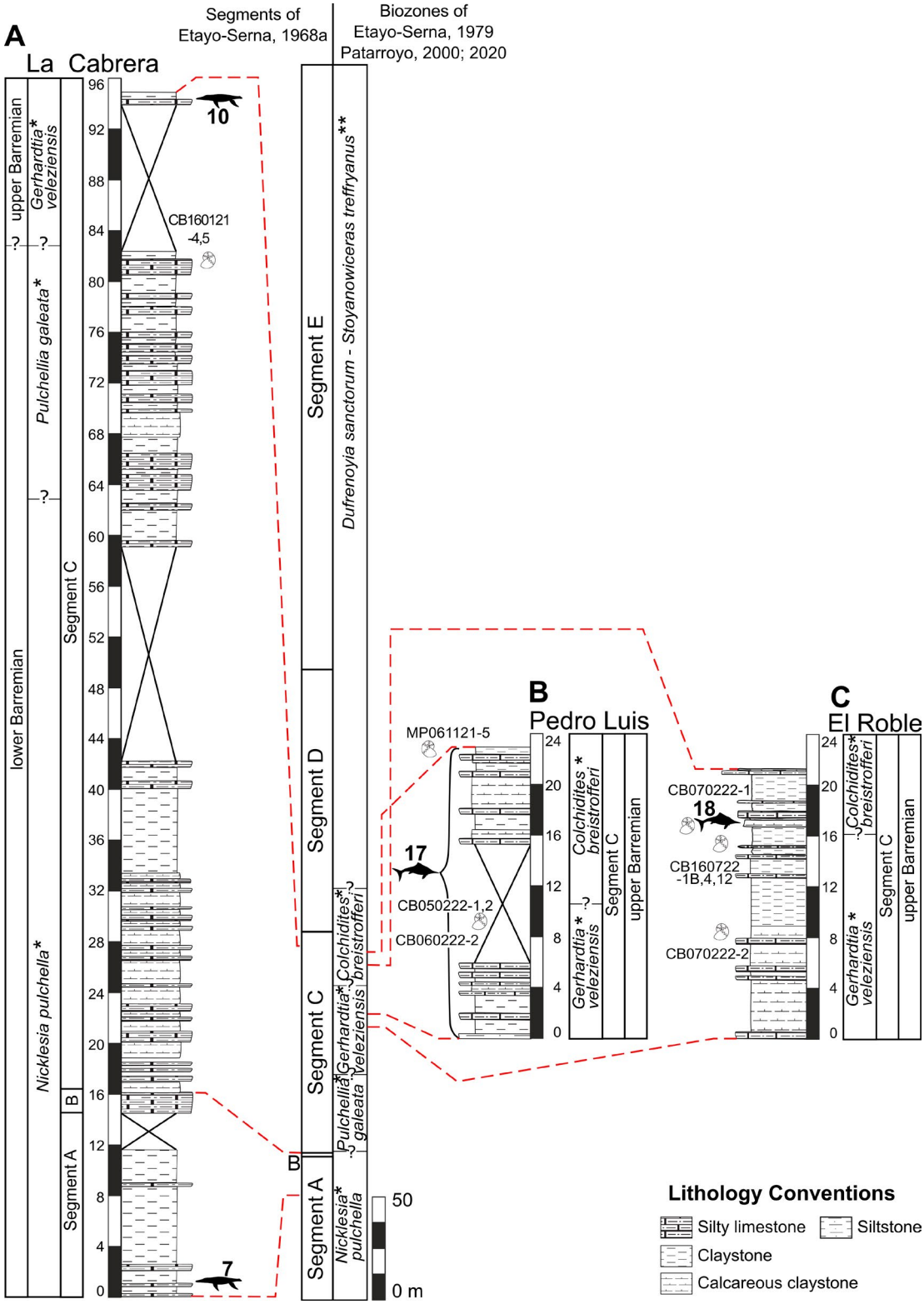

Figure 3. Generalized stratigraphic columns from three localities of Villa de Leiva, correlated with the segments stated by Etayo-Serna (1968a) within the Arcillolitas abigarradas Member, and with the Barremian ammonoid biozones of Patarroyo (2000). A, La Cabrera Hill section; B, Pedro Luis Hill section; C, El Roble section.*, Barremian ammonoid biozones of Patarroyo, 2000; 2020; **, Aptian ammonoid biozones of Etayo-Serna, 1979. The information associated with the number accompanying the marine vertebrate silhouettes can be consulted in Table 1.

MONSALVE-3 SECTION

This section was described in the Monsalve hill, west of Villa de Leiva town, outcropping between coordinates N 5º37'49.2"; W73º35'10.6" and N 5º37'41.3"; W73º35'08.9" (Fig. 1). One published and three unpublished (currently under study) specimens come from the locality where this section was described. The published specimen is the ichthyosaur *Muiscasaurus catheti* (FCG-CBP-16) (Páramo-Fonseca *et al.*, 2021). The unpublished specimens include the elasmosaurid FCG-CBP-3, the pliosaurid FCG-CBP-4, and the ophthalmosaurid ichthyosaur FCG-CBP-18. We visited the finding site of the specimen FCG-CBP-16 and refine the coordinates given by Páramo-Fonseca *et al.* (2021) in N 5º37'43.12"; W73º35'11.12", that correspond to the Monsalve hill (the authors gave a wrong name for this hill). According to Páramo-Fonseca *et al.* (2021) the specimen was found in beds equivalent to the segment E of Etayo Serna (1968a), and numerous ammonoids collected in the ichthyosaur finding site indicated the upper Aptian *Dufrenoyia sanctorum – Stoyanowiceras treffryanus* biozone of Etayo-Serna (1979). The stratigraphic position of all the specimens collected in the Monsalve-3 section was determined based on the geographic location of their finding sites.

This section comprises 40 meters of claystones, interspersed with sporadic layers of calcareous claystones and regular competent layers of silty limestone. Calcareous concretions are found throughout the section. The concretions tend to be primarily small (diameter <10 cm), although some medium-sized are found in the upper part of the section (diameter 10 – 20 cm). In the first 12 meters, it is common to find gypsum lenses and concretions covered by gypsum; however, after 12 meters, the gypsum disappears (see Supplemental Data 1).

The specimens FCG-CBP-4, FCG-CBP-3, come from levels of calcareous claystones corresponding to meter 27 of the described section (Fig. 4C and Supplemental Data 1). The specimens FCG-CBP-16 and FCG-CBP-18 come from levels of calcareous claystones corresponding to meter 39 of the described section (Fig. 4C and Supplemental Data 1).

In this section, we did not find lithological characteristics or stratigraphic boundaries that would allow a correlation of our section with the segments of Etayo-Serna (1968a). However, given the spatial and stratigraphic relationship of this section with the other two sections described in the Monsalve hill, it was estimated that our described section corresponds to a portion of the segment E of Etayo-Serna (1968a). To achieve a more precise correlation of our described section within the segment E of Etayo-Serna (1968a), we measured over the map published by Etayo-Serna (1968a) the distance between the GPS point corresponding to the uppermost level described in our section and the drawn upper limit of the Arcillolitas abigarradas Member. We calculated an approximate thickness of the uppermost missing portion of the Arcillolitas abigarradas Member in our section from this distance. This calculated thickness was 34 meters. Therefore, the specimens FCG-CBP-4, FCG-CBP-3, come from layers 45 to 47 meters below the upper limit of segment E, and the specimens FCG-CBP-16 and FCG-CBP-18 come from layers 35 to 36 meters below the upper limit of segment E. Thus, it is established that all the specimens included in the Monsalve-3 section come from the upper half of segment E of Etayo-Serna (1968a) (Fig. 4C).

A clayey level with abundant remains of crushed ammonoids was found at meter 30, approximately 9 m below the stratigraphic provenance of the ammonoids reported by Páramo-Fonseca *et al.* (2021) with the ichthyosaur FCG-CBP-16. Some of these ammonoids were identified as *Dufrenoyia* sp. Kilian and Reboul,1915 (CB070321-1, 2 and CB070321-4 to 10) and *Stoyanowiceras* sp. Karsten, 1858 (CB070321-3) (see Supplemental Data 2, Fig. 5; 6A-C, E-J). These taxa are included by Etayo-Serna (1979) in the biozone of *Dufrenoyia sanctorum – Stoyanowiceras treffryanus*, which according to this author indicates the upper Aptian in Colombia.

LA CATALINA SECTION

This section was described in the La Catalina hill, near the San Roque rural school, west of Villa de Leiva town, outcropping between coordinates N 5º37'49.2"; W73º35'10.6" and N 5º37'41.3"; W73º35'08.9" (Fig. 1). In this section, we located the stratigraphic provenance of the published plesiosaur *Callawayasaurus colombiensis* specimens UCMP 38349 and UCMP 125328; IGMp174997 (Welles, 1962) and the shark *Protolamna ricaurtei* specimen FCG-CBP-93 (Carrillo-Briceño *et al.*, 2019), and the unpublished (currently under study) specimen CFSTA090318 containing remains of shark and turtle. According to Welles (1962), the specimens UCMP 38349 and UCMP 125328; IGMp174997 were found in La Catalina hill. Etayo-Serna (1968a) states that these specimens come from his segment E. According to Carrillo-Briceño *et al.* (2019), the specimen FCG-CBP-93 was collected from the Arcillolitas abigarradas Member; however, the authors did not provide further details on the stratigraphic origin of the specimen.

This section comprises 24 meters of claystones, interspersed with occasional layers of calcareous claystone, silt, and competent layers of silty limestone. The concretions are small in size (diameter <10 cm) and are rare in the entire described section (see figure 3 and Supplemental Data 1). Gypsum is scarce, and only appears in the form of lenses in some intervals (meters 5-6, 9-11, and 20-21). In the first basal 7 meters of the described section, whitish clays with crushed ammonites covered by gypsum were found (see Supplemental Data 1).

Both specimens CFSTA090318 and FCG-CBP-93 come from a calcareous clay layer corresponding to meter 21 of the described section (Fig. 4D and Supplemental Data 1). A precise geographical location of the specimens UCMP 38349 and UCMP 125328; IGMp174997 is unknown; however, according to the figure 2 of Welles (1962), the specimens were found in the structural slope of the hill, which allow us to locate the specimens in the upper levels of the described section. As for section Monsalve-2, the level of whitish claystones with flattened ammonoids at the base of the section is correlated with the top of segment D of Etayo-Serna (1968a). According to the stratigraphic position of this level, it was determined that the described section correlates with the top of segment D and the base of segment E from Etayo-Serna (1968a). In agreement with this, all the specimens located in this section come from the basal layers of segment E of Etayo-Serna (1968a) (Fig 4D). Furthermore, several ammonoids were found in different layers of the first 6 meters of the section. These ammonoids were identified as *Cheloniceras* (*Epicheloniceras*) *carlosacostai* (CB120121-2,3 and CB130121-7), *Dufrenoyia* sp. (CB120121-1), and *Riedelites obliquum* (Riedel, 1938) (CB130121-1,4) (see Supplemental Data 2, Fig. 4A-C; 6D; 7A-B). Following Etayo-Serna (1979), these taxa are included in the upper Aptian biozone of *Dufrenoyia sanctorum – Stoyanowiceras treffryanus*. Thus, the stratigraphic provenance of the specimens UCMP 38349, UCMP 125328; IGMp174997, CFSTA090318 and FCG-CBP-93 is also correlated with the *Dufrenoyia sanctorum – Stoyanowiceras treffryanus* biozone of Etayo-Serna (1979).

EL FÓSIL SECTION

This section was described in vicinities of the Museo El Fósil, west of Villa de Leiva town, outcropping between coordinates N 5º38'14.6"; W73º33'32.6" and N 5º38'13.3"; W73º33'31.2" (Fig. 1). In this section, we located the stratigraphic provenance of the published pliosaurid *"Monquirasaurus" boyacensis* specimen MJACM1 (Hampe, 1992; Noè and Gómez-Pérez, 2020). Hampe (1992) indicates that the specimen comes from segment V of Forero and Sarmiento (1985), which is equivalent to segment E of Etayo-Serna (1968a) (see Forero and Sarmiento, 1985 fig. 2).

In this section, only 1.5 meters were described due to the high vegetation coverage in the area. It consists of a layer of light gray clay covered by a reddish silty limestone with irregular concretions (diameter <20 cm) (see Supplemental Data 1). To achieve a more precise correlation of the described section within the segment E of Etayo-Serna (1968a), we calculated the thickness of the upper portion of the Arcillolitas abigarradas Member missing in our section based on the geological map of Etayo-Serna (1968a). The calculated thickness was 66 meters, indicating that the described section and the stratigraphic provenance of the specimen MJACM1 correlate with the upper half of the segment E of Etayo-Serna (1968a) (Fig. 4E). The numerous ammonoids reported by Etayo-Serna (1968a; pp 28-29) from his segment E and those collected from the same segment in the other stratigraphic sections here described correlate with the *Dufrenoyia sanctorum – Stoyanowiceras treffryanus* biozone of Etayo-Serna (1979), which according to this author indicates the upper Aptian in Colombia.

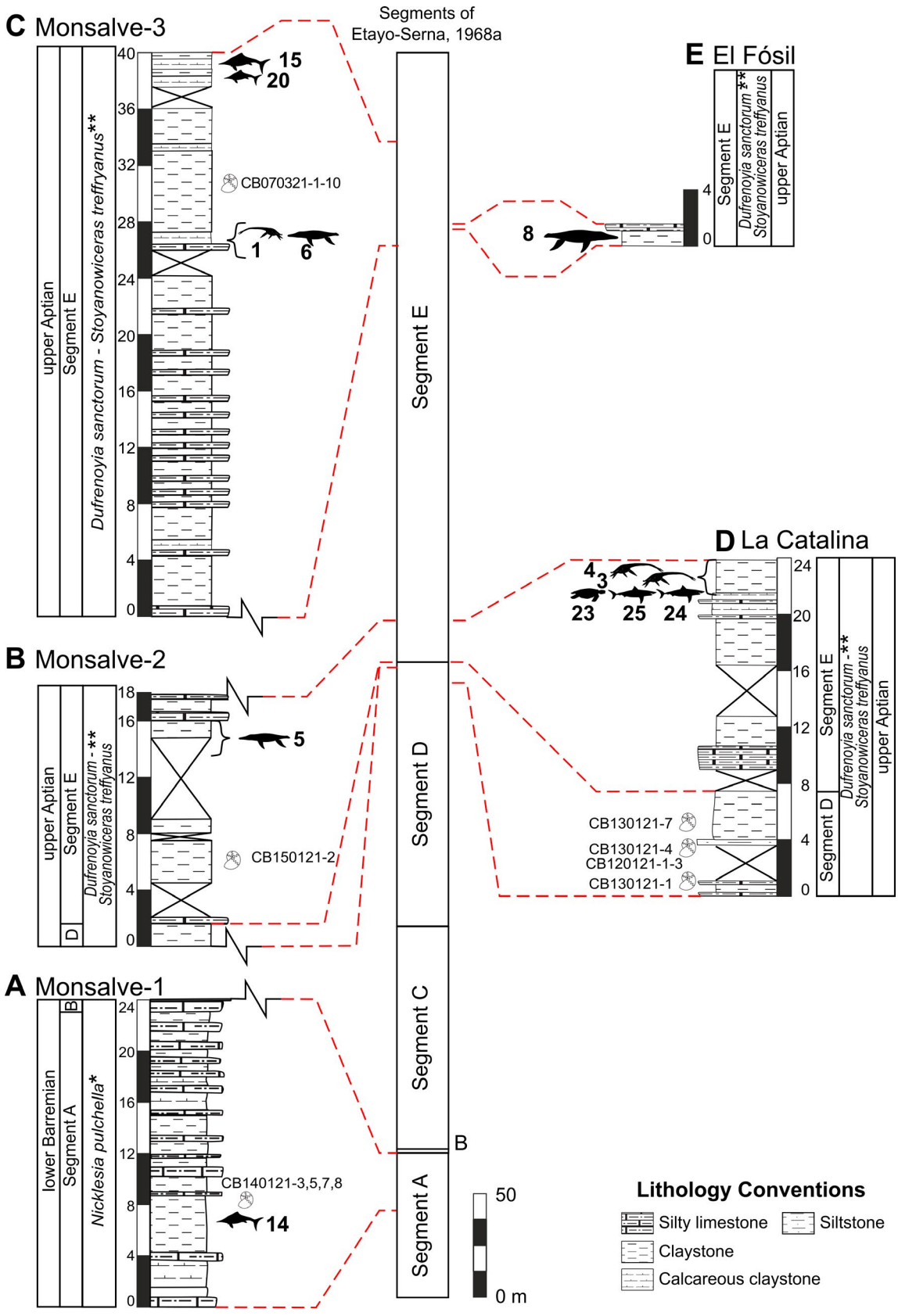

Figure 4. Generalized stratigraphic columns from three localities of Villa de Leiva, correlated with the segments stated by Etayo-Serna (1968a) within the Arcillolitas abigarradas Member. A-C, Monsalve Hill sections. D, La Catalina hill section; E, El Fósil section. *, Barremian ammonoid biozones of Patarroyo, 2000; 2020; **, Aptian ammonoid biozones of Etayo-Serna, 1979. The information associated with the number accompanying the marine vertebrate silhouettes can be consulted in Table 1.

Specimens not located in the stratigraphic sections

Specimen UN-DGR-1000

The description of the pliosaurid *Acostasaurus pavachoquensis* specimen UN-DGR-1000 was published by Gómez-Pérez and Noè (2017). According to these authors, the specimen was found in the Pavachoque creek in La Yuca Hill (municipality of Sutamarchán), in the lower part of the Arcillolitas abigarradas Member with the ammonoid *Nicklesia pulchella*, which dates the beds as lower Barremian. Accordingly, the stratigraphic position of the specimen UN-DGR-1000 can be correlated with segment A of Etayo-Serna (1968a).

Specimen CIP-0001

The description of the teleosauroid specimen CIP-0001 was published by Cortés *et al.* (2019). According to these authors, the specimen was found in La Cabrera Hill (Villa de Leiva). Although the authors give coordinates of the finding site, it is unknown if the specimen was found in situ or as a tumbled concretion, as it is common to find fossils in Villa de Leiva. Therefore, it was not possible to establish its exact stratigraphic provenance. Cortés *et al.* (2019) report the ammonoid genus *Gerhardtia* in association with the teleosauroid that the authors relate with the upper Barremian *Gerhardtia veleziensis* zone of Patarroyo (2000; 2020). According to this, the stratigraphic provenance of the specimen CIP-0001 is here located in segment C of Etayo-Serna (1998) without specifying its position within this segment.

Specimen FCG-CBP-22

The description of the specimen FCG-CBP-22 of the elasmosaurid plesiosaur *Leivanectes bernardoi* was published by Páramo-Fonseca *et al.* (2019a). According to these authors, the specimen was found in La Cabrera Hill (Villa de Leiva), but the exact location of the finding site is unknown. However, on the base of one ammonoid identified as *Cheloniceras* (*Epicheloniceras*) *carlosacostai*, found in the matrix surrounding the plesiosaur specimen, Paramo-Fonseca *et al.* (2019a) state that the specimen comes from upper Aptian rocks of the Arcillolitas abigarradas Member and locate it in the segment E of Etayo-Serna (1968a).

Specimen FCG-CBP-87

The description of the ichthyosaur specimen FCG-CBP-87 (*Platypterygius* sp.) was published by Cortés and Páramo-Fonseca (2018). Following these authors, the specimen was collected in La Cabrera Hill (Villa de Leiva), but the exact location of the finding site is unknown. Cortés and Páramo-Fonseca (2018) state that the specimen comes from the Arcillolitas abigarradas Member, and, based on the ammonoid *Nicklesia pulchella* found in the matrix surrounding the ichthyosaur specimen, they conclude that the specimen comes from lower Barremian rocks. This information allows us to locate the stratigraphic provenance of the specimen FCG-CBP-87 in segment A of Etayo-Serna (1968a).

Specimen FCG-CBP-28

The ichthyosaur specimen FCG-CBP-28 (Ophthalmosauridae) is currently under study. This specimen was found as a tumbled concretion in La Cabrera Hill (Villa de Leiva), so its exact geographical origin is unknown. Therefore, it is not possible to establish its exact stratigraphic position. However, in the rock surrounding the fossil, there are numerous ammonoids, some of which were identified as *Acanthoptychoceras* sp. (see Supplemental Data 2, Fig. 1). This ammonoid genus is included by Patarroyo (2000) in his lower Barremian *Nicklesia pulchella* biozone. This information allows us to locate the stratigraphic provenance of the specimen FCG-CBP-28 in segment A of Etayo-Serna (1968a).

Specimen MPVL-667

The pliosaurid specimen MPVL-667 was described and identified as *Stenorhynchosaurus munozi* by Páramo-Fonseca *et al.* (2023). This specimen was collected from a trundled concretion found in La Yuca creek (Sutamarchán). The only available information about its stratigraphic provenance allows us to state that the specimen comes from the Barremian Beds of the Arcillolitas abigarradas Member (see Páramo-Fonseca *et al.*, 2023). With this information, we can only locate the stratigraphic provenance of the specimen MPVL-667 within segments A, B, or C of Etayo-Serna (1968a).

Discussion

Stratigraphic distribution of marine vertebrate specimens

We performed a lithostratigraphic, biostratigraphic, and graphic correlation between all stratigraphic columns, the specimens with associated biostratigraphic information and the reference segments defined by Etayo-Serna (1968a) for the Arcillolitas abigarradas Member. This correlation shows us that almost all the marine vertebrate specimens originate from four stratigraphic intervals (Fig. 5). Each of these stratigraphic intervals contains a vertebrate assemblage. Two of these assemblages are found in Barremian levels (vertebrate assemblages 1 and 2), and two in upper Aptian levels (vertebrate assemblages 3 and 4) (Fig. 5). Although the vertebrate assemblages 3 and 4 come from a single ammonoid biozone, they were here separated because a significant stratigraphic interval without vertebrates (approximately 150 m) is present between them.

Barremian vertebrate assemblages

Vertebrate assemblage 1. This assemblage includes two specimens of pliosaurid plesiosaurs *Acostasaurus pavachoquensis* (UN-DGR-1000) and MPVL-MP110210-1 and three specimens of ichthyosaurs: *Platypterygius* sp. (FCG-CBP-87), and the ophthalmosaurid FCG-CBP-8 and FCG-CBP-28 These specimens come from layers of Segment A of the Arcillolitas abigarradas Member of Etayo-Serna (1968a) (Fig. 5) and correlate with the *Nicklesia pulchella* biozone (sensu Patarroyo, 2000; 2020) or the *Nicklesia* biozone (sensu Bürgl, 1956a), which, according to these authors, represent the lower Barremian in Colombia.

Vertebrate assemblage 2. This assemblage includes three specimens of pliosaurid plesiosaurs, two specimens of *Stenorhynchosaurus munozi* (VL17052004-1 and MP050310-1), and one specimen of *Sachicasaurus vitae* (MP111209-1), two ichthyosaur specimens of *"Kyhytysuka" sachicarum* (CIP-GA-01042014 and DON-19671) and a specimen of a teleosauroid (CIP-0001). All these specimens come from the upper part of Segment C of the Arcillolitas abigarradas Member of Etayo-Serna (1968a) (Fig. 5). Except for the ichthyosaurs, all the specimens correlate with the *Gerhardtia veleziensis* biozone of Patarroyo (2000; 2020) or the *Pulchellia* biozone of Bürgl (1956a), which allows uniting them together in an assemblage. These biozones represent the lower upper Barremian (sensu Patarroyo, 2000; 2020) or the middle Barremian (sensu Bürgl, 1956a).

Although the ichthyosaur specimen CIP-GA-01042014 was found with an ammonite indicative of the *Colchidites breistrofferi* biozone of Patarroyo (2000), only one stratigraphic meter below the occurrence of this ammonite was found another ammonite indicative of his *Gerhardtia veleziensis* biozone. Therefore, this short stratigraphic distance does not justify separating this ichthyosaur specimen into a different vertebrate assemblage. Therefore, specimen CIP-GA-01042014 is linked to assemblage 2.

As discussed above, the ichthyosaur specimen DON-19671 was found as a detached concretion coming from segment C of the Arcillolitas abigarradas Member of Etayo-Serna (1968a). However, its association with one of the two ammonoid biozones of Patarroyo (2000) (*Heinzia velenziensis* or *Colchidites breistrofferi*) related to this segment, cannot be specified. Nevertheless, its origin from the upper Barremian beds (sensu Patarroyo, 2000; 2020) or middle to upper Barremian beds (sensu Burgl, 1956a) within the segment C of Etayo-Serna (1968a) allows us to include it in the vertebrate assemblage 2 (Fig. 5).

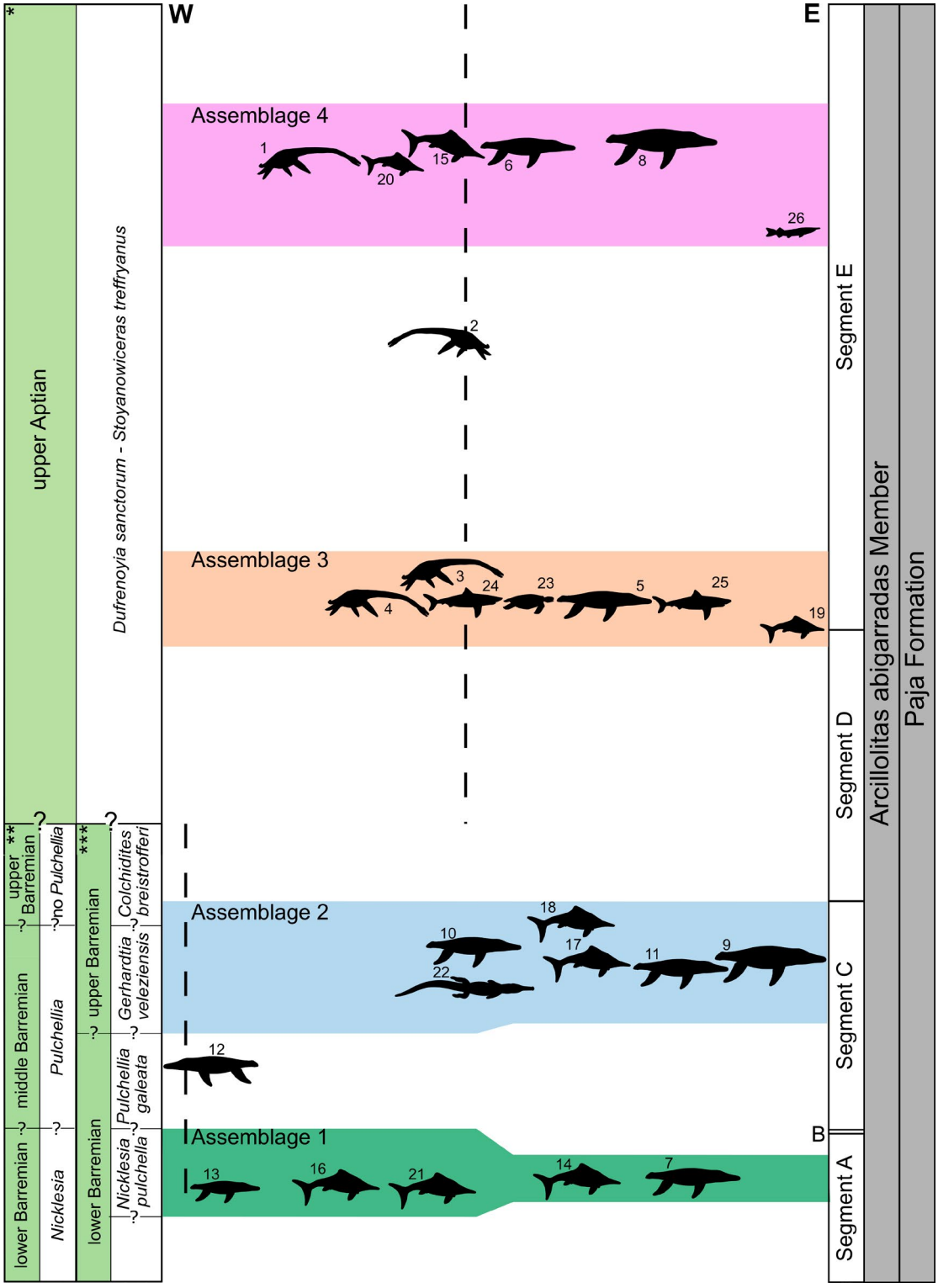

Figure 5. Diagram showing the vertebrate assemblages resulting from the correlation of the stratigraphic provenance of the specimens included in this work. *, Aptian ammonoid biozones of Etayo-Serna, 1979; **, Barremian biozones of Bürgl, 1956a; ***, Barremian biozones of Patarroyo, 2000; 2020. Specimens: 1- Elasmosauridae (FCG-CBP-3); 2- *Leivanectes bernardoi* (FCG-CBP-22); 3- *Callawayasaurus colombiensis* (UCMP 38349); 4- *C. colombiensis* (UCMP 125328; IGMp174997); 5- Pliosauridae (CFSTA 2-1); 6- Pliosauridae (FCG-CBP-4); 7- Pliosauridae (MPVL-MP110210-1); 8- *"Monquirasaurus" boyacensis* (MJACM 1); 9- *Sachicasaurus vitae* (MP111209-1); 10- *Stenorhynchosaurus munozi* (VL17052004-1); 11- *S. munozi* (MP050310-1); 12- *S. munozi* (MPVL-667); 13- *Acostasaurus pavachoquensis* (UN-DGR-1000); 14- Ophthalmosauridae (FCG-CBP-8); 15- Ophthalmosauridae (FCG-CBP-18); 16- Ophthalmosauridae (FCG-CBP-28); 17- *"Kyhytysuka" sachicarum* (DON-19671); 18- *"K." sachicarum* (CIP-GA-01042014); 19- *Muiscasaurus catheti* (FCG-CBP-74); 20. *M. catheti* (FCG-CBP-16); 21- *Platypterygius* sp. (FCG-CBP-87); 22- Teleosauroidea (CIP-0001); 23- Testudines (CFSTA090318); 24- Lamniforme (CFSTA090318); 25- *Protolamna ricaurtei* (FCG-CBP-93); 26- *Vinctifer* sp. (MB f. 3500).

Upper Aptian vertebrate assemblages

Vertebrate assemblage 3. This assemblage includes two specimens of the elasmosaurid plesiosaur *Callawayasaurus colombiensis* (UCMP 38349 and UCMP 125328; IGMp174997), one specimen of a pliosaurid plesiosaur (CFSTA 2-1); one specimen of the ichthyosaur *Muiscasaurus catethi* (CIP-FCG-CBP-73); one specimen of a turtle (CFSTA090318), and two specimens of lamniform sharks, one of *Protolamna ricaurtei* (FCG-CBP-93) and other not yet identified (CFSTA090318). These specimens come from the lower part of the segment E of the Arcillolitas abigarradas Member of Etayo-Serna (1968a) (Fig. 5) and correlate with the *Dufrenoyia sanctorum - Stoyanowiceras treffryanus* b iozone o f E tayo-Serna (1979) w hich, a ccording t o t his a uthor, represents the upper Aptian in Colombia.

Vertebrate assemblage 4. This assemblage includes one specimen of elasmosaurid plesiosaur (FCG-CBP-3); two specimens of pliosaurid plesiosaurs, one of *"Monquirasaurus" boyacensis* (MJACM1) and the unidentified pliosaurid FCG-CBP-4, two specimens of ophthalmosaurid ichthyosaurs, one of *Muiscasaurus catheti* (FCG-CBP-16) and the unidentified ophthalmosaurid FCG-CBP-18, and one specimen of a bony fish *Vinctifer* sp. (MB f. 3500). These specimens come from the upper part of the E segment of the Arcillolitas abigarradas Member of Etayo-Serna (1968a) (Fig. 5) and, like the specimens of assemblage 3, correlate with the *Dufrenoyia sanctorum - Stoyanowiceras treffryanus* biozone of Etayo-Serna (1979) which, according to this author, represents the upper Aptian in Colombia.

Specimens with imprecise stratigraphic provenance

Two of the specimens in this study, the *Leivanectes bernardoi* specimen FCG-CBP-22 and the pliosaurid specimen MPVL-667 could not be included in one of the vertebrate assemblages because their imprecise stratigraphic or biostratigraphic provenance.

As mentioned above, the plesiosaur specimen FCG-CBP-22 comes from the segment E of the Arcillolitas abigarradas Member of Etayo-Serna (1968a) and was correlated with the *Dufrenoyia sanctorum - Stoyanowiceras treffryanus* biozone of Etayo-Serna (1979). However, without more precise information, the stratigraphic provenance of this specimen within the thick segment E cannot be specified. Therefore FCG-CBP-22 could be part of the assemblage 3 or 4 (Fig. 5).

The stratigraphic provenance of the pliosaurid specimen MPVL-667 was established in the Barremian interval of the Arcillolitas abigarradas Member, correlating with the segments A, B, and C of Etayo-Serna (1968a). Therefore, it could be linked to either of the two Barremian assemblages, meaning that the specimen MPVL-667 could be part of the vertebrate assemblage 1 or 2 (Fig. 5).

4. Conclusions

We defined the stratigraphic position of 26 specimens of marine vertebrates from beds of the Arcillolitas abigarradas Member of the Paja Formation in the Villa de Leiva – Sáchica - Sutamarchán region. We described a complete stratigraphic section of the Arcillolitas abigarradas Member from Sáchica, Boyacá, and eight partial stratigraphic sections of this Member from Villa de Leiva. We refine the information on the stratigraphic provenance of some of the specimens included in this study, mainly that of three holotype specimens (*Muiscasaurus catheti* (CIP-FCG-CBP-73), *"Kyhytysuka" sachicarum* (DON-19671) and *Protolamna ricaurtei* (FCG-CBP-93)), which stratigraphic origin was not previously specified beyond the Arcillolitas abigarradas Member. A lithostratigraphic, biostratigraphic, and graphic correlation of the gathered information allowed us to establish four vertebrate assemblages representing coeval faunas within the Arcillolitas abigarradas Member, two from the Barremian and two from the upper Aptian. The paleoecological implications of the marine vertebrae assemblage established in this work are currently under study.

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Supplemental Material

- Supplemental Data 1: Detailed stratigraphic columns described in this study.
- Supplemental Data 2: Identification of ammonoids collected in this study.
- Supplemental Data 3: Detailed stratigraphic column of Arrayán Alto section and identified ammonoids.

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