

Plesiosaurs, Palaeoenvironments, and the Paja Formation Lagerstätte of Central Colombia: An Overview

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Abstract The Cretaceous Paja Formation of the alto Ricaurte of the Eastern Cordillera of central Colombia was laid down under an epicontinental sea during Hauterivian – Aptian times. The Paja Formation epicontinental sea was home to a diverse, and now well-preserved, pelagic marine fauna that includes members of Plesiosauria, other marine reptiles, fish, and ammonites. However, the benthic fauna is depauperate, preserving just a few thin-shelled bivalves and evidence of microbial mats. This suggests dysoxic–anoxic bottom waters, separated from oxic surface waters by a chemocline–pycnocline. The exceptional preservation of the Paja Formation fauna makes the alto Ricaurte a unique Lower Cretaceous marine vertebrate Lagerstätte. Previous palaeoenvironmental interpretations of the Paja Formation, based on observations of the gypsiferous, dark mudrock sequence, suggested an intertidal evaporitic (sabkha) environment. However, integration of sedimentological, palaeobiological, taphonomic, and diagenetic data provides evidence for deeper water conditions. The exquisite preservation and articulation of the skeletons of large marine reptiles, three-dimensionally preserved fish, beautifully ornamented ammonites, and delicate plants, do not accord with a sabkha environment. Sabkha is typical of mid-latitude, dryer climates under the descended limb of the Hadley atmospheric cell, rather than a wet tropical equatorial location of the Paja Formation. Mineralogical arguments used to infer the presence of sabkha are not primary depositional features, but due to secondary migration of mineral-rich fluids. These fluids probably had their source in the earliest Cretaceous topographic high now beneath the Sabana de Bogotá, and were driven by hydraulic pressure generated by volumetric changes due to hydration of anhydrite into gypsum due to the post-Cretaceous rise of the northern Andes mountain chain. The separation of primary and secondary diagenetic features is thereby critical for understanding the evolution of the Paja Formation sedimentary basin in the alto Ricaurte.

Keywords: Lagerstätte, Lower Cretaceous, Paja Formation, palaeoenvironments, Plesiosauria.

Resumen La Formación Paja de la región del alto Ricaurte en la cordillera Oriental de Colombia se depositó en un mar epicontinental durante el Hauteriviano–Aptiano. Este mar tenía una fauna marina pelágica diversa que se encuentra hoy en día muy bien preservada e incluye miembros del orden Plesiosauria, otros reptiles marinos, peces y amonitas. Sin embargo, la fauna bentónica está empobrecida, se conservan solo algunos bivalvos de conchilla delgada y evidencia de tapetes microbiales. Esto sugiere que las aguas profundas eran de carácter disódico–anódico, separadas de las aguas

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superficiales oxigenadas por la quimoclina–picnoclina. La preservación excepcional de la fauna de la Formación Paja hace que el alto Ricaurte sea un Lagerstätte de vertebrados marinos del Cretácico Inferior único a nivel mundial. Interpretaciones previas del paleoambiente de la Formación Paja, basadas en observaciones de la secuencia de lodolitas oscuras yesosas, sugirieron un ambiente evaporítico intermareal (*sabkha*). Sin embargo, la integración de datos sedimentológicos, paleobiológicos, tafonómicos y diagenéticos proporciona evidencia de condiciones de aguas más profundas. La exquisita preservación y la articulación de los esqueletos de grandes reptiles marinos, peces, amonitas bellamente ornamentadas y plantas delicadas no concuerdan con un ambiente de *sabkha*. Los *sabkhas* son característicos de latitudes medias y climas más secos, localizados bajo la rama descendente de la celda atmosférica de Hadley, antes que típicos de la localización más ecuatorial tropical húmeda de la Formación Paja. Los argumentos mineralógicos utilizados para inferir la presencia del *sabkha* no son característicos de deposición primaria, sino debido a la migración secundaria de fluidos ricos en minerales. Estos fluidos probablemente tenían su origen en la topografía alta del Cretácico más temprano, ahora debajo de la Sabana de Bogotá, y fueron impulsados por la presión hidráulica generada por los cambios volumétricos debidos a la hidratación de la anhidrita en yeso como un resultado del levantamiento pos–Cretácico de la cadena montañosa norte de los Andes. Por lo tanto, la separación entre características diagenéticas primarias y secundarias es crítica para comprender la evolución de la cuenca sedimentaria de la Formación Paja en el alto Ricaurte.

Palabras clave: Lagerstätte, Cretácico Inferior, Formación Paja, paleoambientes, Plesiosauria.

1. Introduction

The Cretaceous was a “greenhouse” world (Hu et al., 2012; Larson & Erba, 1999) with high partial pressure of atmospheric carbon dioxide, high global temperatures, high rates of plate tectonic (mid–ocean ridge) activity, and no or very restricted polar ice caps (Fluteau et al., 2007; Hay, 2008; Mann & Stein, 1997; Miller et al., 2003b; Poulsen et al., 2007). These conditions resulted in high global sea levels which, associated with the generally subdued Cretaceous terrestrial topography, brought about flooding of large areas of the low lying continental margins, producing numerous shallow epicontinental, epeiric, or epicratonic seas (Bornemann et al., 2005; Immenhauser, 2009; Miller, et al., 1988). These epicontinental seas were especially prevalent in tropical and subtropical regions, with water depths typically in the range of 100 m or less, and sluggish circulation compared to modern shallow marine shelf settings (e.g., Miller & Foote, 2009). Epicontinental seas were dominated by the deposition of fine–grained siliciclastic mudrocks (silt and clay grade in varying proportions, variably termed mudstones, claystones, siltstones, and shales), and/or carbonate–rich sediments (Ruppel & Loucks, 2008), which were highly susceptible to water column stratification and bottom water and/or sediment dysoxia or anoxia (Mann & Stein, 1997; Miller & Foote, 2009; Weissert, 1981; Wignall, 1989). These oxygen–poor epicontinental seafloor conditions, associated with occasional oceanic anoxic events (OAEs) (Jenkyns, 1980, 1997; Schlanger & Jenkyns, 1976), led to frequent pres-

ervation of appreciable amounts of organic carbon (C_{org}). Total organic carbon was typically >1%, but commonly much more (Tourtelot, 1979; Tyson & Pearson, 1991; Weissert, 1981), producing black mudrock successions, which often resulted in exceptional fossil preservation.

The Paja Formation forms part of the exposures within the Eastern Cordillera of modern–day central Colombia (Figure 1). The depositional environment of the Eastern Cordillera of Colombia (ECC) is interpreted as part of a shallow, epicontinental sea lying over an extensional back–arc basin (Martínez et al., 2007) due to subduction of the Farallón Plate under the South American Plate. Roll–back of the overlying continental plate led to crustal stretching and thinning, with downwarping, which generated a low lying marine sedimentary basin (Maccellari, 1988). Later inversion of this extensional tectonic regime formed a compressional zone as the proto–Andes mountain range began to rise, resulting in uplift and ultimate unroofing and exposure of the ECC Cretaceous sedimentites (Mosolf et al., 2010). Today, the Paja Formation preserves “typical” epicontinental sea deposits, with a lithology of predominantly dark–coloured organic–rich mudrocks and a rich fossil fauna.

The thickest known outcrops of the Paja Formation are approximately 940 m (Etayo–Serna, 1979), and occur in Villa de Leiva, Sáchica, and Sutamarchán, an area known as the alto Ricaurte (Figure 1d), Boyacá Department which forms part of the altiplano Cundiboyacense of the ECC (Etayo–Serna, 1968). Around alto Ricaurte, the Paja Formation is a sequence of typically finely laminated mudrocks (shales) with occasional ar-

gillaceous limestones, fine-grained sandstones, and abundant calcareous concretions; intercalations of gypsum and calcite are frequent, and pyrite is abundant (Etayo–Serna, 1979). The Paja Formation of the alto Ricaurte is richly fossiliferous, preserving both autochthonous marine and allochthonous terrestrial faunas (Carballido et al., 2015; Etayo–Serna, 1968, 1979; Huertas, 1970). The number of fossils preserved in national and local museums, and private collections, indicates the richness of the fossiliferous deposits of alto Ricaurte.

The warm Cretaceous “waterworld” produced ideal conditions for marine organisms to flourish. Cretaceous epicontinental seas teemed with life, including the large marine reptiles and their prey: numerous fish, and uncountable invertebrates. One of the longest-lived groups of marine reptiles were Sauropterygia (Early Triassic – Late Cretaceous; Bardet, 1995; Carroll, 1988). Plesiosauria are advanced members of Sauropterygia, which during the Jurassic and Cretaceous acquired a global distribution (Bardet et al., 2014), and as large (>2 m length) marine predators and mega-predators, were important faunal elements of Cretaceous oceans (Massare, 1984, 1997). However, our understanding of Lower Cretaceous Plesiosauria is very limited (e.g., Benson & Druckenmiller, 2014; Gasparini & Goñi, 1985; Hampe, 1992), producing a major lacuna in our understanding of Cretaceous seas, and leading to the designation of this interval as the “Lower Cretaceous Gap” (Gómez–Pérez & Noè, 2017). In addition to plesiosaurs, a wide range of marine reptiles inhabited Early Cretaceous seas: the fish-shaped Ichthyosauria (ichthyosaurs), the marine Chelonia (turtles), and marine members of Crocodylia (crocodiles). Of the invertebrates, the ammonites are so abundant that it has become a tradition in alto Ricaurte to use their fossils in local buildings, and the genus *Dufrenoyia* has become a symbol of the region (Figure 2).

The Early Cretaceous is a key time for understanding the evolution of marine life, following the extinctions at the end of the Jurassic (Benson & Druckenmiller, 2014). However, relatively few complete or well-preserved Lower Cretaceous sections exist worldwide. The deposits of the alto Ricaurte preserve a comparatively complete Lower Cretaceous sedimentary sequence, of which the Hauterivian – Aptian Paja Formation forms part. The Paja Formation thereby represents one of the few epicontinental sea deposits recording the history of the Lower Cretaceous Gap. The Paja Formation preserves both a marine and terrestrial fossil fauna that is exceptional in terms of the quantity and quality. Hence, the Paja Formation is a fossil *Lagerstätte* (Gómez–Pérez & Noè, 2017; Maxwell et al., 2016), a geological formation that exhibits great diversity and exceptional fidelity of preserved palaeobiodiversity (Selden & Nudds, 2012). Of the numerous invertebrates and vertebrates recovered from the Paja Formation, some of the most important are the ammonites, which are used for global correlation, and Plesiosauria, which have begun to fill the marine reptile Lower Cretaceous Gap. This combination of completeness of

the deposits, and the exceptional fossil fauna, makes the Paja Formation of the alto Ricaurte globally important.

1.1. The Problem

The Paja Formation of the alto Ricaurte is one of the best-studied sedimentary sections in Colombia, yet numerous questions remain unanswered. Much of the primary work is in the form of unpublished undergraduate theses (e.g., Espinel–Arias & Hurtado–Henao, 2010; Galvis–Arenas & Valencia–Escobar, 2009), or has been presented as conference abstracts of restricted availability, and without full supporting data (e.g., Etayo–Serna et al., 1978; Patarroyo–Camargo et al., 2011). The environment of deposition of the Paja Formation has been interpreted as a marginal marine succession, with water depths ranging from outer-shelf to upper shore slope (e.g., Huber & Wiedmann, 1986). Interpretations based on sedimentological studies have concluded that the Paja Formation was laid down in a closed basin with restricted circulation and tranquil sedimentation, including periods of subaerial exposure resulting in an evaporitic sabkha environment (Etayo–Serna, 1968; Forero–Onofre & Sarmiento–Rojas, 1985). However, a greater water depth, comparable to the Tethyan Vocontian Basin (Bornemann et al., 2005; Mattioli et al., 2008), has been proposed based on palaeontological studies (Maxwell et al., 2016; Welles, 1962). However, this relatively deep bathymetric interpretation has been countered by evidence from the presence of turtle eggs and benthic algal mats (Etayo–Serna et al., 2015), suggesting a nearshore, terrestrial breeding ground for the turtles, and a shallow water, nearshore, subtidal environment for algal growth. In this model, marine reptile carcasses are interpreted as having floated into the Paja Formation Basin after death (Etayo–Serna, 1968), yet the often exceptional, fully articulated nature of the large vertebrates argues against a “float and bloat” model of post-mortem transport and deposition (Schäfer, 1972). Currently, these major discrepancies in interpretation remain unresolved, and hinder our understanding of Paja Formation palaeoenvironments. Hence, former interpretations require critical reappraisal based on a combination of sedimentological and palaeontological data.

1.2. Materials and Methods

In this contribution, we concentrate on the Paja Formation exposed within the alto Ricaurte, in Sáchica, Sutamarchán, and Villa de Leiva. We base our interpretations on published and other widely available data, both sedimentological (including mineralogical) and palaeobiological (vertebrate, invertebrate, and microfossil; marine and terrestrial), supplemented by personally collected specimens. We combine palaeontological, sedimentological, and diagenetic data with published studies on the modern shallow marine realm and ancient epicontinental

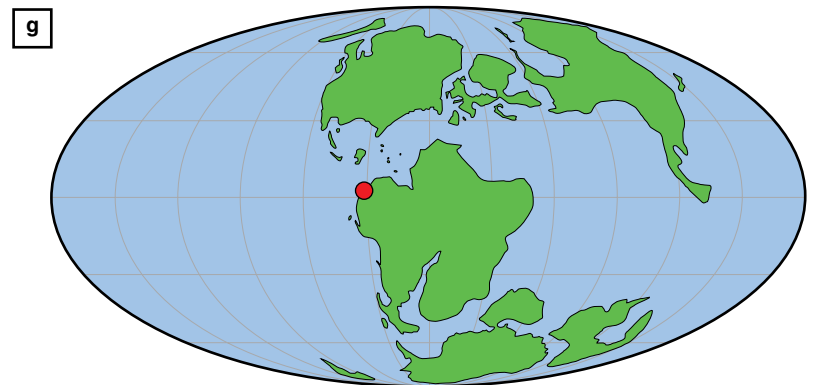
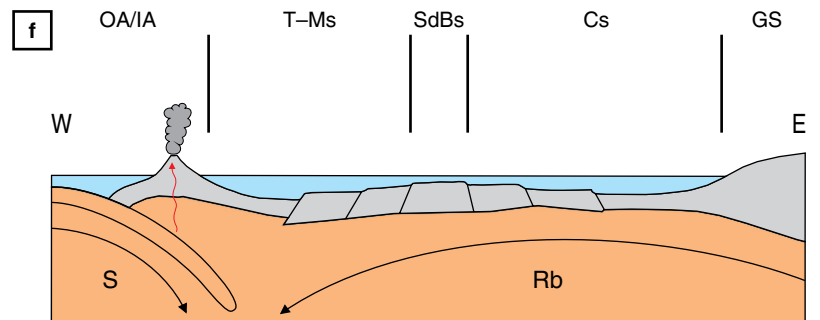
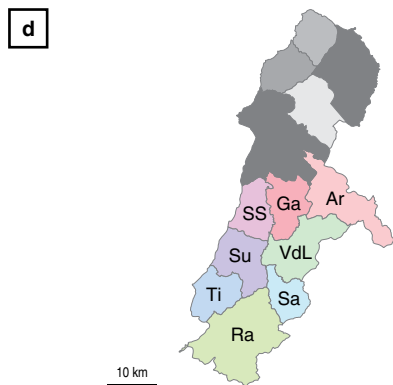
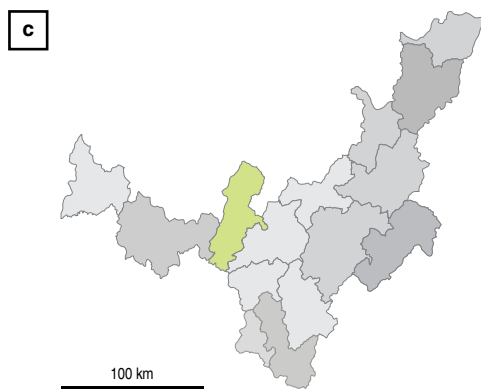


Figure 1. Maps and cross-section showing the location of the Paja Formation Basin and palaeogeological interpretations. **(a)** World map showing the position of Colombia (green). **(b)** Map of Colombia showing the departments (Department of Boyacá, green; Bogotá, red). **(c)** Department of Boyacá showing the provinces (Ricaurte Province, green). **(d)** Ricaurte Province showing municipalities (alto Ricaurte coloured showing the municipalities: (Ar) Arcabuco, (Ga) Gachantivá, (Ra) Râquira, (Sa) Sâchica, (SS) Santa Sofia, (Su) Sutamarchân, (Ti) Tinjacá; (VdL) Villa de Leiva), and bajo Ricaurte, greys. **(e)** Topographic map showing the three Colombia cordilleras (mountain chains): (WC) Western Cordillera, the currently active volcanic mountain chain resulting from subduction of the Nazca Plate to the west; (CC) Central Cordillera, separated from the Western Cordillera by the Cauca River, the former island arc to the west of the Eastern Cordillera Basin; and (ECC) Eastern Cordillera of Colombia within which the Paja Formation lies (approximate position of Paja Formation Seas, red circle). **(f)** Conceptual model showing a cross-section through the Eastern Cordillera Basin sedimentary basin during the Early Cretaceous: (Cs) Cocuy Sub-basin, a series of half-grabens; (E) east; (GS) Guiana Shield of the South American Plate; (OA/IA) open ocean/island arc (the future Central Cordillera); Rb—roll-back of the edge of the South American Plate, leading to lithospheric stretching, thinning, and down-warping; (S) subduction of the Farallón Plate under the South American Plate; (SdBs) Sabana de Bogotá (or Cundinamarca) Sub-basin, a horst over which salts were deposited during the earliest Cretaceous; (T-Ms) Tablazo–Magdalena Sub-basin, a series of half-grabens, of which the Paja Formation deposits form part; (W) west. **(g)** Hauterivian – Barremian palaeogeography, with the approximate position of Paja Formation Seas, red circle; land, green; seas and oceans, blue. Base maps (a–e) from various government websites; (f) original; (g) modified from Smith et al. (1994; map 18).



Figure 2. Ammonite sculpture mounted in the alto Ricaurte. Ammonites are so abundant, that the genus *Dufrenoyia* has become a symbol of the region. Sculpture located along the Villa de Leiva–Sutamarchân road (location indicated by an asterisk on Figure 3).

sea deposits, and thereby provide a comprehensive and integrated overview of the Paja Formation.

2. Overview of Paja Sedimentology and Palaeoenvironmental Interpretations

2.1. Tectonic Setting

The Paja Formation rocks of the ECC form part of the Chibcha Terrane (Gómez & Almanza, 2015). The regional tectonic structure of the ECC is broadly a horst (comprising the Sabana de Bogotá or Cundinamarca Sub-basin), which lies between a pair of half grabens, the Tablazo–Magdalena Sub-basin to the west and the Cocuy Sub-basin to the east (Gaona–Narváez, 2015; Jiménez et al., 2014; Teixell et al., 2015); the Paja Formation of the alto Ricaurte forms part of the Tablazo–Magdalena Sub-basin (Gaona–Narváez, 2015). The majority of the ECC Cretaceous rocks are of marine origin, with the (presumably deeper) western margin dominated by mudrocks (Teixell et al., 2015).

Early Cretaceous sedimentation of the ECC occurred in an extensional back-arc basin (Martínez et al., 2007), the result of complex interactions between the Caribbean, Nazca (a remnant of the Farallón), and South American plates. Subduction of the oceanic Farallón Plate beneath the continental South American Plate (Teixell et al., 2015) caused roll-back and extension of the western margin of the South American Plate (Figure 1f). This extensional regime resulted in normal faulting, which produced a “block-basin” topography; however, it is not known if extension was sufficiently great to produce rifting and emplacement of mid-ocean ridge basalt-type magmas. The extensional regime initially caused thermal expansion, followed by thermal sag (Jiménez et al., 2014) which produced a tectonically controlled deepening of the basin. Although the Cretaceous has been hypothesised as a time of generally subdued topographic relief, this does not accord well with a hypothesised increase in mid-ocean ridge spreading rates, which would have led to increased rates of subduction and elevated topography in the form of the Central Cordillera island arc to the west of Paja Formation Seas. Paja Formation sedimentation was therefore controlled by tectonically induced normal faulting, and bounded by a magmatic arc to the west (the future Central Cordillera), and the Guiana Shield to the east, both of which acted as potential sediment sources (Gaona–Narváez, 2015).

2.2. The Paja Formation

The type section for the Paja Formation lies on the north bank of the La Paja Creek, where it enters the Sogamoso River, close to Bucaramanga, Santander Department, in the Middle Magdalena Valley on the western flank of the ECC (Etayo–Serna, 1965, 1979; Guerrero, 2002b). The Paja Formation was first described by WHEELER (in Morales, 1958), as composed of

black shales with abundant calcareous concretions, which preserves a Hauterivian to Aptian ammonite fauna including the genera *Nicklesia*, *Pulchellia*, *Heteroceras*, *Santandericeras*, *Chelonicerias*, and *Colombiceras* (Guerrero, 2002b; Renzoni, 1981). In the type locality, the Paja Formation overlies the coarse-grained limestones of the Rosablanca Formation, and underlies the mixed carbonate and clastic sedimentites of the Tablazo Formation, the lateral time equivalent of the lower part of the San Gil Group of the alto Ricaurte (Guerrero, 2002b; Moreno et al., 2013).

Within alto Ricaurte, the Paja Formation overlies the Ritoque Formation. Although the contact between the Ritoque and Paja Formations was originally thought to be conformable (Etayo–Serna, 1979; Guerrero, 2002a; Huber & Wiedmann, 1986), it is now considered a paraconformity due to missing upper Valanginian ammonite biozones (Etayo–Serna et al., 2015). The upper contact of the Paja Formation with the Lower San Gil Formation (San Gil Group) is gradational (Etayo–Serna, 1979; Guerrero, 2002b). The Paja Formation crops out almost continuously along road cuttings (e.g., Tunja–Sáchica), rivers (e.g., Samacá River), creeks (such as Negra Creek) and hillsides (loma La Yuca, loma Monsalve, loma La Cabrera, loma La Catalina, loma La Yesera, and loma Blanca) and is divided into three members, which in ascending stratigraphic order are: *Lutitas Negras Inferiores*, *Arcillolitas Abigarradas*, and *Arcillolitas con Nódulos Huecos* (Etayo–Serna, 1965) (Figure 3). These deposits surround the Upper Jurassic or lowest Cretaceous sandstones of the Arcabuco Anticline (Etayo–Serna, 1968; Huber & Wiedmann, 1986). However, despite the complex tectonic environment that has raised the alto Ricaurte sections of the Paja Formation to around 2150 m above modern day sea levels, the deposits are well-exposed and exhibit limited structural complications (Etayo–Serna, 1968).

2.2.1. Sedimentology

2.2.1.1. *Lutitas Negras Inferiores* (LNI)

The lowermost member of the Paja Formation is the LNI, and it is this unit on which the town of Villa de Leiva lies (Etayo–Serna, 1968). The LNI has a sharp contact with the underlying grey siltstones of the Ritoque Formation (Etayo–Serna, 1965, 1968; Guerrero, 2002a) and is subdivided into five lettered segments, A–E. Along the Cucaita–Samacá Road the LNI exhibits a thickness of 340–380 m, and the sedimentites are mainly black, fissile claystones with intercalations of micrite, and occasional sandier interbeds in the middle of the unit (Etayo–Serna, 1965, 1968, 1979; Etayo–Serna et al., 2015). The LNI has been considered a distinct lithostratigraphic unit, the Villa de Leiva Formation (Guerrero, 2002a), as the LNI is absent from Paja Formation type area near Bucaramanga. The proposed type section for the Villa de Leiva Formation is 5 km south-southeast

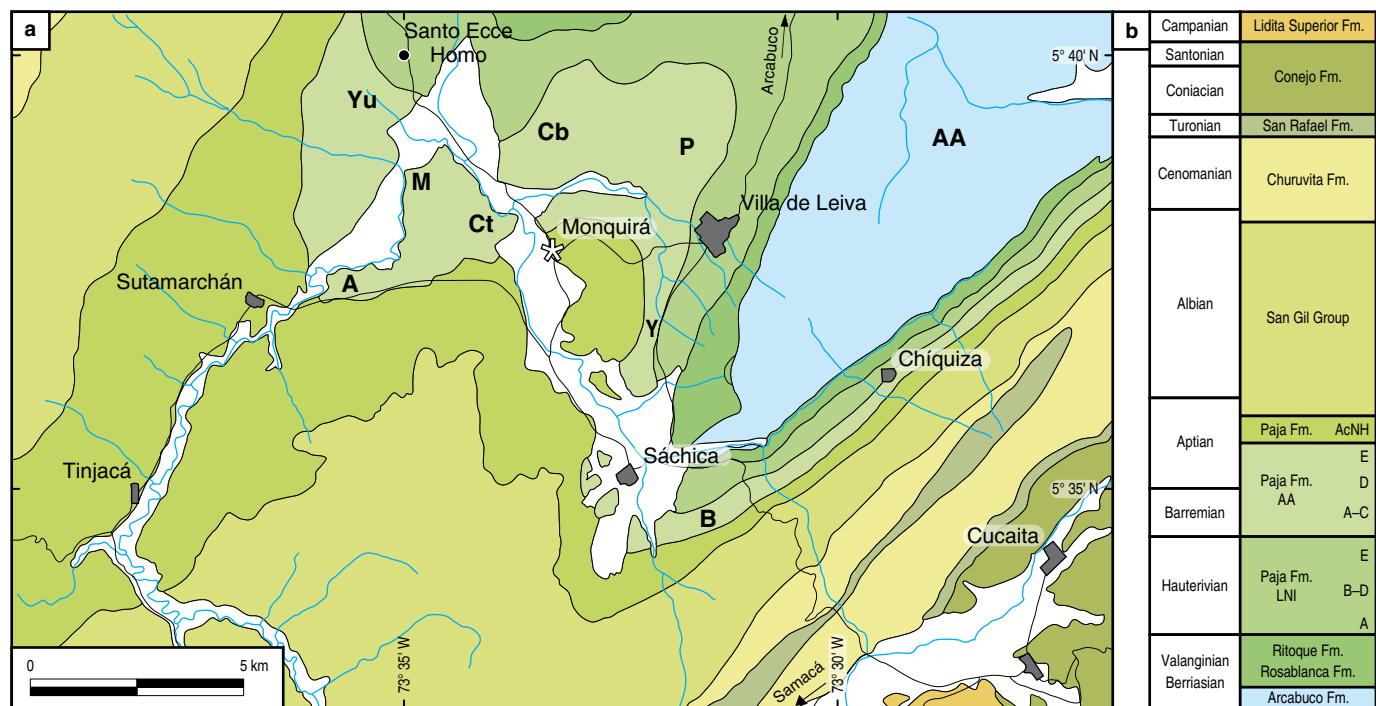


Figure 3. The southern alto Ricaurte. **(a)** Geological map and **(b)** stratigraphic column, indicating localities mentioned in the text. The map extends from Tinjacá in the west to Cucaita in the east and is centred on SÁCHICA–Villa de Leiva with directions to Arcabuco and Samacá indicated (alluvium, white; asterisk, location of ammonite sculpture (Figure 2); rivers, blue; towns, grey; principal roads, black). Abbreviations: (A) loma La Asomada; (AA) Arcabuco Anticline; (B) loma Blanca; (Cb) loma La Cabrera; (Ct) loma La Catalina; (M) loma Monsalve; (P) loma Pedro Luis; (Y) loma La Yesera; (Yu) loma La Yuca; (Fm.) Formation. The stratigraphic column shows geological age (left), formation or group (centre), with members and lettered segments for the Paja Formation. Modified from Etayo–Serna et al. (2015).

of Villa de Leiva along Negra Creek to the southeast of the Arcabuco Anticline (Guerrero, 2002a). However, this proposal of an independent Villa de Leiva Formation has not been widely adopted (however, see Patarroyo, 2009).

Segment A of the LNI comprises 110–120 m of black, red-weathering, normally finely-laminated claystones that are sandier towards the base (Etayo–Serna, 1965, 1968). Calcareous concretions are dispersed throughout the segment and are occasionally concentrated into bands; gypsum is present in the segment but is more common higher in the sequence. Fossils are scarce, although some concretions are fossiliferous and some fossils are covered with or shattered by gypsum (Etayo–Serna, 1968).

Segment B of the LNI consists of 20 m of dark-coloured, very fine-grained sandy clay-shales. The base and top of the segment are formed by two bands of very fine-grained sandstone, and between these marker horizons, the shales exhibit “swirling” boundaries (Etayo–Serna, 1968), possibly representing dewatering structures. The segment also contains both calcareous concretions and gypsum (Etayo–Serna, 1968). Segment C is 30 m of black shales, with calcareous concretions up to 250 mm in diameter, and occasional fossils some of which are pyritized. Approximately in the middle of the segment is a 1.3 m thick, contorted sandy-shale bed, which may represent slump folding, with intercalations of gypsum (Etayo–Serna,

1968). Segment D is 15 m of very fine-grained, compact, siliceous sandstone, which is banded and apparently forms banks (Etayo–Serna, 1968). Some calcareous concretions are present.

Segment E of the LNI, consists of 165 m of predominantly dark mudstones, occasionally finely-laminated, with some micaceous siltstone intercalations (Etayo–Serna, 1965, 1968). Concretions are common, many calcareous, but others are small and clay-rich. Towards the top of the segment the concretions are occasionally fossiliferous and coated, or radially crossed, by layers of gypsum (Etayo–Serna, 1968). Fossils are generally scarce in this segment, although most abundant towards the top.

2.2.1.1.1. Environment of Deposition

The LNI has been considered a period of relative geological stability, with nearly uniform environmental conditions prevailing during deposition of the member (Etayo–Serna, 1968). By LNI times, the generation of accommodation space and rates of sedimentation are considered to have been subequal, with environmental conditions remaining approximately uniform throughout deposition (Etayo–Serna, 1968). The black shale units (segments A, E) are considered to have been deposited in a low energy, reducing environment with little or no bottom currents (Etayo–Serna, 1968). However, it has been speculated that

this was not the result of deep marine conditions (Etayo–Serna, 1968), but due to restricted access to the open sea. This suggested the LNI black shales did not represent deep water deposition, but rather sedimentation in anoxic conditions below storm wave base (Etayo–Serna et al., 2015). The sandier segments (B, the centre of C, D) have been seen as the edges of a northward thickening sandstone unit, representing former offshore littoral marine bars lying parallel to the palaeocoastline (Etayo–Serna, 1968, 1979; Etayo–Serna et al., 2015). The presence of littoral sand bars is equivocal, as it was based on lithological correlation between segments B–D of the LNI, and an unnamed thick sandstone unit lying west of the town of Arcabuco (Etayo–Serna, 1965, 1968, 1979; Etayo–Serna et al., 2015). Correlation was also based on both units overlying sedimentites containing *Olcostephanus* ammonites (Etayo–Serna, 1968).

2.2.1.2. *Arcillolitas Abigarradas* (AA)

The middle unit of the Paja Formation is the AA Member, which along the Cucaita–Samacá Road exhibits a thickness of 480 m (Etayo–Serna, 1965, 1968, 1979). The AA is predominantly composed of fissile, light-coloured claystones, sandier in the lower part, and exhibiting intercalations of calcareous claystones and gypsum higher in the succession (Etayo–Serna, 1979). This unit is subdivided into five segments lettered A–E.

Segment A of the AA, is up to 57 m of weathered black claystones, with intercalations of harder calcareous clayey-sandstones, some of which preserve evidence of cross-bedding (Etayo–Serna, 1965, 1968, 1979). The segment contains calcareous concretions 0.5 m or more in maximum dimension and often clay coated, some of which are septarian and crossed internally by veins of calcite. The surrounding beds arch both above and below the concretions. Gypsum forms interstratified, bedding parallel layers, but also cuts the bedding and forms coatings around concretions. In places it is possible to observe layers of fibrous calcite, especially along the margins of the clayey-sandstone beds. The base of the segment preserves an event horizon consisting of a mixture of ammonites (some fragmentary), wood, and benthic foraminiferans (Patarroyo–Camargo et al., 2009; Patarroyo, 2009). In the top few metres of segment A at lomas La Yesera and Blanca, fossils and concretions are poorly preserved due to accumulations of gypsum.

Segment B of the AA is a marker horizon, 1.6 m thick, formed from very compact clay-rich limestones in thin beds, some separated by thin clay lenses towards the top; these beds contain some poorly preserved concretions and fossils (Etayo–Serna, 1968). Segment C comprises 86 m of grey claystones, with calcareous concretions, and harder marlstone intercalations. Gypsum fills fissures throughout the segment, with marl layers overlain by bedding parallel layers of gypsum up to 10 mm thick. Calcareous concretions are frequently surrounded by layers of gypsum and iron oxides (Etayo–Serna, 1968). Except for the base, segment

C typically preserves no fossils. Segment D is formed from 102 m of claystones, less sandy than the underlying layers, and with a white clay-rich bed towards the top (Etayo–Serna, 1968); this may be a bentonite (Bürgli, 1954). The middle of the segment preserves gypsum exploited by local farmers, and smaller gypsum veins fill cracks and fissures. The segment preserves abundant small, calcareous concretions and prominent, hard calcite levels (Etayo–Serna, 1968). Fossils are rare at the base of the segment, but occur sporadically above; fossils in the white clay layer are strongly compressed and covered in gypsum.

Segment E of the AA comprises 235 m of weathered claystones, some finely laminated, and intercalated with thin calcareous clays bands. The claystones are interstratified with gypsum, which in places has been exploited by local farmers; gypsum-filled cracks and fissures are frequently present. Calcareous concretions are dispersed throughout the segment (Figure 4) together with hard bands of calcite (Etayo–Serna, 1968). The entire segment is richly fossiliferous, with many concretions full of well-preserved ammonites; fossils are often at the centres of the concretions.

2.2.1.2.1. Environmental Interpretation

The base of segment A of the AA, has been interpreted as showing the action of density driven (turbidity) currents, which flowed from east to west (Etayo–Serna, 1968). These turbidity currents were interpreted as reworking previously deposited organic remains (principally cephalopod shells and wood) and produced little sorting in terms of size of the transported materials. Large ammonites were deposited parallel to the stratification, with the remains of smaller ammonites within the living chambers of the larger specimens. The east–west direction of the flow was based on a westerly reduction in calcium carbonate deposition, which resulted in an increase in the size and richness of cephalopod fragments, an increase in heteromorphic ammonites, and a reduction in fossil wood towards the east. Hence, segment A of the AA was seen as having mobile bottom conditions that inhibited benthic fauna (Etayo–Serna, 1968). However, although turbidity currents may have affected the Paja Formation Basin, no data is available on the flow direction(s) indicated by the cross-bedding within the hard bands of segment A, and as intermittent events, turbidity currents would not have produced constantly shifting bottom conditions. The variation in ammonites considered current transported (Etayo–Serna, 1968), is only marginally statistically significant, and the distances are probably too short for reliable analysis. The preservation of delicate organic structures, such as spines on ammonite shells, strongly argues against dynamic transport of these organisms from within or outside the Paja Formation Basin. In addition, supporting arguments based on fossils being located at the centres of the concretions, or the possibility of concretions concentrated by current action (Etayo–Serna, 1968), are

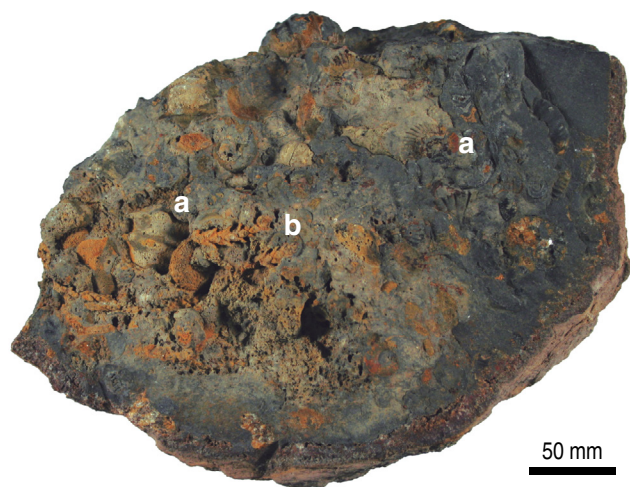


Figure 4. Concretion from the alto Ricaurte (UADG LM 15.57f) with a mixture of autochthonous ammonites (a) and allochthonous terrestrial plant material (b). Collected from loma La Cabrera.

fallacious as concretions are of early diagenetic origin (Lash & Blood, 2004; Witkowska, 2012), and therefore not related to depositional processes.

Segments B–E of the AA were interpreted as representing a wide, shallow bay in the neritic zone of a platform sea, with alternating restriction and access to the open ocean (Etayo–Serna, 1968). Restriction was seen as the result of more complete development of the littoral bars hypothesised for LNI times. This periodic restriction was hypothesised to lead to changes in bottom waters, with west–east flowing currents that produced oscillating bottom water dynamics. During times of restriction there were gentle bottom currents with deposition of mostly complete and well–preserved ammonites, and increased salinity which led to development of sabkha and deposition of gypsum (Etayo–Serna, 1968; Forero–Onofre & Sarmiento–Rojas, 1985). Times of greater access to the open sea produced more dynamic bottom currents, with winnowing of ammonites by shell shape, and the introduction of decomposing marine reptile carcasses in from the west, which floated belly up into shallow Paja Formation waters, to become beached and preserved (Etayo–Serna, 1968). However, salinity increase would have led to the deposition of halite (NaCl) prior to gypsum, for which there is no evidence in the Paja Formation. In addition, many of the characteristic features of sabkha (e.g., birdseyes, boudinage, scour and fill, ripples, cross–bedding; Townson, 1975) are absent from the AA, and setulfs (Sarkar et al., 2011), although reported from the Paja Formation are not supported by images or locations (Forero–Onofre & Sarmiento–Rojas, 1985), casting doubt on their validity. Sabkha development requires hypersalinity for gypsum to be deposited, leading to a sparse fauna (Townson, 1975) and this is at odds with abundant, unbroken, three–dimensionally preserved ammonites in segments B–E of the AA. The floating of decomposing vertebrate carcasses

does not match the taphonomy of fully articulated fossils, many of which (e.g., *Callawayasaurus*) are also associated with the presence of gypsum (Welles, 1962).

2.2.1.3. *Arcillolitas con Nódulos Huecos* (AcNH)

The uppermost unit of the Paja Formation is the 80 m thick and undivided AcNH Member, which consists of claystones, with intercalations of shiny white clays, although the deposits become more micaceous and sandy towards the top of the unit. Numerous hollow concretions, up to 200 mm in diameter, and smaller massive clay concretions up to 50 mm in diameter, characterize the unit (Etayo–Serna, 1968). Fossils occur sporadically within the claystones, white clays, and concretions. Although vertebrate fossils are rare in the AcNH, one of the authors (M.G.–P.) has found indeterminate fragments of a very weathered vertebrate in this member.

2.2.1.3.1. Environmental Interpretation

The environmental conditions of the AcNH are interpreted as a similar to the AA, but without the calcite– and gypsum–rich layers. This suggested more access to the open sea, with reduced deposition of evaporitic minerals (Etayo–Serna, 1968). The white clays have been considered volcanic ash deposits (Bürl, 1954), although these were not subsequently recognised as such (Etayo–Serna, 1968).

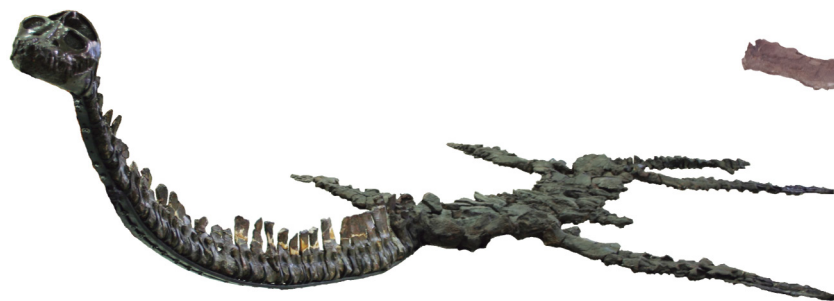
2.2.2. Palaeontology

Fossils, especially marine reptiles, fish, and ammonites (Figures 5–7), are common in the Paja Formation around the alto Ricaurte (Huber & Wiedmann, 1986). Here we summarize the palaeontology of the Paja Formation, with special emphasis on the autochthonous marine reptiles (plesiosaurs, ichthyosaurs, marine turtles), followed more briefly by fish, invertebrates, and microfossils.

2.2.2.1. *Plesiosaurs*

The Paja Formation, in terms of abundance, variety, and exceptional preservation of Plesiosauria, is the most important Lower Cretaceous plesiosaur assemblage in the world. In pre-cladistic studies, Plesiosauria was divided into two groups, the long-necked plesiosauromorphs (Figure 5a) and the short-necked pliosauromorphs (Figure 5b). Rather confusingly, both Plesiosauria and the plesiosauromorphs have been referred to as “plesiosaurs”; however, here we use the term “plesiosaur” to refer only to Plesiosauria. Both plesiosauromorph and pliosauromorph plesiosaurs are represented in the Paja Formation deposits of the alto Ricaurte. Plesiosauria are the second most common large vertebrate faunal elements after the ichthyosaurs,

a



b



c



d



e



f



Figure 5. Representative marine reptile fossils from the alto Ricaurte. **(a)** The Bogotá specimen of the plesiosauiromorph plesiosaur *Callawayasaurus colombiensis* (SGC MGJRG.2018.V.1), the skull is a replica based on combined information from the original of this specimen and the holotype (UCMP 38349); length along the vertebral column 7 m. **(b)** The pliosauiromorph plesiosaur *Kronosaurus boyacensis* (MJACM 1) in situ where discovered, preserved length 7.35 m. **(c)** Skull of the ophthalmosaurid ichthyosaur *Platypterygius sachicarum* (SGC DON-19671), length 890 mm. **(d)** Skull and anterior vertebral column of the ophthalmosaurid ichthyosaur *Muisacasaurus catheti* (CIP-FGC-CBP-74), length 800 mm. **(e)** The protostegid marine turtle *Desmatochelys padillai* (CIP-FGC-CBP 01), length 1.44 m along the midline; it is likely the eggs illustrated in Figures 9, 10 belong to this species. **(f)** The sandownid marine turtle *Leyvachelys cipadi* (CIP-FGC-CBP-71), length 1 m.

represented by four published genera, all of which are currently monospecific, although further specimens await description.

The first published plesiosaurs from the Paja Formation were two substantially complete skeletons of the plesiosauiromorph *Callawayasaurus colombiensis* (Welles, 1962) Carpenter, 1999, the holotype (UCMP 38349) and second specimen (SGC MGJRG.2018.V.1; Figure 5a). The two specimens were originally described as new species of the North American genus *Alzadasaurus* Welles, 1943, as *Alzadasaurus colombiensis* Welles, 1962, although following revision, the species was transferred to the new genus *Callawayasaurus* (Carpenter, 1999), as *Callawayasaurus colombiensis* (Welles, 1962) Carpenter, 1999. Unfortunately, during this revision, both the name of the country (“Columbia”) and the original species name (“*C. colombiensis*”) were misspelt (Carpenter, 1999, 172).

The two skeletons of *Callawayasaurus* were excavated from grey-coloured red-weathering siltstones of segment E of the AA Member of the Paja Formation by teams led by Ruben Arthur STIRTON of the UCMP (Páramo-Fonseca, 2015; Welles, 1962). The holotype was recovered from loma La Catalina, approximately 6 km to the west of Villa de Leiva, and about 300 m to the north of the Villa de Leiva-Chiquinquirá road (Welles, 1962). The second specimen (or “paratype”) was discovered approximately 100 m to the north, and stratigraphically 10 m from the holotype; however, there is confusion as to the exact relative positions of the two skeletons, as the original description records conflicting locality information (see Welles, 1962, 1, 13, 32), although this discrepancy is in the process of being resolved. The holotype of *Callawayasaurus* was transferred to the University of California, Berkeley under the 1944–1945 Comisión de Vertebrados (Espinosa, 2016), whilst the second specimen remained in Bogotá (Welles, 1962, 17, 32); the skull, formerly registered to the museum in Berkeley as UCMP 125328, has recently been returned to the Servicio Geológico Colombiano (SGC).

The preservation of the holotype and second specimens of *Callawayasaurus colombiensis* are remarkably similar. Both skeletons were found in the supine (“belly-up”) position, are almost complete and articulated, and exhibit minimal crushing (Páramo-Fonseca, 2015; Welles, 1962). The holotype is missing the ilia, ischia, tail, and some distal limb elements, all of which can be attributed to recent weathering and/or collection failure due to digging for gypsum (Welles, 1962). The second specimen of *Callawayasaurus* (Figure 5a) is somewhat more

complete, although the skull is imperfect, missing the left mid-portion between the external naris and orbit, which was not found in the field. Both specimens are largely articulated, with the holotype exhibiting slight movement of the right paddles, ribs, gastralia, and a few other elements (Welles, 1962), all attributable to the settling of the carcass during decomposition. Both specimens are mostly uncrushed, with the holotype exhibiting slight compression of the skull (a pit in the snout, between the orbits, the parietal crest, part of lower temporal arch, and the palate), the left scapula, right coracoid, and a few distal limb elements (Welles, 1962).

Both the holotype and Bogotá specimens of *Callawayasaurus* are remarkably well-preserved (Welles, 1962). Using the holotype as an example, the skeleton preserves the jaws tightly closed, most of the teeth in situ in their alveoli, the delicate hyoid bones under the skull, and gastroliths in and around the rib cage. The bone surface is excellently preserved, with the internal spongy bone texture present in many places without mineral infill; this has been attributed to rapid burial by fine-grained sediments that sealed the carcass from permineralizing groundwaters (Welles, 1962). The casts of bivalves and ammonites are common in the surrounding matrix. The bones are frequently surrounded by extensive limestone concretions, especially the skull, shoulder girdle, and vertebral column, which has reduced the crushing from subsequent overburden. The bones are typically chocolate brown-coloured and coated in red-coloured iron oxide, or surrounded by cm scale red- or yellow-weathering iron oxide-rich concretions. In addition, gypsum is common as crystals in the sedimentary matrix, and infilling veins and cracks (Figure 8). A layer of gypsum approximately 6 mm thick covered the skull and palate, with gypsum penetrating the skull and other bones.

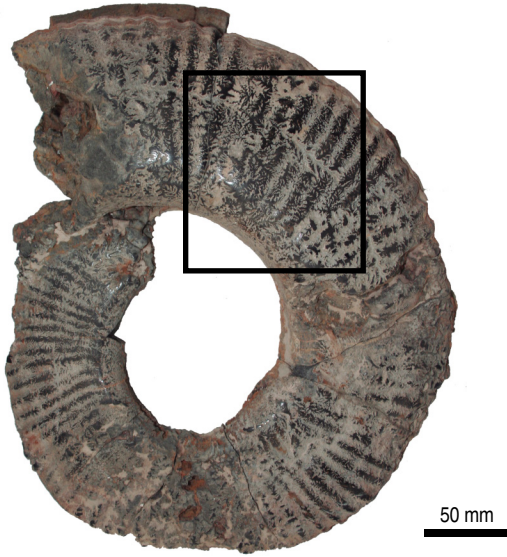
After the discovery of *Callawayasaurus*, two incomplete plesiosauiromorph specimens, exhibiting good three-dimensional preservation, have been recovered from the alto Ricaurte, and attributed to the genus (Goñi & Gasparini, 1983; Jerez-Jaimes & Narváez-Parra, 2001). The first was the anterior of a skull and mandible preserved to level with the rear of the orbits (UN ICNMHNR-081) recovered from loma La Cabrera, some 4 km to the west of Villa de Leiva (Goñi & Gasparini, 1983). The second was a much more complete, and at least partially articulated, skeleton discovered at an unrecorded locality and horizon in the Paja Formation near Villa de Leiva. Discovered



Figure 6. Fish remains preserved in three-dimensions from the alto Ricaurte showing a range of sizes and morphotypes, none of which have been formerly described. Specimen numbers **(a)** MJACM 13; **(b)** MJACM 17; **(c)** MJACM 29; **(d)** MJACM 16a–c, a complete specimen of *Vincitifer* species; **(e)** MJACM 269, scales from the flanks of a large fish; **(f)** MJACM 270, scales of *Vincitifer* species. No collection localities recorded, but all specimens are likely derived from Paja Formation, vereda Monquirá.

Figure 7. Ammonites from the alto Ricaurte showing a range of sizes and morphotypes (both planispiral and heteromorph forms), none of which have yet been formerly described. Specimen numbers **(a)** MJACM 35, large planispiral ammonite missing central whorls and **(b)** detail of the boxed area showing suture pattern; **(c)** MJACM 202, a smaller planispiral ammonite; **(d)** MJACM 117, a criocone (open planispiral) heteromorph ammonite; **(e)** MJACM 112, “hairpin-shaped” heteromorph ammonite preserved in association with two planispiral ammonites; **(f)** MJACM 137, a moderately sized planispiral ammonite missing the central whorls, and **(g)** detail of the boxed area showing suture pattern. No collection localities recorded, but all specimens are likely derived from Paja Formation, vereda Monquirá.

a



b



c



d



e



f



g



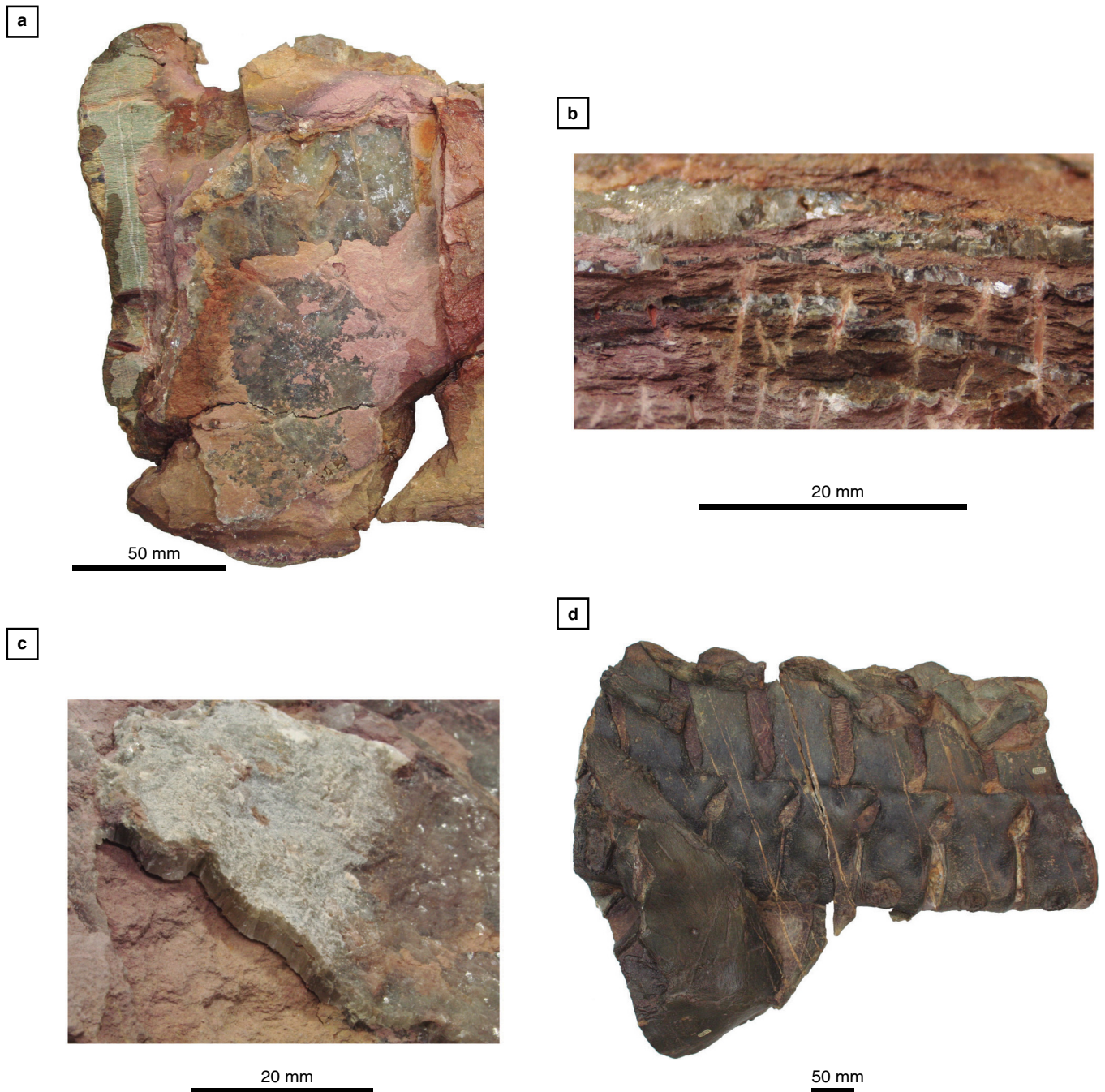


Figure 8. Gypsum “beef” associated with the holotype of *Callawayasaurus colombiensis* (UCMP 38349) showing **(a)** the unprepared (originally upper) surface of cervical vertebra 22 (anterior, left; dorsal, top) showing a gypsum sheet sub-parallel to the bone surface, that splits into two to the left; notice also the vertical veins of gypsum cutting the bone and matrix. **(b)** Layers of gypsum “beef” within the sediments as seen from anterior view (i.e., to the left of (a)). **(c)** Bi-layered sheet of gypsum “beef” on the unprepared (original upper) surface of a block containing cervical vertebra 29 (pars) to 31. **(d)** Prepared (originally lower) surface of posterior cervical and ?anterior “pectoral” vertebrae partly covered by the coracoid of the shoulder girdle (anterior, right; dorsal, top), showing vertical veins of gypsum cutting the bones. Collected by a party from the Tropical Oil Company and Ruben Arthur STIRTON (UCMP) from loma La Catalina.

in 1999, the specimen was tentatively attributed to *Callawayasaurus* (Jerez-Jaimes & Narváez-Parra, 2001), although the current whereabouts is unknown. Numerous additional specimens of plesiosauiromorphs, some probably attributable to *Callawayasaurus* but others that represent new genera, are held

by various institutions and await formal scientific description (Gómez-Pérez & Noë, 2017; Páramo-Fonseca, 2015).

The second described plesiosaur from the Paja Formation of the alto Ricaurte was a plesiosauiromorph (MJACM 1) discovered in June 1977 (Acosta et al., 1979), and later described as

the new species *Kronosaurus boyacensis* Hampe, 1992 (Figure 5b). The skeleton was discovered by local farmers in the upper Aptian segment E of the AA Member of the Paja Formation in Monquirá, 4 km to the west of Villa de Leiva (Acosta et al., 1979). The skeletal remains are currently the centrepiece of the community run Museo El Fósil built over the site of the find. MJACM 1 lies in the prone (dorsal up) position, is substantially complete and mostly articulated, although the skeleton is missing the upper surface of the posterior of the skull, some elements of the posterior of the pelvis, the rear right limb beyond the femur, the tail, and numerous distal limb elements (Hampe, 1992). However, all missing elements can be attributed to recent weathering or collection failure. The skull is somewhat crushed and some elements such as the ribs and some vertebrae are slightly displaced due to post-mortem movement of the carcass. However, the skeleton is mostly articulated, with the teeth in their alveoli, and the bones preserved in three-dimensions; there is no evidence of scavenging or colonization by epibionts. The surrounding sediments are fine-grained, grey-weathering, and fissile (Acosta et al., 1979), and many of the bones are surrounded by calcareous and/or iron-rich concretions (Hampe & Leimkuehler, 1996), which helped to maintain the original three-dimensional shape of the animal.

The third plesiosaur described from the Paja Formation of alto Ricaurte was *Stenorhynchosaurus munozi* Páramo-Fonseca et al., 2016 (SGC VL17052004-1), discovered on the land of Jorge MUÑOZ on the eastern slope of loma La Cabrera, some 4 km to the west of Villa de Leiva. The specimen was originally published as *Brachauchenius* sp. (Hampe, 2005), whilst under the study of María Eurídice PÁRAMO-FONSECA and colleagues. *Stenorhynchosaurus* was recovered from segment C of the AA Member of the Paja Formation, and ammonite biostratigraphy permitted dating of the specimen to the early late Barremian (Páramo-Fonseca et al., 2016). The skeleton was discovered in a variegated clay-grade, calcareous and kaolinitic, laminated mudstone. The animal was articulated and substantially complete, lying in the prone position with the paddles spread out laterally. The bone surface is generally very well-preserved. *Stenorhynchosaurus* is missing the tip of the snout, distal elements of the left anterior paddle, the entire right posterior paddle, and the tail. There is some crushing to the rear of the skull and neural arches, and some of the ribs and posterior elements are displaced, but there is no evidence of scavenging or epibionts.

The fourth plesiosaur from the alto Ricaurte Paja Formation is the newly described genus and species of pliosauro-morph, *Acostasaurus pavachoquensis* Gómez-Pérez & Noè, 2017 (UNDG R-1000). This specimen was recovered in 1967 by a French Technical Cooperation team working with the Hydrology Section of the Ministry of Public Works of Colombia; however, no contemporary collection records exist (Acosta et al., 1979). The specimen was recovered close to the Santo Ecce

Homo Convent, in Sutamarchán. The specimen consists of a largely complete and articulated pliosauro-morph from the lower Barremian segment A at the base of the AA Member of the Paja Formation. The specimen was surrounded by a fine-grained, very dark-coloured matrix, and encased in a single large, non-septarian concretion which preserved ammonites, used for biostratigraphically dating the skeleton. No gypsum was preserved with this specimen. Currently only the skull and anterior cervical vertebrae are prepared; however, the skull is substantially complete and three-dimensional, with delicate structures such as sclerotic plates well-preserved, which are only infrequently encountered in plesiosaurs (Andrews, 1913; Gómez-Pérez & Noè, 2017). *Acostasaurus* is therefore one of the most complete members of Plesiosauria from the Lower Cretaceous, and one of the best preserved pliosauro-morphs anywhere in the world.

2.2.2.2. *Ichthyosaurs*

The second common group of marine reptiles reported from the Paja Formation of alto Ricaurte are the ichthyosaurs. Numerous examples of ichthyosaurs are known, but the majority remain unpublished (e.g., Páramo-Fonseca, 2015); however, many specimens represent new taxa, and are likely to completely re-write our current understanding of post-Jurassic ichthyosaur diversity and evolution, and deserve publication in the highest-quality international journals. The work reinterpreting Cretaceous ichthyosaur diversity and evolution has begun on other faunas worldwide (e.g., Fernández & Aguirre-Urreta, 2005; Fernández et al., 2005; Fischer et al., 2014; Zammit, 2012), and the Colombian specimens from the Paja Formation are likely to prove key to this work.

The first named ichthyosaur from Colombia was the ophthalmosaurid *Platypterygius sachicarum* Páramo-Fonseca, 1997 (SGC DON-19671), recovered from loma Pedro Luis, 1.5 km northwest of Villa de Leiva by Jorge CÁRDENAS and presented to the SGC Museum in 1967 (Figure 5c). No detailed stratigraphic information is available; however, the specimen was recovered from the lower part, probably segment A, of the AA Member (see Páramo-Fonseca, 1997, Figure 1). The specimen consists of a substantially complete skull, originally preserved in a hard calcareous-rich matrix (probably a non-septarian concretion), which permitted acid preparation of the left side of the skull; the right side was earlier mechanically prepared. The specimen is essentially three-dimensionally preserved, with some lateral crushing, and is largely complete, but missing the tips of the jaws. The skull bones are articulated, with the sclerotic rings partly preserved in life position, and almost all teeth on the left side in situ; the teeth on the right are more disordered. Bone preservation is generally good on the left of the skull, although the surfaces of some bones are incomplete or fractured, whereas the right side is much more heavily weathered, indicating the specimen lay in the sediment

on its left side, with the right side exposed to weathering prior to collection. The surrounding matrix is organic-rich, with some carbonized plant remains preserved in and around the tightly closed jaws. No ammonites or other macrofossils, palynomorphs or foraminiferans, were encountered in the matrix during preparation (Páramo-Fonseca, 1997).

Muiscasaurus catheti Maxwell et al., 2016 (CIP-FGC-CBP-74) was the second described ophthalmosaurid ichthyosaur from the alto Ricaurte Paja Formation, preserving an incomplete cranium associated with 10 articulated cervical vertebrae with attached neural arches and some ribs (Figure 5d). The specimen was recovered from vereda Arrayanes, municipio de Sáchica, from an unspecified horizon within the AA Member of the Paja Formation. The remains were preserved in two calcareous concretions; however, the orientation of discovery was not recorded. Although the skull is essentially three-dimensionally preserved, there is some lateral compression. The anterior of the snout of *Muiscasaurus* is unnaturally curved to the right; this curvature has been attributed to arrival of the carcass head first on the sea floor (Maxwell et al., 2016). However, there is no known mechanism for plastic deformation (rather than breakage) of fresh bone due to impact, making it more likely the deformed snout was due to diagenetic concretionary growth or overburden pressure. As with most of the alto Ricaurte vertebrate specimens, the jaws are preserved tightly closed, the teeth are in position, and delicate structures including sclerotic rings and probable hyoid elements are preserved in or close to their original life positions. The vertebral centra of *Muiscasaurus* are exceptionally well-preserved (Maxwell et al., 2016), the bone retaining the open, porous texture observed in *Callawayasaurus* (Welles, 1962).

2.2.2.3. Marine Turtles

Turtles are abundant in many Cretaceous marine deposits (Cadena & Parham, 2015), although they are most commonly found disarticulated (Cadena, 2014); however, articulated turtles are well represented in the Paja Formation deposits of alto Ricaurte. The first published turtle remains, attributed to a eucryptodire, were a cranial mould and associated mandible (UN ICN-MHNR-083) discovered at loma La Asomada. However, the first turtle named from the Paja Formation was *Desmatochelys padillai* Cadena & Parham, 2015, a member of the Protostegidae, a group of specialized marine turtles that radiated during the Early Cretaceous (Figure 5e); this specimen was considered the oldest known marine turtle, depending on the definition of this group (Cadena & Parham, 2015). The holotype (CIP-FGC-CBP 01) includes a complete skull with articulated lower jaw, a partial hyoid, some cervical vertebrae, both forelimbs (missing most of the phalanges), a left scapula and coracoid, a nearly complete carapace, and parts of the plastron (Cadena & Parham, 2015). Referred specimens include both adults and juveniles with complete or near complete skulls, all with the lower jaws

articulated (CIP-FGC-CBP 13, 15, 39, 40, and UCMP 38346), an incomplete vertebral column with attached fragmentary carapace (UCMP 38245A), and a posterior fragment of a carapace (UCMP 38245B). The specimens were found in dark grey limestone concretions, the bones covered, and cavities filled, with a layer of iron oxides. UCMP 38245B preserves possible evidence of predation, in the form of two sub-circular holes, that have been attributed to the teeth marks of a predatory pliosauromorph (Cadena & Parham, 2015). Most specimens were recovered from loma La Catalina, but one (FCG-CBP 15) was found nearby at loma La Cabrera. Although the exact locality of the Berkeley specimens (UCMP 38345A, B, and 38346) was assumed to be from the alto Ricaurte region (Cadena & Parham, 2015), examination of the UCMP archives (by LFN) indicates all three turtle remains were recovered from loma La Catalina, at the same date and site as the holotype of *Callawayasaurus*. All three remains, therefore, most probably belong to the same individual. Hence the UCMP referred specimens, and probably all the material mentioned above, were derived from segment E of the AA Member of the Paja Formation.

The second new genus and species of turtle described from the Paja Formation was *Leyvachelys cipadi* Cadena, 2015, the most complete sandowniid turtle (Tong & Meylan, 2013) thus far known (Figure 5f). The holotype skeleton (CIP-FGC-CBP-71) was discovered in 2009 at loma La Catalina in a calcareous claystone, surrounded by abundant calcareous-iron nodules and concretions, presumably from segment E of the AA Member of the Paja Formation. The specimen consists of an incomplete but articulated skeleton, including the united skull and lower jaw, cervical and caudal vertebrae, parts of both limb-girdles, distal limb elements, and an almost complete carapace (Cadena, 2015). The preservation and preparation is sub-optimal, due to the attached iron-rich nodules, with some erosion of the bone surface. The skull is three-dimensionally preserved, with the jaws articulated and minimal evidence of distortion; however, the postcrania is generally flattened.

The Paja Formation of the alto Ricaurte has revealed several spherical objects (UMCP 38348) interpreted as fossilized turtle eggs (Etayo-Serna et al., 2015; Páramo-Fonseca, 2015), which are closely associated with the bones of the mother (Figures 9, 10). The eggs were discovered in segment E of the AA Member at loma La Catalina, the locality that produced the holotype of *Callawayasaurus*, and at the same time as the *Leyvachelys cipadi* specimens (UCMP 38245A, B, 38346); it is therefore probable the eggs belonged to the same individual. The eggs are spherical, a common shape for modern sea turtle eggs (Mikhailov, 1997), and three measurable specimens have diameters of 50, 61, and 64 mm, which is slightly larger than modern sea turtle eggs which range between 32.1–55.2 mm in diameter (Dodd Jr, 1988; Hirth, 1980; Miller et al., 2003a; Pritchard & Mortimer, 1999). The outer surfaces of the preserved eggs exhibit irregularly arranged, sub-millimetric, raised swellings, different to the

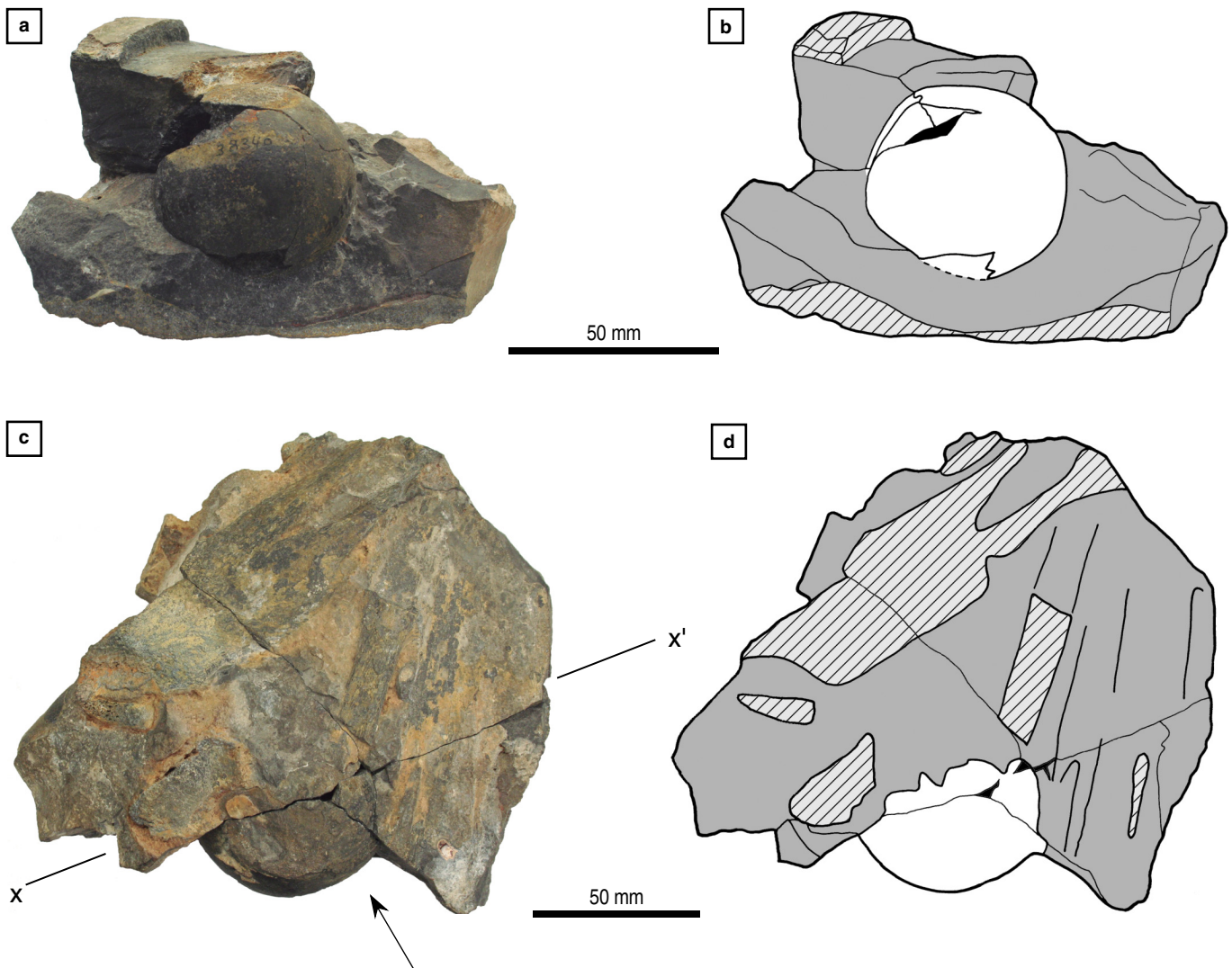


Figure 9. Two turtle eggs preserved in non-septarian concretions, which also preserve the bones of the mother enclosing the eggs (UCMP 38340), (a, c) photographs and (b, d) interpretive drawings. The eggs, probably belong to *Desmastrochelys padillai*, were collected in 1945 by a party from the Tropical Oil Company and Ruben Arthur STIRTON (UCMP) from loma La Catalina, at the same time as the holotype of *Callawayasaurus colombiensis*. Line x-x' represents the section of the surface shown in Figure 10 (a, c), as viewed from the direction of the arrow. In the drawings: bones, hatched; concretion, grey; eggs, white. Scale bars represent 50 mm.

smooth shelled eggs of modern marine turtles (Imai et al., 2016; Mikhailov, 1997). The eggs are preserved with approximately 3 mm thick calcite “shells”, which are much thicker than the leathery shells of modern turtle eggs (Nuamsukon et al., 2009; Philloft & Parmenter, 2006), although in contrast to modern turtles, the fossil eggs are likely to have been hard-shelled (Winkler & Sánchez-Villagra, 2006). Two distinctly coloured calcite layers form the “shell”, a dark outer layer and a lighter inner layer, and the eggs are more-or-less completely filled with dark-coloured, coarsely crystalline (sparry) calcite. The mammilated structure, “shell” thickness, and bi-coloured external layering suggests the preserved external surface of the eggs is a result of calcite crystals lining the inside of the original aragonite shell (Isaji et al., 2006; Mikhailov, 1997), which was later lost during diagenesis.

2.2.2.4. Fish

Planktonic fish are numerous and diverse from the Paja Formation of alto Ricaurte (Álvarez-León et al., 2013; Etayo-Serna, 1968), are preserved in numerous collections, but are currently understudied (Figure 6). A specimen of the aspidorhynchid fish *Vinctifer* (MB f. 3500), was recovered from Aptian strata of loma Blanca near Sáchica in segment E of the AA Member of the Paja Formation (Schultze & Stöhr, 1996). The specimen is incomplete, but preserved in three-dimensions. In addition, numerous fish in a range of institutions await formal description, but appear to include amiids, “semionotiforms”, ichthyodectiforms, pachyrhizodontids, aspidorhynchids, and araripichthyids which are similar to, or possibly congeneric with, fish collected

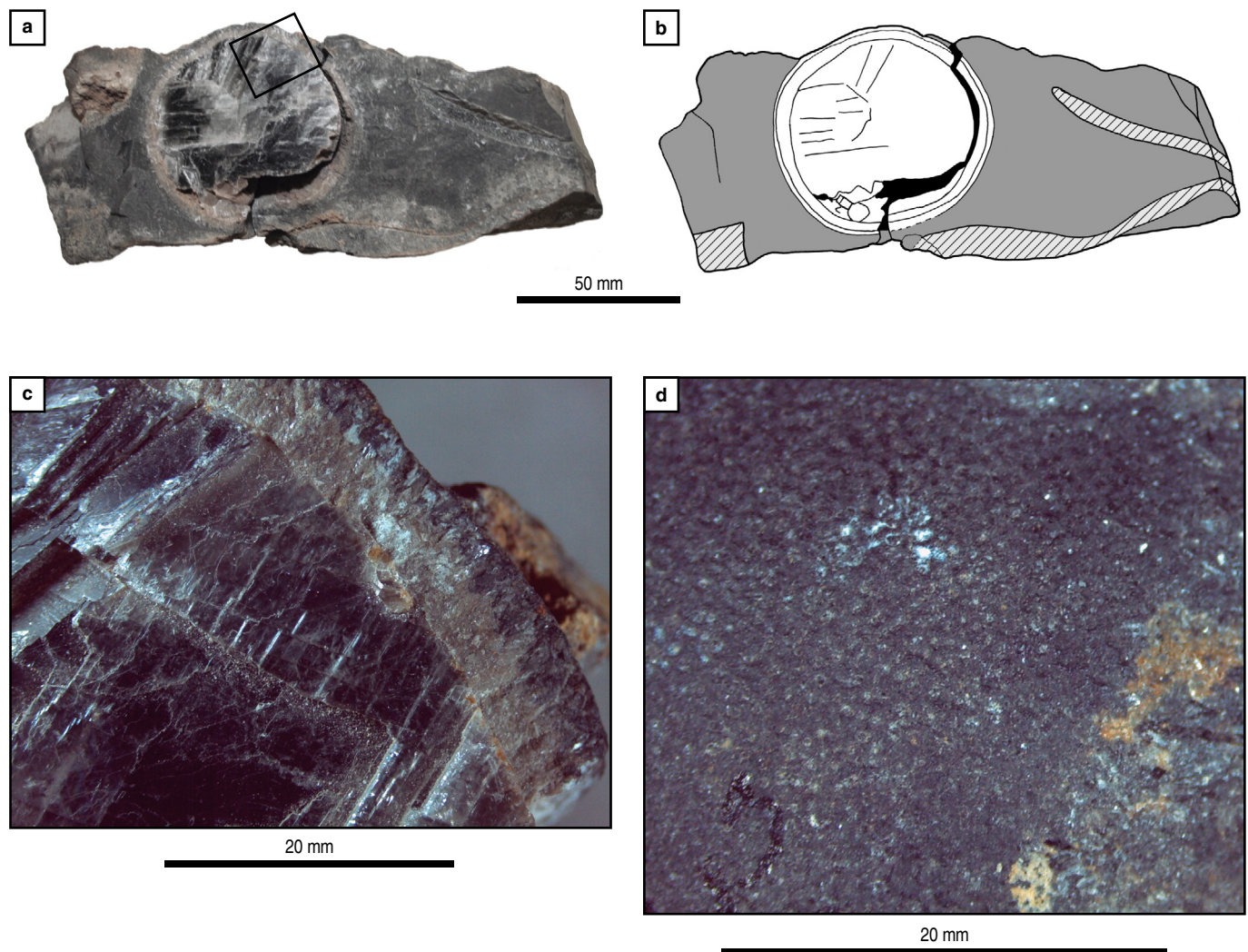


Figure 10. Cross-section through the turtle egg (UCMP 38340) shown in Figure 9c, probably belonging to *Desmatochelys padillai* (a) photograph and (b) interpretive drawing; in the drawing: bone, hatched; concretion, grey; egg, white; voids, black. (c) Photomicrograph close up of section of the “shell” boxed in (a), notice the “shell” is a double layer of differentially coloured calcite, and the coarsely crystalline (sparry) calcite infill. (d) Photomicrograph of the external surface of the “shell”. In (c, d) the “shell” most likely represents calcite lining the inner surface of the original aragonite invested shell, which is not now preserved. Collected by a party from the Tropical Oil Company and Ruben Arthur STIRTON (UCMP) from loma La Catalina.

from the slightly younger Santana Formation of Brazil (Selden & Nudds, 2012).

2.2.2.5. Marine Macro-invertebrates

Here we briefly summarize the marine invertebrate palaeontology of the Paja Formation, with special emphasis on the range of organisms present. In contrast to the taxonomic treatment of the vertebrates above, we explore the macroinvertebrates in stratigraphic order to show the range of organisms living in the Paja palaeoenvironments at any one time. As with much of the Mesozoic marine world, ammonites (Figure 7) are key elements for Colombian and Paja Formation biostratigraphy (e.g., Etayo-Serna, 1964, 1979; Hoedemaeker

& Kakabadze, 2004; Kakabadze & Hoedemaeker, 1997), and include diverse planispiral and heteromorphic forms (Bogdanova & Hoedemaeker, 2004; Etayo-Serna, 1968; Kakabadze & Hoedemaeker, 1997, 2004; Sharikadze et al., 2004; Vašíček & Hoedemaeker, 2003). The age of the Paja Formation had been ascertained as Hauterivian to part way through the late Aptian (Etayo-Serna, 1965), with one of the most intractable problems being the definition of the lower Barremian boundary (Etayo-Serna, 1964; Patarroyo, 1997, 2000b, 2009). Biostratigraphic work has included ammonites from the Creutzberg Collection (see the volume prefaced by Hoedemaeker & Kakabadze, 2004), however these specimens were not collected with robust stratigraphic horizons, with inferred geological ages assigned based on comparison to European ammonite

faunas. Details of the complex ammonite zonation are not discussed here.

2.2.2.5.1. Lutitas Negras Inferiores (LNI)

Ammonite biostratigraphy indicates a late Hauterivian age for the LNI (Etayo–Serna, 1965), although the lowermost part of segment A has occasional preserved lower Hauterivian ammonites (Etayo–Serna et al., 2015). Segment A of the LNI preserves occasional accumulations of invertebrates, which are mostly preserved flattened in the mudstones, rather than within the concretions. Occasional accumulations of large sized *Olcostephanus* ammonites occur (Etayo–Serna, 1968), and the segment also preserves a few other indeterminate cephalopod fossils (Etayo–Serna et al., 2015), but no bivalves or gastropods. Segment C also preserves a few *Olcostephanus* ammonites (Etayo–Serna, 1968). Within segment E fragments or impressions of indeterminate ammonites are occasionally locally abundant (Etayo–Serna, 1968), with *Crioceratites* present close to the top of the segment (Etayo–Serna, 1968). Rare thin-shelled bivalve molluscs are also found at this horizon (Etayo–Serna, 1968).

2.2.2.5.2. Arcillolitas Abigarradas (AA)

The ammonite fauna preserved in the AA indicates an age range from Barremian to early Aptian (Etayo–Serna, 1968). The fossils in segment A of the AA are distributed across a series of localities; however, not all fossils are found at all sites, and when present the genera are found in varying proportions (Etayo–Serna, 1968). The lower part of the segment preserves a rich ammonite fauna, often with very well-preserved delicate organic structures, including *Acrioceras*, *Ancyloceras*, *Hamulina*, *Heteroceras*, *Paracrioceras*, *Phylloceras*, *Pulchelliidae*, *Pseudohaploceras*, *Spitidiscus*, and *Valdedorsella* ammonites typical for the base of the local Barremian (Etayo–Serna, 1964). This horizon has also yielded a rare example of an ammonite aptychus, attributed to *Nicklesia pulchella* (Patarroyo, 2000a). The ammonites are found together with a few turrillid gastropods, fragments of bivalve molluscs, but notably no echinoderms (which are stenohaline taxa; Townson, 1975) and some benthic foraminiferans (Etayo–Serna, 1968). The middle of the segment preserves ammonites typical of the Colombian Barremian, including *Crioceratites*, *Karsteniceras*, *Nicklesia*, *Pedioceras*, *Phylloceras*, and *Pseudohaploceras*, together with indeterminate, thin-shelled bivalves and a few gastropods. Towards the top of the segment, the upper lower Barremian ammonites *Phylloceras*, *Pulchellia*, *Karsteniceras*, *Parasaynoceras*, and *Pseudohaploceras* are found, together with other heteromorphs and some indeterminate bivalves. The fossils are frequently three-dimensionally preserved when in the centres of the concretions, whereas those in the mudstones are more commonly compressed and fragmented (Etayo–Serna, 1968).

Segment B of the AA preserves a few poorly preserved enrolled and heteromorph ammonites, whereas segment C has revealed various, well-preserved ammonites, mostly belonging to *Pulchelliidae*, including the genera *Colchidites*, *Heinzia*, *Phylloceras*, *Pseudohaploceras*, *Pulchellia*, *Karsteniceras*. Segment D has produced *Chelonicerases*, *Neodeshayesites*, and *Prochelonicerases* ammonites (Etayo–Serna, 1968).

Ammonite fossils are incredibly abundant within the concretions of segment E of the AA. Large forms are often found isolated, whereas smaller specimens are frequently preserved complete and in dense accumulations, and may be associated with fragments. The ammonites recovered from segment E include the genera *Acanthohoplites*, *Australiceras*, *Colombiceras*, *Chelonicerases*, *Epicheloniceras*, *Dufrenoyia*, *Gargasiceras*, *Neodeshayesites*, *Phylloceras*, *Pseudoaustraliceras*, *Riedelites*, and *Zurcherella* (Etayo–Serna, 1964, 1979, 1981). In addition to the ammonites, marine Teredinidae bivalves (or “shipworms”) that live by boring into floating wood (Evans, 1999; Gingras et al., 2004) are common in the segment (Figure 11). Towards the top of segment E, a fibrous calcite band, when split along the middle, reveals extremely abundant remains of inoceramid bivalves, representing the preservation of a short-lived event horizon (Figure 12).

2.2.2.5.3. Arcillolitas con Nódulos Huecos (AcNH)

The ammonite fauna of the AcNH indicates a late Aptian age (Etayo–Serna, 1968). Ammonites are frequently preserved as internal moulds within the mudstones and concretions, and dense accumulations of thin-shelled bivalves and occasional gastropods occur at some horizons. The fauna was taken to indicate well-oxygenated waters with a soft bottom that limited the development of benthic life (Etayo–Serna, 1968). This in turn was used as evidence to infer abundant life throughout the AcNH, which was concentrated by currents, but only sporadically fossilized due to unspecified taphonomic effects (Etayo–Serna, 1968).

2.2.2.6. Marine Microorganisms

Within the Paja Formation, finely-laminated wavy, somewhat dome-like, sedimentary structures are common at some horizons. These structures, with 92% micrite and parallel lamination have been interpreted as cryptalgal mats (Etayo–Serna et al., 2015), providing evidence for shallow water conditions, as marine algae usually live in the permanently wet, but well-lit zone immediately below the low tide mark. Other microfossils are rarely preserved in the Paja Formation; however, an event horizon at the base of the AA (segments A–B) preserves the calcareous benthic foraminifera *Epistomina caracolla* (Patarroyo–Camargo et al., 2009; Patarroyo, 2009). The low diversity of *Epistomina* was used to support an anoxic nearshore evapo-

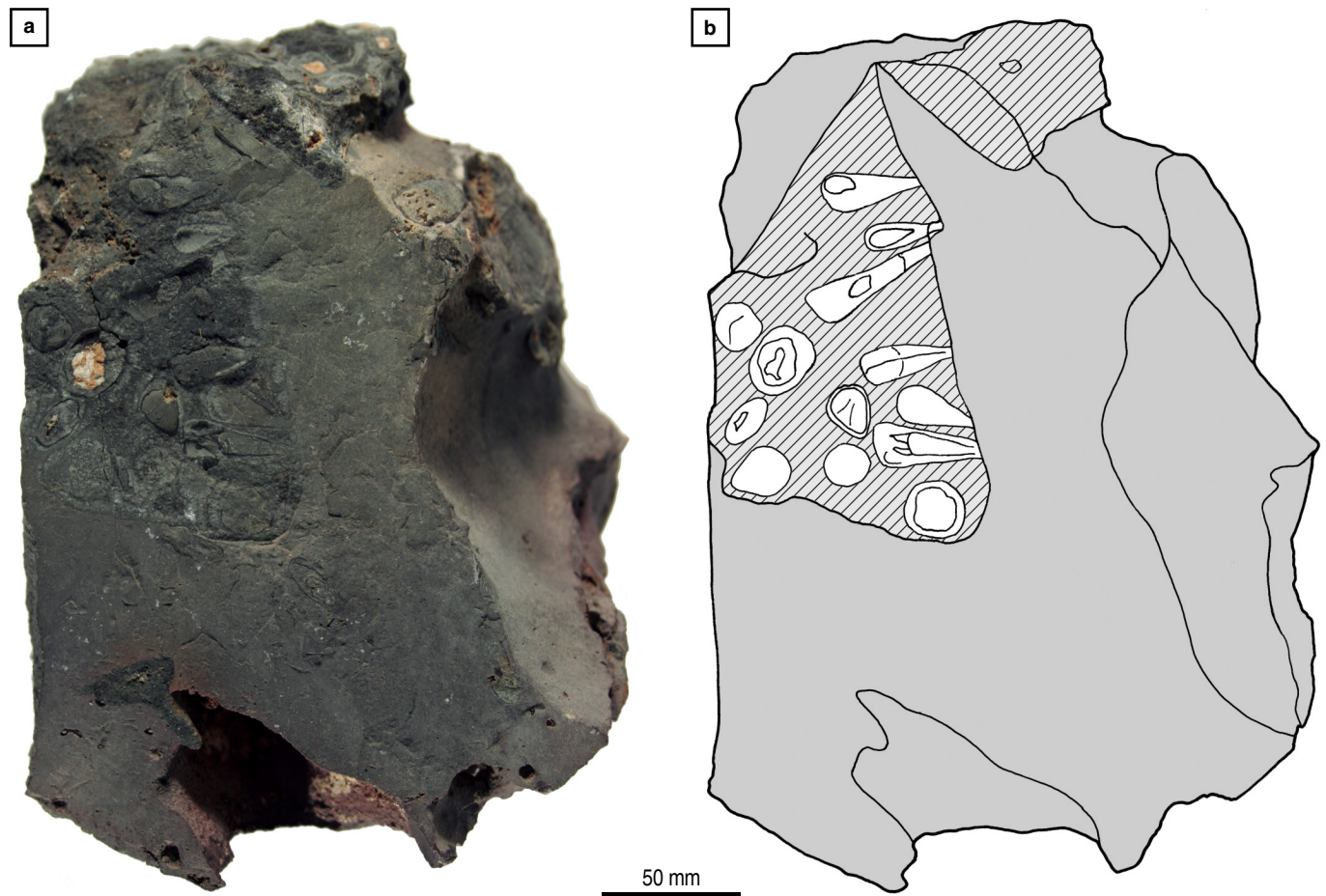


Figure 11. *Teredolites* “wood-ground” ichnofossils, with body fossils of the original bivalves that inhabited the burrows, preserved in a non-septarian concretion (UADG LM 15.10), (a) photograph and (b) interpretive drawing of. In (b) calcite replaced wood, hatched; concretion, grey; ichnofossils and inhabitants, white. Collected by LFN from loma La Cabrera.

ritic environment for the AA; however, *Epistomina caracolla* is typical of oxic watermasses (Gradstein et al., 1999) from mid-shelf neritic to bathyal depths (Decker & Rögl, 1988; Wightman, 1992), and hence cannot support this conclusion. It is more likely this assemblage represents temporary seafloor oxygenation following a storm event (Figure 13).

2.2.2.7. Terrestrial Organisms

In addition to the autochthonous marine fauna of the Paja Formation, alto Ricaurte rocks preserve abundant remains of allochthonous terrestrial plants and occasional terrestrial vertebrates and invertebrates.

2.2.2.7.1. Terrestrial Vertebrates

Mesozoic terrestrial vertebrates are extremely uncommon in Colombia, with the only diagnostic dinosaur being the sauropod *Padillasaurus leivaensis* Carballido et al., 2015 from the Paja Formation of the alto Ricaurte (MJACM 4; originally published as JAVCM 0001). Although originally considered a brachio-

saurid titanosauriform (Carballido et al., 2015) *Padillasaurus* is now considered to be a basal member of the non-brachiosaurid titanosauriform clade Somphospondyli (Mannion et al., 2017). The exact geographical location where *Padillasaurus* was found is not known, although the source of the specimen is reported as the La Tordoya area of vereda Monquirá (Carballido et al., 2015); however La Tordoya is located in vereda El Roble, northeast of Villa de Leiva. Based on the presence of *Gerhardtia galeatoides* and *Lytoceras* sp. ammonites (JAVCM 2, 3, and 4 of Carballido et al., 2015) the remains have an early late Barremian age, and were derived from an unspecified segment (but probably segment C) of the AA Member of the Paja Formation.

The remains of *Padillasaurus* consist of three non-articulating units that contain the incomplete posterior dorsal, sacral, and anterior caudal regions interpreted as the parts of a single animal (Carballido et al., 2015). The first unit consists of part of an isolated mid- to posterior dorsal cervical centrum, the second (unprepared) unit is interpreted as the last dorsal and two anterior sacral vertebrae, and the third unit consists of two posterior sacral and eight anterior caudal vertebrae in articulation. Although incomplete, the vertebrae are well-preserved

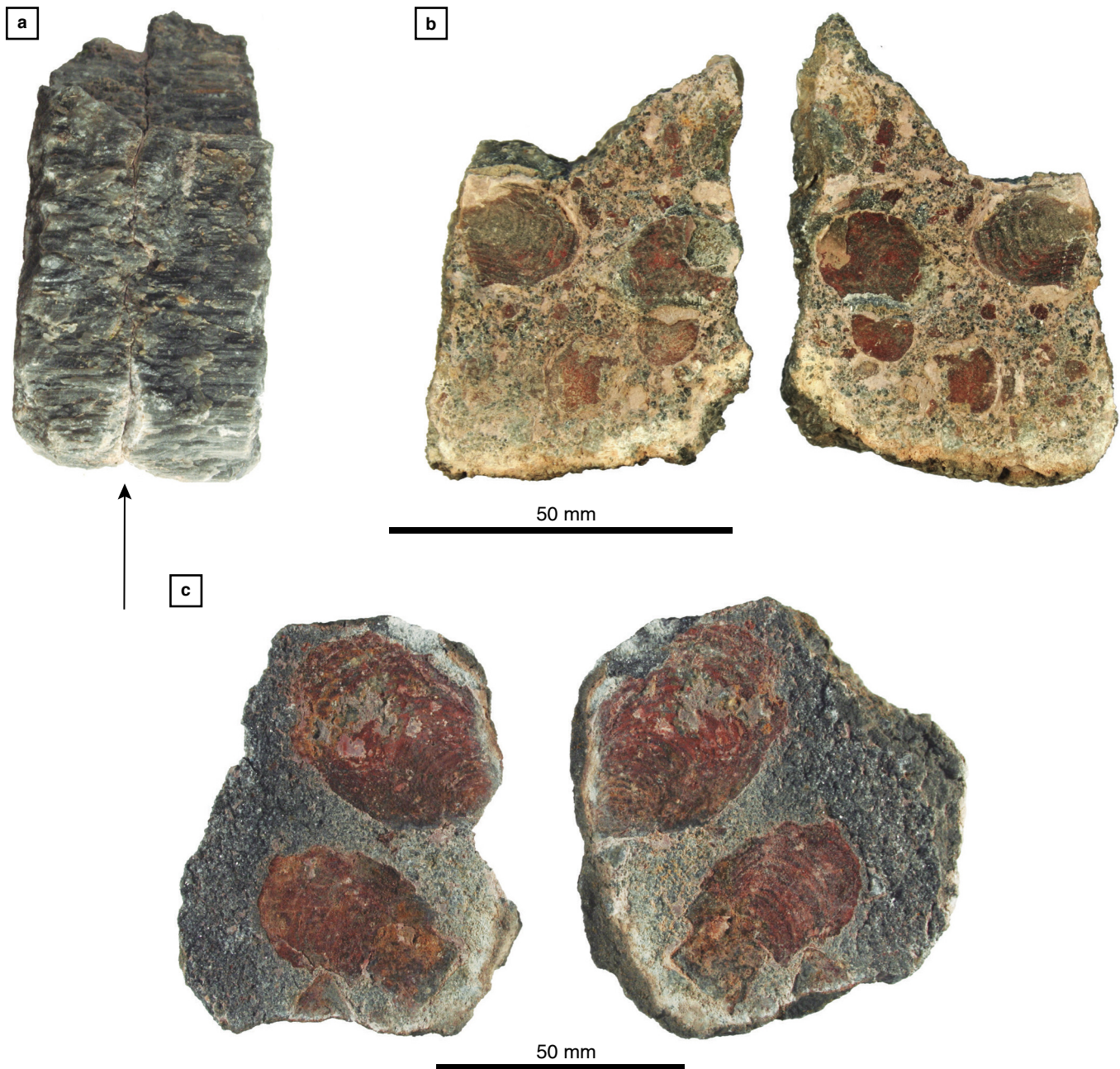


Figure 12. Bivalves preserved in calcite “beef”. **(a)** Bi-layered calcite “beef” showing the “fibrous” nature of the mineral, with the calcite crystals oriented normal to the edges of the vein (UADG LM 17.560). **(b)** The same specimen split open along the central “suture” (arrowed in (a)), showing the preservation of inoceramid bivalve shells within the “beef”. **(c)** A second specimen showing somewhat larger inoceramid shells (UADG LM 17.564). The presence of the bivalves in the centres of the veins indicates antitaxial (from the centre outwards) growth of the calcite. Presumably, the bivalves colonized the seafloor following an environmental perturbation that temporally oxygenated the seafloor, and after lithification the vein nucleated along the calcium carbonate of the shells. Collected by LFN from loma La Cabrera.

including large pleurocoels and some delicate vertebral laminae (Carballido et al., 2015). The almost complete posterior dorsal vertebra is better preserved on its right, suggesting this part of the specimen was discovered sediment side down. This dinosaur fossil appears to be the incomplete remains of a floated carcass, with only the most tightly fused (sacral) or ligamentously tied (anterior caudal) regions remaining articulated.

2.2.2.7.2. Terrestrial Invertebrates

The only reported insect remains from the Paja Formation belong to the family Aeschniidae (Insecta: Odonata), the group to which dragonflies belong (McGavin, 2001). The material includes a beautifully preserved four-winged insect collected from the upper part of segment E of AA. Although no full de-

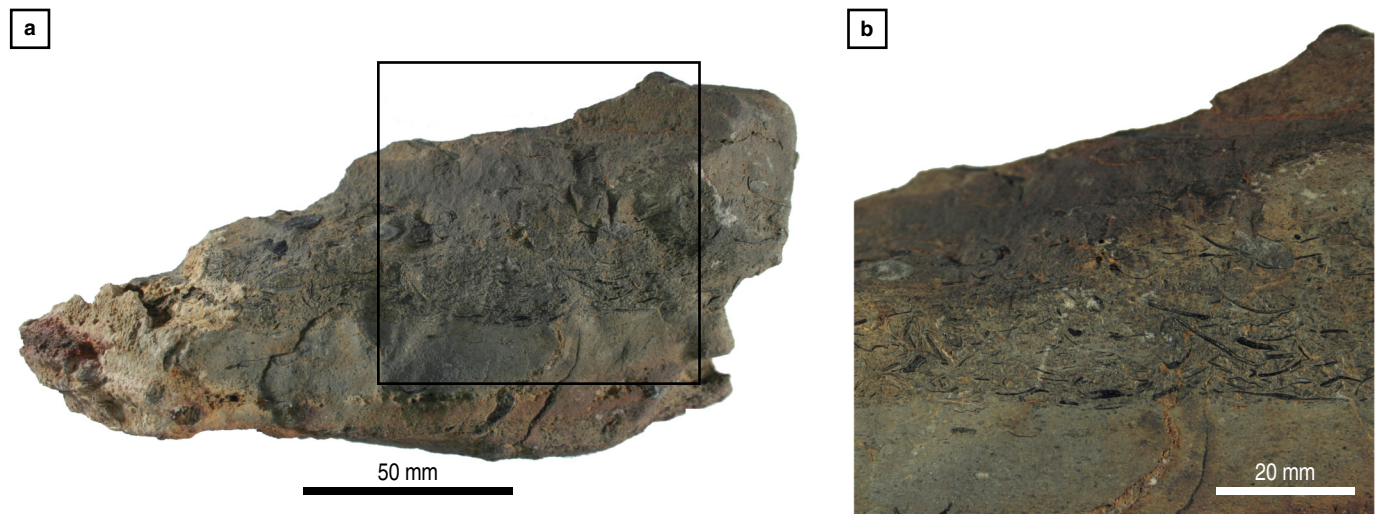


Figure 13. A non-septarian concretion containing a horizon rich in chaotically arranged bivalve fragments, interpreted as a storm bed (UADG LM 17.478). **(a)** Complete block, **(b)** close up of boxed section indicated in (a). Way up interpreted as to the top of the page, based on relatively sharp base and more diffuse upper boundary, but uncertain as the specimen was recovered as a loose block. Collected by LFN from Salto y La Lavendera.

scription is yet available, the environment of deposition has been interpreted as very shallow marine (Gómez-Cruz et al., 2011). However, this does not account for taphonomic aspects such as transportation and burial, so it is uncertain how the specimen was preserved in the Paja Formation Basin. It is possible the insect either flew or was blown into Paja Formation Seas and was deposited in the basin after becoming water saturated and sinking. Preservation of the relatively delicate soft parts, such as the wings, indicates rapid burial, and an absence of oxygen and bioturbation.

2.2.2.7.3. Terrestrial Plants

Allochthonous terrestrial plants (Pteridophyta) are relatively common elements of the Paja Formation deposits of alto Riquarte. LNI segments A and E preserve some scattered plant remains (Etayo-Serna, 1968; Etayo-Serna et al., 2015), but plants are most abundant in the concretions of segment E of the AA (Etayo-Serna, 1968). Described taxa include ferns (Polypodiopsida, part of the former “Pteridophyta”), and seed plants (Spermatophyta) including Bennettitales and cycads (Cycadophyta), conifers (Pinophyta) (the latter two forming part of the former “Gymnospermae”), and angiosperms (Magnoliophyta) (Willis & McElwain, 2002). The ferns are referred to the Weichseliaceae genus *Paradoxopteris* (van Waveren et al., 2002), and Cycadophyta include the genera *Macrotaeniopteris*, *Nilssonia* (Huertas, 1967, 1970), *Pterophyllum*, and *Taeniopteris* (van Waveren et al., 2002). Pinophyta includes a range of families: *Cupressinocladus* (formerly referred to *Thuites* and *Brachyphyllum*; Huertas, 1967, 1970), *Brachyphyllum*, and *Pagiophyllum* (van Waveren et al., 2002) (family Cupressineae); *Frenelopsis* (Moreno-Sánchez et al., 2007)

(family Cheirolepidiaceae); *Araucariostrobus* (Huertas, 1970, 1976; van Waveren et al., 2002), *Conites* (van Waveren et al., 2002), and *Damarites* (Huertas, 1976) (family Araucarineae); *Pinostrobus* and *Pityostrobus* (Huertas, 1967; van Waveren et al., 2002) (family Pinaceae); and *Podozamites* (Huertas, 1967; van Waveren et al., 2002) (family Podocarpaceae). Magnoliophyta includes the genus *Ficus* (family Moraceae) (Huertas, 1967) and the putative angiosperms *Sterculiocarpus* (Huertas, 1967) and *Carpolithes* (van Waveren et al., 2002); however, the latter two may be conifers with large seeds (van Waveren et al., 2002). In addition to the species named above, fossil wood, which cannot easily be attributed to a genus (van Waveren et al., 2002), is extremely common in the Paja Formation. Many of the plant remains are extremely well-preserved externally, often as casts filled with black, macrocrystalline calcite (sparite) (Huertas, 1967; van Waveren et al., 2002), but with no original internal structure (Figure 14); however some wood in the Paja Formation is silicified (Figure 15), and preserves detail to the cellular level.

3. Discussion

The Paja Formation is a thick sequence of fine-grained siliclastic, predominantly dark-coloured pyrite-enriched mudrocks with some calcareous and sandier interbeds, and abundant fossils. Such “monotonous” mudrock successions (Mann & Stein, 1997), make up 75–80 % of crustal strata (Ruppel & Loucks, 2008); however, black mudrock deposits like the Paja Formation are poorly understood, although with the advent of hydraulic fracturing (“fracking”) an increasing number of studies are being undertaken (e.g., Ruppel & Loucks, 2008; Sageman et al., 1991; Schieber, 2016; Tourtelot, 1979). Organic-rich

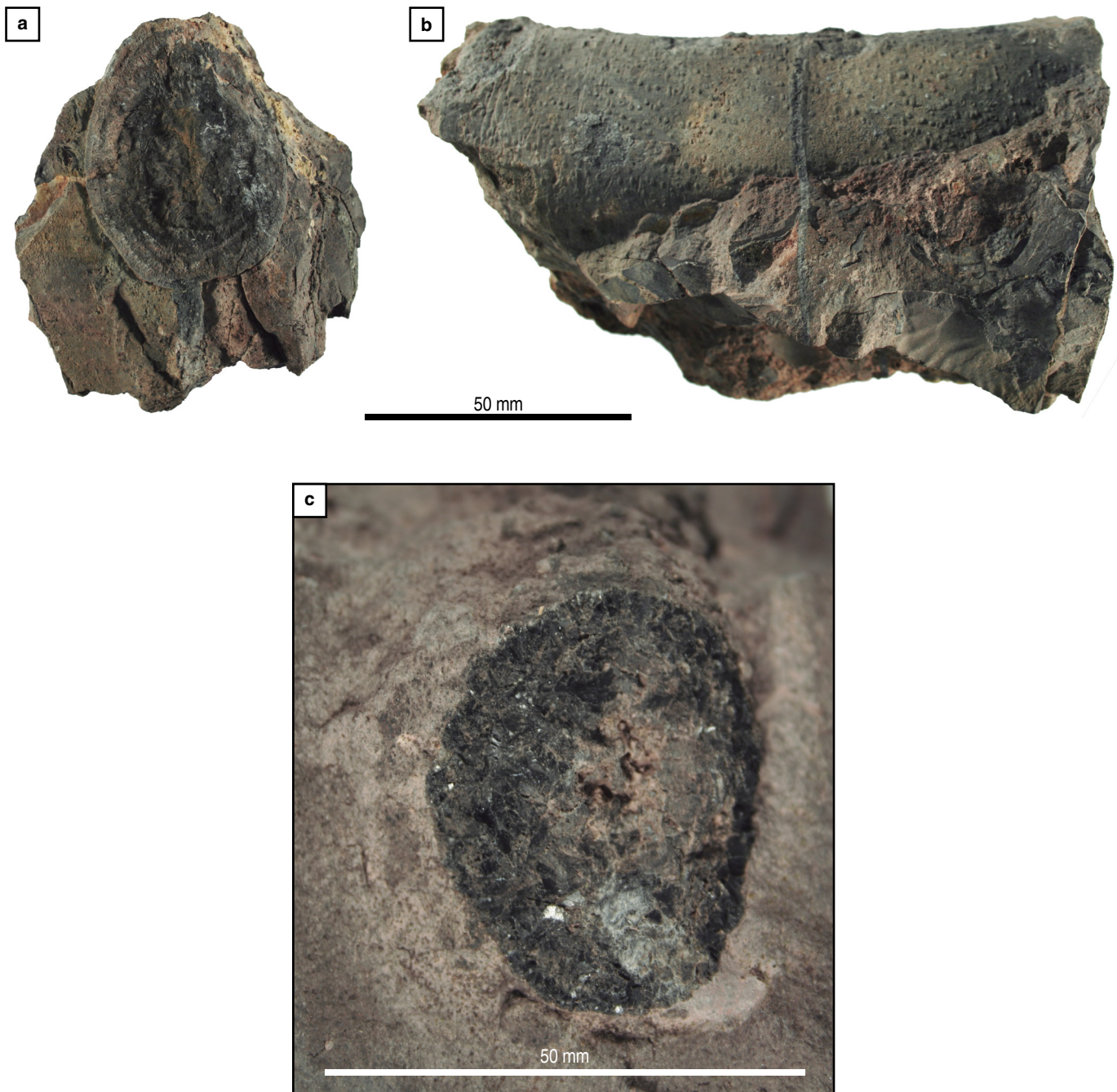


Figure 14. Wood preserved as external moulds filled with coarsely crystalline (sparry) black calcite. **(a)** Cross-section showing the internally layered calcite infill, and **(b)** lateral surface with well-preserved external surface ornamentation of small rugosities (UADG LM 14.50h). **(c)** A second specimen with coarser external ornamentation, filled with non-layered, coarsely crystalline black calcite (UADG 17.537). Both specimens preserved within non-sectarian concretions. Collected by LFN from loma La Cabrera.

mudrocks accumulate in a wide range of depositional settings, many of which are highly complex to understand (Ruppel & Loucks, 2008), in part due to a lack of modern analogues for Cretaceous high-stand epicontinental seas (Algeo et al., 2008; Schieber, 2016; Wignall, 1991a). Hence, to understand the dynamics of former Paja Formation Seas, and the organisms that inhabited them, it is essential to consider diverse evidence for physical water body properties, sedimentary environments, and

biogeochemical parameters (Sageman et al., 1991; Tyson & Pearson, 1991).

3.1. Reinterpretation of the Physical and Biotic Environment of the Paja Formation

Deposition of the Paja Formation in the alto Ricaurte took place during Hauterivian – Aptian times, in a world with high global

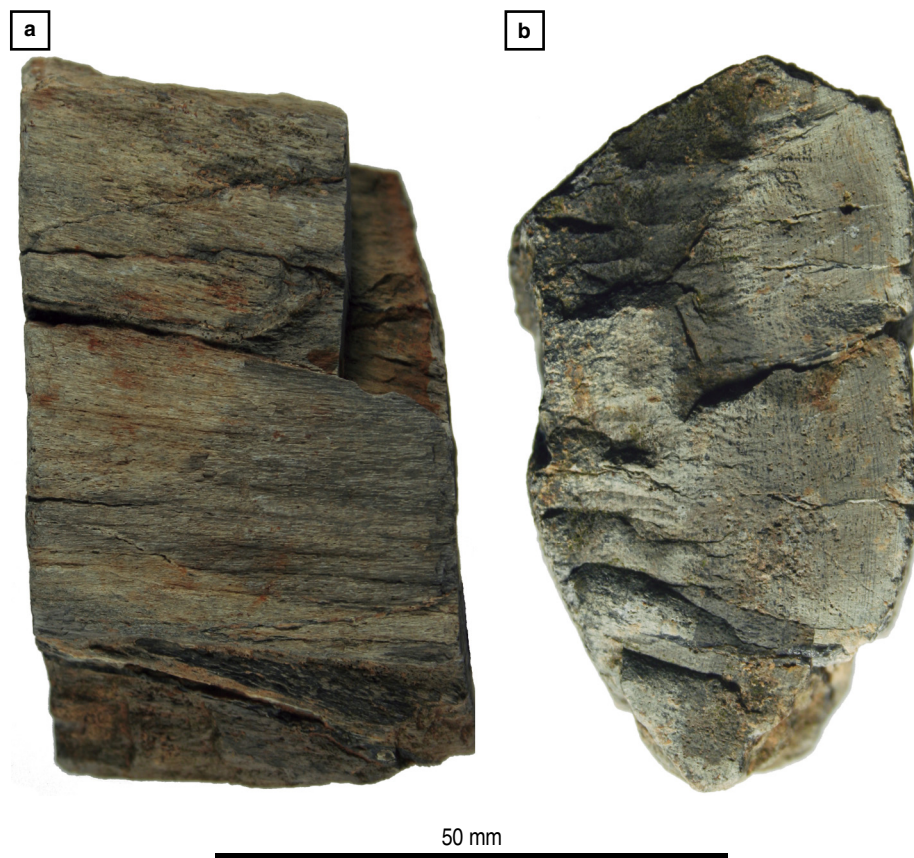


Figure 15. Silicified wood, (a) showing external fibrous woody texture and (b) rotated 90 degrees to show the cross-section with the outer surface (a) to the right (UADG LM 17.407a). Note the faint growth lines to the right of (b) with coarser textured (heart) wood to the left. The preservation of the internal structure contrasts markedly with specimens preserved in calcite (Figure 14). Collected by LFN from El Roble.

sea levels, warm and equitable global temperatures (Tyson & Pearson, 1991; van Helmond et al., 2015; Weissert, 1981), and seas dominated by marine reptiles, fish, and ammonites. The Paja Formation Basin lay in an equatorial location, 5–7° north of the equator (Smith et al., 1994), beneath the ascending limb of the Hadley atmospheric cell (Ziegler et al., 2003). This location, associated with high solar insolation and warm sea surface temperatures, enhanced the hydrological cycle (Poulsen et al., 2007; Ufnar et al., 2002) and produced high evaporation and precipitation rates (van Helmond et al., 2015). Modern tropical shelf seas are well-mixed by the action of tides and/or wind driven waves; although tides would have been damped by friction over shallow epicontinental sea floors (Bádenas & Aurell, 2008). Hence, most energy in Cretaceous tropical epicontinental seas came from the wind (Tyson & Pearson, 1991), and this atmospheric disturbance incorporated abundant O_2 and CO_2 into surface waters, despite a decrease in atmospheric gas solubility in sea water with increasing temperature (Tyson & Pearson, 1991; van Helmond et al., 2015).

3.1.1. Water Depth in Paja Formation Seas

Water depth is a key environmental parameter, and yet absolute palaeowater depths are one of the most poorly constrained boundary conditions of epicontinental seas (Immenhauser, 2009; Ruppel & Loucks, 2008; Tyson & Pearson, 1991; Wig-

nall, 1991a). The Paja Formation Seas flooded continental lithosphere, producing a marine incursion extending into the continental interior (Immenhauser, 2009). Hence, water depth in Paja Seas would have been “shallow” compared to abyssal depths, as high global sea levels increase the aerial extent of continental flooding more rapidly than water depth (Tyson & Pearson, 1991). Modern shelf seas range in depth from 0 m (at the shoreline) to around 200 m (close to the continental slope) (Immenhauser, 2009), but are typically <130 m deep. Anoxia does not occur in waters shallower than about 10–15 m (due to atmospheric surface mixing), and does not normally occur below 60 m, the depth where organic matter is fully degraded in oxic waters (Tyson & Pearson, 1991). The thermocline typically lies at 10–40 m water depth, and a pycnocline may occur at 1–10 m above the sediment–water interface (Tyson & Pearson, 1991). However, with their unique characteristics, Cretaceous epicontinental seas are not directly comparable to modern peri-continental (shelf) seas (Immenhauser, 2009; Meyer & Kump, 2008).

Water depths in epicontinental seas undoubtedly varied in space and time. Estimates of water depth vary from a few to tens to hundreds of metres (Etayo-Serna, 1968; Forero-Onofre & Sarmiento-Rojas, 1985; Miller et al., 1988; Sageman et al., 1991; Wignall, 1991a), but maximum water depth is commonly cited as <100 m (e.g., Miller & Foote, 2009; Mutterlose et al., 2009). Water depth is controlled, and modified, by global sea-levels, and rates of sedimentation and subsidence (Wig-

nall, 1991a). However, anoxic bottom waters must be below fair weather wave base (typically around 15 m water depth), and the generally fine-grained mudrocks of the Paja Formation (Etayo–Serna, 1965, 1968) suggest a water depth below normal storm wave base (Miller et al., 1988), which is typically around 30–60 m (Bádenas & Aurell, 2008). However, occasional distal tempestites (Figure 13) indicate the Paja Formation sediment–water interface was within reach of exceptional storms, which in modern seas may affect waters below 100 m (Tyson & Pearson, 1991). This is corroborated by a lack of shallow water sedimentary structures (desiccation cracks, wave-formed ripples, seafloor mineralization) or common tempestite deposits (erosive bases, coarse-grained lags, hummocky cross stratification) (Immenhauser, 2009; Miller et al., 1988), and may be further constrained by the presence of sandownid turtles that have been considered to inhabit the near shore–littoral zone (Cadena, 2015). Hence, we suggest a water depth for Paja Formation Seas in the range of 60–130 m.

3.1.2. Paja Formation Surface Waters

Cretaceous atmospheric (and oceanic) partial pressures of carbon dioxide ($p\text{CO}_2$) were high (Zhang et al., 2016), which together with high water temperatures and a well-lit equatorial location (due to daytime solar input being directly overhead; Sageman et al., 1991), led to elevated rates of marine photosynthesis (Caplan & Bustin, 1998; van Helmond et al., 2015). In modern seas, nutrient availability, water temperature, salinity, and water clarity all control photosynthetic rate (Tourtelot, 1979), so for continued primary productivity in Paja Seas, constant input or recycling of biologically limiting nutrients (especially N, K, Fe) was essential (Moore et al., 2013). Most nutrients in the modern shallow marine realm come from continental weathering and are delivered by freshwater runoff (Keller, 2008). For Paja Formation Seas, sediments and nutrients were sourced from neighbouring landmasses or topographic highs forming islands, which included the Guiana Shield to the east, and the Central Cordillera island arc to the west (Campos–Álvarez & Roser, 2007). The island arc may also have contributed volcanic ash during eruptions (Hoedemaeker & Kakabadze, 2004), and thus influenced Cretaceous ocean fertility (Petrash et al., 2016; van Helmond et al., 2015). Wind-blown continental dust may also have contributed nutrients (Schieber, 2016), but as Paja Formation Seas were outside the desert climatic belt, this was likely to have been a minimal input.

The climate of adjacent landmasses controls the rate of terrestrial organic matter input into a marine basin (Weissert, 1981). During Paja Formation times, elevated $p\text{CO}_2$, equatorial temperatures, and abundant water availability enhanced rates of terrestrial tropical deep weathering (Petrash et al., 2016; van Helmond et al., 2015). There is ample evidence from the Paja Formation that these nearby landmasses, like the Paja Seas, ex-

hibited high primary productivity, and were therefore covered in an abundance of vegetation. Terrestrial vegetation acts to stabilize weathering products, especially if land surface gradients are subdued (Schieber, 2016), although vegetation may also have generated high levels of weathering, both physical (through root action) and chemical (through release of organic acids). There is abundant evidence for higher plant input into Paja Formation Seas (e.g., Huertas, 1967, 1970), and this abundance of terrestrially sourced vegetation indicates high levels of run off, which would have brought abundant detrital grains and nutrients, as ions in solution, into the Paja Formation Basin (Tyson & Pearson, 1991), together with the organic material. These terrestrially sourced weathering products, together with the organic material, were presumably delivered to Paja Formation Seas via rivers (Tyson & Pearson, 1991; van Helmond et al., 2015) as a result of high tropical precipitation rates and following intense runoff resulting from storms. Once in the shallow marine realm, high sea surface temperatures ensured rapid biochemical recycling of biological limiting nutrients. High nutrient input, associated with elevated temperatures may also have been a key factor in bottom water anoxia (Meyer & Kump, 2008).

There is no absolute method for determining Paja Formation palaeosalinity (Tyson & Pearson, 1991). Rainfall and freshwater runoff from adjacent landmasses can decrease surface seawater salinity, but wind mixing would have limited this to local variability near-shore (Sageman et al., 1991; Tyson & Pearson, 1991). The abundant ammonite fossils (e.g., Etayo–Serna, 1979; Patarroyo, 2000b), members of Cephalopoda, are indicative of marine conditions with near normal salinity, as all modern cephalopods are intolerant to greatly increased or lowered salinities (Moore, 2001). That most ammonites are autochthonous to the Paja Formation Basin, and did not experience significant post-mortem transport, is demonstrated by their frequent exceptional preservation, including the most delicate shell structures such as spines (e.g., Etayo–Serna, 1968; Patarroyo, 2000a). Hence, near normal marine conditions, as indicated by the fossil fauna, implies an open connection to wider Cretaceous oceans which maintained normal marine salinity. Thus, surface waters of Paja Formation Seas would have been warm, well-lit, and well mixed, with abundant O_2 and CO_2 , and normal marine salinity.

3.1.3. Pelagic Fauna

Interpreting a living community from fossil evidence requires rigorous analysis, but this is only partly possible for Paja Formation Seas due to lack of study. Paja Formation Seas were home to a diverse, autochthonous pelagic fauna consisting of numerous marine reptiles, fish, and ammonites (Figures 5–7), although marine crocodiles and belemnites, common in other Lower Cretaceous marine deposits (Mutterlose et al., 2009), are entirely absent from the Colombian Cretaceous. Marine rep-

tiles, all air breathing, are represented by abundant and diverse plesiosaurs (both plesiosauiromorphs and pliosauiromorphs), ichthyosaurs, and marine turtles. Fish are abundant and diverse, and ammonites, both planispiral and heteromorphic, some large, are incredibly abundant. The fish and ammonites, both of which obtain O_2 for respiration dissolved in the water column, provide evidence for abundant oxygenation of surface waters. The high pelagic biodiversity is also an indication of the productivity of Paja Formation Sea surface waters, as all organisms are ultimately dependent on phytoplankton as a source of energy. The organic-rich Paja Formation sediments are thus indicative of rich phytoplankton and zooplankton in the oxic, photic zone waters of this former epicontinental sea.

Marine reptiles may have been attracted to Paja Formation Seas to exploit feeding grounds rich in fish and ammonites. Additionally, Paja Formation Seas may have acted as relatively safe breeding- or birthing-grounds for marine reptiles (cf. to the Posidonien-schiefer deposits of Holzmaden, Germany; Bottjer et al., 2002). However, gravid females and juveniles are rare in the fossil record, and poorly known from the Paja Formation, so the topic requires additional research. Currently, the only direct evidence for marine reptile reproduction in Paja Formation Seas is the presence of turtle eggs (Figures 9, 10), and juveniles of *Desmatochelys padillai* (Cadena & Parham, 2015). However, as the turtle eggs are surrounded by the bones of the mother, this excludes the possibility the eggs had been laid. Hence, the current data cannot support the hypothesis of a turtle breeding ground (Etayo-Serna et al., 2015), and in any case, marine turtle eggs require both water from the environment (Wallace et al., 2006) and low salinity (Miller et al., 2003a) to develop. Hence, the previously hypothesised sabkha environment for the Paja Formation (Forero-Onofre & Sarmiento-Rojas, 1985) is incompatible with the terrestrial deposition of turtle eggs, which in an evaporitic environment will rapidly dehydrate and die.

In addition to the free-swimming pelagic organisms, the Paja Formation preserves abundant evidence of pseudoplanktonic bivalves, or lignophagous “shipworms” (Evans, 1999; Gingras et al., 2004) that lived by burrowing into floating driftwood (Figure 11). That this is pseudoplankton, rather than bottom living bivalves colonizing wood falls, is clear from the presence of boring bivalves all around the wood, which would not be the case for bottom colonization, where wood in contact with the sediment surface would be free of boring organisms. The presence of xylic bivalves is also evidence that woody plant material was a common resource in Paja Formation Seas, and that some floated for a considerable time. In addition to the preserved pseudoplankton, it is likely other organisms hitched a ride on swimming marine reptiles, fish, and cephalopods, or floating objects, as occurs in modern oceans (Wignall & Myers, 1988). However, this is aspect of Paja Formation palaeoecology requires additional research.

3.1.4. Paja Formation Bottom Waters

The sedimentology of the Paja Formation is predominantly fine-grained mudrocks, which are frequently finely-laminated, but exhibit limited evidence for abiotic sedimentary structures, and typically lack coarse-grained clastic materials (Tyson & Pearson, 1991). These muddy sediments are indicative of a low energy depositional environment (Townson, 1975; Wignall & Myers, 1988), with sediments gradually settling through a tranquil water column, and little disturbed by bottom currents (cf. Etayo-Serna, 1968). This is supported by the low-level of mechanical fragmentation and disarticulation observed in many invertebrate and vertebrate fossils, but which may also be due to the rarity of scavengers on the sea floor (Wignall & Myers, 1988). However, infrequent silt laminae and sandier interbeds indicate occasional high-energy events that deposited coarser-grained material in the Paja Formation Basin. These event horizons produced large, infrequent perturbations of Paja Formation Seas, likely generated by very large tropical storms, tsunamis or turbidity currents. Tectonic activity probably produced earthquakes (Wignall, 1989) from the nearby subduction zone beneath the Central Cordillera island arc to the west (Gaona-Narváez, 2015), or as a result of extensional crustal faulting beneath the Paja Formation sedimentary basin (Jiménez et al., 2014).

The predominantly dark colour of Paja Formation sedimentites is indicative of a high organic carbon (C_{org}) content (Tourtelot, 1979). Total organic carbon (TOC) values in the Paja Formation are on average >1%, and in some exceptionally horizons TOC reaches >15% in (Campos-Álvarez et al., 2002). However, C_{org} is only incorporated into seafloor sediments when organic matter supply is greater than biochemical breakdown. Aerobic metabolism consumes O_2 , and when consumption is higher than supply, dysoxic or anoxic bottom waters and/or sediments, together with enhanced preservation of C_{org} result (Caplan & Bustin, 1998; Tourtelot, 1979; Tyson & Pearson, 1991). In addition, the dark mudrocks of the Paja Formation frequently preserve iron pyrite (Fe_2S) (Etayo-Serna, 1979). In the absence of O_2 , photosynthetic (green, purple) or non-photosynthetic sulphate-reducing bacteria thrive, decompose organic matter, invade the sediments, and generate hydrogen sulphide (H_2S) (Tourtelot, 1979; Tyson & Pearson, 1991). The organic matter thereby acts as fuel for seawater sulphate reduction. H_2S is produced close to the sediment-water interface, combines with iron derived from sediments, and is ultimately preserved in the form of iron pyrite (Fe_2S) (Schieber, 2011). Hence, the common presence of iron pyrite (Etayo-Serna, 1979) is evidence for the anoxic nature of Paja Formation epicontinental sea sediments. The less-common silt-rich and sandier interbeds, on the other hand, are of lighter colour as they contain much less C_{org} , and little or no Fe_2S . These lighter coloured beds were probably the result of

low-frequency high-energy perturbations that stirred up the water column, introducing both coarser sediments and dissolved oxygen into the benthic realm. Short-term oxidation of the sea floor permitted oxidative decomposition of organic matter raining down from the surface waters, and temporally changed biological seafloor dynamics.

The muddy Paja Formation Sea floor was probably soft, possibly with a “soupy” (water-rich) consistency (Martill, 1993). Muds, when initially deposited, typically contain a high percentage of water (Nicholls & Russell, 1990), leading to a fluidized upper sedimentary pile. These muds may contain up to 80% water by volume, which can be reduced to as little as 30% upon compaction (Nichols, 2009). It is possible to estimate the volume of dewatering for the Paja Formation by comparing the thickness of bedding preserved within early diagenetic concretions, to the compacted sediments that wrap around those concretions; this differential compaction indicates a loss of original sediment thickness of at least 80% (Figure 16). In addition to the sedimentary evidence, the fully articulated nature of many Paja Formation marine reptile skeletons (plesiosaurs, ichthyosaurs, turtles) suggest the carcasses sank into soft muds (Martill, 1985, 1988), partially or completely burying the organisms. This would have aided their preservation, and may help explain differential preservation on the two sides of the ichthyosaur *Platypterygius sachicarum* (SGC DON-19671), and the titanosauriform dinosaur *Padillasaurus leivaensis* (MJACM 4) (Carballido et al., 2015; Páramo-Fonseca, 1997). The numerous articulated fish, many bearing scales and/or preserved in three-dimensions (Figure 6), also strongly argues for rapid burial close to the site of death, and preservation in anoxic sediments (Martill, 1993). The presence of soft or soupy sediments inhibited the growth of “normal” marine benthos, except perhaps for a few reclining species of inoceramid bivalves, dysoxia–anoxia at the base of the water column prevented the growth of epifauna on exposed skeletal elements (Etayo–Serna, 1965), and minimized the action of scavengers.

3.1.5. Benthic Fauna

The Paja Formation preserves a depauperate benthic fossil fauna compared to the pelagic realm (Macellari & de Vries, 1987), with typically low levels of bottom-living macrofossil diversity and abundance. This indicates non-normal bottom conditions, most likely lacking in oxygen, but also possibly with toxic H_2S generated on the sea floor or periodically released from within the sediments. However, some thin-shelled, epifaunal bivalve molluscs (e.g., inoceramids) are tolerant of low oxygen tensions, and even small amounts of H_2S (Wignall, 1991b; Wignall & Myers, 1988), and it is probably these species that are preserved in the Paja Formation (Etayo–Serna, 1968). In addition, the Paja Formation occasionally preserves gastropods,

and extremely rarely echinoderms, crustaceans, and benthic foraminiferans (Etayo–Serna, 1968; Patarroyo, 2009). Hence, as with the sedimentology, there is good biological evidence for short-term benthic oxidation of the Paja Sea floor. These oxygenation events are recorded as occasional bivalve-rich horizons (Figure 12), and the rare presence of “normal” marine benthic faunal elements (Etayo–Serna, 1968). Periodically oxygenated Paja Formation bottom waters is in line with our developing more general understanding of epicontinental seas dynamics (e.g., Brady & Bowie, 2017; Sageman et al., 1991; Selden & Nudds, 2012).

Wavy, finely laminated sedimentary structures preserved with cubes of iron pyrite (Fe_2S) are common within the Paja Formation of alto Ricaurte. These sedimentary structures have been interpreted as algal mats (Etayo–Serna et al., 2015), living in shallow, well-lit (euphotic) waters that permitted sufficient light penetration to maintain photosynthesis. However, the lack of grazing macrofauna, normally abundantly associated with Phanerozoic well-lit, well-oxygenated algal mat ecosystems (Eriksson et al., 2007), indicates dysoxic–anoxic conditions at least at the sediment–water interface. Hence, although microbial mat communities may at times have had oxic photosynthetic microorganisms (such as cyanobacteria) on the surface, it is likely that at most times these environments were dysoxic–anoxic and consisted of surface-living, sulphate-reducing microbial mat communities (e.g., green sulphur bacteria; Hay, 2008), producing H_2S to which algae are entirely intolerant. Hence, the Paja Formation microbial laminates, with the common presence of pyrite, are not necessarily indicative of well-lit, shallow-water, oxic conditions, but are better interpreted as deeper water, low oxygen, possibly H_2S -rich environments dominated by sulphate-reducing microbes. However, even in the presence of somewhat oxygenated near-bottom waters, anoxic microbial mats may flourish, with a strong O_2 (and H_2S) gradient immediately above the sediment water interface. The interpretation of wavy lamination as anoxic microbialites, rather than oxic cryptoalgal structures, is of importance as it accords more closely with the deeper, anoxic interpretation of the fine-grained organic-rich sediments generally observed in the Paja Formation.

The well-laminated fabric of many Paja Formation beds, and the scarcity of ichnofossils, indicates an almost entire lack of bioturbating infauna. Absence of burrowing forms implies anoxia at the sediment water interface (Mann & Stein, 1997; Wignall & Myers, 1988), most likely with the presence of H_2S , which produces conditions chemically hostile to most macro-infaunal and epifaunal life (Macellari & de Vries, 1987; Sageman et al., 1991). However, laminated sediments may not be entirely lifeless (Tyson & Pearson, 1991), although the organisms are likely to be soft-bodied polychaetes, which are unlikely to leave evidence of their presence in the sedimentary or fossil records.

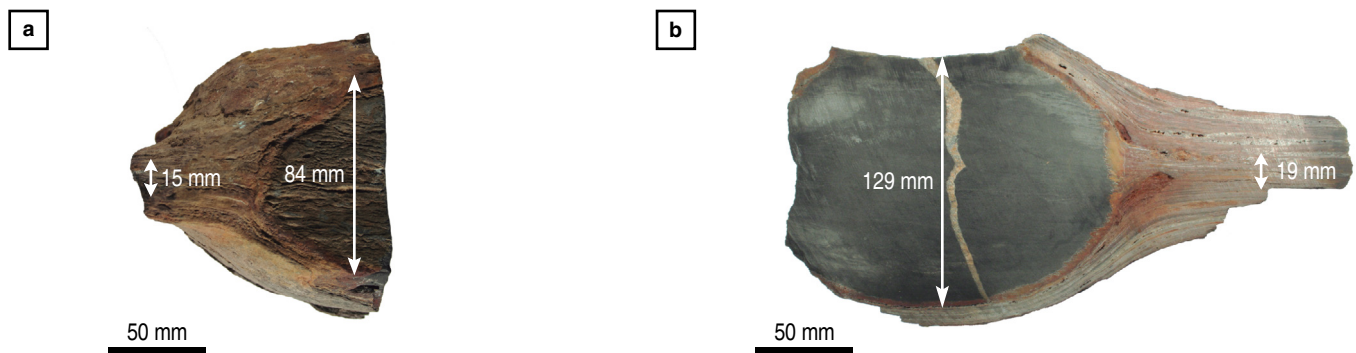


Figure 16. Non-septarian, early diagenetic concretion surrounded by non-concretionary sediments that “wrap around” the concretion (UADG LM 17.369). **(a)** “End” of the concretion showing the bedding (picked out by recent weathering) passing through the concretion, whereas the surrounding non-concretionary sediments “wrap” around the concretion. **(b)** Cut, right side, of (a) showing the lack of obvious bedding within the concretion (but which is faintly visible in the original specimen), the wrapping of sediments not invested by early diagenetic concretion growth, and a later phase calcite vein cutting the concretion sub-vertically. This specimen gives details of both pre- and post-compaction thicknesses of the sediment pile; in (a) concretion 84 mm, same laminae 15 mm post-compaction gives 82.14% compaction ($100 - (15/84 \times 100)$); in (b) concretion 129 mm (minimum), same laminae 19 mm post-compaction gives a minimum of 85.27% compaction ($100 - (19/129 \times 100)$). Collected by LFN from Salto y La Lavendera, way up not known but overburden pressure was in the sense top–bottom.

3.1.6. A Tripartite Division of Paja Formation Waters

Dark, laminated mudrocks largely devoid of benthic macrofauna and trace fossils, beneath a stratified water mass were episodically developed in shallow epicontinental seas during the Jurassic and Cretaceous (Petrash et al., 2016; van Helmond et al., 2015). Paja Formation Seas were thereby divided into a three-phase environment (Tyson & Pearson, 1991): firstly, near-normal marine surface waters; secondly, non-normal dysoxic–anoxic bottom waters and anoxic sediments; and thirdly, these two semi-independent water masses were separated by a chemocline or pycnocline (density interface). However, development of a chemocline–pycnocline will trap nutrients in the bottom waters, which, unless nutrients are available from elsewhere, will lead to reduced surface water primary productivity (Tyson & Pearson, 1991), however, abundant nutrients appear to have been available in Paja Formation Seas from terrestrial sources as argued above. The interface between the upper and lower waters was not a sharp line, but rather a transition zone, which restricted vertical mixing of oxygen-rich surface waters and nutrient-rich but oxygen-poor bottom waters (Sageman, 1985; Wignall, 1991a). Hence, the development of a semi-permanent chemocline–pycnocline acted as a control on both fauna and C_{org} burial (Pacton et al., 2011; Sageman et al., 1991).

With water depth greater than fair weather atmospheric mixing, an oxygen and temperature gradient can develop due to incomplete mixing. With highly productive surface waters, the degradation of dead organic matter settling through the water column is incomplete, and below the well-mixed zone organic matter degradation consumes more oxygen than can be replaced by diffusion, especially in periods of high global temperatures

such as the Cretaceous (Meyer & Kump, 2008; Tourtelot, 1979). This generates an oxygen gradient, and an oxygen minimum zone at or above the sediment–water interface (Jenkyns, 1980). Hence, dead organic matter normally oxidized within the water column, reaches the sediment–water interface, using up dissolved oxygen as it goes. Any aerobic decomposition on the seafloor further reduces benthic oxygen availability, and low oxygen tensions gradually reduce benthic faunal species richness, biomass, and body size. The elimination of thick-shelled forms occurs first, although some smaller shelly forms can survive in dysoxic environments (Wignall & Myers, 1988). In the Paja Formation, the thickness of the lower (sub chemocline–pycnocline) dysoxic–anoxic water layer was probably in the order of centimetres to a metre (cf. Tyson & Pearson, 1991).

Ultimately, organic matter on the seafloor becomes incorporated into sediments, as it can no longer be completely consumed by aerobic epifauna. In organic-rich sediments without infauna, even in the presence of partially oxic bottom waters, anoxic conditions will exist a few millimetres below the sediment–water interface (May & Harvey, 1995). In anoxic conditions, sulphate-reducing bacteria act on the organic matter, producing hydrogen sulphide, which is preserved in the rock record as iron pyrite (Tourtelot, 1979). Indeed, the incomplete breakdown of organic matter may produce compounds that preferentially act as substrates for anaerobic bacteria on the seafloor (Tourtelot, 1979). These conditions are most likely to occur in the deepest part of the basin, producing an oxygen-deficient “puddle” (Wignall, 1991a). However, oxygen levels also depend on the rate of surface organic primary productivity, clastic sedimentation rates (so as not to over dilute organic matter), oxygen diffusion rates (lower in warmer waters), and the intensity of oxidation (Tourtelot, 1979).

The interface between the upper and lower water masses developed due to differences between surface and bottom water bodies in terms of (Hay, 2008; Meyer & Kump, 2008; Wignall, 1989): temperature as a result of solar heating of surface waters (likely); chemical differences due to slow oxygen diffusion and high nutrient availability (likely); and/or salinity differences (less likely). In modern environments, shelf anoxia is normally due to thermal stratification of the water column, but can be a result of dense saline bottom waters (Tyson & Pearson, 1991). In Paja Formation Seas, salinity differences seem an unlikely cause because, although salinity is a potent stratifying agent, it is improbable a halocline could develop across an entire epicontinental sea basin (Tyson & Pearson, 1991). However, sediment cracking is observed in the Paja Formation, and underwater this could be related to syneresis (sub-aqueous sediment shrinkage due to osmotic dewatering into a halocline). However, the cracking seen in Paja Formation sediments seems more likely to be a result of diagenetic sediment dewatering and shrinkage (cf. to septarian nodule formation). Hence, thermal stratification of Paja Formation Seas, associated with oxygen starvation of the bottom waters and high nutrient input into surface waters (and hence high primary productivity), leading to biochemical water mass differences, seems the most likely reason for Paja Formation chemocline–pycnocline development and maintenance.

Shallow water black mudrock facies are often considered broadly transgressive (Tourtelot, 1979). However, although transgression may help explain the initial development of anoxia in Paja Formation Seas, it cannot explain the maintenance of that system. Paja Formation Seas existed from Hauterivian to Aptian times (approximately 18 Ma based on current understanding, Cohen et al., 2013; updated 2017/02), and marine transgression did not continue unabated throughout this time (Guerrero, 2002a, 2002b). In modern subtropical and temperate seas, stratification is commonly linked to seasonality, with summer primary productivity sufficient to induce bottom water dysoxia–anoxia, and winter storms sufficiently strong to breakdown the chemocline–pycnocline (Bádenas & Aurell, 2008; Miller et al., 1988). However, the latitudinal position of the Paja Formation Seas indicates a non-seasonal equatorial climate, with constant high primary productivity and therefore continual organic matter loading.

The majority of modern, and many ancient, dysoxic–bottom marine environments are enclosed, but it is perhaps possible to develop shelf anoxia in an open setting. However, the Paja Formation is best seen as a semi-enclosed sea, bordered by land to the east (and at different times to the north and south), with an incomplete barrier to the west formed by the Central Cordillera island arc. Hence, none of the commonly cited causes of density stratification appears to apply to Paja Formation Seas, and this reinforces the uniqueness of each individual epicontinental sea. Hence, the tripartite division of Paja Formation waters

initially developed, and was later maintained, through surface water heating, and differential surface and bottom water biochemical processes (Meyer & Kump, 2008). Once developed, dysoxic or anoxic bottom conditions are self-perpetuating. Some phytoplankton live along the chemocline–pycnocline, obtaining sunlight for photosynthesis from above and nutrients for growth from below (Tyson & Pearson, 1991). The gill-bearing fish and cephalopods will not enter dysoxic bottom waters, as they require oxygenated waters to survive. Marine reptiles, as air breathing organisms, could potentially cross the chemocline–pycnocline to enter dysoxic bottom waters, but a lack of prey items would normally restrict these organisms to the well-mixed surface waters. This lack of macroscopic predators in Paja Formation bottom waters, together with soft sediments, helps to explain the absence of scavenging on marine reptile skeletons and fish carcasses preserved in the Paja Formation. A “snapshot” model for the environment for the Paja Formation is presented in Figure 17.

3.1.7. Dynamics of Paja Formation Seas

Epicontinental seas were dynamic places (Sageman et al., 1991). Modern shallow seas are rarely beyond the reach of storm mixing (Tyson & Pearson, 1991), and Paja Formation Seas were undoubtedly affected by storms, and possibly earthquakes, tsunamis, and turbidity currents. Equatorial regions are subject to short but intense thunderstorms, and at 5–7° north of the equator (Smith et al., 1994), Paja Formation Seas were on the lower latitudinal limits of the tropical storm (hurricane–typhoon–cyclone) belt, but were undoubtedly occasionally affected by these large atmospheric perturbations (Emanuel, 2003). In shallow shelf or epicontinental seas, storms affect a large proportion of the water column (Tyson & Pearson, 1991). Exceptional storms may completely break down chemical or density interfaces (Wignall & Myers, 1988) although the greater the depth of water, the greater the energy required to breakdown stratification, making permanency of the chemocline–pycnocline a depth dependant parameter (Wignall, 1991a). Large storms that breach the chemocline–pycnocline will temporally introduce oxygen into normally dysoxic–anoxic bottom waters (Miller et al., 1988; Wignall & Myers, 1988), but may also release toxic H₂S from bottom waters or sediments (Meyer & Kump, 2008).

Evidence for storms in deep water environments are typically preserved as distal tempestites (Figure 13), often just a few mm thick, characterized by graded rip-up clasts, silt laminae, and thin graded mud horizons (Miller et al., 1988; Wignall, 1989). The aftermath of storm events may be recognised in the rock record by the presence of brief colonization events preserved as shell pavements (Figure 12), surrounded above and below by dysoxic–anoxic sediments (Miller et al., 1988; Wignall, 1989). In addition, the wide range of terrestrial material within the Paja Formation Basin (including logs, branches, leaves, fruit, insects,

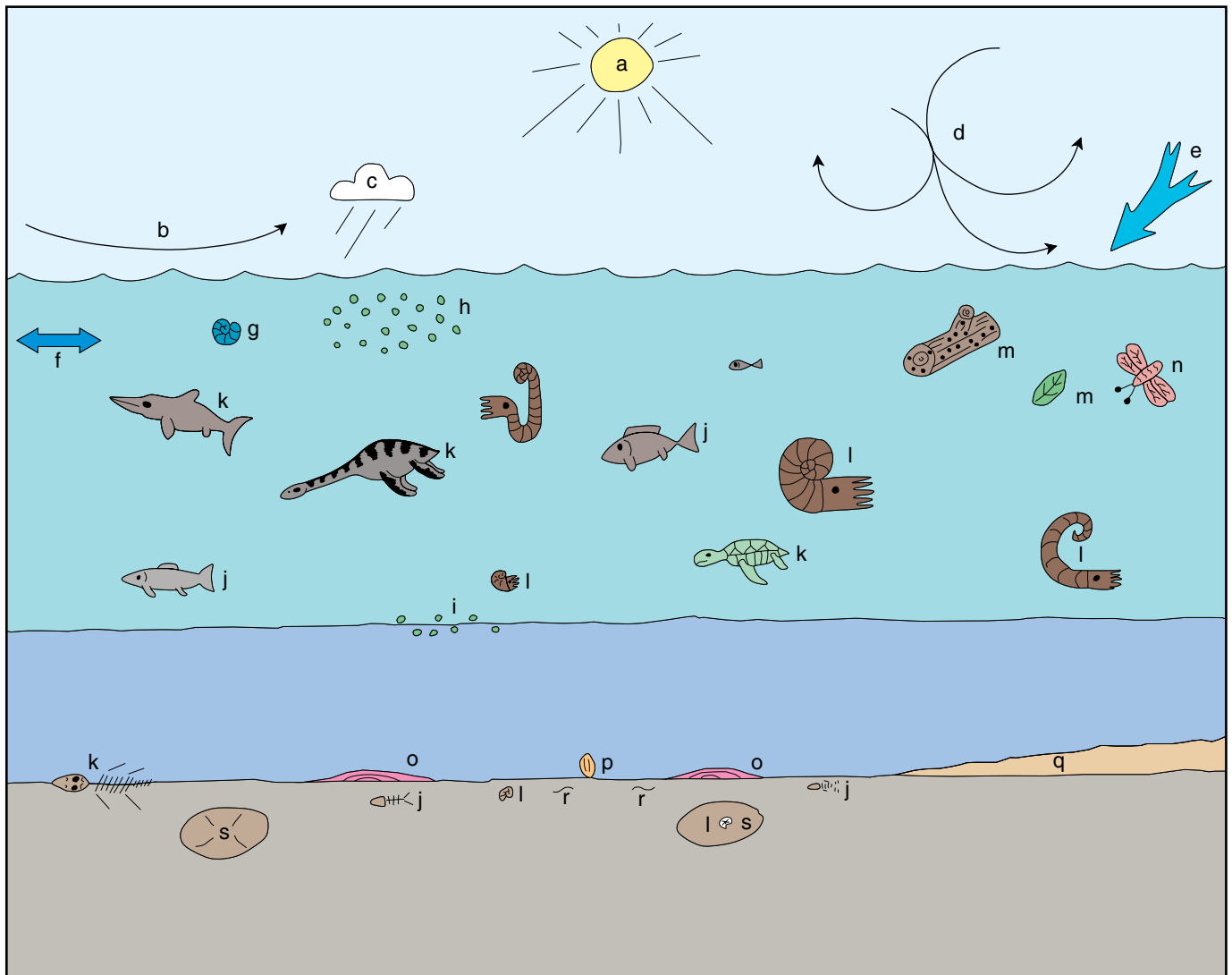


Figure 17. A diagrammatic representation of Paja Formation Seas, with inputs from sun, rain, wind, storms, and the terrestrial realm. Surface waters with a restricted circulation and tidal influence, and with a diverse pelagic fauna. Dysoxic-anoxic bottom waters with a depauperate benthic fauna of a few thin-shelled bivalves, separated from the surface waters by a chemocline-pycnocline. The dysoxic-anoxic bottom waters largely excluded burrowing and surface living organisms and permitted exceptional fossil preservation. Abbreviations: (a) solar input; (b) wind; (c) rain; (d) tropical storms; (e) terrestrial freshwater and organic matter; (f) subdued tidal or current action; (g) zooplankton; (h) surface water phytoplankton; (i) phytoplankton exploiting the chemocline-pycnocline; (j) fish and their fossils; (k) marine vertebrates and their fossils; (l) ammonites and their fossils; (m) floating logs with boring bivalves (“shipworms”), and other terrestrial plant material; (n) insects; (o) sulphate-reducing bacterial mats; (p) depauperate benthic fauna; (q) occasional storm deposits; (r) low oxygen tension and hydrogen sulphide-tolerant annelid worms; (s) early diagenetic concretions, which may or may not contain fossils, and/or be septarian in nature. Water depths not to scale, with chemocline-pycnocline a transition zone. See text for details.

and a dinosaur) is evidence for intense tropical storms blowing or washing terrestrial faunal and floral elements into Paja Formation Seas. However, it is worth noting, that no pterosaur or bird remains have yet been reported from the Paja Formation, although both of these groups should be expected to be occasionally found. Storms may mix the water column to the seafloor (Tyson & Pearson, 1991); however, high-energy storm events are the rarest (Wignall, 1989). With the perturbation over, the seafloor may remain oxygenated for a period of years, depending on water depth and surface water primary productivity, which allowed

the development of short-term post-event biofacies (e.g., Figure 12). However, the chemocline-pycnocline was self-restoring and with time bottom water dysoxia-anoxia developed, re-establishing the former tripartite division. A model for the possible development and dynamics of the Paja Formation epicontinental sea is presented in Figure 18.

Hence, Paja Formation Seas had surface waters that were warm and buoyant, well-lit, well-oxygenated, and with a near-normal salinity. Surface waters had strong solar input, a freshwater contribution derived from precipitation and runoff

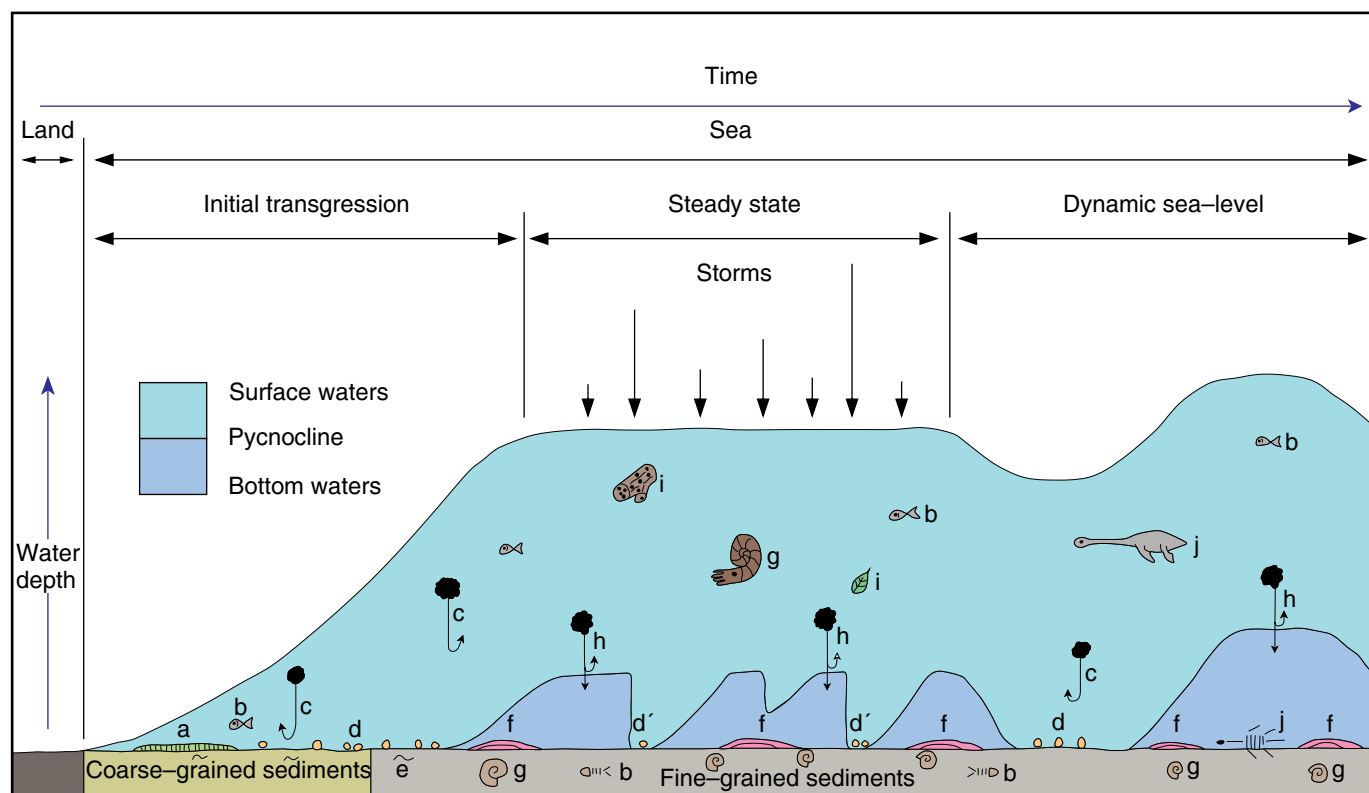


Figure 18. Conceptual diagram for the development, maintenance, breakdown, and re-initiation of a chemocline-pycnocline and dysoxic-anoxic bottoms water in Paja Formation epicontinental seas. Left to right: transgression over the land surface deposited coarse-grained nearshore sediments and a shallow water fauna developed. Organic carbon is almost completely recycled, either within the water column, or on or close to the seafloor. As sea level continues to rise, finer-grained sediments are deposited, and bottom waters are no longer well mixed or oxygenated. With high surface water primary productivity, organic carbon is incompletely degraded, and in the lower water column oxygen demand is greater than availability leading to bottom water dysoxia-anoxia. The two water masses are separated by a chemocline-pycnocline zone, which was reinforced by a relative lack of solar heating of bottom waters. With steady-state (non-fluctuating) sea levels, large storms may lower or breakdown the chemocline-pycnocline briefly oxygenating the sea floor, however, the chemocline-pycnocline is self-restoring. With fluctuating sea levels, regression may lead to the lowering or complete removal of the chemocline-pycnocline, and transgression may raise the chemocline-pycnocline. Paja Formation Seas were probably affected by a combination of fluctuating sea levels and storm events producing a complex, everchanging dynamic. Abbreviations: (a) algal mats; (b) fish and their fossils; (c) recycled organic matter; (d) bottom living epifauna, d' epifaunal invasions due to brief oxygenation events; (e) infauna; (f) sulphate reducing microbial mats; (g) ammonites and their fossils; (h) incompletely recycled organic matter; (i) floating logs with boring bivalves ("shipworms"), and other terrestrial plant material; (j) marine vertebrates and their fossils. Horizontal and vertical axes not to scale. See text for details.

(which provided nutrients and terrestrial organic matter), and were mixed by wind and to a lesser extent tidal action. The surface waters were home to a pelagic flora of phytoplankton, with high rates of photosynthetic primary productivity (Pacton et al., 2011), and a fauna of zooplankton, which acted as the base of a complex food web dominated by ammonites, fish, and marine reptiles (Figures 5–7). In addition, floating terrestrial wood acted as a substrate for pseudoplanktonic, wood-boring bivalves (Figure 11). By contrast, the bottom waters of Paja Seas were C_{org} -rich, oxygen-starved (anoxic-dysoxic), and affected by the production of H_2S . This led to a low diversity, low abundance depauperate benthos, dominated by microbial mat communities that thrived at low oxygen tensions. These two water masses were separated by a chemocline-pycnocline, making the Paja Formation a Type II, pelagic dominated facies (Sageman et al.,

1991). However, Paja Formation Seas were highly dynamic, leading to periodic breakdown of the boundary between surface and bottom waters by large-impact physical perturbations such as passing tropical storms, tsunamis or turbidity currents (Hay, 2008; Miller et al., 1988). Nonetheless, the tripartite division of Paja Seas was re-established through the same biochemical and physical processes that initiated the system (Sageman et al., 1991), producing a dynamic equilibrium that did not rely upon sluggish circulation of bottom currents (Meyer & Kump, 2008).

3.2. Taphonomy and Diagenesis

Preservation affects both sediments and fossils, and many processes are common to both inorganic particles and organic remains. Taphonomy is commonly divided into two comple-

mentary studies: biostratinomy, the biological, chemical, and physical processes occurring prior to final burial, or organisms (or their parts) acting as sedimentary particles; and diagenesis, the chemical and physical processes which affect both rocks and enclosing fossils following final burial (Lash & Blood, 2004; e.g., Martin, 1999; Witkowska, 2012). The taphonomy of the Paja Formation is understudied (but see Etayo–Serna, 1968); however, below we discuss the taphonomy of the marine reptiles, knowing that further work is required to fully understand Paja Formation deposits, post–depositional history, and the preservation of diverse faunal elements.

3.2.1. Biostratinomy

Following death, a vertebrate carcass may float, beach or sink. In the taphonomic model proposed for the Paja Formation (Etayo–Serna, 1968), marine reptile decomposing carcasses floated in from the west, eventually beaching along the palaeoshoreline. The assumption that marine reptile carcasses floated may or may not be true. For instance, humans have hunted modern marine mammals, preferring “right” whales—those that floated when harpooned, over other species that sank (Clapham, 1997; Würtz & Repetto, 1998)—but it is not known whether marine reptiles floated or sank upon death, or if like modern marine mammals it varied between species. However, marine mammals are insulated with a thick layer of low-density blubber, which increases their propensity to float, whereas modern reptiles typically have little subcutaneous fat deposits (Shirihai & Jarrett, 2006). If Mesozoic marine reptiles were akin to modern reptiles, it is more likely they sank upon death, at least until the gases of decomposition developed to a sufficient degree to re-float the carcass. However, the beautifully preserved specimens of marine reptiles from the Paja Formation are often fully articulated (Figure 5), with the jaws tightly closed, teeth in their alveoli, and delicate structures such as sclerotic plates and hyoid apparatus preserved in situ (e.g., Maxwell et al., 2016; Páramo–Fonseca, 1997; Welles, 1962). Based on actualistic taphonomic studies of modern mammals, floating carcasses rapidly decay and are subject to scavenging and disarticulation, and the lower jaw is one of the first elements to drop from a carcass (Schäfer, 1972). Hence, assuming similar patterns of necrolysis in Mesozoic marine reptiles and modern mammals, a “float and bloat” model for marine reptile preservation in the Paja Formation (Etayo–Serna, 1968) would predict loss of elements, starting with the lower jaw, distal limb elements, and the tail, and carcasses would present evidence of scavenging. However, modern mammal and Mesozoic marine reptile taphonomy are not the same, with examples of ichthyosaurs known that “nose-dived” into sediments with the lower jaws intact (Martill, 1993; Wahl, 2009). However, the residence times in water (i.e., when sinking occurred) of these carcasses after death, are not known. Equally, beaching of marine reptiles following death (as proposed by Etayo–Serna, 1968) would predict that, as a large

potential food supply, the body would be rapidly consumed by aerial, marine or terrestrial predator–scavengers, and that the bones would become scattered by wave action (Schäfer, 1972), which this is not seen in Paja Formation fossils.

The exceptionally well-preserved, articulated, little crushed preservation of the Paja vertebrates, including the preservation of delicate structures such as hyoid bones, sclerotic rings, scales, and eggs, requires a different explanation, where normal biostratinomic decay and destructive processes were “short-circuited”. The articulated nature of the skeletons argues strongly for rapid burial (Brenchley & Harper, 1998), which may have been due to rapid sedimentation rates, but is more likely a result of a soft or soupy substrate consistency (Martill, 1993). Complete or partial burial in soft sediments would also decrease the chances of re-flotation of a carcass during the generation of gases of decomposition, depending on the weight of the overlying water column. The presence of organic carbon-rich sediments and dysoxic–anoxic bottom waters would also have precluded scavenging by fish and cephalopods, reduced or prevented epibiont encrustation, and minimized the possibility of scavenging by air-breathing marine reptiles.

3.2.2. Diagenesis

Following final burial, diagenetic processes begin. The soft tissues of a dead organism are a vast potential energy source for microorganisms, which rapidly reduce oxygen availability around the carcass, and produce dysoxic–anoxic conditions at or close to the sediment–water interface. The subsequent anaerobic breakdown of soft tissues and interaction with seawater releases H_2S , which reacts with iron released from sediments to produce iron pyrite (Fe_2S). Hence, the presence of pyrite in alto Ricaurte sediments strongly suggests anoxic pore waters, and future study of pyrite morphology may be indicative of the oxygen content of Paja Formation bottom waters (Gallego–Torres et al., 2015; Roychoudhury et al., 2003).

Calcareous- and iron-rich concretions are abundant throughout the Paja Formation (Figure 4). Concretions are often richly fossiliferous (Etayo–Serna, 1968), but even those devoid of macrofossils are likely to have nucleated around microfossils or amorphous C_{org} . Concretions are also indicative of reduced sedimentation rates (Martin, 1999), and localized, pre-compaction diagenesis at shallow depths within the sediment pile, prior to dewatering. The early diagenetic nature of Paja Formation concretions can be ascertained by the “wrapping” of enclosing sediments (Figure 16), which is indicative of concretionary growth within the sediment body and later differential dewatering and compaction of the surrounding non-concretionary sediments. As burial depth increased, early diagenetic concretions resisted compaction of the sediments and, where they formed around fossils, led to exceptional three-dimensional preservation (Páramo–Fonseca, 1997; Welles, 1962).

Gypsum and calcite are common in many parts of the Paja Formation, and have been considered syndepositional (Etayo–Serna, 1968; Forero–Onofre & Sarmiento–Rojas, 1985). Both calcite and gypsum are encountered as sheet-like bodies (gypsum veins are commonly 1–2 mm thick, whereas calcite veins are often 10 mm or more in thickness; Figures 8, 12), with internal bi-layered fibrous-like crystals (“satin spar” for gypsum or “sparite” for calcite), distributed approximately symmetrically around a central junction (Cobbold et al., 2013; Philipp, 2008). As the crystals lie approximately normal to the edges of the mineral sheets, this form of gypsum or calcite is commonly termed “beef” as it has the appearance of cut meat (Cobbold et al., 2013); cone-in-cone calcite is also occasionally present. The calcite and gypsum sheets may follow bedding, but also commonly cross or cut sedimentary layers and concretions, or divide to surround fossils (Etayo–Serna, 1968). In addition, antitaxial growth (from the vein centre) means fossils may be found in the centre of calcite “beef” (Figure 12), and as the crystals of the minerals are arranged perpendicular to the centre of the vein, vague impressions or “shadows” of the fossils may be visible on both outer surfaces of the mineral veins (Cobbold et al., 2013).

The perpendicular arrangement of gypsum and calcite fibres is evidence for extensional vein growth, with cracking and deposition from hydrothermal fluids occurring along the vein walls (Philipp, 2008). The fracturing of mudrocks indicates vein growth and deposition must have taken place in consolidated sediments. Gypsum “beef” typically forms at temperatures of up to 60 °C, whereas calcite “beef” is deposited at temperatures of 70–120 °C or within the “oil window” (Cobbold et al., 2013). Thus, formation of gypsum and calcite “beef” occurs at temperatures (and pressures) higher than those at the surface of the earth (Kershaw & Guo, 2016), so interpretations of sheet gypsum or calcite as syndepositional, are erroneous. The temperatures of formation of gypsum and calcite “beef” suggest emplacement of gypsum after the calcite, probably during relatively recent unroofing of the ECC (Mosolf et al., 2010), although further work is required to determine the cross-cutting relationships of gypsum and calcite in the Paja Formation, and hence the relative timing of vein emplacement. However, as gypsum deposition did not occur during Paja Formation times, this leaves open the source of the calcium sulphate. One possible source is vertical migration from underlying or now missing overlying sediments, rich in calcium sulphate. However, contiguous formations show no evidence of extensive original gypsum precipitation (Etayo–Serna, 1965, 1968), which suggests lateral migration of calcium sulphate-rich fluids from a geographically more distal source.

3.3. A Regional and Global Overview

During the Cretaceous, sea levels were globally high compared to today (Haq et al., 1987; Miller et al., 2005). Flooding of the Early Cretaceous western basins of Colombia commenced

during the Berriasian, gradually extending from west to east (Gaona–Narváez, 2015). During this time, the Cundinamarca or Sabana de Bogotá Sub-basin horst was periodically flooded, as a result of constantly changing global sea levels (Haq et al., 1988; Müller et al., 2008), which led to the deposition of evaporitic deposits (Cortés et al., 2006). Evaporation of seawater is likely to have produced a range of salts, including calcium carbonate, gypsum (hydrated calcium sulphate), and halite (sodium chloride). However, as sea levels were constantly changing, repeated flooding and evaporation would have built complex salt deposits. Following tectonic inversion, these salts may have been the source of the post-depositional minerals (gypsum and possibly calcite) in the Paja Formation.

During Paja Formation times (Hauterivian to early Albian) global sea levels continued to fluctuate (Haq et al., 1988; Müller et al., 2008), leading to complex and dynamic cycles that affected the Paja Formation depositional environment (Mann & Stein, 1997). The causes (and effects) of these high but constantly changing sea levels have been the subject of much debate with increased seafloor spreading rates and superplume induced large igneous province volcanism (e.g., the Ontong Java Plateau) evoked as possible mechanisms (Keller, 2008; Kominz, 2001; Seton et al., 2009). Superimposed over global sea-level changes, where a series of oceanic anoxic events (OAEs), which occurred throughout the Cretaceous (Hesselbo et al., 2007; Jenkyns, 2010). The Paja Formation of alto Ricaurte is likely to record evidence for two of these events. The OAE 1a (Selli) event of the early Aptian (Jenkyns, 2010; Leckie et al., 2002; Pictet et al., 2015) probably occurred in segment D (or possibly the base of segment E) of the AA Member. OAE 1b (the Paquier event), which occurred close to the Aptian – Albian boundary (Jenkyns, 2010; Zhang et al., 2016), is likely to have occurred in the AcNH Member. The causes of OAEs may have been many and varied, but possibly include increased mid-ocean ridge volcanism producing gasses and nutrients, and release of methane gas hydrates, both leading to higher than normal ocean primary productivity (Jones & Jenkyns, 2001; Larson & Erba, 1999; Méhay et al., 2009; Petrash et al., 2016; van Helmond et al., 2015; Zhang et al., 2016). In northern South America, facies changes appear to broadly match these global trends in sea-level and ocean dynamics (Macellari, 1988).

During the latest Cretaceous, collision of the Pacific Plate with the South American Shield began the process of tectonic inversion of the ECC Basin, producing an intracontinental doubly vergent mountain chain (Jiménez et al., 2014; Teixell et al., 2015). This compression resulted in a combination of thick- and thin-skinned faulting (Babault et al., 2013; Moreno et al., 2013), with a major decollement (basal detachment fault) in the lowermost Cretaceous salt-rich layers, that today lie at around 4 km depth (Teixell et al., 2015). Inversion of the ECC resulted in halite diapirs (e.g., at Nemocón and Zipaquirá; Babault et al., 2013), and may have been the source for the lateral migration of

mineral-rich fluids that gave rise to both Colombian emeralds (Cobbold et al., 2013) and the gypsum “beef” in the Paja Formation. The calcite “beef” could have been sourced from the same fluids, intrabasally, or a combination of both. Hence, rapid Miocene uplift of the Andes (Babault et al., 2013; Bayona et al., 2013), may have been the trigger for fracturing, vertical salt dome diapirism, and lateral migration of over pressurized, calcium- and sulphate-rich fluids.

One salt deposited during the Berriasian was presumably calcium sulphate, originally in the form of gypsum, but at depth converted by dehydration to anhydrite, which produces a reduction of the original volume of around 10% (Philipp, 2008). Following tectonic inversion, the anhydrite was exposed to circulating groundwaters, causing hydration to gypsum, and a volume increase of 60% (Philipp, 2008), generating fluid over pressurisation and salt mobilization. Over pressurisation would have led to hydrothermal fluid movement along faults and fractures reactivated or produced due to crustal shortening, or developed as a result of natural hydraulic fracturing, and along bedding planes between the largely impermeable mudrocks within the Tablazo–Magdalena Sub–basin. Successive mineral-rich fluid flows, over a period of several millions of years (Cobbold et al., 2013), would thereby have deposited fibrous gypsum (and possibly calcite) “beef” within Paja Formation rocks. Hence, the source of the over pressurization is likely to have been conversion of anhydrite to gypsum (Philipp, 2008), driven by deep water circulation as a result of changing precipitation and runoff resulting from the rise of the Andes mountain chain (Mora et al., 2008).

Ultimately, uplift of the Andes brought Paja Formation rocks to 2150 m above sea level, and unroofing led to modern subaerial weathering and erosion. This produced recent oxidation of iron-rich clay minerals, leading to the typically variegated colours of the Paja Formation outcrops. A small amount of gypsum in the Paja Formation may have been produced close to the surface by recent weathering.

4. Conclusions

The Paja Formation was deposited in a moderately deep (~60–130 m) marine basin, formed as a result of extensional tectonics and high sea levels during Hauterivian to Aptian times. By uniting sedimentological, paleobiological, taphonomic, and tectonic data with literature on modern shelf and ancient epicontinental seas, we have been able to reconstruct and reinterpret the palaeoenvironment of the Paja Formation of alto Ricaurte. The Paja Formation Seas were tripartite, with normal marine surface waters inhabited by a diverse pelagic fauna of marine reptiles (plesiosauro-morph and pliosauro-morph plesiosaurs, ichthyosaurs, and marine turtles), numerous fish, and extremely abundant ammonites. The food web is inferred to have been based on abundant phyto- and zoo-plankton. Surface waters were warm,

well-lit, well-mixed, and of normal salinity. This was in marked contrast to the bottom waters, which were dysoxic–anoxic, and inhabited by low oxygen- and hydrogen sulphide-tolerant species, such as thin-shelled bivalves, probable annelid worms, and sulphide reducing bacteria that formed seafloor mats. Dysoxia–anoxia in the sediments and lower water column was due to the accumulation of incompletely degraded organic matter. The upper and lower portions of the water column seem to have been separated by a chemocline–pycnocline, which may have arisen due to temperature driven chemical or density differences between surface and deeper waters, but could (less probably) have been due to differences in salinity, or a combination of factors. However, Paja Seas were dynamic, and occasional breakdown of the chemocline–pycnocline occurred as a result of large tropical storms, but Paja Formation Seas may also have been affected by earthquake generated tsunamis and/or turbidity currents.

A paucity of Lower Cretaceous marine reptile bearing strata has long been noticed (e.g., Hampe, 1992). However, the Paja Formation of the alto Ricaurte, Eastern Cordillera of Colombia is a very complete succession of Hauterivian to Aptian rocks, which preserves an exceptional pelagic fauna. The excellent preservation of the fossil fauna around alto Ricaurte opens a new window on marine reptile, and particularly plesiosaur, diversity in the Early Cretaceous. The Paja Formation can therefore be considered one of very few Lower Cretaceous marine reptile Lagerstätte.

Data supporting an evaporitic environment for the Paja Formation, based on the presence of gypsum, is shown to be erroneous and the result of secondary, diagenetic processes. Gypsum (and possibly calcite) “beef” is likely to have been emplaced as the result of hydrothermal fluid migration, with the gypsum probably sourced from Berriasian salts deposited over the Sabana de Bogotá high. Fluid migration was likely driven by over pressurisation due to rehydration of anhydrite to gypsum as a result of Andean uplift, unroofing, and resultant changing climatic patterns. Hence, two aspects critical to a full understanding of the geological history of the Paja Formation, are the taphonomy of the fossil remains, and the clear separation of original depositional features from the products of diagenesis. This work thereby suggests that although the deposits of the alto Ricaurte region are some of the best studied in Colombia, there remains much to understand about these fascinating rocks, and the times in which they were deposited.

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Explanation of Acronyms, Abbreviations, and Symbols:

AA	Arcillolitas Abigarradas	OAEs	Oceanic anoxic events
AcNH	Arcillolitas con Nódulos Huecos	SGC	Servicio Geológico Colombiano Dirección de Geociencias Básicas Museo Geológico José Royo y Gómez Diagonal 53 n.º 34–53, Bogotá D. C., Colombia
CIP	Centro de Investigaciones Paleontológicas km 4, vía Santa Sofía, Villa de Leiva, Boyacá, Colombia	TOC	Total organic carbon
ECC	Eastern Cordillera of Colombia	UCMP	University of California Museum of Palaeontology 1101 Valley Life Sciences Building, Berkeley California 94720, USA
JAVCM	Junta de Acción Comunal, vereda Monquirá (now MJACM)	UN	Universidad Nacional de Colombia Departamento de Geociencias Carrera 45 n.º 26–85, Bogotá D. C., Colombia
LFN	Leslie Francis NOË		
LNI	Lutitas Negras Inferiores		
MG-P	Marcela GÓMEZ-PÉREZ		
MJACM	Museo El Fósil, vereda Monquirá, Boyacá, Colombia		

Authors' Biographical Notes



Leslie F. NOË is a vertebrate palaeontologist, stratigrapher, and historian of science, with special interests in the palaeobiology and evolution of the Sauropterygia. Leslie undertook his undergraduate studies in the School of Environmental and Applied Sciences at the University of Derby, UK, and graduated with honours with a Combined Subjects

(Biology, Geology, and Physical Geography) degree. Leslie subsequently undertook doctoral studies, at the University of Derby, under the supervision of Dr. Don SMITH, Dr. Arthur CRUICKSHANK (Leicester Museums), and Dr. Derek WALTON, and wrote his PhD thesis on the cranial osteology of the Callovian (Middle Jurassic) Oxford Clay Formation plesiosaurian genera *Liopleurodon*, *Simolestes*, and *Pachycostasaurus*. Leslie gained a wide range of experience during seven years in the Sedgwick Museum, University of Cambridge, UK, as well as undertaking undergraduate and postgraduate supervision, and undergraduate teaching in both the Department of Earth Sciences and the Department of Zoology. A curatorship at Thinktank, the Birmingham Science Museum, UK, followed, together with an honorary position at the University of Birmingham. Leslie returned to Cambridge as curator of the globally important Harland Collection of rocks, fossils, and minerals, before moving to Colombia, where he is currently Associate Professor in the Departamento de Geociencias, Universidad de los Andes in Bogotá. As the first geologist in the newly formed Geociencias Department, Leslie has written numerous undergraduate courses, and continues to publish on Mesozoic marine reptiles, with special reference to Colombian Cretaceous faunas.



Marcela GÓMEZ-PÉREZ is a vertebrate palaeontologist and sedimentary geologist with special interests in pliosauro-morph marine reptiles, museology, and geological outreach. Marcela undertook her undergraduate studies in the Departamento de Geociencias of the Universidad Nacional de Colombia, Bogotá, where she graduated with

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