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**Palynology of Aptian – Albian amber deposits of the Oriente Basin-Ecuador and the
Eastern Cordillera-Colombia**

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Manizales, Colombia

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Eastern Cordillera-Colombia**

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Abstract

Two Cretaceous localities with presence of amber were identified, one in the Oriente Basin of Ecuador (Genoveva Mine), and another in the Eastern Cordillera of Colombia (La Popa Mine). A palynological study was developed in these units and it was determined that the formations present in both localities correspond to the uppermost part of the lower Hollin Formation (early Albian) and the lower Une Formation (Albian), respectively. In Ecuador, the study was also realized in other localities near to the mine, both in the Hollin Formation and of the overlying Napo Formation.

The palynomorphs found in the studied locations were grouped into five groups: angiosperm pollen, non-gnetalean gymnosperm pollen, gnetalean pollen, spores, and marines. The question of whether the tropical belt in the Albian was arid or humid is still controversial, but in these studied localities, spore diversity predominates in comparison with the other groups of plants, especially some gymnosperms that indicate aridity (*Classopollis*, ephedroid pollen grains and elater-bearing species) which would suggest predominant humid climate conditions in the northwestern margin of Gondwana for this time.

Keywords: Palynology, Cretaceous, Amber, Colombia, Ecuador.

Resumen

Se identificaron dos localidades cretácicas con presencia de ámbar, una en la Cuenca de Oriente de Ecuador (Mina Genoveva), y otra en la Cordillera Oriental de Colombia (Mina La Popa). En estas unidades se desarrolló un estudio palinológico y se determinó que las formaciones presentes en ambas localidades corresponden a la parte superior de la Formación Hollín inferior (Albiano temprano) y a la Formación Une inferior (Albiano), respectivamente. En Ecuador, el estudio se realizó también en otras localidades cercanas a la mina, tanto de la Formación Hollín como de la suprayacente Formación Napo.

Los palinomorfos encontrados se agruparon en cinco grupos: polen de angiospermas, polen de gimnospermas no gnetales, polen gnetales, esporas y marinos. La cuestión de si el cinturón tropical en el Albiano era árido o húmedo sigue siendo controversial, pero en las localidades estudiadas predomina la diversidad de esporas en comparación con los otros grupos vegetales, especialmente de algunas gimnospermas que indican aridez (*Classopollis*, granos de polen efedroides y especies portadoras de eláteres) lo que sugeriría un clima predominantemente húmedo en el margen noroccidental de Gondwana para este momento.

Palabras clave: Palinología, Cretácico, Ámbar, Colombia, Ecuador.

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1. Introduction

The main sources of information about early angiosperm diversification have been dispersed pollen and detached leaves (e.g., Doyle & Hickey, 1976; Hughes, 1976; Hickey & Doyle, 1977; Hughes, 1994) and also pollen grains found in-situ within flowers (Friis *et al.*, 2011). Most of the research on the subject has been done at temperate latitudes and there is not a distinct pattern in the latitudinal distribution of the early angiosperm records. There is extensive information on Early Cretaceous angiosperms from middle paleolatitudes in the Northern Hemisphere, but angiosperms were also diverse and abundant at low paleolatitudes (Friis *et al.*, 2011). Macrobotanical evidence from North America indicates that angiosperms only became ecologically significant at high latitudes by the earliest Late Cretaceous, but mostly restricted to riparian environments (Wing *et al.*, 1993). Estimates based on pollen (diversity and abundance) suggest that angiosperms were already dominant in some environments at mid-paleolatitudes by the Cenomanian (Lupia, 1999). In contrast, the patterns of angiosperm radiation and diversification at low latitudes are not well understood (Mejia-Velasquez *et al.*, 2012; Jaramillo, 2012, 2019), particularly because of the few studies from tropical latitudes (e.g., Crane & Lidgard, 1989; Lupia *et al.*, 1999).

In this study, the results of the palynological analysis of two Cretaceous successions in Ecuador (Hollin Formation) and Colombia (Une Formation) are presented, in order to date the sites, determine the floristic composition, and assess whether the climate on the western margin of South America was humid or arid.

Two localities were studied (Figure 1): 1) The Genoveva Mine in the Oriente Basin, Ecuador (Figure 2A), which belongs to the lower Hollin Formation (Lat: -0.71102, Long: -77.78778) with Albian Paleolatitude: -6.92 and Paleolongitude: -53.87, according to the reconstructions made by Muller *et al.* (2016). 2) La Popa Mine in the Eastern Cordillera of Colombia (Figure 2B), from the Une Formation (Lat: 4.70866, Long: -73.95213) with Albian Paleolatitude: -1.77 and Paleolongitude: -50.29, according to the reconstructions made by Muller *et al.* (2016).



Figure 1. Location of the two study sites (Genoveva Mine in Ecuador and La Popa Mine in Colombia).

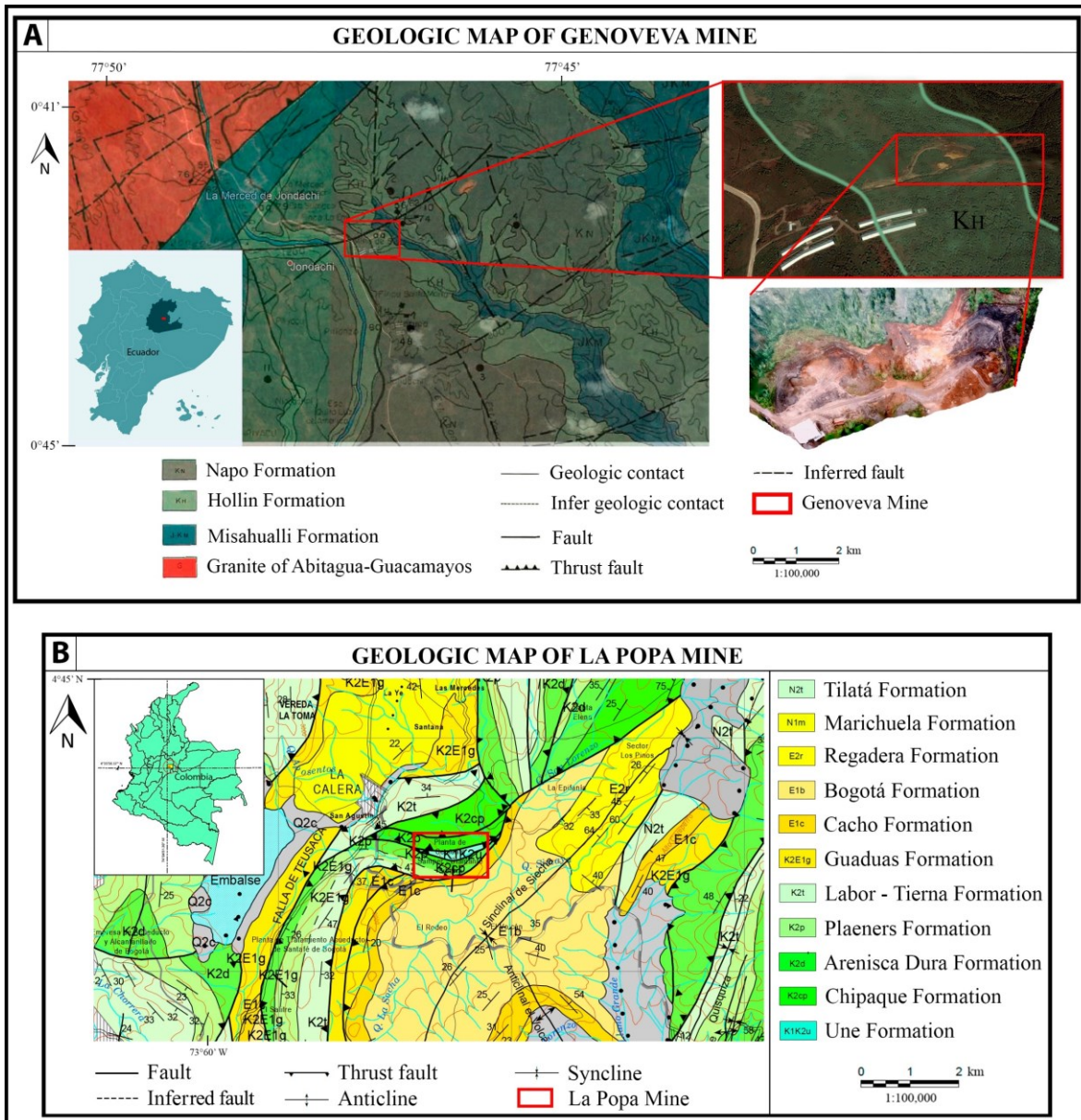


Figure 2. Geologic maps. A. Genoveva Mine in Ecuador. Information from Eguez *et al.* (2017). B. La Popa Mine in Colombia. Information from Buitrago *et al.* (2008) and Alcárcel & Gómez (2019).

2. Objectives

General objective

To study the palynological assemblages from rocks associated with Early Cretaceous amber deposits in two different localities of South America: the Oriente Basin of Ecuador and the Eastern Cordillera of Colombia.

Specific objectives

- To identify the palynological content of the samples from Genoveva Mine and La Popa Mine.
- To date both sites using palynology.
- To discuss the rainfall conditions (humidity versus aridity) using palynological proxies.

3. Geological setting

3.1. Stratigraphy

In the Oriente Basin of Ecuador, Paleozoic basement, Mesozoic–Cenozoic volcanic rocks, and sedimentary units are exposed (Vallejo *et al.*, 2002). One of the most studied units is the Hollin Formation because it is the main oil reservoir in the Oriente Basin (Dashwood & Abbotts, 1990). The Eastern Cordillera of Colombia is composed of Phanerozoic sedimentary rocks, with local exposures of Proterozoic-lower Paleozoic basement with multiple orogenic episodes (Etayo-Serna *et al.*, 1983; Cediél *et al.*, 2003; Horton *et al.*, 2010; Saylor *et al.*, 2012). The Une Formation is widely distributed in the Eastern Cordillera and corresponds to a clastic unit (Zavala *et al.*, 2009).

3.1.1. Hollin Formation

The Hollin unit comprises two formations, the lower Hollin Formation, known as the Main Hollin Sandstone (Baby *et al.*, 2004), and the Lower Sandstone, known as the Upper Hollin Sandstone or upper Hollín Formation (Jaillard *et al.*, 1997). The age of this unit ranges from middle-late Aptian to middle Albian (White *et al.*, 1995; Jaillard *et al.*, 1997; Vallejo *et al.*, 2002; Ordoñez *et al.*, 2006; Romero *et al.*, 2017) while Sarmiento-Rojas (2019) suggests an early Aptian – middle Albian age. The lower Hollin Formation is dominated by conglomeratic sandstones graded to quartz sandstones with cross-bedding, deposited in braided river channels (White *et al.*, 1995; Romero *et al.*, 2019). The upper Hollin Formation is characterized by sandstones intercalated with mudstones rich in organic matter and leaf fragments accumulated in coastal plains to shallow platforms (White *et al.*, 1995; Romero *et al.*, 2019; Sarmiento-Rojas, 2019). The levels containing amber at the Genoveva Mine are within the lower Hollin Formation. The upper limit of this unit with the overlying Napo Formation corresponds to a major flooding surface (Romero *et al.*, 2019).

3.1.2. Napo Formation

The Napo Formation ranges from late Albian to early Campanian (Mello *et al.*, 1995; Vallejo *et al.*, 2002; Sarmiento-Rojas, 2019) and consists of organic-rich shales, limestones, and sandstones. It is subdivided into several informal members, that can be correlated over large distances in the Oriente Basin of eastern Ecuador (Tschopp, 1953). Two sandstone units (labelled T and U sandstones) constitute the most important hydrocarbon reservoirs, and the organic-rich zones (e.g., Basal Shale Member) are considered the source of almost all hydrocarbons in the basin (Rivadeneira, 1986; Dashwood & Abbotts, 1990; Mello *et al.*, 1995; Vallejo *et al.*, 2002). The Napo Basal member has been dated as late Albian by palynological studies (Vallejo *et al.*, 2002) and has been interpreted as deposited in dysoxic-anoxic, paralic-neritic environments (Mello *et al.*, 1995) or by deposition of inner shelf mudstones (Sarmiento-Rojas, 2019).

3.1.3. Une Formation

The Une Formation forms a strong geomorphological escarpment that contrasts with the underlying Fόμεque Formation and the overlying Chipaque Formation with fine-grained lithologies that generate valleys (Ulloa *et al.*, 2001; Corredor & Terraza, 2015). The Une Formation is composed by black mudstones, dark grey quartz-siltstones and white quartz-sandstones with dark siltstone intercalations that are found in thin to very thick tabular layers. The siltstones are locally calcareous and fossiliferous, while the mudstones have lenticular bedding with the presence of fossil bivalves and abundant plant remains (Reyes, 1984; Corredor & Terraza, 2015). The unit has been dated as Albian – Cenomanian (Renzoni, 1981; Fabre, 1985; Montoya & Reyes, 2003) and interpreted as formed by accumulation of sediments in very shallow marine settings and deltaic deposits (Renzoni, 1962; Ulloa *et al.*, 2001; Sarmiento-Rojas, 2019).

3.1.4. Chipaque Formation

The Chipaque Formation is characterized mainly by thick and very thick layers of claystones and mudstones, alternated with siltstones and fine-grained sandstones in medium and thin

layers (Renzoni, 1962; Guerrero & Sarmiento, 1996; Corredor & Terraza, 2015). This formation has been dated as late Cenomanian to Santonian (Montoya & Reyes, 2003; Corredor & Terraza, 2015), while Guerrero & Sarmiento (1996) indicated that the lower part of the Chipaque Formation is early Turonian. It was accumulated in a shallow marine platform (Ulloa & Rodríguez, 1976; Villamil, 1998; Garcia *et al.*, 2009; Sarmiento-Rojas, 2019) when the tectono-eustatic base level reached its maximum level during the Mesozoic (Sarmiento-Rojas *et al.*, 2006; Corredor & Terraza, 2015; Sarmiento-Rojas, 2019).

3.2. Paleogeography and climate

The paleogeographic evolution of South America during the Early Cretaceous is driven by two main tectonic events: an active western continental margin with permanent subduction of the Pacific plates and its concomitant magmatic arc; and the separation of Africa from South America with an expansion of the ocean floor initiating in the southern South Atlantic Ocean (Spalletti *et al.*, 1999; Prámparo *et al.*, 2007).

The Aptian – Albian was characterized by elevated worldwide temperatures and high mean annual tropical temperatures, which reached ~32 °C (Schouten *et al.*, 2003) and levels of CO₂ up to ~1000 ppm (Haworth *et al.*, 2005). The Cenomanian was even warmer with temperatures reaching 32 – 36 °C (Schouten *et al.*, 2003) and >1000 ppm of CO₂ (Haworth *et al.*, 2005; Fletcher, 2006; Barclay *et al.*, 2010). Whether the Early Cretaceous tropical belt was arid or humid remains controversial (Mejia-Velasquez *et al.*, 2012). Several climatic reconstructions based on lithological evidence and palynological data suggested aridity conditions for that time (Ziegler *et al.*, 1987; Chumakov *et al.*, 1995; Herngreen *et al.*, 1996). In contrast, other palynological studies suggested that tropical latitudes were humid (de Lima, 1983; Thusu *et al.*, 1988; Herngreen & Dueñas-Jimenez, 1990; Schrank, 1992; Mejia-Velasquez *et al.*, 2012). Mejia-Velasquez *et al.* (2018) indicated that a humid climate prevailed in northwestern South America during the Berriasian – Hauterivian and the Albian intervals, although it does not preclude that the interior of the South America-Africa presented much drier conditions.

For the study areas, published climate models for Albian – Cenomanian indicated a Mean Annual Temperature (MAT) of ~30 °C (Barron & Peterson, 1993; Barron *et al.*, 1995; Poulsen *et al.*, 2001; Donnadieu *et al.*, 2006) (Figures 3 and 4; Table 1). Some climate models indicated a tropical humid climate (Fluteau *et al.*, 2007; Hay & Floegel, 2012; Kuethe, 2016) while Parrish *et al.* (1982) indicated a moderately low Mean Annual Precipitation (MAP) (Figure 4C; Table 1). Global atmospheric CO₂ levels for the middle Cretaceous were estimated at up to 2000 ppm (Table 2) (Wang *et al.*, 2014).

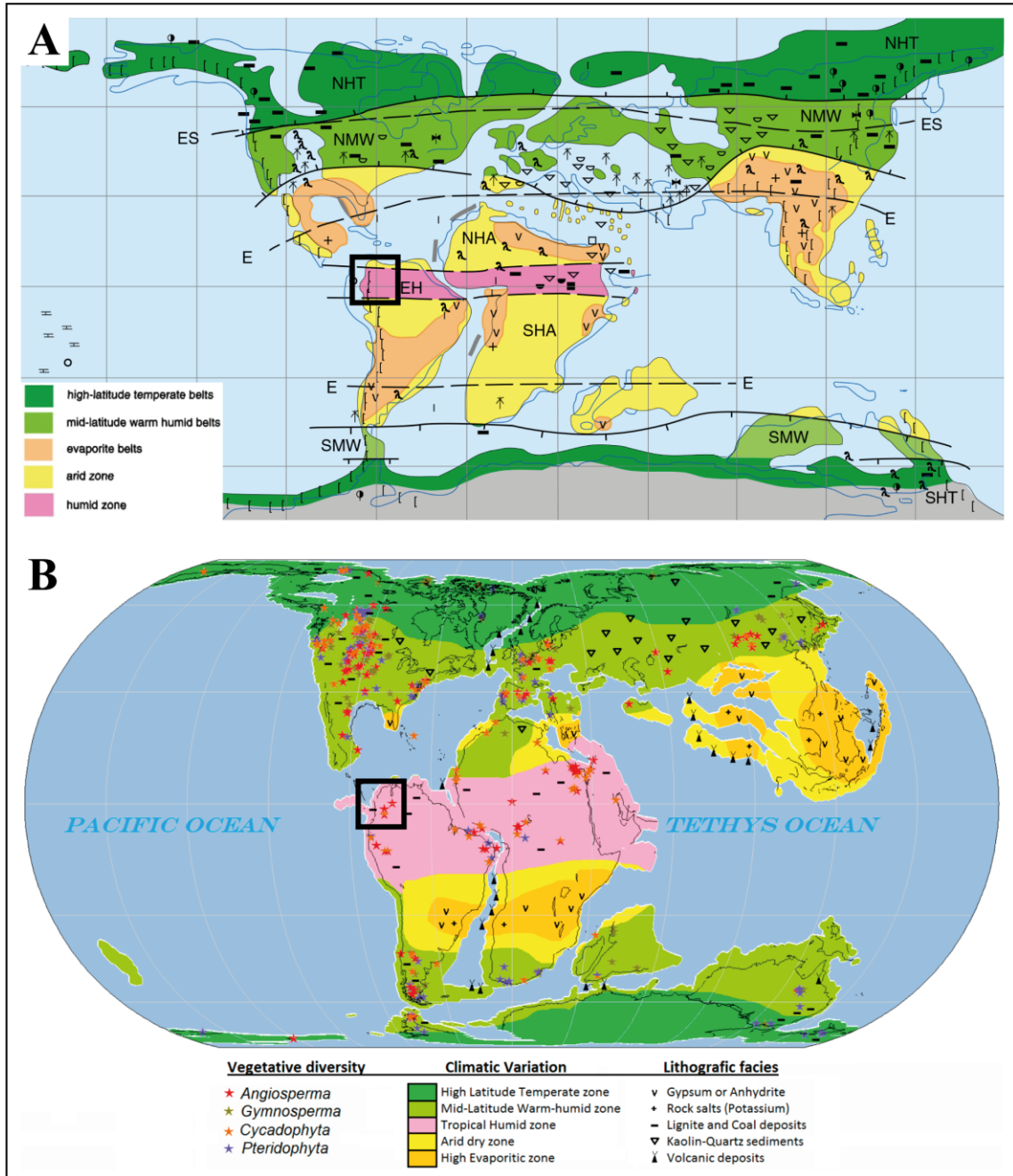


Figure 3. Climatic models proposed for the Albian. A. Albian climate indicators and zones (Hay & Floegel, 2012); B. Climatic model of the late Albian (Kuethe, 2016).

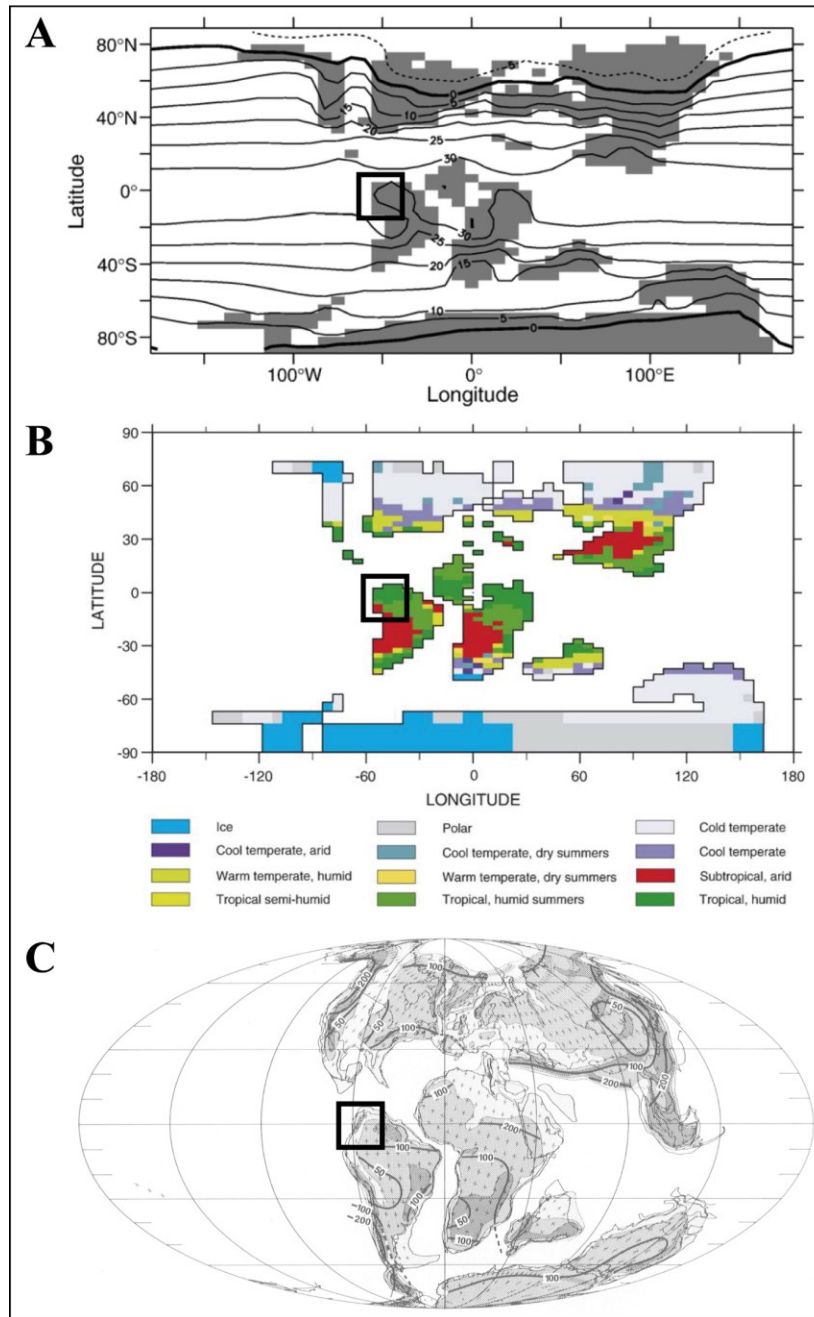


Figure 4. Climatic models proposed for the Cenomanian. A. Mean annual surface temperature (°C) simulated for the Cenomanian (Donnadieu *et al.*, 2006); B. Simulated climate for the Cenomanian (Fluteau *et al.*, 2007); C. Predicted distribution of rainfall patterns for the Cenomanian, the rainfall was divided into four categories: < 50 = low rainfall, 50 – 100 = moderately low rainfall, 100 – 200 = moderately high rainfall, > 200 = high rainfall (Parrish *et al.*, 1982).

Table 1. Mean Annual Temperature (MAT) and Mean Annual Precipitation (MAP) estimates for the Albian – Cenomanian in tropical latitudes for the study area.

Reference	MAT	MAP	Proxy
Parrish <i>et al.</i> , 1982		Moderately low rainfall	Atmospheric circulation
Barron & Peterson, 1993	20-30 °C		Global Environmental and Ecological Simulation of Interactive System (GENESIS)
Barron <i>et al.</i> , 1995	27-32 °C		Global Environmental and Ecological Simulation of Interactive System (GENESIS)
Poulsen <i>et al.</i> , 2001	24-30 °C		Ocean general circulation model
Donnadieu <i>et al.</i> , 2006	30 °C		Fast Ocean-Atmosphere Model (FOAM)
Fluteau <i>et al.</i> , 2007		Tropical humid	Atmospheric circulation
Hay & Floegel, 2012		Tropical humid	Climate-sensitive fossils and sediments
Kueth, 2016		Tropical humid	Climate-sensitive fossils and sediments

Table 2. CO₂ estimations for the middle Cretaceous (Wang *et al.*, 2014).

Age	Stage	CO₂ (ppm)	Proxy	Locality	Reference
Late Cretaceous	Cenomanian	37-2000-500	Stomata	USA	Barclay <i>et al.</i> , 2010
		700-1400	Stomata	UK, USA	Haworth <i>et al.</i> , 2005
		1000-1400	Liverwort isotope	Antarctica	Fletcher, 2006
Early Cretaceous	Albian	620-1200	Stomata	UK, USA	Haworth <i>et al.</i> , 2005

3.3. Cretaceous sedimentation

The Aptian – early Albian deposition of shallow marine to coastal sandstone facies in the Oriente Basin in Ecuador (Hollin Formation) was capped by a middle Albian Transgression Surface (TS) that corresponds to the Hollin/Napo boundary, and it is genetically associated with a subsequent Maximum Flooding Surface (MFS) 10 in the lower Napo Formation (Figure 5) (Sarmiento-Rojas, 2019). The Une-Chipaque boundary corresponds to a late Cenomanian – early Turonian TS 8, and it is associated to the maximum flooding surface at the Cenomanian – Turonian boundary that represents the highest sea-level of the Cretaceous (MFS 8; Figure 5) (Sarmiento-Rojas, 2019). The MFS 10 regionally could correspond to either one of two Albian Oceanic Anoxic Events (OAEs), the middle Albian OAE 1c or the late Albian OAE 1d (Figure 6). The MFS 8 corresponds to OAE 2, the Cenomanian – Turonian boundary (Figure 6) (Villamil, 1998; Villamil & Arango, 1998).

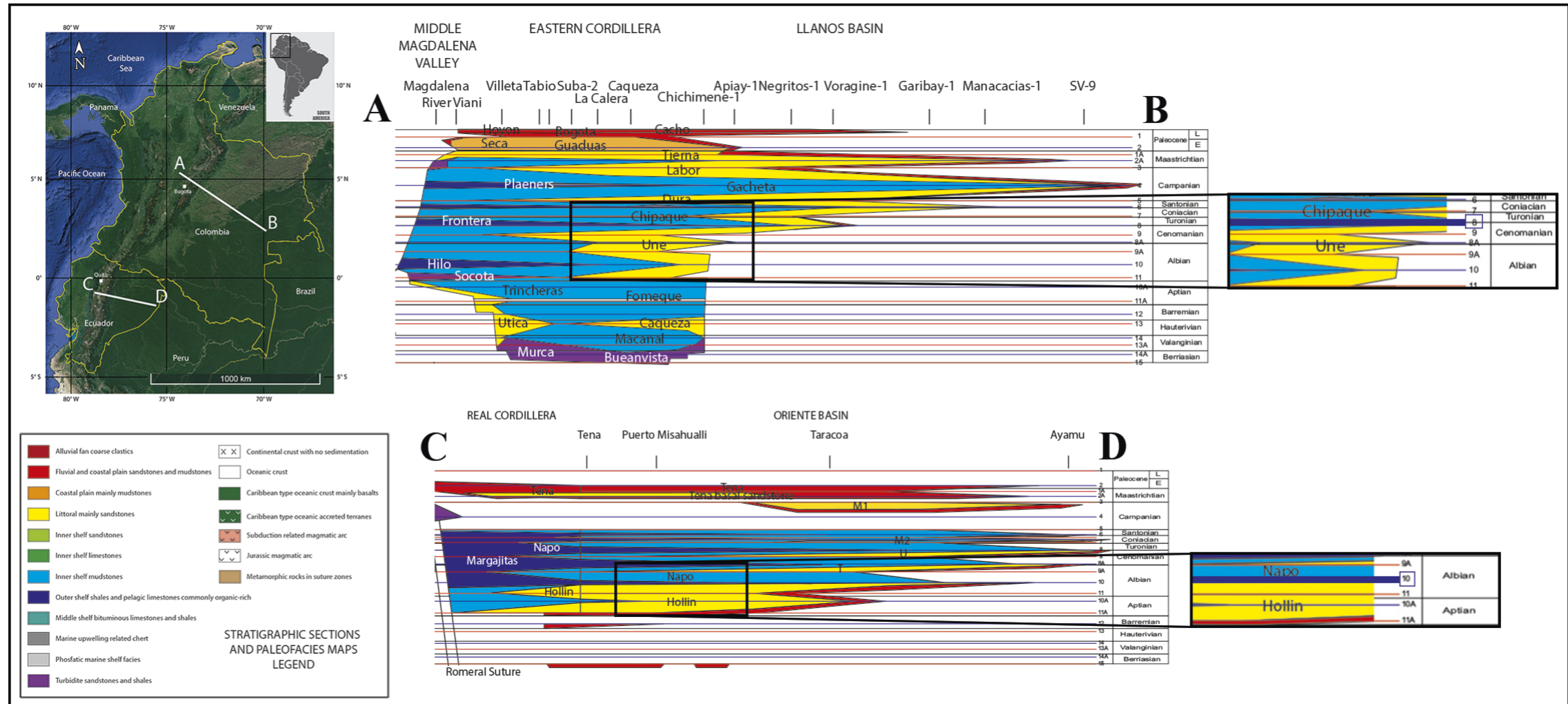


Figure 5. Stratigraphic sections along central Colombia (A-B) and Ecuador (C-D). Geological time in vertical axis. Horizontal red lines indicate proposed Sequences Boundaries (SB); horizontal blue lines indicate Maximum Flooding Surfaces (MFS) for the proposed stratigraphic sequences (Sarmiento-Rojas, 2019).

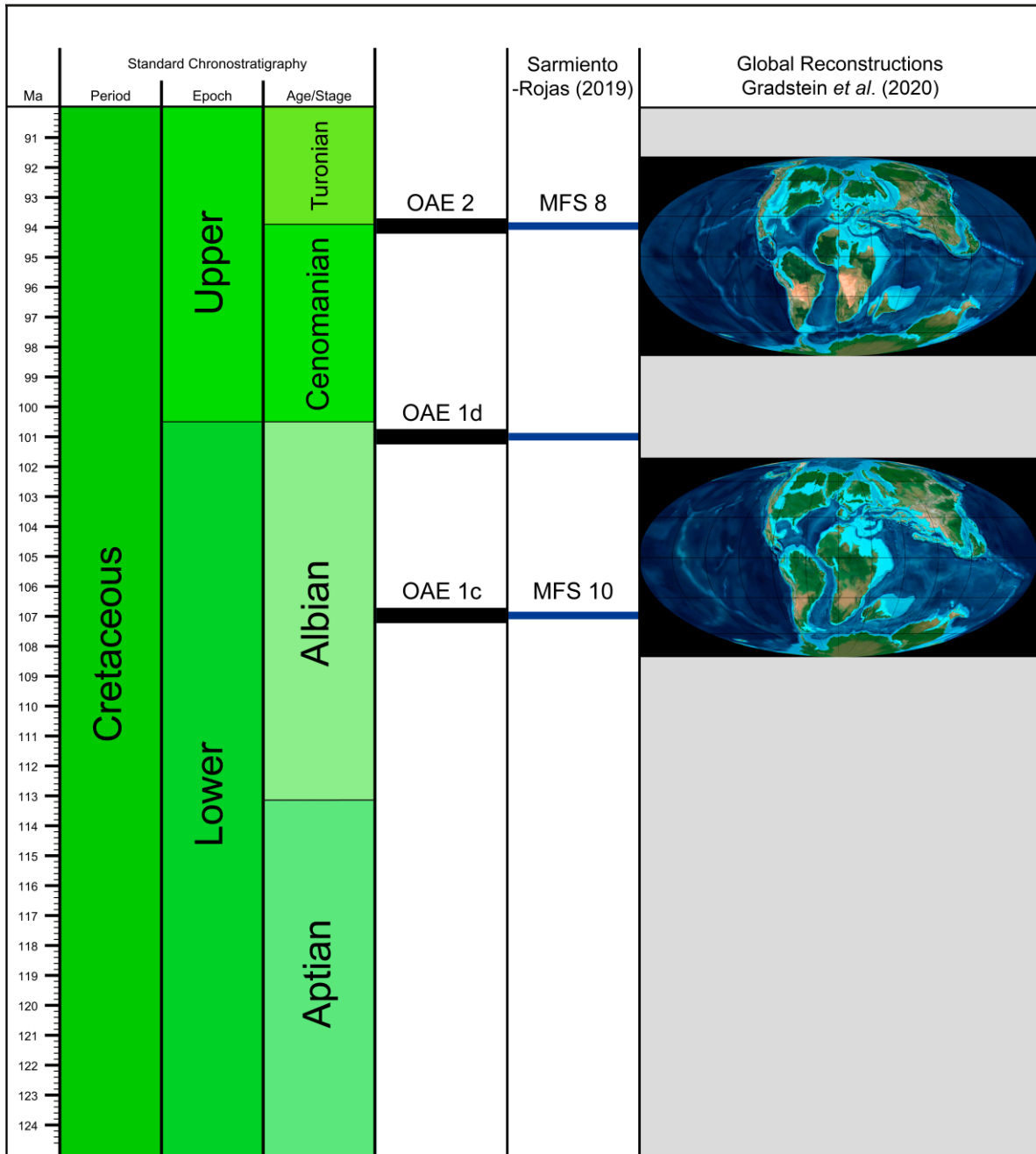


Figure 6. Oceanic Anoxic Events (OAEs); Maximum Flooding Surfaces (MFS) 8 and 10 according to Sarmiento-Rojas (2019).

4. Theoretical framework

This study examines the palynological assemblages from strata associated with amber in two localities of South America: The Oriente Basin of Ecuador and the Eastern Cordillera of Colombia. The palynoflora found in these sites will be useful to understand the origin and radiation of angiosperms during the Albian in tropical latitudes.

4.1. Origin and radiation of angiosperms

The Early Cretaceous radiation of angiosperms was one of the major biotic events in the history of life yielding dramatic consequences for the composition and subsequent evolution of terrestrial ecosystems (Doyle & Hickey, 1976; Dilcher, 1979; Hughes, 1994; Friis *et al.*, 2011; Friis *et al.*, 2015; Shi *et al.*, 2022). However, the timing of their origin still remains as a controversial topic (Silvestro *et al.*, 2021; Cui *et al.*, 2022).

One of the oldest reliable angiosperm fossil records are *Nymphaeales* reproductive structures with *in-situ* pollen from the Barremian – Albian in Portugal (Friis *et al.*, 2000, 2001). Older records are controversial. Some examples are the dispersed pollen with morphological characteristics of angiosperms found in the Middle Triassic? of the Barents Sea, Norway (Hochuli & Feist-Burkhardt, 2004) or the Late Triassic in Virginia, USA (Cornet, 1989), the isolated Triassic leaf imprints in northwestern Texas, USA (Cornet, 1986), and the Early Cretaceous *Archaeofructus* in Northeast China (Zhou *et al.*, 2003) previously dated as Late Jurassic (Sun *et al.*, 1998). A particular case, it is the pre-Cretaceous origin of angiosperms postulated by Silvestro *et al.* (2021), who, using Bayesian statistics, demonstrated that this age is supported not only by molecular clock approaches but also by analyses of the fossil record that explicitly fill the incomplete sampling. The estimated age, however, has strongly conflicted with the known temporal distribution of angiosperm fossils (Budd *et al.*, 2021). Another important case is *Florigerminis jurassica*, a very well-preserved fossil flower bud discovered in the Jurassic of Inner Mongolia, China; the developed interpolated existence of a blooming flower between the flower bud and mature fruit in *Florigerminis* suggests an earlier origin of angiosperms (Cui *et al.*, 2022).

New evidence shows that the transition to widespread angiosperm-dominated biomes was delayed until the Paleocene (66 – 56 Ma) and families with the shortest lags to dominance are overrepresented in temperate and arid biomes compared with tropical biomes (Ramírez-Barahona *et al.*, 2020). Today, there are more living species of angiosperms than all other groups of land plants combined (Friis *et al.*, 2011).

4.2. Cretaceous palynological zonation

There are only two palynological zonation schemes for the Cretaceous of tropical South America which were used to assess the age of the study sites, Regali *et al.* (1974) (Figure 7) and Muller *et al.* (1987) (Figure 8).

In Regali *et al.* (1974) the Aptian – Turonian interval is divided into three superzones:

1. *Exesipollenites tumulus* superzone (Aptian): The base is characterized by the Last Appearance Datum (LAD) of *Cedripites?* sp. and the top by the LAD of *Exesipollenites tumulus*. It is divided into six zones (Table 3).
2. *Inaperturopollenites microclavatus* superzone (early – middle Albian): The base is characterized by the LAD of *Exesipollenites tumulus* and the top by the LAD of *Inaperturopollenites microclavatus*. It is divided into three zones (Table 3).
3. *Elateroplicites africaensis* superzone (late Albian – Turonian): The base is characterized by the LAD of *Inaperturopollenites microclavatus* and the top by the LAD of *Elateroplicites africaensis*. It is divided into four zones (Table 3).

Table 3. Palynological zones of Regali *et al.* (1974).

Palynological superzone	Palynological zone	Palynological zone-Base	Palynological zone-Top
<i>Exesipollenites tumulus</i>	<i>Inaperturopollenites Crisopolensis</i>	LAD <i>Aequitriradites spinulosus</i>	LAD <i>Inaperturopollenites crisopolensis</i>
	<i>Inaperturopollenites curvimuratus</i>	LAD <i>Inaperturopollenites crisopolensis</i>	LAD <i>Inaperturopollenites curvimuratus</i>
	<i>Foveotriletes</i> sp.	LAD <i>Inaperturopollenites curvimuratus</i>	LAD <i>Foveotriletes</i> sp.
	<i>Inaperturopollenites turbatus</i>	LAD <i>Foveotriletes</i> sp.	LAD <i>Inaperturopollenites turbatus</i>
	<i>Sergipea variverrucata</i>	LAD <i>Inaperturopollenites turbatus</i>	LAD <i>Sergipea variverrucata</i>
	<i>Caytonipollenites?</i> sp. 1	LAD <i>Sergipea variverrucata</i>	LAD <i>Caytonipollenites?</i> sp. 1
<i>Inaperturopollenites microclavatus</i>	<i>Pentapsis valdiviae</i>	LAD <i>Caytonipollenites?</i> sp. 1	LAD <i>Pentapsis valdiviae</i>
	<i>Elateropollenites jardinei</i>	LAD <i>Pentapsis valdiviae</i>	LAD <i>Elateropollenites jardinei</i>
	<i>Steevesipollenites alatiformis</i>	LAD <i>Elateropollenites jardinei</i>	LAD <i>Steevesipollenites alatiformis</i>
<i>Elateroplicites africaensis</i>	<i>Elaterosporites protensus</i>	LAD <i>Steevesipollenites alatiformis</i>	LAD <i>Elaterosporites protensus</i>
	<i>Psilatricolpites papilioniformis</i>	LAD <i>Elaterosporites protensus</i>	LAD <i>Psilatricolpites papilioniformis</i>
	<i>Gnetaceaepollenites diversus</i>	LAD <i>Psilatricolpites papilioniformis</i>	LAD <i>Gnetaceaepollenites diversus</i>
	<i>Gnetaceaepollenites crassipoli</i>	LAD <i>Gnetaceaepollenites diversus</i>	LAD <i>Gnetaceaepollenites crassipoli</i>

In Muller *et al.* (1987) the Aptian – Turonian interval is divided into four superzones:

1. Superzone II (early – middle Aptian) comprises the “*Inaperturopollenites*” *crisopolensis*-*Afropollis* zone. The base of the superzone is the LAD of *Dicheiropollis etruscus*; the top of the superzone is the First Appearance Datum (FAD) of (*Psila*-), (*Reti*-), *Striatricolpites* sp. (Table 4).
2. Superzone III (late Aptian – middle Albian) comprises both the “*Tricolpites*”-*Exesipollenites tumulus* and *Elateropollenites jardinei* zones. The base of the

superzone is the FAD of (*Psila-*), (*Reti-*), *Striatricolpites* sp.; the top of the superzone is the FAD of *Psilatricolporites* sp. (Table 4).

3. Superzone IV (late Albian – Cenomanian) comprises both the *Elaterosporites protensus/verrucatus-Afropollis* and *Triorites africaensis* zones. The base of the superzone is the FAD of *Psilatricolporites* sp.; the top of the superzone is the LAD of *Triorites africaensis* and *Corollina* sp. (Table 4).
4. Superzone V (Turonian) comprises the “Interval zone”. The base of the superzone is the LAD of *Triorites africaensis* and *Corollina* sp.; the top of the superzone is the FAD of *Droseridites senonicus* (Table 4).

Table 4. Palynological zones of Muller *et al.* (1987).

Palynological superzone	Palynological zone	Palynological zone-Base	Palynological zone-Top
Superzone II	“ <i>Inaperturopollenites</i> ” <i>crisopolensis-Afropollis</i>	FAD <i>Afropollis</i> sp.	FAD tricolpate angiosperm pollen LAD “ <i>Inaperturopollenites</i> ” <i>crisopolensis</i>
Superzone III	“ <i>Tricolpites</i> ”- <i>Exesipollenites tumulus</i>	FAD tricolpate angiosperm pollen	FAD <i>Elaterosporites</i> , <i>Elateropollenites</i> , <i>Elateroplicites</i> sp. LAD <i>Exesipollenites</i> <i>tumulus</i>
Superzone IV	<i>Elateropollenites jardinei</i>	FAD <i>Elaterosporites</i> , <i>Elateropollenites</i> , <i>Elateroplicites</i> sp.	FAD triporate pollen types and <i>Psilatricolporites</i> sp.
Superzone IV	<i>Elaterosporites</i> <i>protensus/verrucatus-</i> <i>Afropollis</i>	FAD triporate pollen types and <i>Psilatricolporites</i> sp.	LAD <i>Afropollis</i> sp.
Superzone IV	<i>Triorites africaensis</i>	LAD <i>Afropollis</i> sp. FAD <i>Triorites</i> <i>africaensis</i>	LAD <i>Corollina</i> sp. and <i>Triorites africaensis</i>
Superzone V	“Interval zone”	LAD <i>Corollina</i> sp.	FAD <i>Droseridites</i> <i>senonicus</i>

4.3. Amber

Amber is fossilized resin secreted by a wide range of plant families (Arillo, 2007) (Figure 9), is entirely organic and its composition from the original resin changed over millions of years (Grimaldi, 1996). It is found in several deposits around the world. Fossiliferous ambers have a range of ages from Early Cretaceous to subrecent hardened resins called copal. When the resin is still fresh and sticky, animal and plant remains can become trapped and fossilized as the resin hardens. The result is preserved fossils with extremely fine three-dimensional detail (Poinar, 1992; Grimaldi, 1996; Arillo, 2007).

Amber can be found wherever the hardened resin of various extinct plants is preserved, but special conditions are required to preserve this substance for millions of years, and only occasionally it survived in large enough quantities to be mined. Only a few of these rich amber deposits exist in the world, and the deposits vary greatly in age (Poinar, 1992; Grimaldi, 1996; Seyfullah *et al.*, 2020). Amber has rarely been reported from South America. The only significant described fossiliferous deposit is from the middle Miocene Pebas Formation of Peru and is probably of angiosperm origin (Antoine *et al.*, 2006; Seyfullah *et al.*, 2020). Older Early Cretaceous (late Aptian – early Albian) South American amber has been reported from Brazil (Pereira *et al.*, 2007).



Figure 9. A. Amber from Genoveva Mine, Oriente Basin-Ecuador. B. Amber from La Popa Mine, Eastern Cordillera-Colombia.

4.4. Oceanic Anoxic Events

The OAEs (Oceanic Anoxic Events) are global perturbations in the ocean–atmosphere system during periods of organic-carbon burial (Schlanger & Jenkyns, 1976; Jenkyns, 2010). They represent an important case of study for modern trends because there were widespread anoxia events and enhanced organic carbon burial linked to exceptionally warm climates and high atmospheric CO₂ concentrations (van Helmond *et al.*, 2013). These events also had elevated the organic carbon preservation in multiple ocean basins and under various paleo-water depths, paleolatitudes and depositional conditions (Arthur *et al.*, 1987; Jenkyns, 2010; Kuroda & Ohkouchi, 2006; Schlanger *et al.*, 1987; Takashima *et al.*, 2006; Owens *et al.*, 2018). The magnitude of these excursions recorded in marine organic and carbonate carbon ranges between ~2 and ~7 ‰ with an average of ~3 ‰ (Schlanger *et al.*, 1987; Erbacher *et al.*, 2005; Jarvis *et al.*, 2006).

5. Methods

5.1. Sampling and processing

Thirty-seven samples of the dark and fine-grained facies were collected including 10 samples along the stratigraphic column in the Genoveva mine. Near this mine, 18 additional samples were collected in six localities from the Hollin Formation and five samples in four localities from the Napo Formation. Moreover, four samples were collected in La Popa Mine, in the Eastern Cordillera of Colombia (Table 5).

Table 5. Analyzed samples information with their locality data and geological formation.

Mine	Sample (STRI-ID)	Locality name	Locality ID	Locality coordinates	Geological Formation
Genoveva Mine	47720	Genoveva Mine	880033	Lat: -0.71102 Long: -77.78778	Hollin
	47721				
	47722				
	47723				
	47724				
	47725				
	47731				
	47732				
	47733				
	47734				
	44661	Pungarayacu Quarry	440071	Lat: -0.70700 Long: -77.74100	Hollin
	44662				
	44663				
	44880				
	44882				
	44883				
	44884				
	46872	NA	880031	Lat: -0.74060 Long: -77.52300	Hollin
	46873	NA	880032	Lat: -0.74036 Long: -77.52401	Hollin
		47726	Pungarayacu	910003	Lat: -0.71161 Long: -77.73966
47727					
47728					
47729					
47730					
47735	Second Genoveva Mine	910004	Lat: -0.71172 Long: -77.79113	Hollin	
	44889	Misahualli Hollin River	440074	Lat: -1.00120 Long: -77.67280	Hollin
	44890				
	44891				
	44886	Misahualli Napo top	440072	Lat: -1.01620 Long: -77.67070	Napo
	44887				

Mine	Sample (STRI-ID)	Locality name	Locality ID	Locality coordinates	Geological Formation
	44892	Misahualli Napo middle	440075	Lat: -1.00470 Long: -77.67120	Napo
	47746	Puerto Napo	910001	Lat: -1.04215 Long: -77.79404	Napo
	47748	Puerto Misahualli	910002	Lat: -1.00964 Long: -77.67011	Napo
La Popa Mine	46426	Chipaque 1	860032	Lat: 4.70967 Long: -73.94975	Une
	46427	Chipaque 2	860033	Lat: 4.70866 Long: -73.95213	Une
	46428	Chipaque 3	860034	Lat: 4.70905 Long: -73.95181	Une
	46487	Chipaque 4	860035	Lat: 4.71265 Long: -73.94826	Une

Samples were prepared following the standard procedure described by Traverse (1988, 2007) and modified in the Laboratorio de Palinología y Materia Orgánica of the Instituto de Investigaciones en Estratigrafía (IIES) at Universidad de Caldas, described as follows:

1. Each sample was washed with neutral soap and water with a coarse bristle brush to remove recent organic matter and possible oxidation.
2. The sample was dried in an oven at 50 °C using aluminum foil.
3. While the sample was drying, the label and container to be used were prepared.
4. Once the sample was dry, it was crushed, 20-30 g, weighed and placed in labeled containers; the remaining material was returned to the airtight bags containing the rest of the sample or preserved material for possible reprocessing.
5. To eliminate the carbonate, in the fume hood, 20 ml of 37% hydrochloric acid (HCl) were added to each sample for 12 hours.
6. The lid and the top of the container were cleaned to make all the material descend using distilled water after 12 hours.
7. The total content obtained from the sample was centrifuged, and the supernatant (water + acid) was discarded in containers for chemical waste. Distilled water was added to the sample residue and agitated with a glass rod to suspend the organic matter.

8. To eliminate the silicates, 70% hydrofluoric acid (HF) was added in the fume hood, approximately 25% of the total volume of the sample, and it remains in acid digestion for 16 to 24 hours under agitation.
9. To clean the palynomorphs and eliminate the excess suspended organic matter, the 10 μm sieves were cleaned using ultrasound. The sample was filtered by adding distilled water as necessary to eliminate the acid fraction. Once filtered and neutralized with distilled water, the material was heated to boiling with 37% HCl for 15 minutes to eliminate the gels and colloidal material (fluorosilicates). An aliquot was extracted in a test tube (marked with the sample data) from the processed organic residue and preserved for first mounting (unoxidized slide). The protocol involves to place the unoxidized slide next to the sample identification label. The remaining residue of organic material was oxidized using 65% nitric acid (HNO_3). This procedure was preformed by pouring a fraction of the content of the test tubes into a beaker and adding HNO_3 for 2-5 minutes (depending on the sample), after that it was neutralized and filtered through a 10 μm sieve again using distilled water. When the sample had a high content of organic material (coals, carbonaceous mudstones, and some lignites), 5% ammonium hydroxide (NH_4OH) was used to remove the dissolved humic substances.
10. Mounting the slide: Two coverslips were mounted, one for the non-oxidized part and the other for the oxidized. Subsequently, a drop of polyvinyl alcohol, which acts as a preservative and adherent, was added to each coverslip.
11. Approximately 100 to 200 ml of the sample both non-oxidized and oxidize were deposited.
12. The slide was dried on a hot plate at a temperature of 70 $^{\circ}\text{C}$ for 15-20 minutes until the aqueous fraction evaporated.
13. Sealing the slide: A drop of Canada balsam was added to each coverslip and then put it in the oven at 70 $^{\circ}\text{C}$ for 1 hour. Subsequently, the slide was placed in oven during 12 hours for final drying. Once the mounting was ready, the excess of Canada balsam was removed using xylene [$\text{C}_6\text{H}_4(\text{CH}_3)_2$] as organic solvent. Finally, the slide was labeled with the respective ID of both the IIES and that one used in the field for

sample identification (STRI-ID). The remaining fractions (oxidized and unoxidized) were stored in 2 ml vials.

The sample 47748 from the lower Napo formation was processed for calcareous nannoplankton by smear slide (Backman & Shackleton, 1983) which is quick, simple and requires a small amount of sediment or rock, described as follows:

1. An agate mortar was used to pulverize the sample. The mortar was washed with HCl between samples to prevent contamination.
2. Small amounts of sediment were deposited on a slide and a couple of drops of buffered water were added to the sediment.
3. The previous solution of sediment and buffered water were distributed as homogeneously as possible on the slide with a suitable utensil (wooden toothpick).
4. The slide was labeled with the sediment to avoid confusion.
5. To dry the preparation, the slide was placed on a hot plate at an intermediate temperature.
6. A drop of Canada balsam (dissolved at 50% with xylene) was added on the spread sediment.
7. A coverslip was placed on the balsam.
8. The material was observed under a polarized light microscope in parallel and crossed nicols.

5.2. Palynological analysis


For the analysis of the palynological slides, a transmitted light microscope (Nikon 50i) with 20X, 40X and 100X objectives was used. The palynomorphs (marine and terrestrial) present in each slide were systematically registered with their respective descriptions and taxonomic classifications on index cards (e.g., Figure 10).

Index Card #76

Elaterosporites verrucatus

(Jardiné & Magloire, 1965) Jardiné, 1967
Major Taxonomic Group: Gnetales

- Pollen.
- Monad.
- Elliptic.
- Distal face strongly convex; proximal face flat to slightly convex.
- Elaterate.
- Distal face with 3 cylindrical expansions of same length? attached to the body in the middle up to 1/3 of the length; the 2 free extremities are rounded; proximal face limited by an annular thickening more or less developed, which structure is similar to the distal elaters.
- Verrucate as secondary sculpture.
- Inaperturate.



Palynological slide: 44892
England Finder: J42-4

Figure 10. Example of a digitized Index Card showing *Elaterosporites verrucatus* and its morphological description.

The preservation grade of the palynomorphs was established as follows: 1) Poor: when the morphological characteristics did not allow the identification of palynomorphs; 2) Moderate: when despite being poorly preserved, some morphological characteristics allowed the identification of the palynomorphs; and 3) Good: when the morphology of most of the palynomorphs allowed their determination.

For the identification of palynomorphs, the morphological database of Jaramillo & Rueda (2021) was used, which includes all palynological publications from South America. The ages of the successions were determined using two biostratigraphic zonations, Regali *et al.* (1974) from Brazil, which is the most complete Lower Cretaceous biostratigraphic work in tropical latitudes of South America, and Muller *et al.* (1987) proposed for northern South America.

The palynomorphs were grouped into five groups including angiosperm pollen, non-gnetalean gymnosperm pollen, gnetalean pollen, spores and marine palynomorphs. Gnetales were placed in their own category rather than with other gymnosperms because they are an important component of equatorial Cretaceous floras (Herngreen *et al.*, 1996) as well as climate indicators. Precipitation was estimated by comparing the total diversity of dry

indicators (*Classopollis*, ephedroid pollen grains and elater-bearing species) versus humid indicators (fern spores) (Herngreen *et al.*, 1996; Mejia-Velasquez *et al.*, 2012; Mejia-Velasquez *et al.*, 2018).

6. Results

6.1. Floristic composition

The overall floristic assemblage is dominated by fern spores with 84 taxa (Figure 11), followed by angiosperms with 63 taxa (Figure 12), while the remaining 40 taxa correspond to gymnosperms (Figure 13), and five taxa are marine palynomorphs (Figure 14).

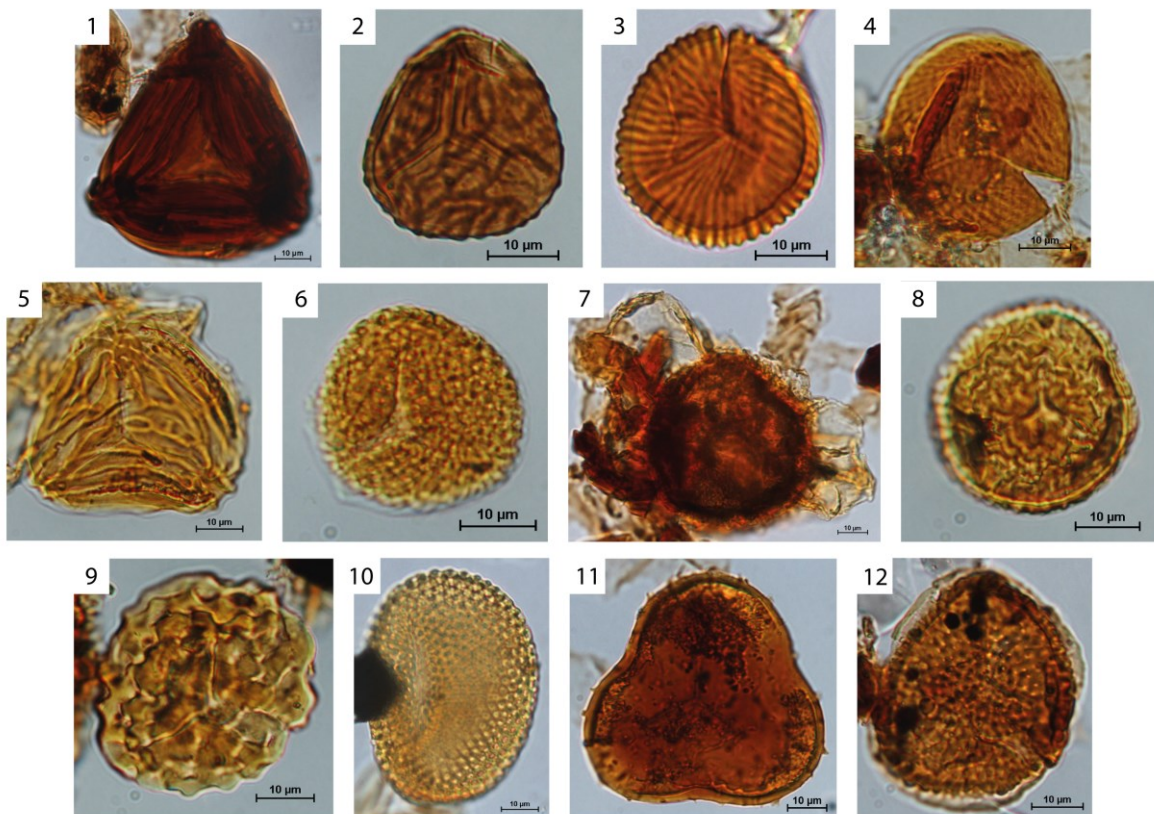


Figure 11. Spore taxa from all localities. 1. *Appendicisporites erdtmanii*; 2. *Camarozonosporites ambigens*; 3. *Cicatricosisporites avnimelechi*; 4. *Cicatricosisporites hallei*; 5. *Cicatricosisporites hughesii*; 6. *Cicatricosisporites kedvesii*; 7. *Crybelosporites pannuceus*; 8. *Hamulatisporis insignis*; 9. *Ischyosporites variegatus*; 10. *Microfoveolatosporis skottsbergii*; 11. *Pilosporites parvispinosus*; 12. *Sestrosporites pseudoalveolatus*.

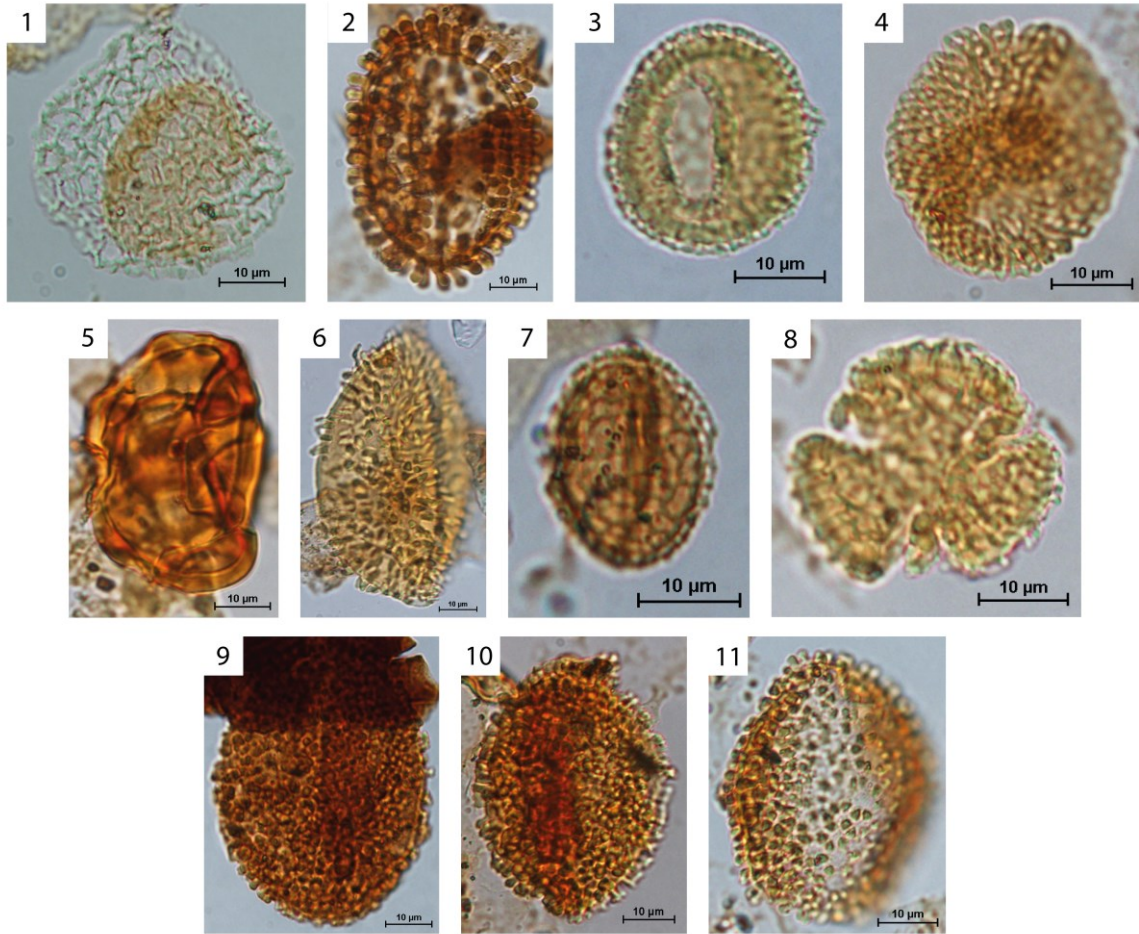


Figure 12. Angiosperm taxa from all localities. Angiosperm taxa from all localities. 1. *Afropollis jordanus*; 2. *Baculamonocolpites* sp.; 3. *Clavatipollenites hughesii*; 4. *Cornetipollis perforatus*; 5. *Cretacaeiporites* sp.; 6. *Echimonocolpites* sp.; 7. *Pennipollis peroreticulatus*; 8. *Retitricolpites operculatus*; 9. *Stellatopollis barghoornii*; 10. *Stellatopollis densiornatus*; 11. *Stellatopollis dubius*.

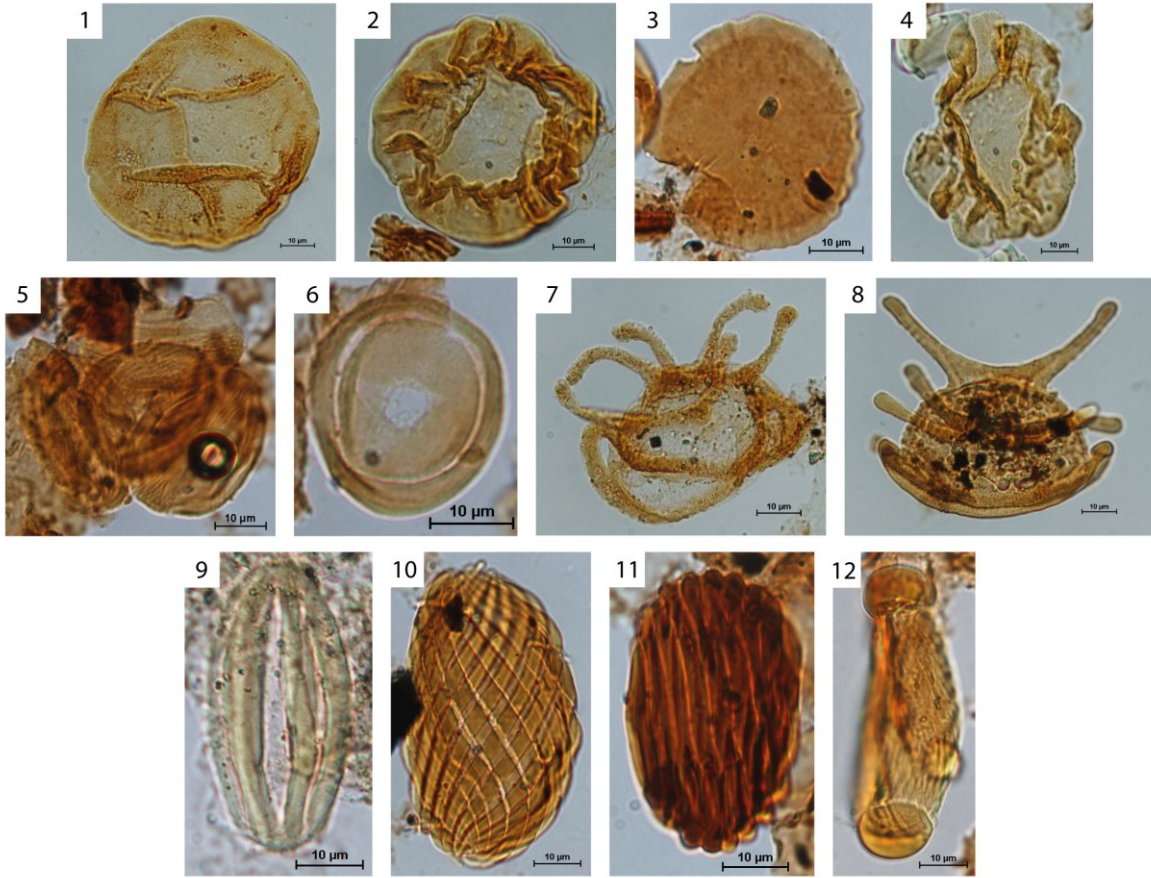


Figure 13. Gymnosperm taxa from all localities. 1-6. Non-gnetalean gymnosperm pollen, 7-12. Gnetalean pollen. 1. *Araucariacites australis*; 2. *Callialasporites dampieri*; 3. *Callialasporites infirmus*; 4. *Callialasporites trilobatus*; 5. *Classopollis classoides*; 6. *Classopollis meyeriana*; 7. *Elaterosporites klaszii*; 8. *Elaterosporites verrucatus*; 9. *Ephedripites ambonoides*; 10. *Ephedripites barghoornii*; 11. *Gnetaceapollenites retangularis*; 12. *Steevesipollenites* cf. *multilineatus*.

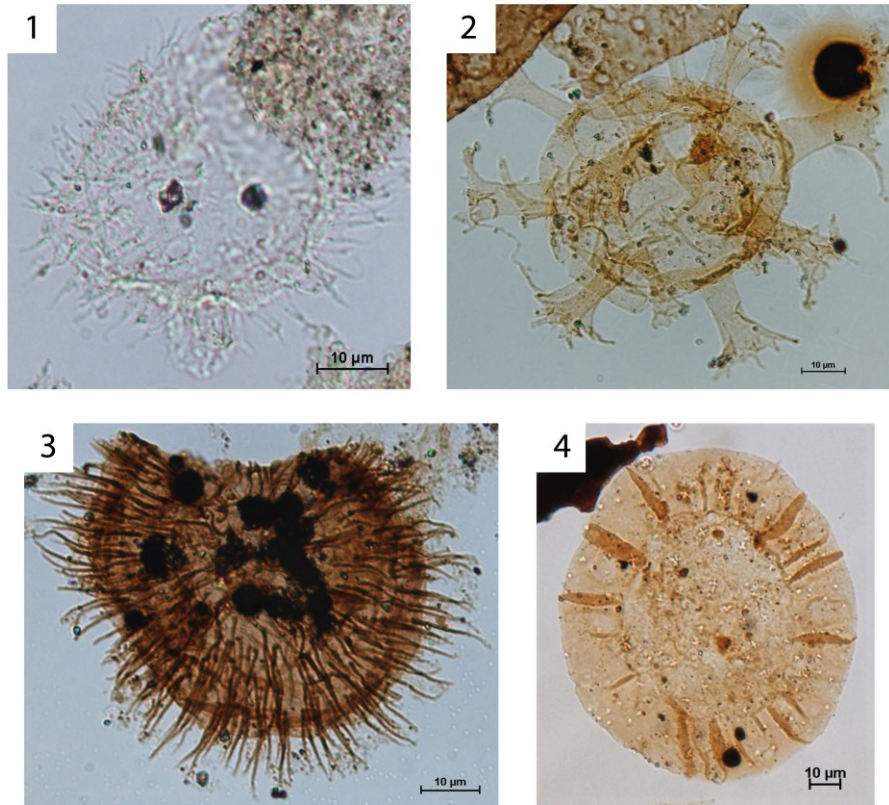
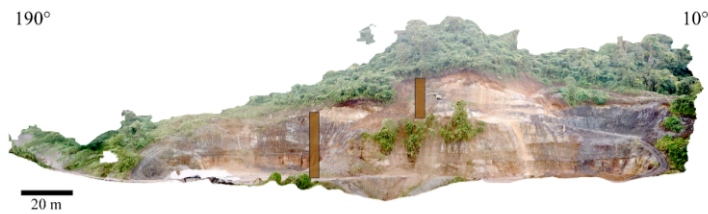


Figure 14. Marine palynomorphs from all localities. 1-2. Dinoflagellates, 3-4. Others. 1. *Coronifera?* sp.; 2. *Hystrichosphaeridium* aff. *tubiferum*; 3. Indeterminate acritarch; 4. *Pterospermella aureolata*.

6.1.1. lower Hollin Formation

The lower Hollin formation in the Genova Mine is 72.5 m thick (Figure 15) and 10 samples were collected there from siltstones and very fine-grained sandstones accumulated in a variety of environments that include proximal braided rivers, lacustrines, hyperpycnal flows and distal braided rivers (Table 6). In the Genova Mine and the other six localities where 18 samples were obtained (see Table 5) a total of 162 taxa were identified including 47 angiosperms, 17 non-gnetalean gymnosperm pollen, 22 gnetalean pollen and 76 spores (Table 7). In general, these taxa present a good preservation.



Stratigraphic Unit	Bed number	Thickness (meters)	Tuff						Lap Agg			Sedimentary structures	Fossils	Sedimentary Facies	Environment		
			Ms	Ws	Ps	Gs	Bs	Cs	f	m	c					vc	fmc
		0.004	clay	silt	vf	f	m	c	vc	f	mc	f	c				
		0.062															
		0.125															
		0.25															
		0.5															
		1															
		2															
		4															
		64															
		256															

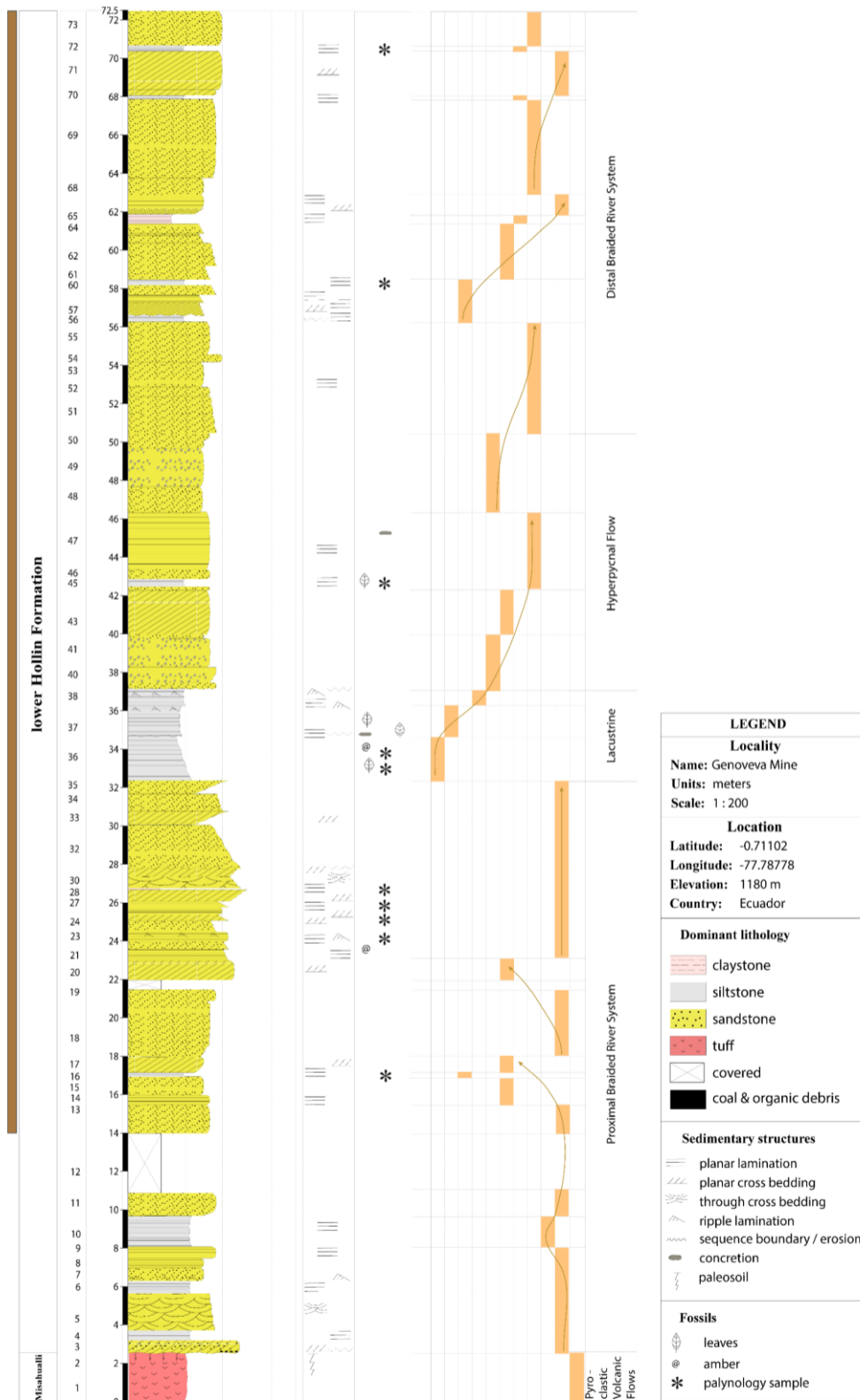


Figure 15. General orthomosaic and stratigraphic column with 1:200 scale of the Genova Mine. In the orthomosaic, the brown bar shows where the stratigraphic column was created. Sedimentary facies and environment information from Quiroz-Cabascango (2021).

Table 6. Samples (top to base) collected from the Genoveva Mine, lithology, sedimentary facies and environment.

Stratum base (m)	Stratum top (m)	STRI ID	Lithology	Sedimentary facies	Environment
70.4	70.7	47733	Dark grey siltstone	Overbank	Distal braided river system
58.2	58.5	47732	Dark grey siltstone	Inner lake	Distal braided river system
42.5	42.9	47731	Grey siltstone	Fluvial plain	Hyperpycnal flow
33.6	33.7	47724	Dark grey siltstone	Outer lake	Lacustrine
32.6	32.7	47723	Dark grey siltstone	Outer lake	Lacustrine
26.7	26.8	47725	Dark grey very fine-grained sandstone	Fluvial channel	Proximal braided river system
25.8	25.9	47722	Dark grey very fine-grained sandstone	Fluvial channel	Proximal braided river system
24.8	24.9	47721	Dark grey very fine-grained sandstone	Fluvial channel	Proximal braided river system
24	24.1	47720	Dark grey very fine-grained sandstone	Fluvial channel	Proximal braided river system
16.9	17	47734	Dark grey siltstone	Inner lake	Proximal braided river system

Table 7. List of palynomorphs found in the Hollin Formation with their natural affinity.

Taxa name	Author	Natural Affinity
<i>Afropollis jardinus</i>	Doyle <i>et al.</i> , 1982	Angiosperm
<i>Arecipites</i> aff. <i>perfectus</i>	Silva-Caminha <i>et al.</i> , 2010	Angiosperm
<i>Baculamonocolpites</i> sp.	Solé de Porta, 1971	Angiosperm
<i>Brenneripollis</i> sp.	Juhász & Goczan, 1985	Angiosperm
<i>Clavamonocolpites</i> sp.	González, 1967	Angiosperm
<i>Clavatipollenites hughesii</i>	Couper, 1958	Angiosperm
<i>Cornetipollis perforatus</i>	Dino, 1992	Angiosperm
<i>Cretacaeiporites</i> sp.	Herngreen, 1974	Angiosperm
<i>Dejaxpollenites</i> sp.	Dino, 1994	Angiosperm
<i>Echimonocolpites</i> aff. <i>tersus</i>	Ward, 1986	Angiosperm
<i>Echimonocolpites</i> sp.	van der Hammen & Garcia, 1965	Angiosperm
<i>Foveomonocolpites</i> cf. “ <i>brevicolpatus</i> ”	Informal	Angiosperm
<i>Foveotricolpites</i> sp.	Pierce, 1961	Angiosperm

Taxa name	Author	Natural Affinity
<i>Foveotricolpites</i> “subgigantoreticulatus”	Informal	Angiosperm
<i>Gemmamonocolpites</i> sp.	van der Hammen & Garcia, 1965	Angiosperm
<i>Liliacidites</i> cf. <i>dividuus</i>	Brenner, 1963	Angiosperm
<i>Liliacidites</i> sp.	Couper, 1953	Angiosperm
<i>Monoporopollenites</i> sp.	Meyer, 1956	Angiosperm
<i>Pennipollis</i> cf. “ <i>echinatus</i> ”	Informal	Angiosperm
<i>Pennipollis peroreticulatus</i>	Friis <i>et al.</i> , 2000	Angiosperm
<i>Perfotricolpites</i> sp.	González, 1967	Angiosperm
<i>Periretisyncolpites</i> sp.	Kieser & Jan du Chene, 1979	Angiosperm
<i>Polyadopollenites</i> aff. <i>microreticulatus</i>	Salard-Cheboldaeff, 1974	Angiosperm
<i>Proxapertites</i> cf. <i>verrucatus</i>	Sarmiento, 1992	Angiosperm
<i>Psilamonocolpites</i> sp.	van der Hammen & Garcia, 1965	Angiosperm
<i>Retibrevitricolpites</i> sp.	van Hoeken-Klinkenberg 1966	Angiosperm
<i>Retimonocolpites</i> sp.	Pierce, 1961	Angiosperm
<i>Retimonoporites</i> cf. <i>operculatus</i>	Brenner & Bickoff, 1992	Angiosperm
<i>Retimonoporites</i> cf. <i>orteguensis</i>	Informal	Angiosperm
<i>Retimonoporites</i> sp.	Brenner & Bickoff, 1992	Angiosperm
<i>Retipollenites</i> sp.	González, 1967	Angiosperm
<i>Retistephanocolpites</i> sp.	Leidelmeyer, 1966	Angiosperm
<i>Retitrescolpites baculatus</i>	Jaramillo & Dilcher 2001	Angiosperm
<i>Retitricolpites</i> “ <i>reticuloghazalensis</i> ”	Mejia <i>et al.</i> , 2017	Angiosperm
<i>Retitricolpites operculatus</i>	Herngreen, 1973	Angiosperm
<i>Retitricolpites</i> sp.	van der Hammen & Wymstra, 1964	Angiosperm
<i>Reyrea</i> aff. <i>polymorphus</i>	Herngreen, 1973	Angiosperm
<i>Rousea</i> aff. <i>miculipollis</i>	Srivastava, 1975	Angiosperm
<i>Scabraperiporites</i> sp.	Regali <i>et al.</i> , 1974	Angiosperm
<i>Scabratricolpites</i> sp.	van der Hammen, 1956	Angiosperm
<i>Senectotetradites</i> aff. <i>varireticulatus</i>	Dettmann, 1973	Angiosperm
<i>Stellatopollis</i> aff. <i>largissimus</i>	Singh, 1983	Angiosperm
<i>Stellatopollis barghoornii</i>	Doyle, 1976	Angiosperm
<i>Stellatopollis densiornatus</i>	de Lima, 1989	Angiosperm
<i>Stellatopollis dubius</i>	de Lima, 1978	Angiosperm
<i>Stellatopollis</i> sp.	Doyle, 1976	Angiosperm
<i>Striatopollis</i> sp.	Krutzsch, 1959	Angiosperm
<i>Tricolpites</i> cf. <i>synstriatus</i>	Jardiné & Magloire, 1965	Angiosperm
<i>Tricolpites</i> sp.	Couper, 1953	Angiosperm
<i>Tucanopollis</i> aff. <i>crisopolensis</i>	Regali, 1989	Angiosperm
<i>Verruperiporites</i> sp.	Dueñas, 1986	Angiosperm

Taxa name	Author	Natural Affinity
<i>Araucariacites australis</i>	Cookson, 1947	Non-gnetalean gymnosperm pollen
<i>Callialasporites dampieri</i>	Dev, 1961	Non-gnetalean gymnosperm pollen
<i>Callialasporites infirmus</i>	Mahmoud, 2003	Non-gnetalean gymnosperm pollen
<i>Callialasporites</i> sp.	Dev, 1961	Non-gnetalean gymnosperm pollen
<i>Callialasporites trilobatus</i>	Dev, 1961	Non-gnetalean gymnosperm pollen
<i>Classopollis brasiliensis</i>	Herngreen, 1975	Non-gnetalean gymnosperm pollen
<i>Classopollis classoides</i>	Pocock & Jansonius, 1961	Non-gnetalean gymnosperm pollen
<i>Classopollis meyeriana</i>	de Jersey, 1973	Non-gnetalean gymnosperm pollen
<i>Classopollis</i> sp.	Pflug, 1953	Non-gnetalean gymnosperm pollen
<i>Cyclusphaera</i> aff. <i>psilata</i>	Volkheimer & Sepulveda, 1976	Non-gnetalean gymnosperm pollen
<i>Inaperturopollenites</i> sp.	Potonié, 1966	Non-gnetalean gymnosperm pollen
<i>Podocarpidites?</i> sp.	Couper, 1953	Non-gnetalean gymnosperm pollen
<i>Taxacites</i> aff. <i>sahariensis</i>	Reyre, 1973	Non-gnetalean gymnosperm pollen
aff. <i>Ephedripites</i> sp. A	Azema & Boltenhagen, 1974	Gnetalean pollen
<i>Elaterosporites</i> sp.	Jardiné, 1967	Gnetalean pollen
<i>Ephedripites</i> aff. <i>regularis</i>	van Hoeken-Klinkenberg, 1964	Gnetalean pollen
<i>Ephedripites barghoornii</i>	Muller, 1968	Gnetalean pollen
<i>Ephedripites</i> cf. <i>procerus</i>	Brenner, 1968	Gnetalean pollen
<i>Ephedripites multicostatus</i>	Muller, 1968	Gnetalean pollen
<i>Ephedripites</i> sp.	Potonié, 1958	Gnetalean pollen
<i>Equisetosporites</i> aff. <i>minuticostatus</i>	de Lima, 1980	Gnetalean pollen
<i>Equisetosporites</i> aff. <i>subcircularis</i>	de Lima, 1980	Gnetalean pollen
<i>Equisetosporites ambiguus</i>	Singh, 1983	Gnetalean pollen
<i>Equisetosporites dudarensis</i>	de Lima, 1980	Gnetalean pollen
<i>Equisetosporites fragilis</i>	de Lima, 1980	Gnetalean pollen
<i>Equisetosporites laticostatus</i>	de Lima, 1980	Gnetalean pollen
<i>Gnetaceaepollenites</i> aff. <i>concisus</i>	Regali, 1989	Gnetalean pollen
<i>Gnetaceaepollenites</i> aff. <i>undulatus</i>	de Lima, 1980	Gnetalean pollen
<i>Gnetaceaepollenites barghoornii</i>	de Lima, 1980	Gnetalean pollen
<i>Gnetaceaepollenites jansonii</i>	de Lima, 1980	Gnetalean pollen
<i>Gnetaceaepollenites retangularis</i>	de Lima, 1980	Gnetalean pollen

Taxa name	Author	Natural Affinity
<i>Singhia multicostata</i>	de Lima, 1980	Gnetalean pollen
<i>Steevesipollenites cupuliformis</i>	Azema & Boltenhagen, 1974	Gnetalean pollen
<i>Steevesipollenites</i> cf. <i>multilineatus</i>	Stover, 1964	Gnetalean pollen
<i>Steevesipollenites pygmeus</i>	Azema & Boltenhagen, 1974	Gnetalean pollen
<i>Aequitriradites</i> cf. <i>verrucosus</i>	Cookson & Dettmann, 1961	Spore
aff. <i>Staplinisporites</i> sp.	Pocock, 1962	Spore
<i>Apiculatasporites</i> sp.	Ibrahim, 1933	Spore
<i>Apiculatisporites</i> aff. <i>levis</i>	Balme & Hennely, 1956	Spore
<i>Appendicisporites erdtmanii</i>	Pocock, 1962	Spore
<i>Baculatisporites</i> sp.	Thomson, 1953	Spore
<i>Balmeisporites</i> sp.	Cookson & Dettmann, 1958	Spore
<i>Camazonosporites ambigens</i>	Playford, 1971	Spore
<i>Camazonosporites</i> sp.	Potonié, 1956	Spore
<i>Camazonosporites vermiculaesporites</i>	Krutzsch, 1963	Spore
<i>Ceratosporites equalis</i>	Cookson & Dettmann, 1958	Spore
<i>Chomotriletes minor</i>	Pocock, 1970	Spore
<i>Cicatricosisporites</i> aff. <i>venustus</i>	Deak, 1963	Spore
<i>Cicatricosisporites avnimelechi</i>	Horowitz, 1970	Spore
<i>Cicatricosisporites hallei</i>	Delcourt & Sprumont, 1955	Spore
<i>Cicatricosisporites hughesii</i>	Dettmann, 1963	Spore
<i>Cicatricosisporites kedvesii</i>	Schrank & Mahmoud, 1999	Spore
<i>Cicatricosisporites sinuosus</i>	Hunt, 1985	Spore
<i>Cicatricosisporites</i> sp.	Potonié & Gelletich, 1933	Spore
<i>Clavatisporites</i> aff. <i>clarus</i>	Kedves & Simoncsics, 1964	Spore
<i>Clavatisporites clarus</i>	Kedves & Simoncsics, 1964	Spore
<i>Clavatisporites</i> sp.	Kedves & Simoncsics, 1964	Spore
<i>Collarisporites fuscus</i>	Deak, 1964	Spore
<i>Concavissimisporites</i> aff. <i>kyrtomatus</i>	Jaramillo <i>et al.</i> , 2014	Spore
<i>Concavissimisporites globosus</i>	Phillips & Felix, 1971	Spore
<i>Concavissimisporites punctatus</i>	Singh, 1964	Spore
<i>Crybelosporites pannuceus</i>	Srivastava, 1975	Spore
<i>Crybelosporites</i> sp.	Dettmann, 1963	Spore
<i>Deltoidospora minor</i>	Pocock, 1970	Spore
<i>Densoisporites perinatus</i>	Couper, 1958	Spore
<i>Dictyophyllidites excellensus</i>	Kar & Singh, 1986	Spore
<i>Distaltriangulisporites</i> aff. <i>irregularis</i>	Singh, 1971	Spore
<i>Echinatisporis</i> aff. <i>circularis</i>	Silva-Caminha <i>et al.</i> , 2010	Spore
<i>Echinatisporis</i> sp.	Krutzsch, 1959	Spore
<i>Echitriletes</i> aff. <i>minispinosus</i>	Jaramillo <i>et al.</i> , 2014	Spore

Taxa name	Author	Natural Affinity
<i>Echitriletes</i> sp.	Potonié, 1956	Spore
<i>Foveotriletes</i> aff. <i>margaritae</i>	Germeraad <i>et al.</i> , 1968	Spore
<i>Foveotriletes</i> aff. <i>ornatus</i>	Regali <i>et al.</i> , 1974	Spore
<i>Foveotriletes</i> sp.	Potonié, 1956	Spore
<i>Gabonisoris</i> <i>vigourouxii</i>	Boltenhagen, 1967	Spore
<i>Gemmatriletes</i> sp.	Pierce, 1961	Spore
<i>Gleicheniidites</i> aff. <i>apilobatus</i>	Brenner, 1963	Spore
<i>Gleicheniidites</i> <i>senonicus</i>	Ross, 1949	Spore
<i>Gleicheniidites</i> sp.	Dettmann, 1963	Spore
<i>Granulatisporites</i> sp.	Potonié & Kremp, 1954	Spore
<i>Hamulatisporis</i> cf. <i>caperatus</i>	Schrank, 1994	Spore
<i>Hamulatisporis</i> <i>insignis</i>	Kedves, 1995	Spore
<i>Ischyosporites</i> aff. <i>badagriensis</i>	Jan du Chene <i>et al.</i> , 1978	Spore
<i>Ischyosporites</i> <i>variegatus</i>	Jansonius & Hills, 1990	Spore
<i>Januasporites</i> sp.	Pocock, 1962	Spore
<i>Leptolepidites</i> <i>macroverrucosus</i>	Schulz, 1967	Spore
<i>Leptolepidites</i> sp.	Couper, 1953	Spore
<i>Leptolepidites</i> <i>verrucatus</i>	Couper, 1953	Spore
<i>Microfoveolatosporis</i> <i>skottsbergii</i>	Srivastava, 1971	Spore
<i>Muerrigerisporis</i> sp.	Solé de Porta, 1972	Spore
<i>Obtusisporis</i> cf. <i>undulus</i>	Kedves, 1995	Spore
<i>Osmundacidites</i> sp.	Couper, 1953	Spore
<i>Osmundacidites</i> <i>wellmanii</i>	Couper, 1953	Spore
<i>Pilosisorites</i> <i>parvispinosus</i>	Dettmann, 1963	Spore
<i>Polypodiisporites</i> sp.	Chlonova, 1961	Spore
<i>Retitriletes</i> aff. <i>eminulus</i>	Srivastava, 1977	Spore
<i>Retitriletes</i> aff. <i>tenuis</i>	Backhouse, 1988	Spore
<i>Retitriletes</i> <i>douglasii</i>	Dettmann, 1986	Spore
<i>Retitriletes</i> sp.	Pierce, 1961	Spore
<i>Ruffordiaspora</i> sp.	Dettmann & Clifford, 1992	Spore
<i>Rugulatisporites</i> sp.	Pflug, 1953	Spore
<i>Sestrosporites</i> <i>pseudoalveolatus</i>	Dettmann, 1963	Spore
<i>Stoverisporites</i> aff. <i>lunaris</i>	Norvick & Burger, 1975	Spore
<i>Striatriletes</i> sp.	van der Hammen, 1954	Spore
<i>Verrucatotriletes</i> aff. <i>tortus</i>	D'Apolito <i>et al.</i> , 2019	Spore
<i>Verrucatotriletes</i> sp.	van Hoeken-Klinkenberg, 1964	Spore
<i>Verrucosisporites</i> <i>rotundus</i>	Singh, 1964	Spore
<i>Verrucosisporites</i> sp.	Ibrahim, 1933	Spore
<i>Verrutriletes</i> sp.	Potonié, 1956	Spore
<i>Verrutriletes</i> <i>virueloides</i>	Jaramillo <i>et al.</i> , 2007	Spore

Taxa name	Author	Natural Affinity
<i>Zlivisporis</i> sp.	Pacltová, 1961	Spore

6.1.2. lower Napo Formation

Five palynological slides were analyzed for four localities (see Table 5) in which a total of 25 taxa were found, corresponding to nine angiosperms, five gnetalean pollen, six spores and five marine palynomorphs (three dinoflagellates and two acritarchs) (Table 8). These taxa presented good preservation.

Table 8. List of palynomorphs found in the Napo Formation with their corresponding natural affinity.

Taxa name	Author	Natural Affinity
<i>Ladakhipollenites?</i> “ <i>pseudosyncolpatus</i> ”	Informal	Angiosperm
<i>Microfoveotripurites</i> aff. <i>cretaceous</i>	van Hoeken-Klinkenberg, 1966	Angiosperm
<i>Monoporopollenites</i> sp.	Meyer, 1956	Angiosperm
<i>Psilabrevitricolporites</i> sp.	van der Kaars, 1983	Angiosperm
<i>Psilamonocolpites</i> sp.	van der Hammen & Garcia, 1965	Angiosperm
<i>Retibrevitricolpites</i> sp.	van Hoeken-Klinkenberg 1966	Angiosperm
<i>Retimonocolpites</i> sp.	Pierce, 1961	Angiosperm
<i>Retipollenites</i> sp.	González, 1967	Angiosperm
<i>Retitrescolpites</i> sp.	Sah, 1967	Angiosperm
<i>Elaterosporites klaszii</i>	Jardiné, 1967	Gnetalean pollen
<i>Elaterosporites verrucatus</i>	Jardiné, 1967	Gnetalean pollen
<i>Ephedripites ambonoides</i>	Brenner, 1968	Gnetalean pollen
<i>Equisetosporites dudarensis</i>	de Lima, 1980	Gnetalean pollen
<i>Sergipea</i> aff. <i>variverrucata</i>	Regali <i>et al.</i> , 1974	Gnetalean pollen
<i>Camarozonosporites</i> <i>ambigens</i>	Playford, 1971	Spore
<i>Clavatisporites clarus</i>	Kedves & Simoncsics, 1964	Spore
<i>Clavatisporites</i> sp.	Kedves & Simoncsics, 1964	Spore
<i>Concavissimisporites</i> aff. <i>punctatus</i>	Singh, 1964	Spore
<i>Echitriletes</i> sp.	Potonié, 1956	Spore
<i>Foveotriletes</i> sp.	Potonié, 1956	Spore
<i>Coronifera?</i> sp.	Cookson & Eisenack, 1958	Dinoflagellate
<i>Hystrichosphaeridium</i> aff. <i>tubiferum</i>	Davey & Williams, 1966	Dinoflagellate
Indeterminate acritarch	NA	Acritarch

Taxa name	Author	Natural Affinity
<i>Oligosphaeridium</i> aff. <i>totum</i>	Brideaux, 1971	Dinoflagellate
<i>Pterospermella aureolata</i>	Eisenack, 1972	Acritarch?

6.1.3. lower Une Formation

Four samples from La Popa Mine were analyzed (see Table 5). A total of 23 taxa were found with relatively good preservation, corresponding to nine angiosperms, three non-gnetalean gymnosperm pollen and 11 spores (Table 9).

Table 9. List of palynomorphs found in the Une Formation with their natural affinity.

Taxa name	Author	Natural Affinity
<i>Afropollis jardinus</i>	Doyle <i>et al.</i> , 1982	Angiosperm
<i>Clavamonocolpites</i> sp.	González, 1967	Angiosperm
<i>Foveotricolpites</i> sp.	Pierce, 1961	Angiosperm
<i>Polyadopollenites</i> cf. <i>mariae</i>	Dueñas, 1980	Angiosperm
<i>Psilamonocolpites</i> sp.	van der Hammen & Garcia, 1965	Angiosperm
<i>Psilatricolpites</i> sp.	van der Hammen & Wymstra, 1964	Angiosperm
<i>Psilatricolporites</i> sp.	van der Hammen & Wymstra, 1964	Angiosperm
<i>Retiacolpites</i> aff. <i>columellatus</i>	Schrank, 2002	Angiosperm
<i>Retitricolpites</i> sp.	van der Hammen & Wymstra, 1964	Angiosperm
<i>Araucariacites australis</i>	Cookson, 1947	Non-gnetalean gymnosperm pollen
<i>Callialasporites dampieri</i>	Dev, 1961	Non-gnetalean gymnosperm pollen
<i>Podocarpidites?</i> sp.	Couper, 1953	Non-gnetalean gymnosperm pollen
<i>Chomotriletes minor</i>	Pocock, 1970	Spore
<i>Cicatricosisporites</i> sp.	Potonié & Gelletich, 1933	Spore
<i>Hamulatisporis insignis</i>	Kedves, 1995	Spore
<i>Ischyosporites variegatus</i>	Jansonius & Hills, 1990	Spore
<i>Laevigatosporites</i> aff. <i>gracilis</i>	Wilson & Webster, 1946	Spore
<i>Osmundacidites wellmanii</i>	Couper, 1953	Spore
<i>Perotriletes</i> sp.	Couper, 1953	Spore
<i>Psilatriletes</i> sp.	van der Hammen, 1954	Spore
<i>Tuberositriletes</i> sp.	Döring, 1964	Spore
<i>Verrucatotriletes</i> sp.	van Hoeken-Klinkenberg, 1964	Spore
<i>Verrutriletes</i> sp.	Potonié, 1956	Spore

6.2. Climatic estimation

The diversity of arid climate-indicating gymnosperms (*Classopollis*, ephedroid pollen grains, and elater-bearing species) was lower than the diversity of spore indicating humid climates (29 taxa versus 83, respectively) (Tables 10 and 11).

Table 10. Indicators of arid climate conditions.

Indicators of arid climates		
1. aff. <i>Ephedripites</i> sp. A	11. <i>Ephedripites barghoornii</i>	21. <i>Gnetaceaepollenites</i> aff. <i>concisus</i>
2. <i>Classopollis brasiliensis</i>	12. <i>Ephedripites</i> cf. <i>procerus</i>	22. <i>Gnetaceaepollenites</i> aff. <i>undulatus</i>
3. <i>Classopollis classoides</i>	13. <i>Ephedripites multicostatus</i>	23. <i>Gnetaceaepollenites barghoornii</i>
4. <i>Classopollis meyeriana</i>	14. <i>Ephedripites</i> sp.	24. <i>Gnetaceaepollenites jansonii</i>
5. <i>Classopollis</i> sp.	15. <i>Equisetosporites</i> aff. <i>minuticostatus</i>	25. <i>Gnetaceaepollenites retangularis</i>
6. <i>Elaterosporites klaszii</i>	16. <i>Equisetosporites</i> aff. <i>subcircularis</i>	26. <i>Singhia multicostata</i>
7. <i>Elaterosporites</i> sp.	17. <i>Equisetosporites ambiguus</i>	27. <i>Steevesipollenites cupuliformis</i>
8. <i>Elaterosporites verrucatus</i>	18. <i>Equisetosporites dudarensis</i>	28. <i>Steevesipollenites</i> cf. <i>multilineatus</i>
9. <i>Ephedripites</i> aff. <i>regularis</i>	19. <i>Equisetosporites fragilis</i>	29. <i>Steevesipollenites pygmeus</i>
10. <i>Ephedripites ambonoides</i>	20. <i>Equisetosporites laticostatus</i>	

Table 11. Indicators of humid climate conditions.

Indicators of humid climates		
1. <i>Aequitriradites</i> cf. <i>verrucosus</i>	29. <i>Crybelosporites</i> sp.	57. <i>Muerrigerisporis</i> sp.
2. aff. <i>Staplinisporites</i> sp.	30. <i>Deltoidospora minor</i>	58. <i>Obtusisporis</i> cf. <i>undulus</i>
3. <i>Apiculatasporites</i> sp.	31. <i>Densoisporites perinatus</i>	59. <i>Osmundacidites</i> sp.
4. <i>Apiculatisporites</i> aff. <i>levis</i>	32. <i>Dictyophyllidites excellensus</i>	60. <i>Osmundacidites wellmanii</i>
5. <i>Appendicisporites erdtmanii</i>	33. <i>Distaltriangulisporites</i> aff. <i>irregularis</i>	61. <i>Perotriletes</i> sp.
6. <i>Baculatisporites</i> sp.	34. <i>Echinatisporis</i> aff. <i>circularis</i>	62. <i>Pilosisporites parvispinosus</i>
7. <i>Balmeisporites</i> sp.	35. <i>Echinatisporis</i> sp.	63. <i>Polypodiaceoisporites</i> cf. <i>reticulatus</i>
8. <i>Camarozonosporites ambigens</i>	36. <i>Echitriletes</i> aff. <i>minispinosus</i>	64. <i>Polypodiisporites</i> sp.
9. <i>Camarozonosporites</i> sp.	37. <i>Echitriletes</i> sp.	65. <i>Psilatrilletes</i> sp.
10. <i>Camarozonosporites vermiculaesporites</i>	38. <i>Foveotriletes</i> aff. <i>margaritae</i>	66. <i>Retitriletes</i> aff. <i>eminulus</i>
11. <i>Ceratosporites equalis</i>	39. <i>Foveotriletes</i> aff. <i>ornatus</i>	67. <i>Retitriletes</i> aff. <i>tenuis</i>
12. <i>Chomotriletes minor</i>	40. <i>Foveotriletes</i> sp.	68. <i>Retitriletes douglasii</i>
13. <i>Cicatricosisporites</i> aff. <i>venustus</i>	41. <i>Gabonisporis vigourouxii</i>	69. <i>Retitriletes</i> sp.
14. <i>Cicatricosisporites avnimelechi</i>	42. <i>Gemmatriletes</i> sp.	70. <i>Ruffordiaspora</i> sp.
15. <i>Cicatricosisporites hallei</i>	43. <i>Gleicheniidites</i> aff. <i>apilobatus</i>	71. <i>Rugulatisporites</i> sp.
16. <i>Cicatricosisporites hughesii</i>	44. <i>Gleicheniidites senonicus</i>	72. <i>Scabratriletes</i> sp.
17. <i>Cicatricosisporites kedvesii</i>	45. <i>Gleicheniidites</i> sp.	73. <i>Sestrosporites pseudoalveolatus</i>
18. <i>Cicatricosisporites sinuosus</i>	46. <i>Granulatisporites</i> sp.	74. <i>Stoverisporites</i> aff. <i>lunaris</i>
19. <i>Cicatricosisporites</i> sp.	47. <i>Hamulatisporis</i> cf. <i>caperatus</i>	75. <i>Striatriletes</i> sp.
20. <i>Clavatisporites</i> aff. <i>clarus</i>	48. <i>Hamulatisporis insignis</i>	76. <i>Tuberositriletes</i> sp.
21. <i>Clavatisporites clarus</i>	49. <i>Ischyosporites</i> aff. <i>badagriensis</i>	77. <i>Verrucatotriletes</i> aff. <i>tortus</i>
22. <i>Clavatisporites</i> sp.	50. <i>Ischyosporites variegatus</i>	78. <i>Verrucatotriletes</i> sp.
23. <i>Collarisporites fuscus</i>	51. <i>Januasporites</i> sp.	79. <i>Verrucosisporites rotundus</i>
24. <i>Concavissimisporites</i> aff. <i>kyrtomatus</i>	52. <i>Laevigatosporites</i> aff. <i>gracilis</i>	80. <i>Verrucosisporites</i> sp.
25. <i>Concavissimisporites</i> aff. <i>punctatus</i>	53. <i>Leptolepidites macroverrucosus</i>	81. <i>Verrutriletes</i> sp.
26. <i>Concavissimisporites globosus</i>	54. <i>Leptolepidites</i> sp.	82. <i>Verrutriletes virueloides</i>
27. <i>Concavissimisporites punctatus</i>	55. <i>Leptolepidites verrucatus</i>	83. <i>Zlvisporis</i> sp.
28. <i>Crybelosporites pannuceus</i>	56. <i>Microfoveolatosporis skottsbergii</i>	

7. Discussion

7.1. Geological Age

7.1.1. lower Hollin Formation

An Albian age was determined for the samples analyzed in the Genoveva Mine and in the other six localities, based on the co-occurrence of *Cretacaeiporites* spp., *Retitricolpites operculatus* and *Callialasporites dampieri* (Table 12; Figure 16). This assemblage is found in the zones *Pentapsis valdiviae* to *Elaterosporites protensus* of Regali *et al.* (1974) and the zones *Tricolpites-Exesipollenites tumulus* to *Elaterosporites protensus/Elaterosporites verrucatus-Afropollis* of Muller *et al.* (1987). Nevertheless, this formation has a middle-late Aptian to middle Albian age (White *et al.*, 1995; Jaillard *et al.*, 1997; Vallejo *et al.*, 2002; Ordoñez *et al.*, 2006; Romero *et al.*, 2017), and that is why a middle-late Aptian age would be expected, however, the found assemblage is Albian. This suggests that the uppermost part of lower Hollin Formation can be associated to early Albian in this study zone.

Two Aptian taxa, *Callialasporites trilobatus* and *Pilosisporites* spp. were also found, which could be reworked, or their age range could be younger as reported by several authors. *C. trilobatus* has been found in the Albian (Morgan, 1978; Zobaa *et al.*, 2013) and Cenomanian (Dino & de Lima, 1991) while for the genus *Pilosisporites*, some species have also been found in the Albian (Norvick & Burger, 1975; Thusu & van der Eem, 1985; Wagstaff *et al.*, 2012; Portela *et al.*, 2014).

7.1.2. lower Napo Formation

In the four studied localities of the lower Napo Formation, a middle – late Albian age was determined by the co-occurrence of *Elaterosporites klaszii* and *Elaterosporites verrucatus* (Figure 16; Table 13). This assemblage is found in the zones *E. jardinei* to *E. protensus* of Regali *et al.* (1974) and the zones *E. jardinei* to *E. protensus*/*E. verrucatus*-*Afropollis* of Muller *et al.* (1987).

Table 13. Age of the taxa found in Napo Formation according to Regali *et al.* (1974) and Muller *et al.* (1987). The ages with asterisk (*) correspond to those used in the Figure 16.

Taxa	Age from Regali <i>et al.</i> (1974)	Age from Muller <i>et al.</i> (1987)
<i>Elaterosporites klaszii</i>	middle Albian – Cenomanian*	Albian – Cenomanian
<i>Elaterosporites verrucatus</i>	middle – late Albian*	Albian – early Cenomanian
<i>Ephedripites</i> complex	NA	middle Aptian – Cenomanian*

The calcareous nannoplankton content of sample 47748 (locality 910002; Table 6) from lower Napo Formation was frequent and showed a good to moderate preservation (Figure 17). Based on the recovery of nannofossils *Gartnerago nanum* and *Gartnerago theta*, this sample is placed between biozones UC0b – UC3a (Burnett *et al.*, 1998), which ranges from late Albian to middle Cenomanian.

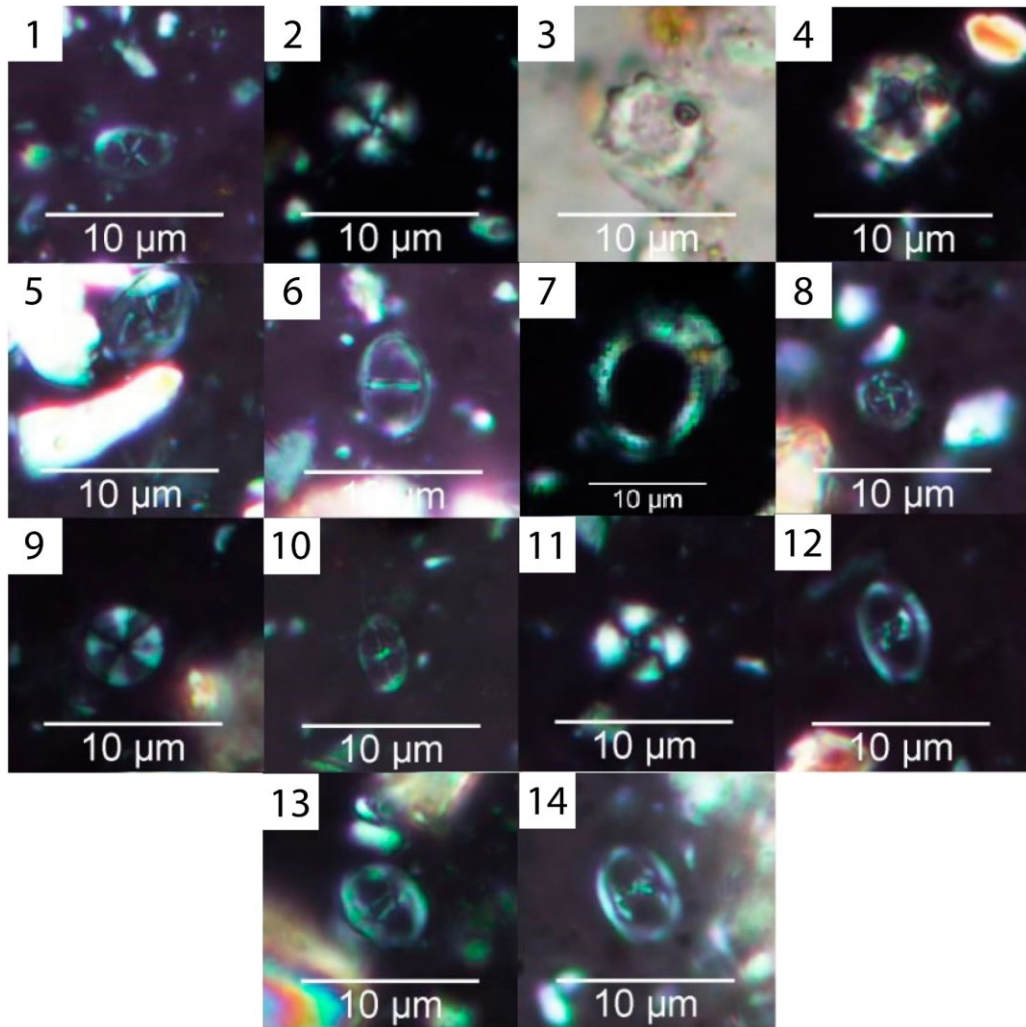


Figure 17. Calcareous nannofossils in sample 47748, lower Napo Formation. **1.** *Chiastozygus* sp.; **2.** *Cyclagelosphaera reinhardtii*; **3-4.** *Rotelapillus crenulatus*; **5.** *Gartnerago nanum*; **6.** *Gartnerago theta*; **7.** *Manivitella pemmatoidea*; **8.** *Prediscosphaera columnata*; **9.** *Radiolithus planus*; **10.** *Staurolithites halfanii*; **11.** *Watznaueria* cf. *Britannica*; **12.** *Zeugrhabdotus scutula*; **13.** *Zeugrhabdotus diplogrammus*; **14.** *Zeugrhabdotus elegans*.

7.1.3. lower Une Formation

In the four studied localities of La Popa Mine, an Aptian – early Cenomanian age was determined based upon the co-occurrence of *Afropollis* complex and *Ischyosporites variegatus* (Figure 16; Table 14). This assemblage is found in the zones *Inaperturopollenites crisopolensis* to *Psilatricolpites papilioniformis* of Regali *et al.* (1974) and the zones *I. crisopolensis*-*Afropollis* to *E. protensus*/*E. verrucatus*-*Afropollis* of Muller *et al.* (1987).

According to some authors (e.g., Renzoni, 1981; Fabre, 1985; Montoya & Reyes, 2003) this unit has been dated as Albian – Cenomanian, however, as was previously mentioned, the age found in the study zone was Aptian – early Cenomanian, which can be related to the few palynomorphs found and to the absence of taxa restricted to the Albian according to the palynological zonations of Regali *et al.* (1974) and Muller *et al.* (1987). Since this formation is not older than Albian, it would be expected for this unit to correspond to the lower Une Formation, and therefore, to have an Albian – early Cenomanian age. Nevertheless, the found Aptian age could be associated to the underlying Fomeque Formation that has an age whose range extends to the late Aptian (Royo, 1939; Hubach, 1957; Campbell, 1962; Etayo-Serna, 1964; Ulloa & Rodriguez, 1979; Ulloa *et al.*, 2000; Patarroyo, 2020).

Table 14. Age of the taxa found in Une Formation according to Regali *et al.* (1974) and Muller *et al.* (1987). The ages with asterisk (*) correspond to those used in the Figure 16.

Taxa	Age from Regali <i>et al.</i> (1974)	Age from Muller <i>et al.</i> (1987)
<i>Afropollis</i> complex	Aptian – middle Cenomanian	Aptian – early Cenomanian*
<i>Araucariacites australis</i>	pre-Aptian – post-Turonian*	NA
<i>Ischyosporites variegatus</i>	Aptian – Cenomanian*	NA

7.2. Rainfall conditions (humid versus arid)

The taxonomic composition indicates a flora dominated by humid indicators for the Albian. This evidence agrees with the previous studies made in the South American west tropics that also shows high levels of rainfall (Mejia-Velasquez *et al.*, 2012; Mejia-Velasquez *et al.*, 2018). However, it is not in accordance with the eastern South American tropics, where the well-studied Crato Formation indicates more arid climate conditions (Mohr & Rydin, 2002; Batten, 2007; Braz, 2012; Bernardes-de-Oliveira *et al.*, 2014).

Assemblages with high abundance and diversity of spores in tropical sediments of similar age have also been found in palynological studies from Colombia (Herngreen & Dueñas-Jimenez, 1990), Brazil (de Lima, 1983) and northeast Africa (Thusu *et al.*, 1988; Schrank, 1992). It is probable that the sites closer to the equatorial tropics, like the localities of this study in Colombia and Ecuador, had a higher rainfall compared to those sites closer to subtropics (Doyle *et al.*, 1982; Schrank, 1990; Brenner, 1996).

de Lima (1983) and Mejia-Velasquez *et al.* (2012) discussed that during the Lower and middle Cretaceous coastal ecosystems were probably more humid than those in the continental interior because of oceanic influences. Our two study localities were located near the coastline at the northwestern corner of South America, where it had the influence of the Pacific Ocean, therefore, higher humidity is possible compared to inland sites. A similar proposal is discussed by Mejia-Velasquez *et al.* (2018) that mention a "supercontinent effect", when the coastal areas of Gondwana were probably more humid than areas in its vast interior, because on the large continents, like Gondwana, the humidity cannot be easily carried from the coast, creating inland deserts at all latitudes (Scotese *et al.*, 1999).

There are other evidences that also supports the presence of a humid climate during the Albian in northwestern Gondwana, such as the isotopic composition of coal layers found in deposits from the Caballos Formation in Colombia that showed mean annual precipitation values slightly higher than the those occurring today in tropical latitudes (Suarez *et al.*, 2010), or global climate models that indicated a humid climate in tropical latitudes (Ufnar *et al.*, 2004; Fluteau *et al.*, 2007; Hay & Floegel, 2012; Kuethe, 2016).

On the other hand, besides of pluviosity, a fluvial system can influence the availability of water for plants in a deltaic system which would affect the amount of the found humid indicators. This is because the vegetation changes following hydrological alterations (Andersson *et al.*, 2000), which has been studied for vascular plants (Nilsson *et al.*, 1991; Toner & Keddy, 1997) and bryophytes (Englund *et al.*, 1997).

It is also important to considerate that high diversity of humid indicators could be biased since the analyses are qualitative. Therefore, it would be required an accounting of the number of palynomorphs per sample to assess the floristic composition in terms of relative diversity and relative abundance. This indicate that the results obtained in this study are preliminary, and further counting could clarify the rainfall conditions (humidity versus aridity) in the northwestern margin of Gondwana.

8. Conclusions

- The lower Hollin Formation at the Genoveva Mine was dated as Albian, palynological zones *Pentapsis valdiviae* to *Elaterosporites protensus* of Regali *et al.* (1974) and the zones *Tricolpites-Exesipollenites tumulus* to *Elaterosporites protensus/Elaterosporites verrucatus-Afropollis* of Muller *et al.* (1987). Specifically, an early Albian age was inferred for the uppermost part of lower Hollin Formation in this locality.
- The lower Napo Formation was dated as middle to late Albian, zones *Elateropollenites jardinei* to *Elaterosporites protensus* of Regali *et al.* (1974) and the zones *Elateropollenites jardinei* to *Elaterosporites protensus/Elaterosporites verrucatus-Afropollis* of Muller *et al.* (1987). Therefore, a late Albian age was inferred for this unit in the study zone. Based on the calcareous nannoplankton, the sample 47748 is late Albian to middle Cenomanian in age, biozones UC0b to UC3a of Burnett *et al.* (1998).
- The lower Une formation outcropping in La Popa Mine was dated as Aptian – early Cenomanian, zones *Inaperturopollenites crisopolensis* to *Psilatricolpites papilioniformis* of Regali *et al.* (1974) and the zones *Inaperturopollenites crisopolensis-Afropollis* to *Elaterosporites protensus/Elaterosporites verrucatus-Afropollis* of Muller *et al.* (1987). In particular, an Albian – early Cenomanian age was inferred in this locality and the found Aptian age could correspond to the underlying Fomeque Formation.
- There is a dominance in spore diversity over the other palynomorph groups, suggesting a humid climate in the northwestern margin of Gondwana. However, further counting of palynomorphs per sample could show more results in terms of diversity and abundance.
- Both pluviosity and the fluvial system can affect the amount of the found humid indicators in this study.
- Angiosperms as the second most diverse group could suggest a rapid angiosperm radiation in tropical latitudes.

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Supplementary material

Supplementary material 1. List of taxa analyzed in this study with their respective coordinates in England Finder. 1 = if taxon is present.

Taxa Name	Pollen Code	England	Samples (STRI-ID)	Geological formation		
		Finder coordinate		Hollin	Napo	Une
<i>Aequitriradites</i> cf. <i>verrucosus</i>	Spore	U44	47731	1		
aff. <i>Ephedripites</i> sp. A (Azema & Boltenhagen, 1974)	Gnetales	V12-4	44661	1		
aff. <i>Staplinisporites</i> sp.	Spore	C9-2	47733	1		
<i>Afropollis</i> <i>jardinus</i>	Angiosperm	T8-2; T19-4; B7-3	47728; 46427; 44661	1		1
<i>Apiculatasporites</i> sp.	Spore	V40-4	44663	1		
<i>Apiculatisporites</i> aff. <i>levis</i>	Spore	F37-3	44663	1		
<i>Appendicisporites</i> <i>erdmanii</i>	Spore	Q28-1	44889	1		
<i>Araucariacites</i> <i>australis</i>	Conifers_other gymnosperms	G2-1; M30-3; E18-1 P2-3 E4	44663; 46427; 44661	1		1
<i>Arecipites</i> aff. <i>perfectus</i>	Angiosperm	F17-4	47723	1		
<i>Baculamonocolpites</i> sp.	Angiosperm	D8-3	47732	1		
<i>Baculatisporites</i> sp.	Spore	D44; U6-4	44661; 47732	1		
<i>Balmeisporites</i> sp.	Spore	M20-2	46873	1		
<i>Brenneripollis</i> sp.	Angiosperm	V9-1	44662	1		
<i>Callialasporites</i> <i>dampieri</i>	Conifers_other gymnosperms	J21	44663	1		1
<i>Callialasporites infirmus</i>	Conifers_other gymnosperms	K40-4; W11- 1	47733; 44889	1		
<i>Callialasporites</i> sp.	Conifers_other gymnosperms	R50-3	47734	1		
<i>Callialasporites</i> <i>trilobatus</i>	Conifers_other gymnosperms	J10	44663	1		
<i>Camazonosporites</i> <i>ambigens</i>	Spore	W16-1	44892	1	1	
<i>Camazonosporites</i> sp.	Spore	H8-2; F29	47735; 47720	1		
<i>Camazonosporites</i> <i>vermiculaesporites</i>	Spore	O44-1	44662	1		
<i>Ceratosporites equalis</i>	Spore	R17-1	44883	1		
<i>Chomotriletes minor</i>	Spore	O6-4; H18-3 H47	44662; 44663	1		1
<i>Cicatricosisporites</i> aff. <i>venustus</i>	Spore	F4	47735	1		
<i>Cicatricosisporites</i> <i>avnimelechi</i>	Spore	O10-2	44661	1		

Taxa Name	Pollen Code	England FINDER coordinate	Samples (STRI-ID)	Hollin	Napo	Une
<i>Cicatricosisporites hallei</i>	Spore	V30	44661	1		
<i>Cicatricosisporites hughesii</i>	Spore	V14-1	44661	1		
<i>Cicatricosisporites kedvesii</i>	Spore	E22-1; P15-1	44662; 44661	1		
<i>Cicatricosisporites sinuosus</i>	Spore	F4-2	47727	1		
<i>Cicatricosisporites</i> sp.	Spore	L10; G3-2; K40; O33-2	44661; 47726; 47724; 47734	1		1
<i>Classopollis brasiliensis</i>	Conifers_other gymnosperms	S9	44883	1		
<i>Classopollis classoides</i>	Conifers_other gymnosperms	U3-4; T5 T39; U41-1	44884; 47726; 44882	1		
<i>Classopollis meyeriana</i>	Conifers_other gymnosperms	M7-2; N14-1	47730; 47726	1		
<i>Classopollis</i> sp.	Conifers_other gymnosperms	K41; T34	44662; 44884	1		
<i>Clavamonocolpites</i> sp.	Angiosperm	K35	44661	1		1
<i>Clavatipollenites hughesii</i>	Angiosperm	F26-1	47725	1		
<i>Clavatisporites</i> aff. <i>clarus</i>	Spore	P45	47724	1		
<i>Clavatisporites clarus</i>	Spore	T16; K7-1	44892; 47725	1	1	
<i>Clavatisporites</i> sp.	Spore	Q18-3; G7-2 P2; N45	44892; 47721; 47733	1	1	
<i>Collarisporites fuscus</i>	Spore	K33-3	44884	1		
<i>Concavissimisporites</i> aff. <i>kyrtomatus</i>	Spore	H49	47735	1		
<i>Concavissimisporites</i> aff. <i>punctatus</i>	Spore	B30	44892		1	
<i>Concavissimisporites globosus</i>	Spore	H32	44663	1		
<i>Concavissimisporites punctatus</i>	Spore	E48-4	47725	1		
<i>Cornetipollis perforatus</i>	Angiosperm	P37-1	47725	1		
<i>Coronifera?</i> sp.	Marine	J43-3	47748		1	
<i>Cretacaeiporites</i> sp.	Angiosperm	T14	47723	1		
<i>Crybelosporites pannuceus</i>	Spore	J15-4; U46-2; T7-4	44661; 44884; 44890	1		
<i>Crybelosporites</i> sp.	Spore	P24	47721	1		
<i>Cycadopites</i> cf. <i>glottus</i>	Conifers_other gymnosperms	J18	46874	1		
<i>Cyclusphaera</i> aff. <i>psilata</i>	Conifers_other gymnosperms	P39-2	47735-1	1		
<i>Dejaxpollenites</i> sp.	Angiosperm	C46-1	47733	1		
<i>Deltoidospora minor</i>	Spore	Y16-4	47728	1		
<i>Densoisporites perinatus</i>	Spore	F40-2	44889	1		
<i>Dictyophyllidites excellensus</i>	Spore	W35	44661	1		

Taxa Name	Pollen Code	England Finder coordinate	Samples (STRI-ID)	Hollin	Napo	Une
<i>Distaltriangulispores aff. irregularis</i>	Spore	O50-4	47731	1		
<i>Echimonocolpites aff. tersus</i>	Angiosperm	R32	47730	1		
<i>Echimonocolpites sp.</i>	Angiosperm	U22	47725	1		
<i>Echinatisporis aff. circularis</i>	Spore	N23-1	44889	1		
<i>Echinatisporis sp.</i>	Spore	Q29	47720	1		
<i>Echitriletes aff. minispinosus</i>	Spore	O2	44661	1		
<i>Echitriletes sp.</i>	Spore	M18-2; V45	44661; 44886	1	1	
<i>Elaterosporites klaszii</i>	Gnetales	X16	44892		1	
<i>Elaterosporites sp.</i>	Gnetales	O37-3	47734	1		
<i>Elaterosporites verrucatus</i>	Gnetales	J42-4	44892		1	
<i>Ephedripites aff. regularis</i>	Gnetales	K45-3	47731	1		
<i>Ephedripites ambonoides</i>	Gnetales	Q19	47748		1	
<i>Ephedripites barghoornii</i>	Gnetales	N45	44889	1		
<i>Ephedripites cf. procerus</i>	Gnetales	E17-4	46872-1	1		
<i>Ephedripites multicostatus</i>	Gnetales	X9-1	44891	1		
<i>Ephedripites sp.</i>	Gnetales	W7-1; F36-3; P43; M5-4	44661; 44663; 46872; 47724	1		
<i>Equisetosporites aff. minuticosatus</i>	Gnetales	W17-4	47729	1		
<i>Equisetosporites aff. subcircularis</i>	Gnetales	X43-3	46872	1		
<i>Equisetosporites ambiguus</i>	Gnetales	P30-4	47733	1		
<i>Equisetosporites dudarensis</i>	Gnetales	K6-3; E11-3	44661; 44886	1	1	
<i>Equisetosporites fragilis</i>	Gnetales	N38	47734	1		
<i>Equisetosporites laticostatus</i>	Gnetales	F36-4	47733	1		
<i>Foveomonocolpites cf. "brevicolpatus"</i>	Angiosperm	W42	44661	1		
<i>Foveotricolpites "subgigantoreticulatus"</i>	Angiosperm	N8	46874	1		
<i>Foveotricolpites sp.</i>	Angiosperm	R11-1	46873	1		1
<i>Foveotriletes aff. margaritae</i>	Spore	K16	44662	1		
<i>Foveotriletes aff. ornatus</i>	Spore	U37-4	47726	1		
<i>Foveotriletes sp.</i>	Spore	Q12-3; U33-2; G22-2	44884; 44889; 44887	1	1	
<i>Gabonispores vigourouxii</i>	Spore	D41	44884	1		
<i>Gemmamonocolpites sp.</i>	Angiosperm	H22-3	46872-1	1		
<i>Gemmatriletes sp.</i>	Spore	C5-3	44889	1		

Taxa Name	Pollen Code	England FINDER coordinate	Samples (STRI-ID)	Hollin	Napo	Une
<i>Gleicheniidites</i> aff. <i>apilobatus</i>	Spore	N3-3	44889	1		
<i>Gleicheniidites</i> <i>senonicus</i>	Spore	M34-1 F34-2 N46-3; H12-2	44662; 47724	1		
<i>Gleicheniidites</i> sp.	Spore	K37-1; M2	44662; 44891	1		
<i>Gnetaceaepollenites</i> aff. <i>concisus</i>	Gnetales	M4	44884	1		
<i>Gnetaceaepollenites</i> aff. <i>undulatus</i>	Gnetales	S5	47730	1		
<i>Gnetaceaepollenites</i> <i>barghoornii</i>	Gnetales	L47-4	44883	1		
<i>Gnetaceaepollenites</i> <i>jansonii</i>	Gnetales	V46-2; J11	47735-1; 47735	1		
<i>Gnetaceaepollenites</i> <i>retangularis</i>	Gnetales	P8-4	44889	1		
<i>Granulatisporites</i> sp.	Spore	S2	44884	1		
<i>Hamulatisporis</i> cf. <i>caperatus</i>	Spore	U30-4	44883	1		
<i>Hamulatisporis insignis</i>	Spore	P17; U20-2; S15	44661; 46427; 46872-1	1		1
<i>Hystrichosphaeridium</i> aff. <i>tubiferum</i>	Marine	F4-4	44892		1	
<i>Inaperturopollenites</i> sp.	Conifers_other gymnosperms	O2-2	44889	1		
Indeterminate acritarch	Marine	R30	44892		1	
<i>Ischyosporites</i> aff. <i>badagriensis</i>	Spore	R13	47727	1		
<i>Ischyosporites</i> <i>variegatus</i>	Spore	O41; K49-2; D31-3	46426; 46427; 47725	1		1
<i>Januasporites</i> sp.	Spore	K25-4	47733	1		
<i>Ladakhipollenites?</i> "pseudosyncolpatus"	Angiosperm	U7-2	44886		1	
<i>Laevigatosporites</i> aff. <i>gracilis</i>	Spore	E48-1	46427			1
<i>Leptolepidites</i> <i>macroverrucosus</i>	Spore	E19	44884	1		
<i>Leptolepidites</i> sp.	Spore	F21-3	47721	1		
<i>Leptolepidites verrucatus</i>	Spore	T31	47720	1		
<i>Liliacidites</i> cf. <i>dividuus</i>	Angiosperm	N14-3	47730	1		
<i>Liliacidites</i> sp.	Angiosperm	G15	47731	1		
<i>Microfoveolatosporis</i> <i>skottsbergii</i>	Spore	U12-4	47725	1		
<i>Microfoveotriporites</i> aff. <i>cretaceous</i>	Angiosperm	E50	47746		1	
<i>Monoporopollenites</i> sp.	Angiosperm	J29-1	44662	1	1	
<i>Muerrigerisporis</i> sp.	Spore	S15	47725	1		
<i>Obtusisporis</i> cf. <i>undulus</i>	Spore	J37-3	44661	1		
<i>Oligosphaeridium</i> aff. <i>totum</i>	Marine	R30	44892		1	

Taxa Name	Pollen Code	England FINDER coordinate	Samples (STRI-ID)	Hollin	Napo	Une
<i>Osmundacidites</i> sp.	Spore	S33	44883	1		
<i>Osmundacidites wellmanii</i>	Spore	U5-1; J9-3	46427; 47722	1		1
<i>Pennipollis</i> cf. "echinatus"	Angiosperm	R24-4	47720	1		
<i>Pennipollis peroreticulatus</i>	Angiosperm	D3-4	47728	1		
<i>Perfotricolpites</i> sp.	Angiosperm	F23-1	47735-1	1		
<i>Periretisyncolpites</i> sp.	Angiosperm	J8-3	47728	1		
<i>Perotriletes</i> sp.	Spore	G21	46426			1
<i>Pilosporites parvispinosus</i>	Spore	H18-1	44889	1		
<i>Podocarpidites?</i> sp.	Conifers_other gymnosperms	E13-2 P40-3; P41-3	46487; 47734	1		1
<i>Polyadopollenites</i> aff. <i>microreticulatus</i>	Angiosperm	N22-1	47725	1		
<i>Polyadopollenites</i> cf. <i>mariae</i>	Angiosperm	K28-1	46487			1
<i>Polypodiaceosporites</i> cf. <i>reticulatus</i>	Spore	Q22-1	46874	1		
<i>Polypodiisporites</i> sp.	Spore	N43	44663	1		
<i>Proxapertites</i> cf. <i>verrucatus</i>	Angiosperm	H13-3	47734	1		
<i>Psilabrevitricolporites</i> sp.	Angiosperm	M8-1	44886		1	
<i>Psilamonocolpites</i> sp.	Angiosperm	U7; V4-2; G8-3	44892; 47728; 47733	1	1	1
<i>Psilatricolpites</i> sp.	Angiosperm	NA	NA			1
<i>Psilatricolporites</i> sp.	Angiosperm	G15-4 P22	46487			1
<i>Psilatriteles</i> sp.	Spore	NA	NA			1
<i>Pterospermella aureolata</i>	Marine	Y11-3	44892		1	
<i>Retiacolpites</i> aff. <i>columellatus</i>	Angiosperm	K36-2	46426			1
<i>Retibrevitricolpites</i> sp.	Angiosperm	P9; L23	44886; 47720	1	1	
<i>Retimonocolpites</i> sp.	Angiosperm	S9-4 V40-1; T7 T6-4; L23-1	44662; 46873; 47748	1	1	
<i>Retimonoporites</i> cf. <i>operculatus</i>	Angiosperm	O6-2	47733	1		
<i>Retimonoporites</i> cf. <i>orteguensis</i>	Angiosperm	H43	47731	1		
<i>Retimonoporites</i> sp.	Angiosperm	Q12-3 W29-3	44662	1		
<i>Retipollenites</i> aff. <i>confusus</i>	Angiosperm	H19-4	46875	1		
<i>Retipollenites</i> sp.	Angiosperm	V5-4; K6	44662; 47748	1	1	
<i>Retistephanocolpites</i> sp.	Angiosperm	J34-4	47723	1		
<i>Retitrescolpites baculatus</i>	Angiosperm	S45	47732	1		
<i>Retitrescolpites</i> sp.	Angiosperm	T32-2	44892		1	

Taxa Name	Pollen Code	England Finder coordinate	Samples (STRI-ID)	Hollin	Napo	Une
<i>Retitricolpites</i> “reticuloghazalatensis”	Angiosperm	U39-2	46872	1		
<i>Retitricolpites operculatus</i>	Angiosperm	P17	47720	1		
<i>Retitricolpites</i> sp.	Angiosperm	U47-3; R20-1 W5-2	46427; 46872-1	1		1
<i>Retitriletes</i> aff. <i>eminulus</i>	Spore	K11	47734	1		
<i>Retitriletes</i> aff. <i>tenuis</i>	Spore	G6	47730	1		
<i>Retitriletes douglasii</i>	Spore	P10-3	47727	1		
<i>Retitriletes</i> sp.	Spore	R23; Q40; D10-1; V26-2	47720; 44662; 44889; 47735-1	1		
<i>Reyrea</i> aff. <i>polymorphus</i>	Angiosperm	K17-2 M20	47731	1		
<i>Rousea</i> aff. <i>miculipollis</i>	Angiosperm	H11	47734	1		
<i>Ruffordiaspora</i> sp.	Spore	P39	44663	1		
<i>Rugulatisporites</i> sp.	Spore	R4-2	44884	1		
<i>Scabraperiporites</i> sp.	Angiosperm	F48	47720	1		
<i>Scabratricolpites</i> sp.	Angiosperm	M33; F23	46875; 47726	1		
<i>Scabratriletes</i> sp.	Spore	F48	46875	1		
<i>Senectotetradites</i> aff. <i>varireticulatus</i>	Angiosperm	H11-1	47733	1		
<i>Sergipea</i> aff. <i>variverrucata</i>	Gnetales	Q6-2	47748		1	
<i>Sestrosporites pseudoalveolatus</i>	Spore	L41-1	44883	1		
<i>Singhia multicostata</i>	Gnetales	F40	47727	1		
<i>Steevesipollenites cupuliformis</i>	Gnetales	W12-4	47731	1		
<i>Steevesipollenites</i> cf. <i>multilineatus</i>	Gnetales	S33-4	47720	1		
<i>Steevesipollenites pygmeus</i>	Gnetales	R4	44889	1		
<i>Stellatopollis</i> aff. <i>largissimus</i>	Angiosperm	H15-4	44889	1		
<i>Stellatopollis barghoornii</i>	Angiosperm	J36-4; P7; R41-3	47728; 44882; 47735-1	1		
<i>Stellatopollis densiornatus</i>	Angiosperm	V7-3 Y16-2	46872-1	1		
<i>Stellatopollis dubius</i>	Angiosperm	Q30-1	44889	1		
<i>Stellatopollis</i> sp.	Angiosperm	U14-3	44889	1		
<i>Stoverisporites</i> aff. <i>lunaris</i>	Spore	K15-4	47720	1		
<i>Striatopollis</i> sp.	Angiosperm	U3-2	44889	1		
<i>Striatriletes</i> sp.	Spore	R24-2	47723	1		
<i>Taxacites</i> aff. <i>sahariensis</i>	Conifers_other gymnosperms	D11	47733	1		
<i>Tricolpites</i> cf. <i>synstriatus</i>	Angiosperm	P39-3	47731	1		
<i>Tricolpites</i> sp.	Angiosperm	S37-2	44661	1		

Taxa Name	Pollen Code	England Finder coordinate	Samples (STRI-ID)	Hollin	Napo	Une
<i>Tuberositriletes</i> sp.	Spore	H12	46428			1
<i>Tucanopollis</i> aff. <i>crisopolensis</i>	Angiosperm	T8	47733	1		
<i>Verrucatotriletes</i> aff. <i>tortus</i>	Spore	N17-1	47720	1		
<i>Verrucatotriletes</i> sp.	Spore	J44-3; E2-4	46427; 44889	1		1
<i>Verrucosisporites</i> <i>rotundus</i>	Spore	U13-3	46872-1	1		
<i>Verrucosisporites</i> sp.	Spore	X28-1; V50-3	44663; 47735	1		
<i>Verruperiporites</i> sp.	Angiosperm	Q3-3	47729	1		
<i>Verrutriletes</i> sp.	Spore	R15; U12; R20	46426; 46427; 47726	1		1
<i>Verrutriletes virueloides</i>	Spore	U40-1	44889	1		
<i>Zlivisporis</i> sp.	Spore	O33-4; R30-2	44663; 44661	1		