
Unusual concentration of Early Albian arthropod-bearing amber in the Basque-Cantabrian Basin (El Soplao, Cantabria, Northern Spain): Palaeoenvironmental and palaeobiological implications

M. NAJARRO^{|1|} E. PEÑALVER^{|1|} I. ROSALES^{|1|} R. PÉREZ-DE LA FUENTE^{|2|} V. DAVIERO-GOMEZ^{|3|} B. GOMEZ^{|3|} and X. DELCLÒS^{|2|}

|1| Instituto Geológico y Minero de España

Ríos Rosas 23, 28003 Madrid, Spain. Najarro E-mail: m.najarro@igme.es
Peñalver E-mail: e.penalver@igme.es Rosales E-mail: i.rosales@igme.es

|2| Departament d'Estratigrafia, Paleontologia i Geociències Marines, Universitat de Barcelona

Campus de Pedralbes, 08071 Barcelona, Spain. Pérez-de la Fuente E-mail: perezdelafuente@ub.edu
Delclòs E-mail: xdelclos@ub.edu

|3| UMR 5125 (PEPS) CNRS, Paléobotanique, Université Lyon-1 (Claude-Bernard)

Campus de la Doua, F-69622 Villeurbanne, France. Daviero-Gomez E-mail: daviero@univ-lyon1.fr
Gomez E-mail: bernard.gomez@univ-lyon1.fr

ABSTRACT

The El Soplao site is a recently-discovered Early Albian locality of the Basque-Cantabrian Basin (northern Spain) that has yielded a number of amber pieces with abundant bioinclusions. The amber-bearing deposit occurs in a non-marine to transitional marine siliciclastic unit (Las Peñas Formation) that is interleaved within a regressive-transgressive, carbonate-dominated Lower Aptian-Upper Albian marine sequence. The Las Peñas Formation corresponds to the regressive stage of this sequence and in its turn it splits into two smaller regressive-transgressive cycles. The coal and amber-bearing deposits occur in deltaic-estuarine environments developed during the maximum regressive episodes of these smaller regressive-transgressive cycles. The El Soplao amber shows Fourier Transform Infrared Spectroscopy spectra similar to other Spanish Cretaceous ambers and it is characterized by the profusion of sub-aerial, stalactite-like flows. Well-preserved plant cuticles assigned to the conifer genera *Frenelopsis* and *Mirovia* are abundant in the beds associated with amber. Leaves of the ginkgoalean genera *Nehvizdya* and *Pseudotorellia* also occur occasionally. Bioinclusions mainly consist of fossil insects of the orders Blattaria, Hemiptera, Thysanoptera, Raphidioptera, Neuroptera, Coleoptera, Hymenoptera and Diptera, although some spiders and spider webs have been observed as well. Some insects belong to groups scarce in the fossil record, such as a new morphotype of the wasp *Archaeromma* (of the family Mymarommatidae) and the biting midge *Lebanoculicoides* (of the monogeneric subfamily Lebanoculicoidinae). This new amber locality constitutes a very significant finding that will contribute to improving the knowledge and comprehension of the Albian non-marine paleoarthropod fauna.

KEYWORDS | Arthropod bioinclusions. Fossil resin. Plant cuticles. Lower Albian. Spain.

INTRODUCTION

Oldest ambers with micro-bioinclusions are known from the Triassic of Italy (Schmidt et al., 2006), but it is not until the Barremian-Aptian of Lebanon that macro-bioinclusions occur more profusely (Azar, 2000; Poinar and Milki, 2001). During the Early Cretaceous, amber-bearing deposits become especially common in the geological record. This was promoted possibly by the rise and spread of conifers, such as the Araucariaceae and Cheirolepidiaceae, and by a palaeoclimate warmer than today due to higher $p\text{CO}_2$ levels and significantly different oceanic circulation and geography (Crowley and North, 1991; Huber et al., 1995; Haywood et al., 2004). Coinciding with the initiation of the moist megathermal zone in the Northern Hemisphere, amber deposits developed between 29°N–50°N during the earliest Cretaceous and extended to 27°N to near 70°N during the Mid Cretaceous (Morley, 2000). During these periods the Iberian Peninsula was situated at low latitude, along the boundary between wet and warm tropical-“paratropical” climates where coal and other organic-rich rocks were deposited.

Early Cretaceous ambers bearing fossil inclusions are scarce, and such localities are of great scientific interest (Fig. 1). In Cantabria (northern Spain), amber is relatively widespread in the Cretaceous deposits, and has been found previously in minor amounts at least at 23 localities. However, in the past none of these localities had provided amber with arthropod inclusions. An intensive geological survey in the Lower Cretaceous succession of northwest Cantabria recently resulted in the discovery of a new amber locality near Rábago village, within the El Soplao territory (Fig. 1B). This site shows a remarkable accumulation of amber with abundant biological inclusions. The El Soplao amber site occurs within a Lower Albian siliciclastic unit (Las Peñas Formation [Fm.]; García-Mondéjar and Pujalte, 1982). Preliminary data for this new amber accumulation indicate that this is probably the largest site of amber with arthropod bioinclusions that has ever been found in Spain so far.

This paper deals with i) documenting this new finding of arthropod bearing amber as an unusual concentration, as well as describing its related deposits in terms of major stratigraphic and sedimentological characteristics, description of the associated plant cuticles and bioinclusions, and preliminary study of the amber geochemistry; ii) discussing geological and depositional features that may help in understanding the palaeoenvironmental implications of these deposits and their palaeogeographic context;

and iii) providing an appropriate introduction for future, more specific studies, on this exceptional new amber site.

Emphasis is given in providing a solid sedimentological, palaeoenvironmental and palaeogeographic framework of this palaeontologically significant deposit for its exceptional preservation and age.

METHODOLOGY AND TECHNIQUES

Sedimentological and palaeoenvironmental interpretations are based on field observations. Four laterally correlative stratigraphic sections (Puente Arrudo, Rábago, La Florida and Plaza del Monte), belonging to the Las Peñas Fm., have been logged at a meter-centimetre scale. From these data a W-E cross-section has been established to display the principal depositional and palaeoenvironmental features and the stratigraphic distribution of the amber and coal-bearing unit. Whenever possible, rock sampling and measurement of palaeocurrent orientations of selected structures were carried out to help in sedimentological interpretations.

Pieces of amber were acquired by surface collection during field work in the area. To characterize the El Soplao amber, three Fourier Transform Infrared Spectroscopy (FTIR) spectra of three separate amber samples and one sample of recent kauri resin -*Agathis australis* (D. Don) Lindl. in Loud., 1829- were obtained using an infrared Fourier Bomem DA3 spectrometer, in the Molecular Spectrometry Unit of the University of Barcelona (SCT-UB).

Palaeobotanical samples from plant cuticle-rich claystones were obtained by macerating the clayey sediment in hydrogen peroxide and air-drying the organic residues. Resulting fossil plant fragments were sorted using both the naked eye and the stereomicroscope.

The amber was kept wet during screening in order to improve visibility and to detect arthropod bioinclusions. Screening was done under a stereoscope, using transmitted and obliquely reflected light. The amber pieces were cut around the detected arthropods and then polished to permit optimal study. Drawings of some specimens were made with the aid of an image drawing tube, an Olympus V-DA mounted on an Olympus BX51 stereoscopic microscope. Photomicrographs were made with a digital camera mounted on the same microscope. The specimens are housed provisionally in the “Museo Geominero of the Instituto Geológico y Minero de España” (IGME), in Madrid, Spain.

PALEOGEOGRAPHICAL DISTRIBUTION OF EARLY-MID CRETACEOUS AMBER

Early-Mid Cretaceous (Aptian to Cenomanian) amber occurrences have great scientific interest owing to their scarcity (Fig. 1). In fact, macrobioinclusion-bearing ambers of this age are basically restricted to four Eurasian areas: Northern Siberia (Taimyr Peninsula), southeastern Asia (Myanmar),

western Middle-East (Lebanon and Jordan), and southwestern Europe (Spain and France). A review of amber localities in the literature was compiled by Martínez-Delclòs et al. (2004). The four areas were located within the warm temperate and tropical-paratropical palaeoclimatic regions (Fig. 1) *sensu* Scotese (2000), also referred to as tropical and south-subtropical Cretaceous climate belts by Spicer et al. (1994).

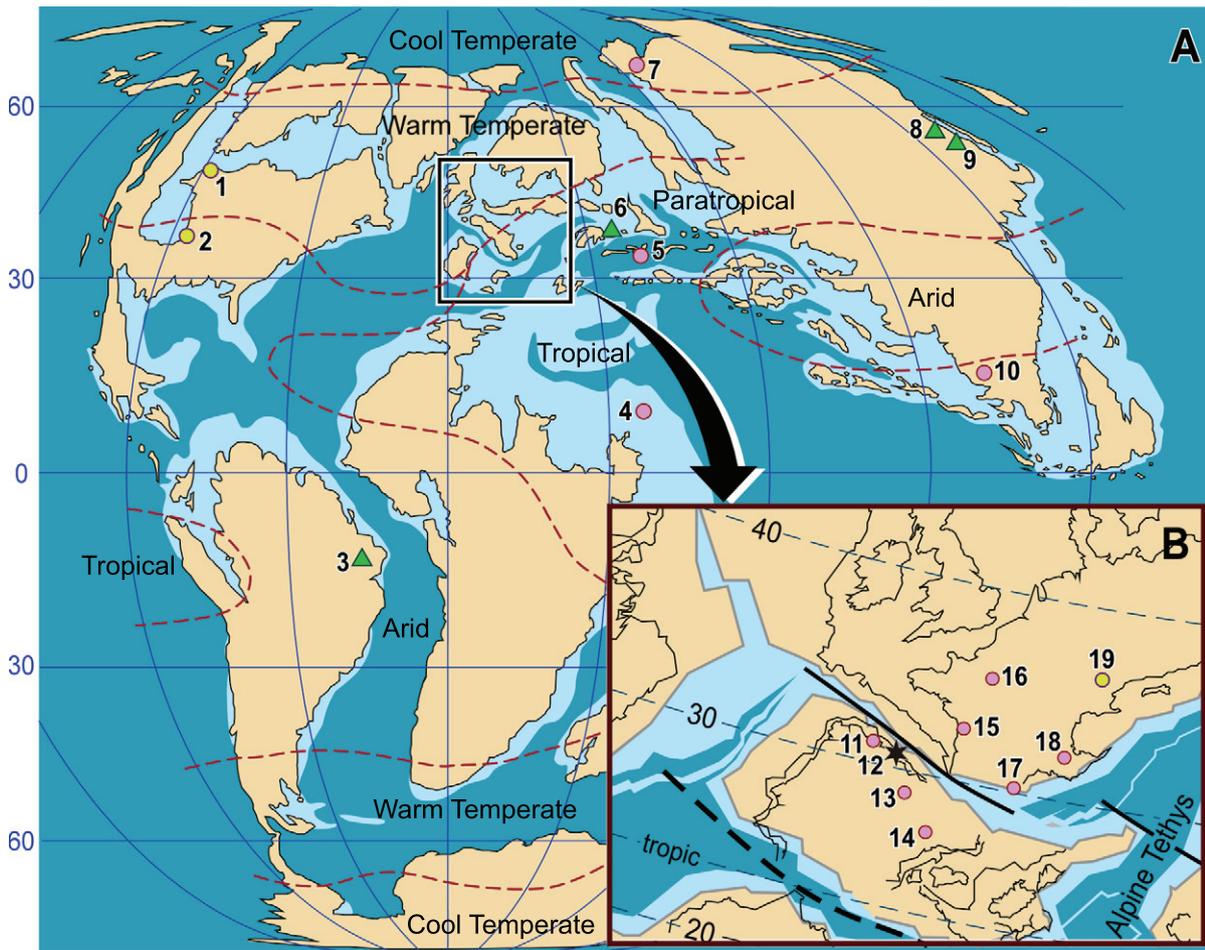


FIGURE 1 | A) Major Early-Mid Cretaceous (Aptian to Cenomanian) amber occurrences (Redrawn from Blakey, 2008). Amber localities with bioinclusions are symbolized by circles, otherwise green triangles are used. Moreover, yellow circles represent ambers that have only provided microbioinclusions (bacteria, protists, algae and/or fungi). Pink circles account for macrobioinclusion-bearing ambers (essentially arthropods), with the exception of El Soplao amber, which is designated out with a black star. Broken purple lines delimit palaeoclimatic regions *sensu* Scotese (2000). (1) Ruby Creek (Alberta, Canada; Medioli et al., 1990). (2) Ellsworth (Kansas, USA; Waggoner, 1996). (3) Nova Olinda-Santana (Ceará, Brazil; Martill et al., 2005). (4) Middle-East. Wadi Zerka (Amman, Jordan; Bandel et al., 1997; Kaddumi, 2005). Bcharreh, Hammana, and Jezzine, among others (Lebanon; Azar, 2000; Veltz, 2008). Mt. Hermon (North District, Israel; Greenblatt et al., 1999). (5) Yukhary Agdzhakend (Goranboy, Azerbaijan; Ratnitsyn and Quicke, 2002). Russia (Zherikhin and Eskov, 1999; Ratnitsyn and Quicke, 2002). (6) Stary Oskol (Belgorod). (7) Taimyr Peninsula (Northern Siberia). Baikura-Neru Bay in Lake Taimyr (Central Taimyr). Nizhnyaya Agapa River (West Taimyr). Begichev Fm. in the Khatanga River (Eastern Taimyr). (8) Khetana River in South of Okhotsk (Khabarovsk Krai). (9) Suyfun Coal Basin (Primorye). (10) Hukawng Valley (Kachin, Myanmar; Cruickshank and Ko, 2003). B) Amplified area squared at subfigure A, corresponding to SW Europe. Spain (Arbizu et al., 1999; Alonso et al., 2000; Peñalver et al., 2007b; Delclòs et al., 2007). (11) El Caleyu and Pola de Siero (Asturias). (12) El Soplao Territory, near Rábago village (Cantabria, in this paper). (13) Moraza and Peñacerrada-Montoria (Burgos and Álava respectively). (14) San Just (Teruel). France (Nel et al., 2004; Perrichot, 2004, 2005; Néraudeau et al., 2005; Perrichot et al., 2007; Néraudeau et al., 2008; Girard, 2008). (15) Archingeay-Les Nouillers, La Buzinie, Cadeuil, Fouras, l'Île d'Aix, and Les Renardières (Les Charentes). (16) Ecommoy and Durtal (Sarthe and Maine-et-Loire respectively). (17) Fourtout (L'Aude). (18) Salignac and Sisteron (Alpes-de-Haute-Provence). (19) Schliersee (Bavaria, Germany; Schmidt et al., 2001).

In Spain, aside from the frequent occurrence of amber in Aptian to Cenomanian deposits, only a few localities show sufficient quantity to be identified as accumulations (Fig. 1B). In the past, only two of these deposits had yielded important amounts of bioinclusions in terms of quantity and quality, specifically the Álava deposits of Peñacerrada and Montoria (Alonso et al., 2000; Delclòs et al., 2007) and the San Just outcrop in Teruel (Delclòs et al., 2007; Peñalver et al., 2007b). In Asturias, although less significant, amber with bioinclusions has been described in El Caleyú and Pola de Siero (Arbizu et al., 1999) (Fig. 1). The identification of the new amber deposit of the El Soplao in Cantabria (Figs. 1 and 2) enlarges the still patchy record of these palaeontological deposits of exceptional preservation in Spain.

GEOLOGICAL AND PALAEOGEOGRAPHIC SETTING

The recently discovered amber outcrop is located in the El Soplao territory in northwestern Cantabria (Fig. 2).

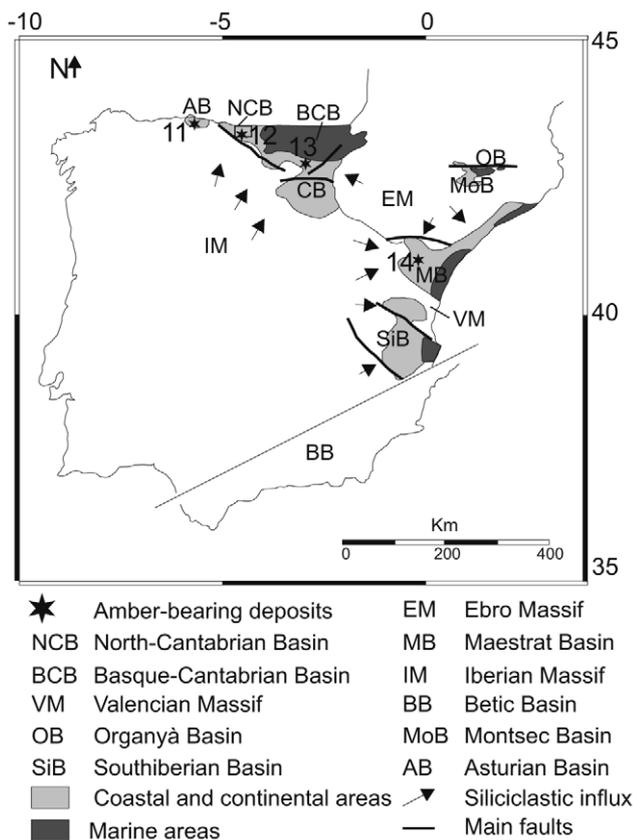


FIGURE 2 | Map of the Iberian Peninsula showing the location of the Lower Albian basins and the distribution of the Lower Cretaceous amber-bearing deposits (same nomenclature as in Figure 1). (11) El Caleyú and Pola de Siero deposits. (12) The El Soplao deposit. (13) Peñacerrada-Montoria deposits. (14) San Just deposit. (Modified from Salas et al., 2001).

This area, located immediately to the north of the Cabuérniga Ridge, constituted the northwestern margin of the Basque-Cantabrian Basin during the Cretaceous (Fig. 3). The evolution and current structure of the Basque-Cantabrian Basin are related to the kinematics between the European and Iberian plates (Malod and Mauffret, 1990; Olivet, 1996). The inception of the basin occurred during a Permo-Triassic rifting event. A second extensional phase was related to the opening of the Bay of Biscay during the Late Jurassic-Early Cretaceous (e.g., Rat, 1988; García-Mondéjar et al., 1996). Renewed extension and perhaps strike-slip faulting along a NW-SE trend occurred during the Aptian-Albian (e.g., García-Mondéjar et al., 1996; Martín-Chivelet et al., 2002; Soto et al., 2007). These tectonic events resulted in the development of several extensional sub-basins bounded by synsedimentary faults, in which great thicknesses of sediments accumulated. These sedimentary sub-basins underwent widespread contraction during the Pyrenean Orogeny in Late Eocene-Oligocene times (Hines, 1985; Fernández Viejo and Gallastegui, 2005). Consequently, the present structure of the study area is the result of the inversion of the previous Mesozoic extensional and strike-slip structures.

The studied succession was deposited in the North Cantabrian sub-basin (NCB) (Fig. 3A), which subsided moderately for most of Cretaceous time (Martín-Chivelet et al., 2002; Wilmsen, 2005). The Cabuérniga Ridge (Fig. 3) is an E-W trending fault zone, which bounds this sub-basin to the south. This palaeo-high represents a previous Variscan structure that was reactivated through extensional faulting during the Mesozoic (Rat, 1988; García-Espina, 1997).

Structurally, the studied succession was deposited during the Cretaceous on an eastward tilted block (Fig. 3B). The tilted block forms the footwall of the N-S Bustriguardo Fault (BF, Figs. 3A and 3C) that bounds to the west the main Cretaceous depocenter (Figs. 3A and 3B). Recent geological mapping has shown that the BF branches at a corner point with the E-W trending North Cabuérniga Fault (NCF; Fig. 3A); (García-Senz “pers. comm.”), forming an extensional-linked system, as in the examples described by Gibbs (1990). Because in the northern margin of the Iberian plate, the direction of extension during the Cretaceous is considered to be roughly orthogonal to the Cantabrian margin (Malod and Mauffret, 1990), the BF is interpreted as a left-lateral transfer fault, and the NCF as the corresponding frontal extensional ramp. The tilted block that contains the El Soplao territory dips and thickens towards the master BF (Fig. 3B), a feature commonly interpreted as the result of extensional fault propagation folding (Withjack et al., 1993). Models of such faults have been described in

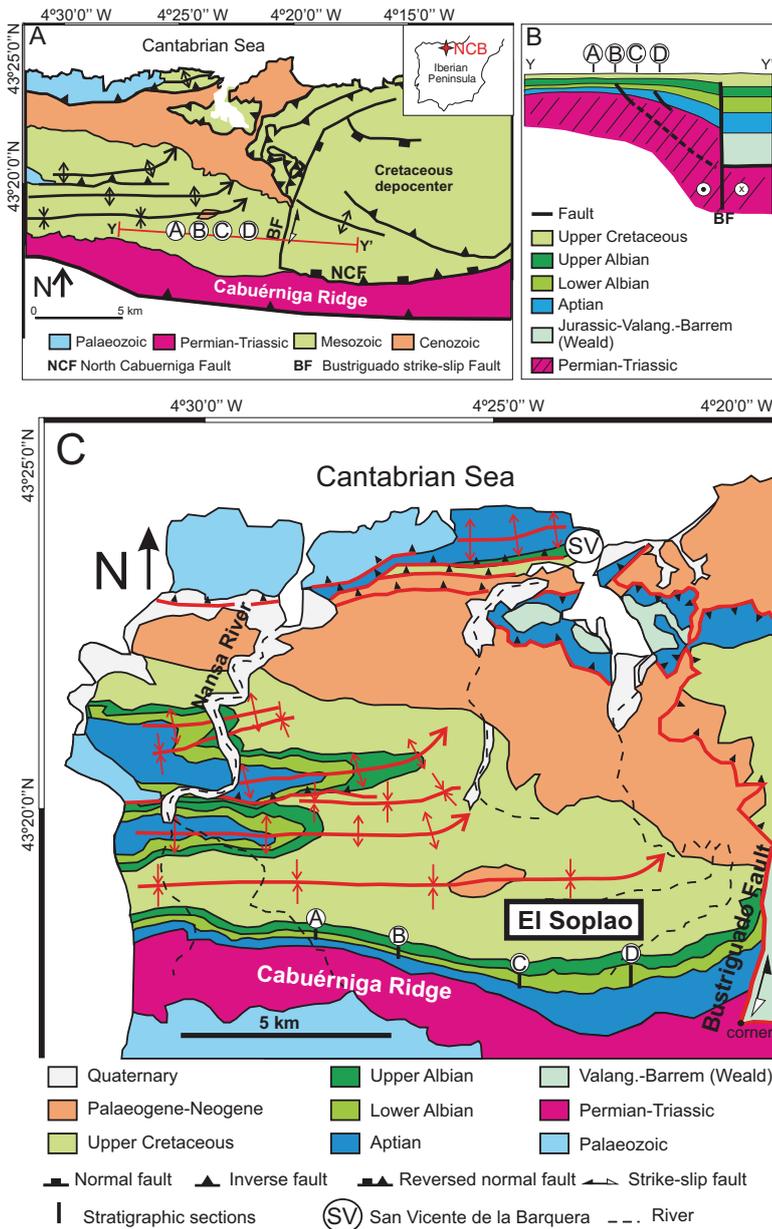


FIGURE 3 | A) Geological sketch with the main structural elements of the North Cantabrian sub-basin (NCB). The red line Y-Y' indicates the position of the cross-section of Fig. 3B. B) Schematic cross-section showing the restored geometry of the NCB in the El Soplao territory during the Cretaceous. Figure not to scale. C) Detailed geological map of the NCB Basin in the El Soplao area with location of the stratigraphic sections studied. (A) Puente Arrudo Section, (B) Rábago Section, (C) La Florida Section, (D) Plaza del Monte Section.

frontal ramps (Withjack et al., 1993) but few examples in transfer faults are known. This Cretaceous configuration was inverted during the Palaeogene folding and the faults reversed their movement. The NCF behaved as a frontal thrust ramp, and the BF as a right-lateral strike-slip fault. The latter passes northwards to an oblique thrust sheet that superposes the Cretaceous on the Cenozoic.

STRATIGRAPHY OF THE EL SOPLAO AREA

The bulk of the Mesozoic succession of the El Soplao area lies unconformably on folded (Variscan deformation) Carboniferous basement (Fig. 4). This succession was initi-

ated with a thick sequence of Lower Triassic continental red sandstones and mudstones (Buntsandstein facies). Late Triassic, Jurassic and earliest Cretaceous sequences are absent in the studied area, probably because during the Late Jurassic-Early Cretaceous rifting stage, the area to the north of the Cabuérniga Ridge was subjected to erosion and nondeposition. Subsidence renewed in the Early Aptian and was accompanied by gradual marine transgression. Thus, the Aptian-Albian succession of the El Soplao area, unconformably overlies Triassic strata and was dominated by shallow marine carbonate deposition (Fig. 4).

As a whole, the Aptian-Albian succession of the El Soplao territory constitutes an E-W elongated lithosome

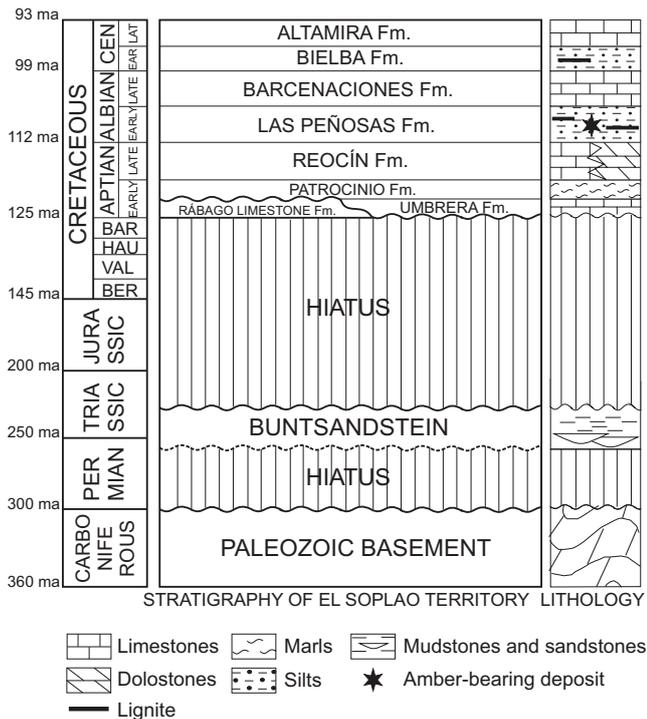


FIGURE 4 | Carboniferous to Upper Cretaceous lithostratigraphy of the El Soplao area (modified from Hines, 1985). Chronostratigraphy after Gradstein (2004).

9 km long with wedge-shaped geometry deepening and thickening eastward, on the slope of the tilted block active during this time (Najarro et al., 2007) (Fig. 3B). Thicknesses vary from about 600 m in the eastern part of the tilted block (Bustriguado area, Fig. 3) to less than 200 m toward the west (Puente Arrudo-Rábago Sections, Fig. 3C). The general stratigraphic and biostratigraphic framework of the Aptian-Albian lithological units has been established by Ramírez del Pozo (1972) and Hines (1985), but the main depositional systems and sequences have been revised recently (Najarro et al., 2007; Najarro and Rosales, 2008). A simplified stratigraphy of this interval is provided, adapted from the terminology by Hines (1985) for the major lithological units (Fig. 4).

The Early Aptian marine transgression led to deposition of shallow platform carbonates of the Lower Aptian Rábago Limestone Fm. and Ubrera Fm. that spread over the studied area. Continued transgression during the Early Aptian caused platform drowning, and resulted in deposition of relatively deep-water marls (Patrocínio Fm.) that covered the entire carbonate platform (Najarro and Rosales, 2008). Subsequent gradual regression led to deposition of shallow water carbonates of the Reocín Fm. during the Late Aptian, and finally delta-estuarine siliciclastics and carbonaceous lutites of the Las Peñas Fm. during the Early Albian (Fig. 4). The vertical evolution

from the Upper Aptian Reocín Fm. to the Lower Albian Las Peñas Fm. is interpreted herein as a relative sea-level fall associated with a deltaic progradation. The Upper Albian succession follows with deposition of the Barcenaciones Fm. (Fig. 4), a shallow water carbonate bank that expands more than 50 km throughout the North Cantabrian sub-basin, as a result of a transgression following deposition of the Las Peñas Fm. A subsequent regression during the Lower Cenomanian deposited the transitional marine siliciclastic Bielba Fm. Later, deeper water conditions were established during the Late Cretaceous, leading to deposition of open-platform carbonates for the remainder of the Cretaceous succession.

LAS PEÑAS FORMATION

Primarily, this paper examines the Lower Albian heterolithic amber-bearing deposit that is included within the Las Peñas Fm. Regional palaeogeographical and palaeoenvironmental reconstructions of the Basque-Cantabrian Basin during this time slice (García-Mondéjar, 1990) indicate that siliciclastic sediment was transported from highlands and continental areas located to the west and south towards the north during deposition of the Las Peñas Fm. This amber-bearing unit is approximately equivalent in age and facies to the broadly extended Escucha Fm., deposited to the south of the Basque-Cantabrian Basin (Barrón et al., 2001; Martínez-Torres et al., 2003), as well as other Mesozoic basins of northeastern Spain, including the Maestrat Basin (e.g., Salas and Martín-Closas, 1991; Salas et al., 1991; Querol et al., 1992; Salas et al., 2001; Rodríguez-López and Meléndez, 2004; Rodríguez-López et al., 2005, 2007; Peyrot et al., 2007; Moreno-Bedmar et al., 2008). These units basically represent littoral facies dominated by delta-estuarine deposits, which can be laterally correlated in a NW-SE direction for more than 500 km, from northeastern Cantabria, through the southeast Basque-Cantabrian Basin in the Álava region (Basque Country), and into the Maestrat Basin in Teruel to the Alicante Province (Fig. 2). These areas, which trace the approximate location of the coastline during the Early Albian, are characterized by the presence of coal-bearing deposits with common presence of amber (Delclòs et al., 2007).

Facies and sequence arrangement

The Las Peñas Fm. previously has been described as a unit formed by a complex of fluvio-estuarine channel sandstones, overbank black carbonaceous mudstones, tidal channel bars and tidal flat facies, and minor intercalations of carbonate beds, exhibiting unclear internal organization (García-Mondéjar and Pujalte, 1982; Hines, 1985). However, detailed stratigraphic and sedimentologi-

cal logging of four W-E correlative stratigraphic sections (the Puente Arrudo, Rábago, La Florida and Plaza del Monte sections; Fig. 3) in the El Soplao region has revealed the depositional architecture of the Las Peñas Fm. and the stratigraphic distribution of the coal- and amber-bearing deposits (Fig. 5). A summary of the general facies associations, depositional environments and their sequential arrangement is given in this section and summarized in Fig. 5 and Table 1.

It is significant that the facies distribution within the Las Peñas Fm. displays a clear tectonic control, as suggested in the study area by the strong lateral thickness

variation in an E-W direction (Fig. 5), which, in the studied area, ranges from between 45 m to the west to more than 100 m to the east. In this way, the Rábago Section that contains the amber deposit represents the highest point of the flexured footwall block of the Bustriguado fault (Fig. 3B) at the time of deposition of the Las Peñas Fm. This flexure seems to be accommodated by several minor synsedimentary faults that delineate the structure observed in the Rábago Section (Figs. 3B and 5).

The Las Peñas Fm. can be informally split into three correlatable units, which are named in this paper, from base to top, Las Peñas 1 to 3 (P1-P3; Figs. 5 and 6A).

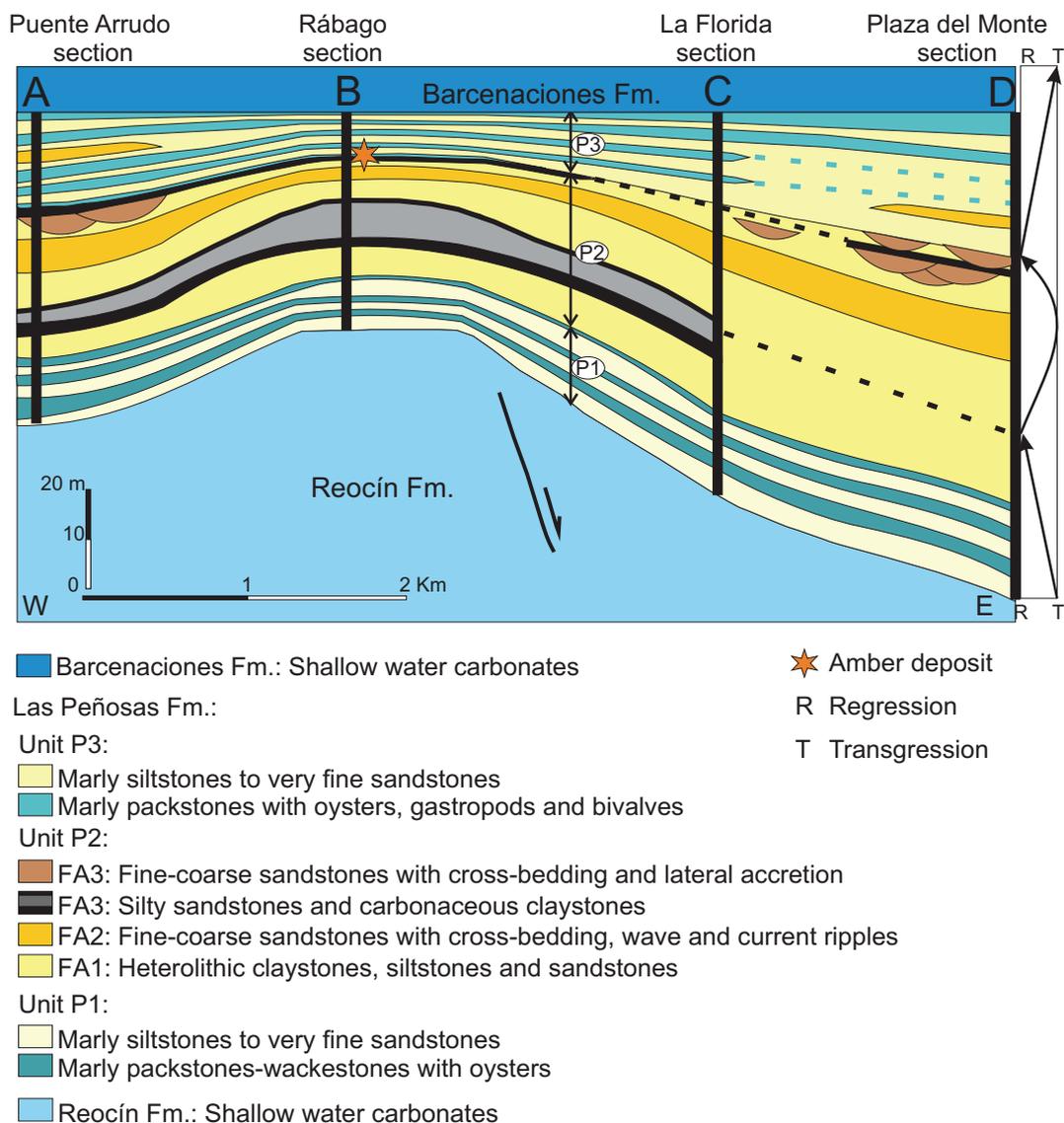


FIGURE 5 | Stratigraphic correlation of the four studied sections (A to D in Figure 3). Note the location of the amber deposit and the thickness variation of the Las Peñas Fm. along the W-E cross section (see also Fig. 3). (P1-P3) Members of the Las Peñas Fm. (see text for explanation). (FA1-FA3) Sedimentary facies associations studied in the Las Peñas Fm. Amber accumulation usually occurs at the P2-P3 unit boundary.

TABLE 1 | Characteristics of the facies associations in the Las Peñasas Fm.

Unit	FA	F	Lithology	Primary Structures	Vertical Stacking	Interpretation
P3			Alternation of nodular marly-packestones with bioclasts and heterolithic levels of mud- silt- and fine to medium grain-sized sandstones	Wavy, flaser and lenticular lamination	Progressive upward increase in carbonate content	Carbonate-siliciclastic mixed platform
P2	FA3	F6	Weakly cemented, moderate-well sorted, very fine- coarse to grained sandstones in erosionally-based, channalized units. Accretion surfaces with silty clay, plant remains, coal and mudclasts. Iron cemented ripples, pyritized trunk fragments and pyritized burrows at the top.	Large scale trough-, longitudinal-, low angle- and small-ripple-cross bedding; lateral accretion; horizontal-and sigmoidal-stratification; complex deformations	Fining upward	Delta plain: Distributary meandering channels
		F5	Dark organic, sulphide-rich mudstones with bivalves, gastropods, leaves, coal, trunks, sulphide nodules and amber	Wavy and lenticular lamination; current ripples	Rhythmic alternations	Delta plain: Interdistributary bay
		F4	Silty very fine sandstones with coal layers, sulphide nodules, trunks and amber		Rhythmic alternations	Delta plain: Interdistributary bay
	FA2	F3	Weakly cemented, moderated to well-sorted fine to coarse-grained sandstones with mud drapes and mudclasts	Large scale trough cross-bedding; planar cross-bedding; wave ripples	Coarsening and thickening upwards	Delta front: Distributary mouth-bars
	FA1	F2	Sulphide mudstone-siltstones with coal and trunk fragments. Minor to moderate bioturbation	Wavy and lenticular lamination	Fining upward	Wave- and tidal influenced estuarine-delta bay
		F1	Pale-yellow, very fine- to medium-grained, well-sorted sandstones. Mudclasts and coal fragments. Minor to abundant bioturbation dominated by <i>Skolithos</i> and track traces.	Low angle and horizontal lamination; planar cross-stratification; flaser and wavy lamination; wave and current-ripples		
P1			Alternation of bioclastic, oyster-rich limestones and bioturbated, nodular marly-silty limestones to siltstones with very fine sand levels	Wavy lamination	Upward decrease in carbonate content and progressive increase in siliciclastics	Transition from shallow carbonate platform to estuarine-delta bay

FA: Facies association. F: Facies

The lower Unit P1 overlies the Reocín Fm. It ranges from about 11 m (Rábago Section) to 40 m (Plaza del Monte Section) and it is characterized by an alternation of bioclastic, oyster-rich limestones and bioturbated, nodular marly-silty limestones to siltstones with intervals of very fine sands. The overall succession presents an upward

decrease of carbonate content and a progressive increase in the quartz silt and sand content of the marly intervals. This succession is interpreted as a transitional unit from a shallow carbonate platform to a siliciclastic estuary-delta bay, caused by rapid change in the sedimentary conditions resulting from deltaic progradation.

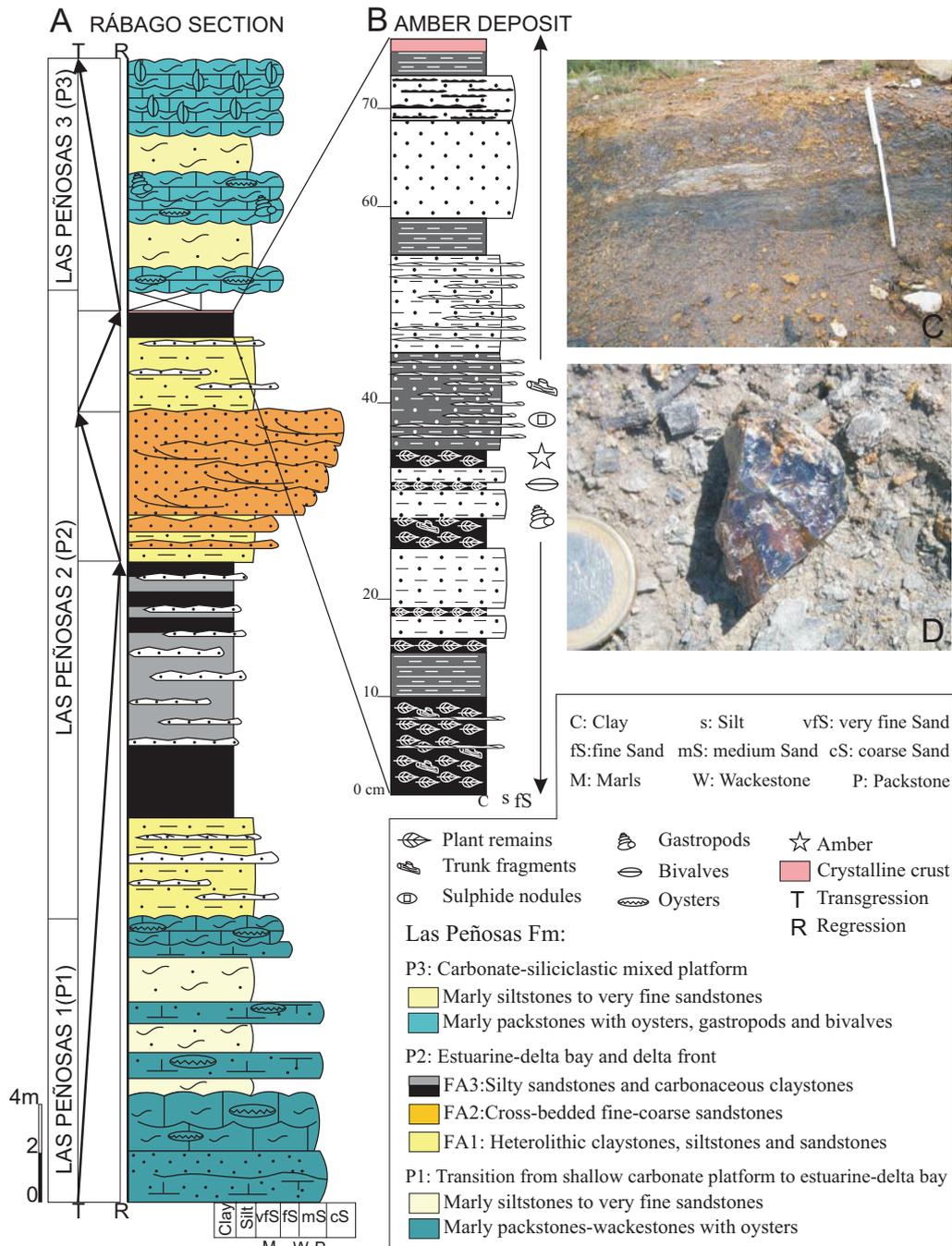


FIGURE 6 | A) Simplified stratigraphic log of the Rábago Section. Two regressive-transgressive cycles are defined. Note that the position of the amber deposit coincides with the maximum regression of the second cycle. B) High-resolution stratigraphy of the amber deposit. C) General view of the amber deposit (scale: 1m). D) Example of a blue amber piece in situ.

The middle Unit P2 contains the amber-rich deposit that has been recently discovered in the Rábago Section (Figs. 6B-D and 7A). It lies on top of P1 and ranges in thickness from 25 m (Rábago Section) to 60 m (Plaza del Monte Section; Fig. 5). This unit consists predominantly of heterolithic sandstones-siltstones and carbonaceous mudstones deposited in broadly coastal estuarine and delta environments. Facies associations can be grouped into three main depositional environments. First is delta front facies association without evidence of emergence,

interpreted largely as shallow marine. This environment includes distributary mouth-bar facies, deposited mostly, if not entirely, under marine conditions, as well as distal bar, nearshore to offshore deposits. Second are wave- and tide-influenced estuarine-delta bay deposits. Third is delta plain facies association, with sedimentary facies that reflect deposition in both distributary meandering channels (Fig. 7B and Table 1) and infilling of interdistributary bays (Figs. 6C and 7C), the latter with high accumulation of coal, plant cuticles (Fig. 7D) and amber pieces



FIGURE 7 | Field pictures of the Las Peñasas Fm. A) General view of the new discovered amber-rich deposit in Rábago Section within the Unit P2. B) FA3: Distributary meandering channel with trough cross-bedding, sigmoidal and horizontal stratification and lateral accretion within the Unit P2 in La Florida Section. C) FA3: Interdistributary bay facies within the Unit P2, capped by an erosive transgressive surface (ravinement), and overlain by marine limestones (Unit P3) (Puente Arrudo Section). D) FA3: Exceptionally well-preserved plant cuticle compressions that appear associated with the amber-rich deposit in Rábago Section. E) Detail of FA1 constituted of interbedded mudstones-siltstones with wavy and lenticular lamination and fine-grained sandstones. Unit P2 in Plaza del Monte Section. F) Marly level with high concentration of bivalves at the top of the Unit P3 in Rábago Section.

(Fig. 6D). Due to the sedimentological and palaeontological importance of this unit, more detailed stratigraphic characteristics and environmental interpretation is provided in the next section.

The Unit P3 superposed the Unit P2 by an erosive transgressive surface (*a ravinement*; Fig. 7C) and in turn is overlain by the Barcenaciones Fm. The thickness of the Unit P3 varies from 13 m to the west (Rábago Section) to 40 m to the east (Plaza del Monte Section; Fig. 5) and is characterized by the stacking of several meter-scale mixed siliciclastic-carbonate sequences. Contrasting with P1, the vertical stacking pattern of P3 presents a progressive increase in the carbonate content toward the top of the unit. This unit is interpreted as a transition from estuarine bay deposits (Fig. 7E) to a shallow carbonate platform system. Thus, a carbonate-siliciclastic mixed platform is proposed. The contact with the overlying Barcenaciones Fm. is taken at the base of a marly-nodular limestone bed with large bivalves that indicates the definitive abandonment of the siliciclastic system (Fig. 7F).

The amber-rich deposit in the Rábago Section

As noted above, the recently discovered site of amber accumulation is located at the top of Unit P2 in the Rábago Section, where this unit is comprised of three facies associations (Fig. 6 and Table 1).

Facies association 1 (FA 1): wave- and tide-influenced estuarine-delta bay

This facies association consists of heterolithic alternations of thinly bedded dark coloured mudstones, siltstones and sandstones, stacked vertically in meter-scale sequences with a general fining-upward trend. The sequences range in thickness from 3 to 4 m. This facies association displays two sedimentary facies. Facies 1 consists of 5 to 40 cm thick, pale-yellow, very fine- to medium-grained, well-sorted sandstones. The basal contacts are flat and sharp, while the contacts in the top are wavy due to ripples. This facies is characterized by low angle and horizontal lamination, planar cross-stratification, flaser and wavy lamination and wave and current ripples at the tops of the beds. Both current and wave ripples are associated with flaser bedding, and current ripples are seen as climbing in some places. Palaeocurrents have been measured in some crests of the wave ripples resulting in a shoreline direction with an overall E-W trend. Mud drapes occur frequently with thicknesses up to 0.5 cm. Mudclasts and coal fragments appear locally. Bioturbation ranges from sparse to elevated but is consistently characterized by a low diversity assemblage dominated by *Skolithos* and various track traces. Facies 2 consists of

beds of mudstone to siltstone. These beds are relatively sulphide-rich and range from 0.5 to 2 m thick, which often combine with facies 1 to form wavy and lenticular bedding (heterolithic facies). Coal and pyritized trunk fragments up to 20 cm long are concentrated at the base of these beds. Minor to moderate bioturbation and sulphide nodules also are present.

The presence of wave and current ripples occurring both as lenticular and flaser bedding, along with the wavy lamination and wave ripples on some sandstone beds, suggests a tidal- and wave-influenced estuarine-delta bay environment (e.g., Reineck and Wunderlich, 1968; Reineck and Singh, 1975; Dalrymple, 1992; Willis, 1997; Kuecher et al., 1990; Folkestad and Satur, 2008). The suite of trace fossils described above may occur in such an environment (Pemberton et al., 1992). The common occurrence of mud drapes and rhythmic bedding of sandstones and mudstones suggests involvement of tidal processes in the formation of this facies (Visser, 1980), but the occurrence of wave-generated structures suggests that reworking also was controlled by waves. The climbing current ripples indicate rapid deposition of sand (Reineck and Singh, 1975). These deposits are interpreted to have originated in the intertidal part of an estuarine-delta bay.

Facies association 2 (FA 2): Delta front distributary mouth-bars

Facies 3 consists of weakly cemented, moderate to well-sorted, fine to coarse-grained sandstone, organized in a coarsening and thickening upwards sequence of about 6 m thick. Sedimentary structures grade vertically from large-scale trough cross-bedding to planar cross-bedding with wave ripples at the top. Mud drapes and mud pebbles are present in foresets. Although preservation at the outcrops prevents detailed sedimentological observations and measurements, in most instances, unidirectional, diffuse palaeocurrent features are observed.

The thickening and coarsening upward trend of this facies association suggests a progradational character. The upward transition from trough cross-bedding to wave ripples at the top suggests decreasing energy conditions. Moreover, the occurrence of mud drapes and mud clasts suggests fluctuating energy conditions likely produced by tidal processes occurring during deposition (Reineck and Singh, 1975; Dalrymple et al., 1990; Shanmugam et al., 2000; Kitazawa, 2007). The presence of wave-ripple lamination also indicates wave influence. As a whole, this facies association is interpreted as a progradation of distributary mouth-bar deposits and sand bars into a wave and tidal influenced estuarine-delta bay.

Facies Association 3 (FA 3): Interdistributary bay

This facies association is composed of a very thin intercalation of silty to very fine sandstones (facies 4) that contain dark organic- and sulphide-rich mudstones (facies 5), ranging in thickness from 0.7 to 2.5 m. Facies 4 is greyish-brown reaching a maximum thickness of 10 cm. It presents wavy and lenticular lamination with current ripples, coal layers (up to 3 cm), sulphide nodules, partially pyritized trunk fragments, minor bioturbation as pyritized burrows, and amber. Facies 5 is mostly composed of layers formed by the accumulation of leaves and other plant remains. These leaves are very well preserved, showing many original details and their venation patterns. When present, the matrix between the plant-bearing levels consists of clay. Also present in this facies are small pyritized moulds of marine gastropods and bivalves, sulphide-nodules (up to 6 cm in size), coal, trunk fragments (up to 15 cm), and abundant pieces of amber. Although amber fragments have been found in all stratigraphic sections, the most abundant yield comes from the Rábago Section, where they consist of both stalactite-shaped and globular or kidney-shaped amber pieces. At the top of this facies association a 5 cm thick crystalline crust appears. The crust surface is colonized by serpulid worm tubes and its genesis remains uncertain. A pale-yellow silty rooting level with associated white mottling occurs in the Plaza del Monte Section at a stratigraphic position laterally equivalent to this crystalline crust.

Dark organic-rich mudstone deposits are interpreted as extensive accumulations of plant remains with a relatively low input of clastic material followed by relatively rapid burial to prevent decomposition (Dalrymple, 1992; Folkestad and Satur, 2008). Mudstones were mostly deposited in interdistributary and coastal bays with a high supply of continental organic matter transported by fluvially associated floods that undoubtedly originated during rainstorm periods. The exceptional preservation of the leaves, along with the presence of pyrite, organic remains, and the low-diversity of fossil traces and benthic fauna, suggest suboxic conditions within the interphase water-sediment. Occasionally, the combined action of spring tides, storms and overbank floods was strong enough to deposit silty and very fine sand layers (Reineck and Singh, 1975; Noe-Nygaard and Surlyk, 1988; Dalrymple, 1992). This inference also is supported by the presence of thin shell remains. The root activity at the top of the infilling sequence implies eventual subaerial conditions, and the development of a horizon exposed to vegetative processes in a palaeosol (McCarthy and Plint, 2003; Folkestad and Satur, 2008). This event is coincident with the maximum regressive stage within the Las Peñas Fm.

Depositional sequences and facies model of the amber-bearing deposits

Within the Las Peñas Fm., amber accumulation occurs principally towards the top of the Unit P2, in dark organic-rich mudstones that deposited in interdistributary bays between meandering distributary channels (i.e., facies association 3; Fig. 8 and Table 1). The vertical stacking of the described facies association of the Unit P2 suggests that it internally displays two smaller transgressive-regressive cycles, with the coal-bearing deposits developing during the regressive phase of the cycles (Fig. 5). These deposits are underlain by shallow marine, siliciclastic and carbonate deposits formed under relatively higher sea-level conditions (Unit P1). The Unit P2 is capped by an erosive transgressive surface (*ravinement*), overlain by full-marine limestones (Fig. 7C). These deposits represent a marked landward shift in the siliciclastic coastal facies, displaying a retrogradation-aggradational stacking pattern (Unit P3). Therefore, deposition of the amber and coal rich levels was coincident with the maximum regressive episode of the estuary-delta progradation (Fig. 5), and represents a relative sea-level fall. The same pattern in coal- and amber-rich deposits has also been described for the Escucha Fm., in the south of the Basque-Cantabrian Basin (Peñacerrada-Montoria outcrops; Martínez-Torres et al., 2003), in the Maestrat Basin (Rodríguez-López et al., 2005), and in the Oliete sub-basin along the San Just outcrop (Peñalver et al., 2007b), both in the Teruel Province. In all these areas amber deposits were related to the progradation of a delta-estuarine system. In Peñacerrada-Montoria, amber accumulated in interdistributary bays within lower delta plain environments (Martínez-Torres et al., 2003), whereas in San Just, amber was deposited in freshwater ponds both within the upper delta plain and in the lower delta plain (Querol et al., 1992). Despite of the similarities between the depositional environments of all the amber-rich deposits of the Lower Cretaceous of Spain, it is worth noting that the depositional environment of the El Soplao amber presents a slight marine influence, as it can be inferred from the presence of some small marine bivalves and gastropods within the amber deposit and bryozoans and serpulids incrusting the surface of some amber samples. In the amber from southwestern France, marine influence has been pointed out as well, but directly evidenced from marine microfossil inclusions like marine diatoms, radiolarians, sponge spicules, and foraminifers (Girard et al., 2008). On the contrary, amber deposits from Lebanon (Azar et al., 2003; Veltz, 2008) and the Isle of Wight (United Kingdom) (Jarzembowski et al., 2008) were accumulated in more proximal delta environments and fluvial channel deposits with a larger continental influence.

Stratigraphic models for clastic deposition generally suggest that regressive wave-dominated shallow marine systems develop during sea-level falls, whereas tidally

influenced paralic coal-rich deposits develop during the transgressive infilling of incised valleys (e.g., Allen and Posamentier, 1993). The majority of these case studies came from areas with relatively simple tectonic settings and subsidence patterns, such as the Cretaceous of the Western Interior Seaway in North America (Posamentier and Vail, 1988) and Quaternary successions along passive margins (e.g., Allen and Posamentier, 1993). In these studies, the tectonic influence on sequence arrangement is relatively minor and the eustatic fluctuation in sea level is the principal control on stratal succession. In contrast, the Las Peñas Fm. was deposited in rifting setting during a period of major tectonic rearrangement across the entire Basque-Cantabrian Basin, with active faulting that resulted in uplift and marked subsidence changes over short distances (García-Mondéjar et al., 1996, 2003). It is in this context that local regression occurred with coeval progradation of siliciclastic coastal deposits.

THE AMBER

General characteristics and morphological types

Trees can produce different kind of resins depending on what structural part is noted, such as roots, trunk,

branches and leaves (Langenheim, 1995). It has long been known that resins are exuded outside the plant as defence from megaherbivores, insects, and pathogens, such as fungi (especially in the tropics), viruses, other microbes and bacteria. Presently, no methodology is available to differentiate what parts of the tree were involved in the origin of different amber types. Due to the relative abundance of amber at several outcrops, it is generally supposed that the exudation of the original resin occurred mainly in trunks. Our observations of *Agathis australis* in New Zealand subtropical forest suggest that roots were probably significant producers of resin during the past, attributable to copious exudations of root-generated resin.

The new Albian deposit described herein is unusually rich in amber flows of different types formed under aerial conditions by liquid resin (containing flow structure). Normally, these flows are very rich in bioinclusions, especially small insects. The richest flows are stalactite-shaped amber pieces (Figs. 9A-9B). These cylindrical or subcylindrical pieces commonly contain very well preserved bioinclusions in clear yellow amber. The amber flows also include sub-spherical or elongated specimens with a pattern of striations and bulges and apparently an attached scar suggesting a bark pattern. This morphology indicates that the flows

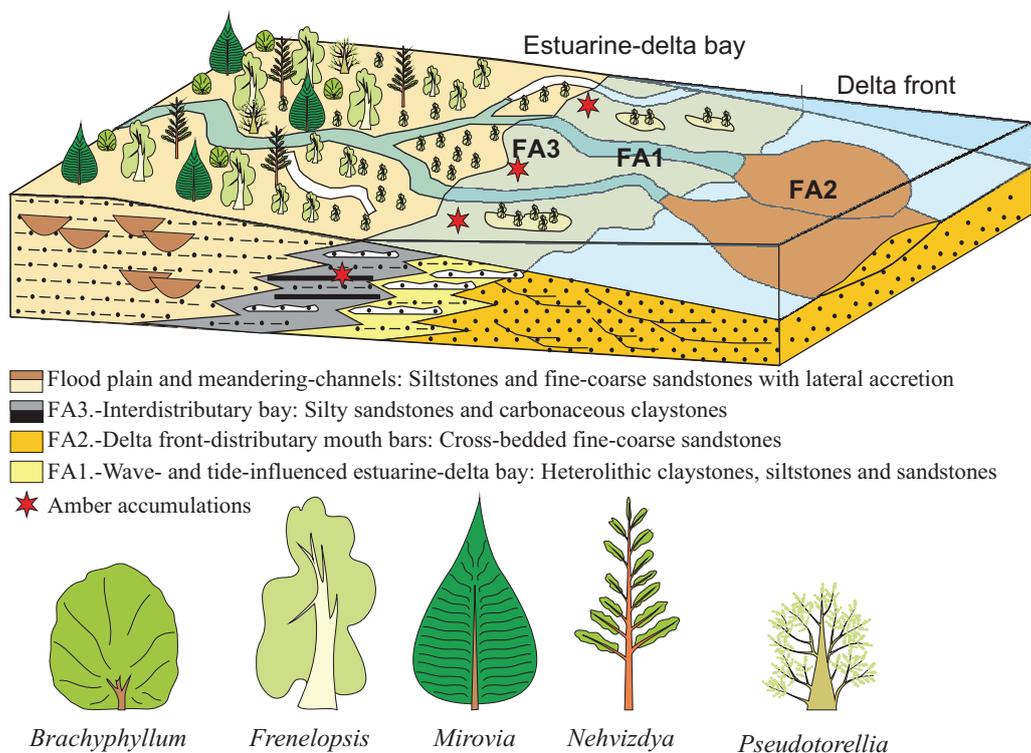


FIGURE 8 | Block diagram illustrating an idealized model of the depositional environments during sedimentation of the amber- and coal-rich levels. The accumulation of amber- and coal-rich sediments took place during the maximum regressive episode of the estuarine-delta progradation. FA: Facies association.

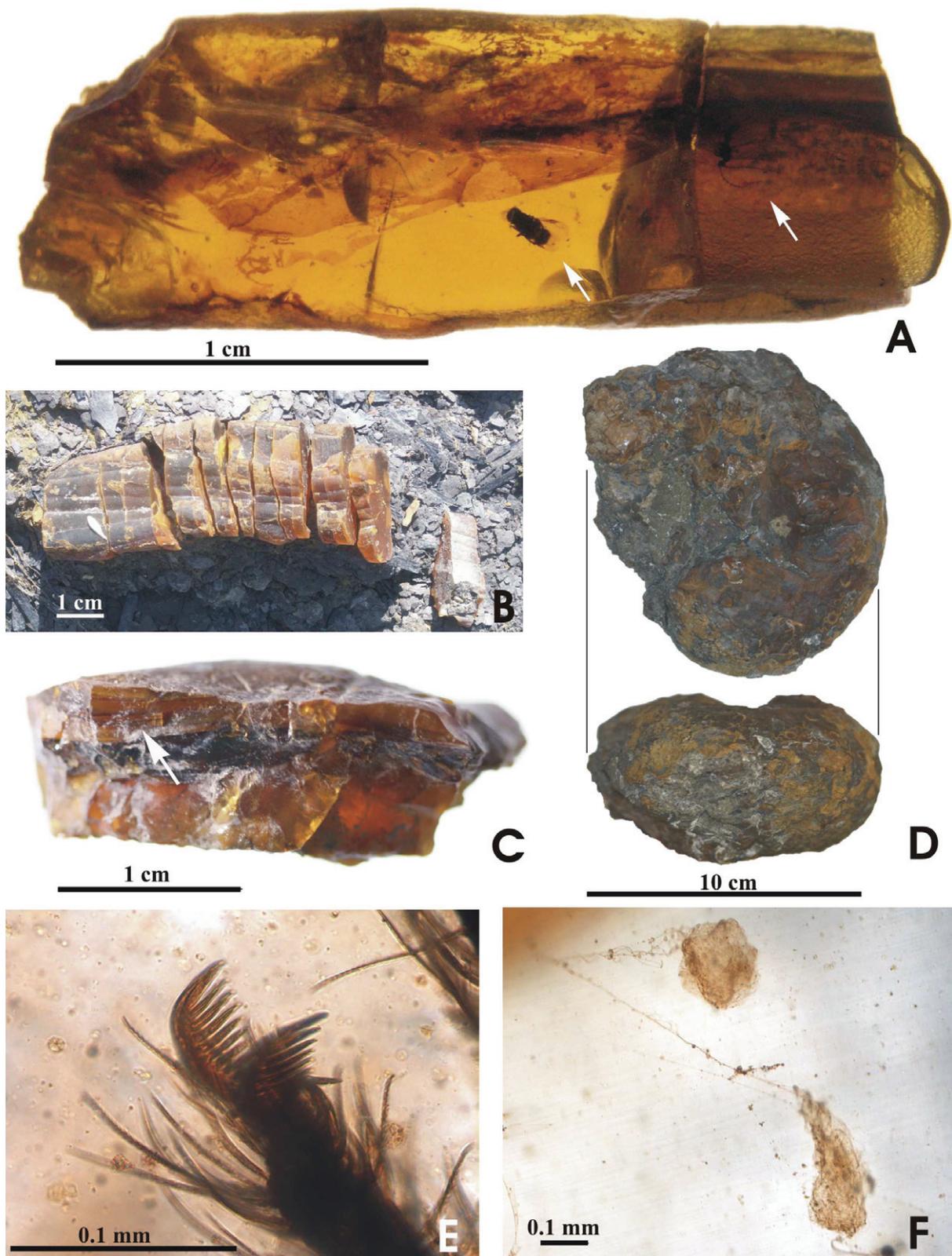


FIGURE 9 | Different types of amber pieces and amber bioinclusions related to spiders from El Soplao (Rábago, Cantabria). A) Stalactite-shaped amber flow with a wasp of the family Megaspilidae -left arrow- trapped on a spider web fragment (see detail of the spider web in 9F) and two insects shown in figure 12C -right arrow-. B) Stalactite-shaped amber flow exposed in situ which contained a scelionid wasp. C) Amber flow (crust); arrow indicates some flows that originated from liquid resin and cover a copious flow of dark amber. D) Big kidney-shaped mass in two views. E) Pectinate paired claws, adapted to efficient handling of silk and locomotion on an aerial web, present in an Araneoidea spider. F) Detail of the spider web fragment which trapped a megaspilid wasp. Images E and F were made with integrated consecutive pictures taken at successive focal planes.

originated by viscous resin under aerial conditions. The viscous resin avoided capture of insects and plant debris due to the short time that these structures remained superficially sticky. Other specimens are plain or unelaborated in shape with several layers accumulating by different flows by less viscous resin with marks indicating aerial conditions (Fig. 9C). This last type usually contains abundant bioinclusions.

A different type are the kidney-shaped masses, normally very large in size (up to a decimetre in diameter) with an external surface slightly granulose that lacks evidence of aerial exposure (Fig. 9D). Some authors consider that this type of mass had formed by subterranean resin secretion from roots, probably explaining their lack of bioinclusions. These amber masses also are abundant in the El Soplao outcrop.

Of gemmological interest, abundant blue amber pieces (Fig. 6D) were found, similar to the noted blue amber from the Dominican Republic (Bellani et al., 2005). Both are the only well-known occurrences of this type of amber. A fluorescent blue glow appears in these pieces under normal sunlight, and under ultraviolet light it glows a bright milky-blue. In contrast, under artificial light these fragments show the typical honey-reddish colour of the Cretaceous amber.

Geochemistry

The Fourier Transform Infrared Spectroscopy (FTIR) is a solid-state spectroscopic technique usually used to characterize ambers (Langenheim and Beck, 1965). Nevertheless, the majority of fossil resins of the same geological range often show similar patterns preventing objective classification. Gas Chromatography-Mass Spectrometry (GC-MS) determines the individual non-volatile amber compounds and their molecular structure, and also suggests the plant producer (Grimalt et al., 1988; Chaler and Grimalt, 2005). Previous GC-MS studies on Cretaceous amber from Álava (southern Basque-Cantabrian Basin) indicate that some isolated compounds found may have originated from agathic acid, suggesting that the genus *Agathis*, or a close genus of Araucariaceae (Coniferales), was the amber producer (Alonso et al., 2000; Chaler and Grimalt, 2005). The palynological study supported this indication, because it revealed that a high percentage of pollen grains related to Araucariaceae (Barrón et al., 2001). Nevertheless, currently no araucariacean meso- or macro-remains have been found within the Álava amber or in the surrounding rock.

Here, we compare the FTIR of recent *Agathis australis* resin and amber samples from El Soplao (Fig. 10).

The *Agathis* resin is a mixture of mono-, sesqui- and diterpenes, and each of its 13 species has a characteristic mixture of diterpenoid acids. Today this araucariacean genus produces large quantities of resin under natural conditions which polymerize rapidly, forming indurated masses. Recent studies from the Álava amber (Chaler and Grimalt, 2005) indicate that all samples show branched monoalkylbenzenes, bicyclic sesquiterpenoids and tricyclic diterpenoids related to pimaric acid precursors, suggesting a distinctive palaeobotanic origin from *Agathis*-like species.

Three amber samples were analysed from the El Soplao amber: i) a fragment of a stalactite-like amber piece from an organic-rich clay level (AMB82); ii) a fragment of large kidney-shaped mass, red in colour, found in an organic-rich sand layer (AMB80), and iii) a fragment of orange kidney-shaped mass from an organic-rich clay level (AMB81). A fragment of stalactite-shaped dry resin from *Agathis australis* also was analysed for comparison (AMB83). The FTIR spectra obtained are shown in Fig. 10.

Structural changes in the organic components of the amber samples are due to maturation processes during rock diagenesis. In the evaluation of the maturity of the coal and organic matter from the Escucha Fm. and other Early Cretaceous Spanish basins, such as the Maestrat Basin and the Basque-Cantabrian Basin, the thermal analysis based on the vitrinite reflectance (%R) suggests around 52°C as maximum temperature from modelling (Sangüesa and Arostegui, 2003; Permanyer, pers. comm.) The FTIR analyses (transmittance and absorbance) of the amber pieces of El Soplao show that all three spectra are practically identical. The IR spectra of all samples exhibited the same bands, but with different intensities (Fig. 10). In absorbance, all spectra show similar relative intensity, but in the sample AMB80, which corresponds to a red amber fragment, the intensity decreases at wave-numbers 727 and 814 cm⁻¹, and increases considerably at approximately wave-number group 1714 cm⁻¹, a complex band associated with carboxyl groups (Fig. 10). In this sample we also observe broad absorption bands at ca. 3460 and 1635 cm⁻¹, the signal due to water or possibly to weathering. The spectra coincide in the major features with the previous results obtained from other Spanish Cretaceous ambers (see FTIR spectra in Alonso et al., 2000; Chaler and Grimalt, 2005; Peñalver et al., 2007a, 2007b; Corchón et al., 2008). All the spectra are dominated by small C-H stretching bands near 2950 cm⁻¹, C-H banding occurs between 1470 and 1380 cm⁻¹, and the carbonyl bands are close to 1700 cm⁻¹. The lack of exocyclic methylenic bands at 880, 1640 and 3070 cm⁻¹ is consistent with the high maturity of the amber.

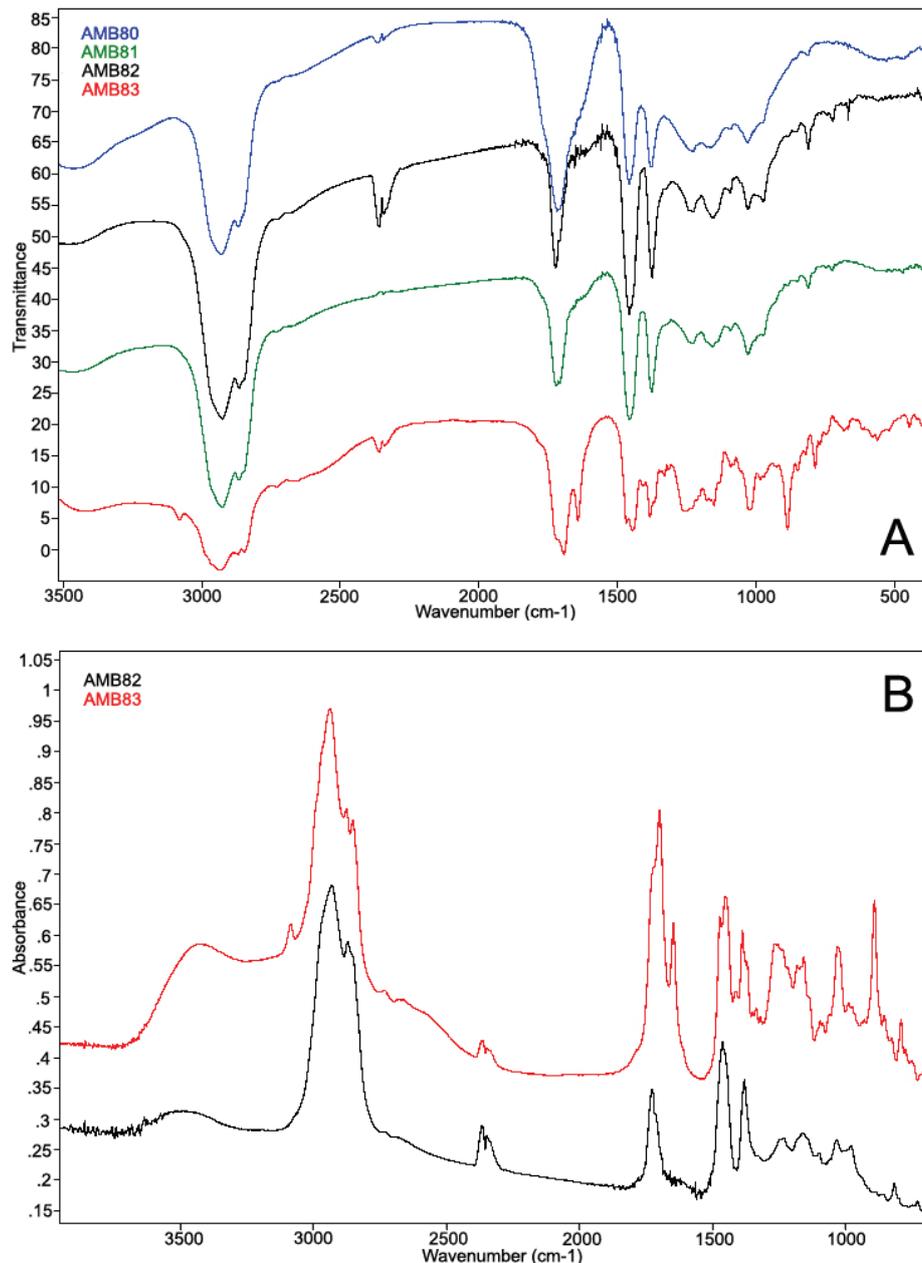


FIGURE 10 | A) Transmittance IR spectra of El Soplao amber: AMB80 red amber from a kidney-shaped mass found within sands; AMB81 orange amber from a kidney-shaped mass found within clays; AMB82 orange amber from a stalactite-shaped flow, found within clays; and AMB83 dry resin from an *Agathis australis* stalactite-like flow, New Zealand in origin. B) IR absorbance spectra from the El Soplao amber and dry resin of *Agathis australis*, both samples analysed came from stalactite-shaped flows.

When the IR absorbance spectra is compared between the amber sample AMB82, an aerial stalactite, and the sample AMB83, a fragment of recent stalactite of the araucariacean *Agathis australis* (Fig. 10), numerous differences may be observed. However, without GC-MS studies, the origin of the variable intensity and the presence of several bands cannot be possibly known. The presence of the absorption maximum in the single-band around 3081 cm^{-1} is typical in *Agathis* resin; however, it is typically absent in

amber due to the polymerization of the resin and increasing maturity. In addition, the spectra around range bands $1650\text{--}1700\text{ cm}^{-1}$, corresponding to the carboxyl groups, is very different between the amber and the resin. The intensity of absorption at wave-numbers 3400 and 1700 cm^{-1} decreases according to an increase in the maturity level of the samples. Other bands observed constitute an unresolved group near wave number 2930 cm^{-1} (C-H st), the most intense group band known for all Cretaceous spectra.

FOSSIL RECORD

Plant cuticle compressions

Exceptionally well preserved plant cuticle compressions are very abundant in the El Soplao amber deposit (Fig. 11), sometimes accumulating in levels up to 10 cm thick. The palaeobotanical samples taken from these levels also show amber and woody fragments, but at less percentage than plant-cuticle compressions (Figs. 11A-11D). Amber pieces show various shapes and colours from yellow to red (Fig. 11A), whereas unidentified, small, dark, woody fragments are preserved as spheroidal, charcoaled masses or charcoals (Fig. 11B). Cuticle fragments of the conifer *Frenelopsis*, of the extinct family Cheirolepidiaceae (Gomez et al., 2002), are the most numerous plant-cuticle components (Fig. 11C). These coniferous axes typically constitute cylindrical internodes bearing apically a nodal whorl of three leaves (Fig. 11E). Some *Frenelopsis* sp. cuticles also show a particular branching of axes borne in the internode (Fig. 11F) (see Daviero et al., 2001 for architectural details). A female cone scale formed by several layers of very thin cuticle (Fig. 11P) constitutes a doubtful record of the genus *Alvinia* Kvaček (Kvaček, 2000), associated with *Frenelopsis* vegetative material. Additionally, the conifer *Mirovia* sp. of the extinct family Miroviaceae (Gomez, 2002) shows about the same quantity of leaf cuticle fragments (Fig. 11D). The leaves clearly display a white central line on one side corresponding to the single middle stomatal-bearing groove, as well as a mucronate apex and suction-pad-shaped base (Figs. 11G-11H). Such leaves have been also described from the Albian of Pyrenees (Corça) and Teruel (Rubielos de Mora) (Gomez, 2002). Also present are two conifer leafy axes of *Brachyphyllum*-type with tiny, helicoidally arranged leaves (Figs. 11L-11M). In addition, two types of ginkgolean leaves also occur. *Nehvizdya* sp. shows obovate leaves with variable apex shapes (Fig. 11I) and attenuate base (Fig. 11J) (Gomez et al., 2000). The venation pattern showing several successive dichotomies and the presence of resin bodies between the veins are clearly seen in the most transparent leaves. In Spain, *Nehvizdya penalveri* has been reported only from the Albian of Rubielos de Mora in Teruel (Gomez et al., 2000). Other ginkgolean leaves are represented by *Pseudotorellia* sp. It has narrow leaves with three stomatal bands located on one side (Fig. 11K). This genus has also been described from the Albian of Rubielos de Mora in Teruel (Gomez, 2000). In addition, it has distinctive reproductive organs similar to the genus *Nehvizdyella* Kvaček (Kvaček et al., 2005), which probably are ovules associated with *Nehvizdya* (Figs. 11N-11O).

Arthropod inclusions

Until now, the arthropods found as inclusions in the El Soplao amber have been spiders and insects. All speci-

mens are small in size, less than 1 cm long, and are well preserved, possessing slight deformation due to pressure. Apparently, the degree of maturation of the amber is slightly higher than the San Just and Álava ambers, because the external surface of the insects is dark, without a silvery gaseous film. That film produces silver-hued reflections under strong direct illumination and makes the appreciation of microsculptural details easier. Formal taxonomy of the new taxa of arthropods will be published elsewhere, principally by Paul Selden and one of us during the completion of a Doctoral Thesis (R.P.F.). Thus, only a brief overview of the most important specimens is presented below.

One of the most remarkable finds is a virtually complete spider specimen. The excellent preservation of the legs shows detailed structure of the tarsal claws (Fig. 9E). The tarsi have large, pectinate paired claws with one row of nine teeth and one small, non-pectinate median claw and numerous serrate bristles, similar to the Araneoidea specimen described by Selden (1989) from the Early Cretaceous limestones of El Montsec (Lleida Province, northeastern Spain). Subsequently, the Montsec specimen was described as *Cretaraneus vilaltae* by Selden (1990) and assigned to the orb-weaver family Tetragnathidae by Selden and Penney (2003). The characteristic claw morphology is structured for an efficient handling of silk and locomotion on an aerial web. Peñalver et al. (2006) published the oldest web with entrapped preys, most likely an orb web, from San Just amber. Penney and Ortuño (2006) described a spider from Álava amber, which displays three tarsal claws and accessory setae, as the oldest true orb-weaving spider, but without illustration and more detailed description of this crucial structure. Also, from the El Soplao amber, a portion of an aerial spider web was found (Fig. 9F), which trapped a small wasp of the family Megaspilidae. This new spider web has a different structure than the specimen from San Just amber. Both the spider specimen and aerial web found in the El Soplao amber shed light on and support the role of aerial webs in the palaeoecology of Cretaceous forests discussed by Peñalver et al. (2006, 2008).

The insect orders found to date in this new site also are the most abundant in other Cretaceous deposits (Fig. 12). These co-occurring orders are Thysanoptera (Fig. 12A), Hymenoptera (Fig. 12B), Blattaria (Fig. 12D), Hemiptera, Coleoptera, and Diptera; the last two are especially plentiful (Figs. 12C-12D). Raphidioptera and Neuroptera have a scarce record in El Soplao as is common in Cretaceous ambers.

Hymenopterans were represented previously by the families Scelionidae (Figs. 12B and 12D), Mymarommatidae, and Megaspilidae (Fig. 9A). The extinct family

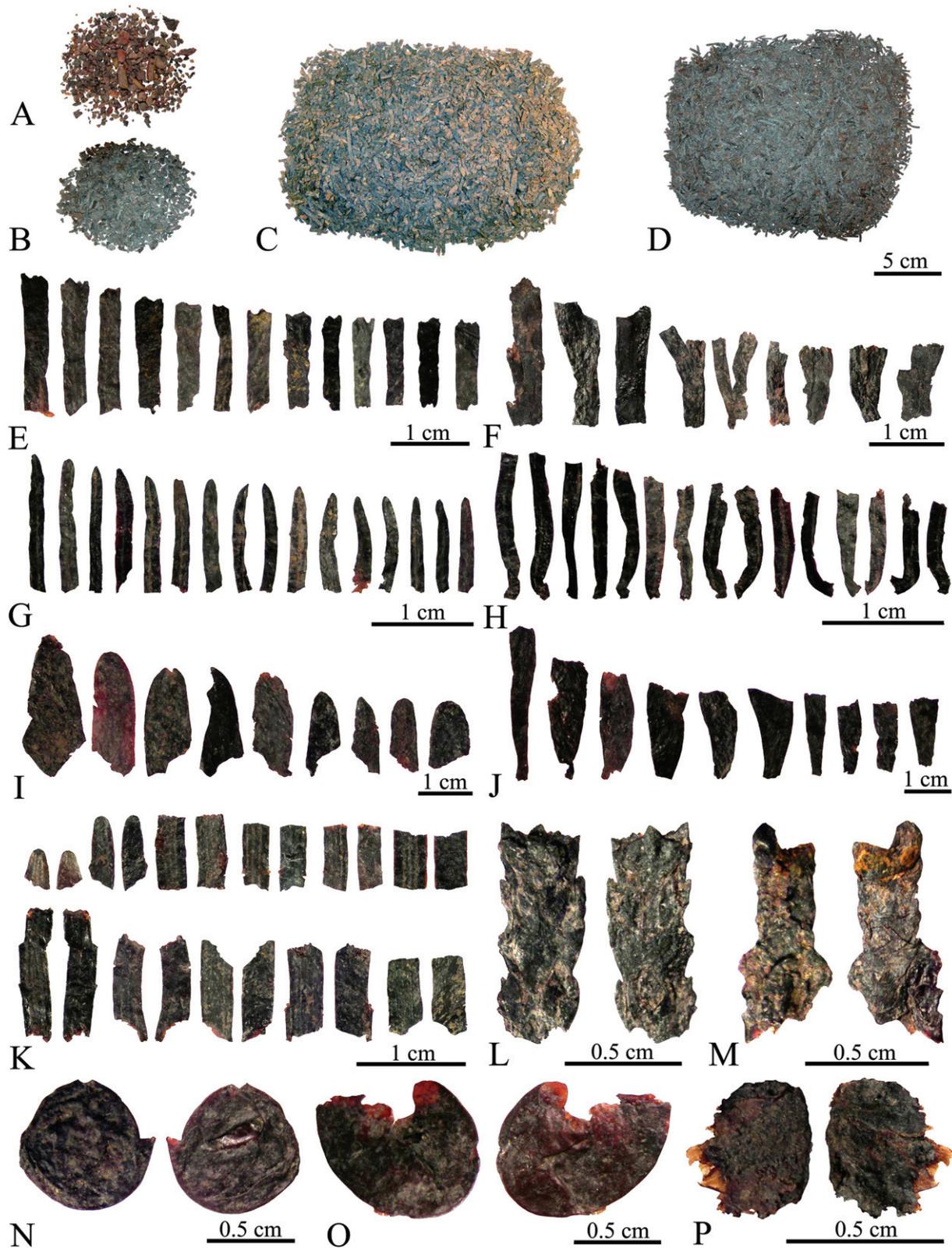


FIGURE 11 | A, D) Four major palaeobotanical components sorted out from a sediment sample (all to the same scale). A) Yellow to red amber pieces. B) Wood fragments. C) *Frenelopsis* sp. cuticles. D) *Mirovia* sp. cuticles. E, F) Internodes of *Frenelopsis* sp. E) Apical nodal whorl of three leaves. F) Intra-internodal branching of axes. G, H) Leaves of *Mirovia* sp. G) A single middle stomatal groove and a mucronate apex. H) Suction-pad-shaped base. I, J) Leaves of *Nehvizdya* sp. I) Variable shapes of apices. J) Attenuate bases. K) Leaves of *Pseudotorellia* sp., showing two apices and three or more stomatal bands on one side of the leaves. L, M) Two *Brachyphyllum*-type leafy axes, showing small, helicoidally arranged leaves. N, O) Ovules of cf. *Nehvizdyella* sp., P) cf. *Alvinia* sp., a multilayered female cone scale of *Frenelopsis* sp.

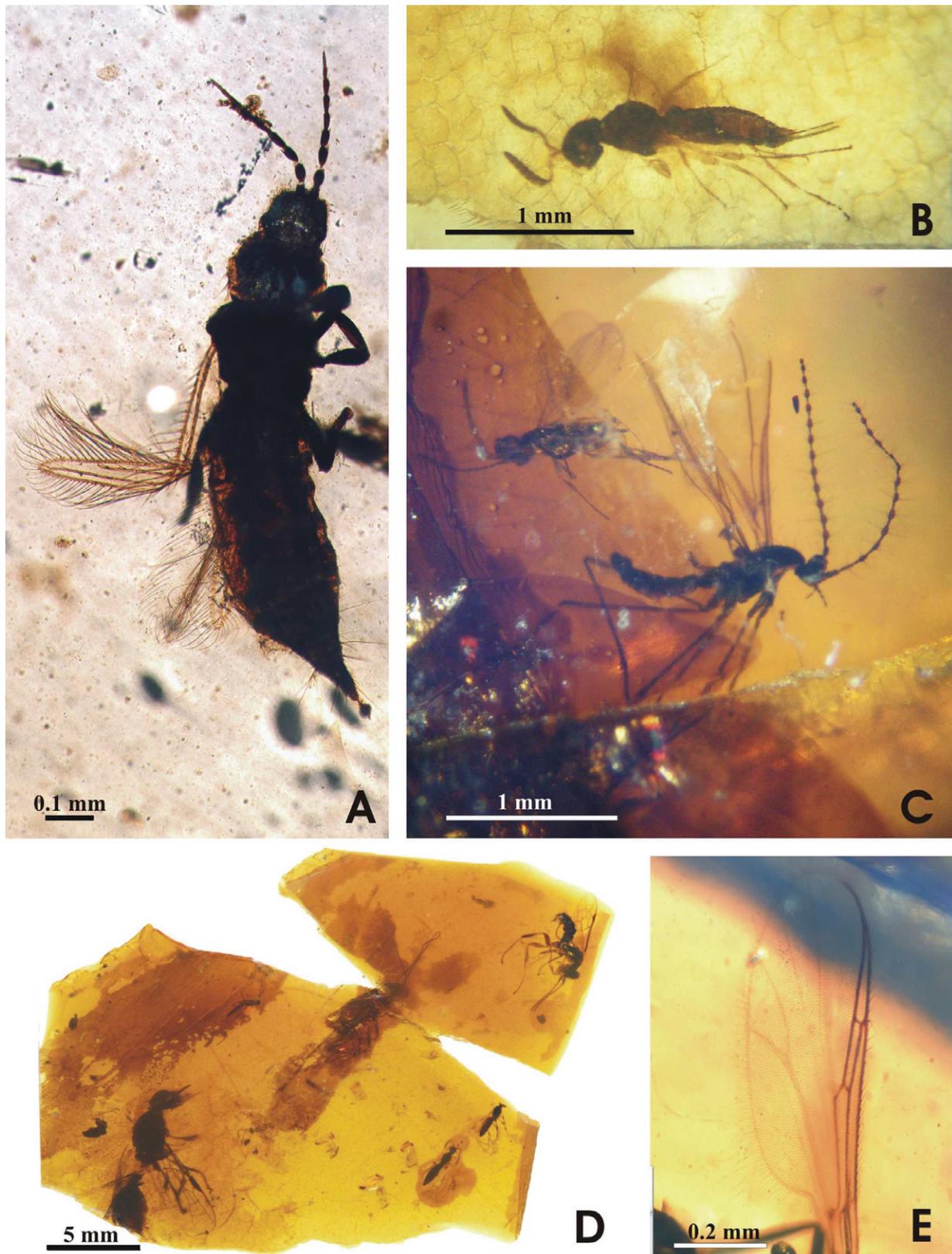


FIGURE 12 | Fossil insects as bioinclusions in El Soplao amber. A) Thysanopteran specimen. B) Female wasp of the family Scelionidae. C) Chalci-doidean wasp -top- and dipteran of the family Cecidomyiidae (gall midges). D) Amber fragment with seven wasps and one immature cockroach in the centre of the preparation. E) Wing of *Archiaustroconops* sp. Images A and E were made with integrated consecutive pictures taken at successive focal planes.

Mymarommatidae, or false fairy wasps, are among the smallest of Hymenoptera and constitute a very important record for the El Soplao amber, represented by a complete winged female of a new morphotype of the extinct genus *Archaeromma*. The family includes only five genera, three extant and two extinct genera (Gibson et al., 2007). The fossil record of this family is very scarce and is only preserved in amber. The genus *Archaeromma* contains eight species (Gibson et al., 2007; Engel and Grimaldi, 2007). This group of minute wasps is characterized by having a head capsule with a hyperoccipital band of pleated membrane separating the frontal plate from the flat occipital plate; an occipital foramen originating at ventral margin of occipital plate; mandibles exodont; female antennae with 6 or 7 funicular segments and 3 or 4 larger distal segments which form a compact tube; and other characters (Gibson et al., 2007). Due to their small size and unusual morphological characters, they are suspected egg parasitoids. The new record from the El Soplao amber is the oldest for this genus.

Among the most interesting insect records in the El Soplao amber are biting midges (Diptera: Ceratopogonidae). The genus *Archiaustroconops*, of the subfamily Austroconopinae, is the only Cretaceous Ceratopogonidae with two well-developed radial cells, an oblique r-m vein (Fig. 12E), and a foreleg/hindleg tarsal ratio ≥ 1.4 (Borkent, 2000). The genus includes six species known only from Lower Cretaceous Lebanese and Álava ambers (Borkent, 2000). It is represented in the El

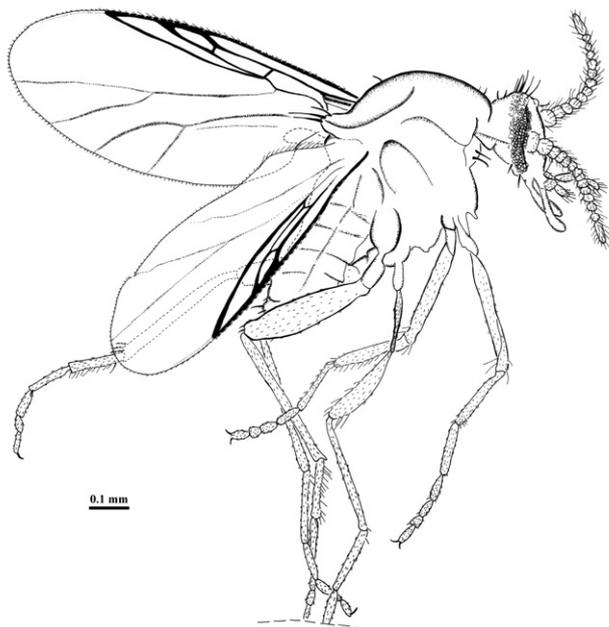


FIGURE 13 | Camera lucida drawing of *Lebanoculicoides* sp. (Ceratopogonidae: Lebanoculicoidinae) in lateral habitus, from the El Soplao amber.

Soplao amber by one new morphotype (Fig. 12E), clearly different from *A. alavensis* found in Álava amber. This new morphotype is characterized by having a strongly elongate first radial cell. Most interesting is the presence of a new taxon of the rare genus *Lebanoculicoides* (Fig. 13), which is only known by two specimens described as *L. mesozoicus* from Lebanese amber (Szadziwski, 1996). This genus is the only member of the Ceratopogonidae having a wing with fully developed R1, R3 and R4+5 veins. This character, among others, indicates that *L. mesozoicus* is the sister group of all other Ceratopogonidae and for that reason it had been included in its own subfamily, named Lebanoculicoidinae by Borkent (2000). The new morphotype differs mainly from the other known species by having ovoidal flagellomeres (not cylindrical) and R4+5 vein terminating in a basal position before reaching the wing apex.

DISCUSSION AND CONCLUDING REMARKS

Stratigraphic and sedimentologic analyses of the amber-bearing deposit of the Lower Albian Las Peñas Fm. indicate that it was deposited on a regressive deltaic-estuarine environment. Facies associations are assigned to three different depositional units (P1 to P3). The stacking of these units and their internal vertical and lateral relationships resulted from an overall marine regressive phase followed by a transgressive marine phase, with the resin accumulation occurring at the most regressive part of the regressive-transgressive sequence (Unit P2). Sedimentological analysis of this unit suggests that the amber deposit constitutes part of the infilling of interdistributary bays, which are laterally associated with distributary meandering channels. The amber-rich beds always contain abundant fragments of carbonaceous material, wood fragments and leaves that still preserve the vegetal textures. The amber-rich beds appear associated with laminated, organic clays, but also with discontinuous beds of massive to laminated sandstones and siltstones with disorganized fragments of woody material. These deposits also contain shells of marine and/or brackish-water molluscs, which suggest a littoral to coastal marsh environment of deposition. Therefore, the suggested depositional scenario for the amber-rich beds is an environment of low-energy coastal and interdistributary bays connected with the sea and affected episodically by higher-energy conditions. Floods during rainstorms eroded and removed the amber and plant remains from their original place of accumulation at the soils of the coast-fringing forest. Then, the amber and plant fragments were transported by density flows that carried large amounts of these materials, mixed with mud and sand, to the coastal and interdistributary bays, where were rapidly accumulated and buried. Most

of the amber pieces show their original form of sub-rounded and stalactite-shape suggesting little erosion during transport. A remarkable characteristic of this amber deposit is the unusual accumulation of aerial amber pieces that contain abundant arthropod and other bioinclusions.

The El Soplao deposit likely originated during a period of abundant production of fluid resin within the palaeoforests, possibly coinciding with a warmer episode. The plant-cuticle assemblage of the El Soplao deposit is quite reminiscent of that from the Albian of Rubielos de Mora (Teruel Province); (Gomez, 2000, 2002; Gomez et al., 2000, 2002). However, the latter deposit has poorly preserved amber and identification at the species level is tenuous, lacking the precision for any determination of amber production. Araucariacean trees are the suggested resin-producing plants during the Cretaceous (Alonso et al., 2000; Chaler and Grimalt, 2005), but leaf remains of this group of conifers are absent from the El Soplao assemblage, although they occur in other similar Spanish deposits. Future palynological studies will complete our understanding of the palaeobotanical context of this deposit.

The abundance of fossil insects in the Early Cretaceous amber of El Soplao is particularly important for further evolutionary studies and palaeoecological reconstructions. This abundance is a consequence of the unusual concentration of amber flows (stalactite-like amber flow pieces and crusts), which contain the most bioinclusions. The fidelity of the arthropod preservation in this amber allows for detailed studies of the ancient forest biota, similar to other Spanish ambers. The Albian age of the El Soplao amber also is of particular importance because during this period certain groups of insects were diversifying to become major pollinators of the first flowering plants. In this context, the presence of spiders and their entrapping aerial webs in El Soplao amber reinforces the hypothesis advocated by Peñalver et al. (2006, 2008) which associates the diversification of spiders to the radiation of winged (pterygote) insects.

Several insect specimens recorded from the El Soplao amber are very scarce in the fossil record, for instance wasps and dipterans. Such is the case for the wasp specimen that belongs to the extinct family Mymarommatidae. Discovery of a new form of the rare dipteran *Lebanoculicoides* in the El Soplao amber indicates that this basal genus had a much more extensive distribution than previously supposed during the Early Cretaceous. Consequently, any new findings of fossil representatives of these groups would be of particular interest.

The FTIR spectra of the El Soplao amber are quite similar to other previously studied Spanish Cretaceous ambers.

However, further investigations are necessary to complete the study of this new locality, including the taphonomic study of the deposit in order to know its origin, the palynological analysis of the amber-bearing stratigraphic sequence, determination of plant species represented as cuticles, and the taxonomic study of the arthropods included within the amber.

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