



Palaeoenvironmental reconstruction of the early Anisian from sedimentology and plant remains in the SE Iberian Range (E Spain)

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ABSTRACT

The end of the Permian period is characterized by the largest mass extinction ever recorded in marine and terrestrial sedimentary rocks. The oldest plant macro-remains after the P–T boundary recorded in the Castilian Branch of the Iberian Range after this mass extinction belong to the Eslida Formation of Anisian age. These associations have been recovered at four localities and include sphenophytes (*Equisetites*, perhaps *Neocalamites* or *Schizoneura*), conifers (*Volzia*, *Albertia*, *Pelourdea*), lycophytes (*Pleuromeia*) and a possible seed fern (*Peltaspermum*).

Facies associations and sedimentological analysis of the Eslida Formation have allowed for distinguishing four architectural elements: CH (channel deposits), LA (lateral accretion), CS (crevasse splay) and FF (overbank fines). The largest fossil remains are associated with CH and LA architectural elements and high-energy events, and they form part of the basal lag or reactivation surfaces. Smaller and well-preserved fragments are associated with the CS architectural elements.

A sedimentologic, taphonomic and palaeoclimatic analysis reveals gradation from riparian hygrophytic vegetation to semi-arid xerophytic vegetation across the alluvial complexes and a progressive aridification through time. A comparison with other areas shows that this association is similar to coeval floras of Iberia and of the “Grès à Voltzia” Formation of northeastern France.

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1. Introduction

The end of the Paleozoic saw the most significant biotic crisis in the history of the Earth. The crisis affected both terrestrial and marine environments, killing over 90% of the species in the oceans and approximately 70% of vertebrate families on land (Erwin et al., 2002; Benton, 2003). Although the causes of this massive extinction are still under discussion, there are several hypotheses about the different processes that could be related to it. Two of the most well-supported processes are a period of volcanic activity in Siberia that lasted over one million years (Heydari et al., 2008; Hong et al., 2011) and emitted CO₂ and other gases into the atmosphere and the release of CH₄ trapped in the sea bottom and in permafrost (Krull et al., 2000; Huynh and Poulsen, 2005). Both processes induced an increase in the global temperature and more widespread arid conditions (Smith and Botha, 2005), changes in the global oceanic and atmospheric circulation (Kidder and Worsley, 2004), a sea-level rise (Kidder and Worsley, 2004) and an anoxic

oceanic event (Wignall and Twitchett, 2002; Woods, 2005), among other consequences. The difficult environmental conditions continued during the Early Triassic and led to a slow biotic recovery compared with the recovery periods of other extinction events (Corsetti et al., 2005).

Studies on how the Permian–Triassic crisis affected plants have proposed a heterochronous and gradual change from opportunistic groups such as lycophytes and ferns to seed ferns and conifers (Retallack, 1995; Benton and Twitchett, 2003), with a “transitional” flora that occurred between the palaeophytic to the mesophytic floras (Willis and McElwain, 2002). In Europe, studies on Triassic plants have suggested an Early Triassic stage with a *Pleuromeia*-dominated flora, followed by a recovery interval with the resurgence of conifers (equatorial forests) during the Middle Triassic. This recovery interval ended in the late Anisian, when a highly diversified flora was re-established (e.g., Grauvogel-Stamm and Ash, 2005; Kustatscher et al., 2010). This reconstruction has been recently discussed again because of the discovery of a well-diversified late Early Triassic flora from Germany with a mixed flora of *Pleuromeia*, ferns, horse-tails and conifers (Kustatscher et al., 2014). Due to the poor and scarce preservation of plant fossils in the first sediments after the end-Permian

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crisis, some aspects of Early Triassic plant communities are still poorly understood, such as the extent of this crisis on species and group levels and the time constraints of the recovery phases. Most data are now based on palynomorphs (e.g., Looy et al., 1999; Hochuli et al., 2010a,b). While it seems to be agreed that the boundary is characterized by a spore peak with a very low diversity (e.g., Looy et al., 1999; Hochuli et al., 2010a,b), the time constraint and dynamics of the biotic recovery are still very much debated.

On the Iberian Peninsula, except for some undetermined plant debris, Triassic plant remains come from the Anisian (Almera, 1909; Schmidt, 1937; Müller, 1969; Boulouard and Vilallard, 1982; Arribas, 1984; Calzada, 1987; Doubinger et al., 1990; Díez et al., 1996, 2007, 2010; Díez, 2000). The so-far best-preserved plant remains have been found in the Aragonian Branch of the Iberian Range (Rodanas section). The flora is dominated by conifers (*Voltzia*, *Albertia*, *Yuccites*, *Willisostrobos*, *Darneya*), while remains of horsetails (*Equisetites*) and *Cycadocarpidium*-like cones are rare. This flora shows a similarity to the early Anisian flora of the Grès à *Voltzia* Formation (Fm.) in the northern Vosges (NE France; Díez et al., 1996).

Considering the open question regarding the recovery time of the plant remains and the palaeoenvironmental changes after the end-Permian mass extinction, any new findings of well-exposed sections yielding plant remains will shed new light on this topic. This paper provides an overview of the sedimentology and architectural elements of the Eslida Fm. in the Cedrillas, Corbalán, Montán and Gátova sections (SE Iberian Range, Spain). The plant remains, together with sedimentological studies of the fossiliferous levels, permit taphonomic interpretations for the plant remains and enable hypotheses on the palaeoenvironmental settings of the earliest Spanish floras after the end-Permian mass extinction.

2. Geological setting

At the end of the Permian and in the Early Triassic, Iberia was located at the eastern side of central Pangea. It was a small plate assembled in the southernmost part of the ancient Laurentia megacontinent (Arche and López-Gómez, 1996; Van Wees et al., 1998; López-Gómez et al., 2002; De Vicente et al., 2009; Vargas et al., 2009).

The present-day Iberian Range is an intracratonic linear alpine structure occupying central and eastern Spain, which was created by inversion tectonics during the Alpine compressive events in an extensional Mesozoic basin: the Iberian Basin. The origin of the Iberian Basin was related to the development of a fault-bounded multistage rift basin during the Cisuralian–Guadalupian (Arche and López-Gómez, 1996; Vargas et al., 2009). This basin started its development on a Variscan basement of Cambrian–Silurian slates and quartzites affected by low-grade metamorphism (Capote and González-Lodeiro, 1983; De Vicente et al., 2009).

The Iberian Range is subdivided into the Castilian and the Aragonian branches towards the southwest and northeast, respectively (Fig. 1). These are morphological alpine structures hundreds of kilometres long, trending NW–SE and separated by different Cenozoic basins. These major structures are controlled by basin boundary faults that acted as normal faults during the Mesozoic development of the basin and were later reactivated as reverse faults during the alpine compression. During the evolution of the rift basin, a series of accommodation faults were developed almost perpendicularly to the main NW–SE extensional faults, which allowed block differentiation during the basin refill.

In the Castilian Branch, the refilling of the Iberian Basin started during the Early Permian and consisted of a well-developed series of alluvial deposits (López-Gómez and Arche, 1993a; Arche and López-Gómez, 1996). Above these rocks, and separated from them by an important hiatus, expressed sometimes as an angular unconformity, are the first Triassic deposits, the so-called Buntsandstein facies of Olenekian–early Anisian (Early–Middle Triassic) age (Fig. 2). These deposits are mainly fluvial but also aeolian in origin (Bourquin et al., 2007, 2011; Soria et al., 2011; López-Gómez et al., 2012). During the Anisian and Ladinian times, these sediments were covered by shallow marine carbonates (Muschelkalk facies) related to the first westward incursion of the Tethys sea (Fig. 2; López-Gómez and Arche, 1993a; López-Gómez et al., 1993, 1998, 2002).

The continental sediments are broadly organized into three main depositional sequences (S1, S2 and S3), the two lower ones for the Permian sediments and the upper one representing the Triassic rocks (Fig. 2). Where the sedimentary record is complete, the Triassic continental sequence consists of the Cañizar and Eslida formations, from base to top,

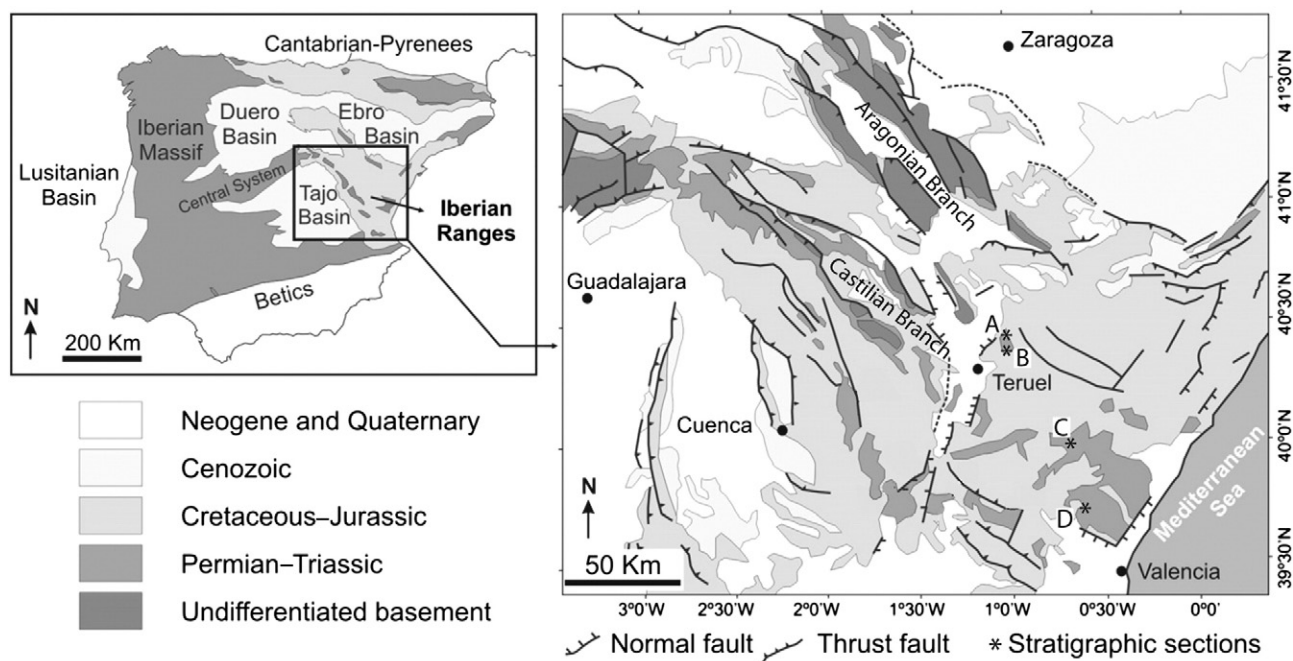


Fig. 1. Geographical location of the studied area with superimposed studied sections. (A) Cedrillas, (B) Corbalán, (C) Montán, and (D) Gátova.

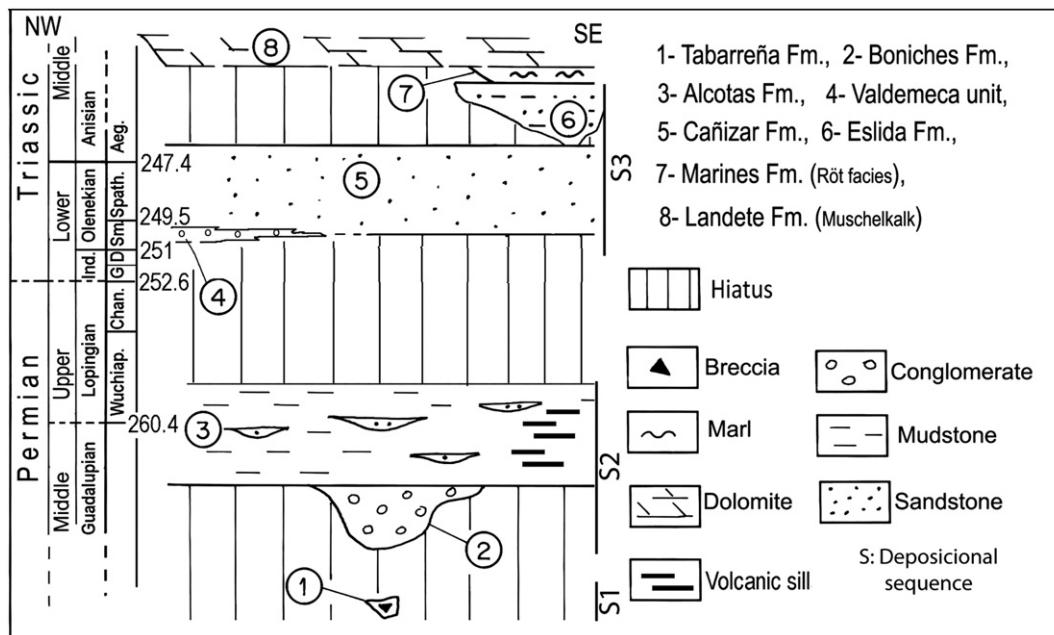


Fig. 2. Scheme of the Permian and Triassic sedimentary successions in the Iberian Ranges, depositional sequences (S1, S2 and S3), associated unconformities and hiatuses.

respectively, and the Valdemeca Unit, which constitutes the lowermost part of the Cañizar Fm. in some areas of the Castilian Branch (Fig. 2). The present work focuses on the Eslida Fm., in the SE of the Castilian Branch, where four sections have been studied, called Cedrillas (40°27'58"N, 0°55'35"W), Corbalán (40°24'25"N, 0° 55'16"W), Montán (40°1'37"N, 0°37'40"W) and Gátova (0°31'12"N, 39°46'15"W) (Fig. 1).

2.1. Stratigraphy

The Cañizar Fm. is mainly constituted by red to pink sandstones. The sandstones are mainly arkoses, although subarkoses and quartzarenites are also present. They have a fine–medium grain size and are composed of subrounded quartz and albite grains embedded in a matrix composed of illite and hematite (Alonso-Azcárate et al., 1997; Benito et al., 2005). This formation has been interpreted as deposited by braided fluvial systems with some aeolian reworking (López-Gómez et al., 2012). Sandstone bodies consist of thinning-upward and fining-upward sequences, tens of centimetres thick that constitute up to six subunits separated by major boundary surfaces (Fig. 3; Arche and López-Gómez, 1999a, 2005). These surfaces are recognized in the entire basin and represent regional erosion surfaces resulting from the reorganization of fluvial depositional systems following pulses of basin-margin faulting and gentle regional tectonic tilting (López-Gómez and Arche, 1993a; Arche and López-Gómez, 1999a,b).

The top of the formation is dated as early Anisian (Middle Triassic) by means of pollen and spores (Doubinger et al., 1990), but the age of the base is not well constrained. It could be Scythian, but is most likely Olenekian, Early Triassic, (López-Gómez and Arche, 1993b.) This would indicate a long period of slow, intermittent deposition. No well-preserved macro-remains have been found in this formation.

The Eslida Fm. normally lays with a hiatus on the Cañizar Fm. and is mainly composed of red siltstones and red or pink sandstones, generally in a 60–40% proportion, and isolated carbonated palaeosols. Sandstones are fine- to coarse-grained arkoses. They are composed of poorly to well-sorted subrounded to subangular–angular quartz and feldspar grains embedded in a clayey matrix. The clay mineral assemblage in these continental sedimentary rocks is dominated by illite, with minor proportions of kaolinite or pyrophyllite (Alonso-Azcárate et al., 1997;

Galán-Abellán, 2011). Large detrital mica crystals are commonly concentrated at the top of the fine-grained sandstones.

The facies represent channels and floodplain sediments deposited in mainly braided but also in meandering fluvial systems into a wide and open basin during a seasonal climate with intercalated dry and more humid periods (Arche and López-Gómez, 1999a). Plant remains and indeterminate organic matter are present in different levels along the studied sections.

In the Eslida Fm., one single pollen and spores assemblage was described by Boulouard and Vilallard (1982) in the Sierra del Espadán section and it was dated as early Anisian (Aegean–Bithynian). Although this association was described as belonging to the Alcotas Fm., we think the position of this sample may be incorrect. Although we have not yet found microflora in this section, a detailed sedimentological study carried out by Arche and López-Gómez (1999b) points to the inclusion of this assemblage in the Eslida Fm., close to the Muschelkalk Facies.

The Eslida Fm. will be the focus of the present study because the first well-preserved Triassic plant macro-remains appear in this formation.

The basal part of this formation was deposited in half-grabens in the eastern part of the Iberian Range, while later, rapid subsidence allowed the development of a wider basin with more symmetrical characteristics (Arche and López-Gómez, 1999a, 2005). As a result, the thickness of this formation is highly variable, being thicker at the centre of the basin and thinner at the border (Fig. 2), where only the uppermost part of the formation is represented.

In the Eslida Fm., six subunits representing main sedimentary sequences can be identified (Fig. 3; Arche and López-Gómez, 2005). These sequences are probably related to different tectonic and climatic pulses that can be followed through the whole basin (López-Gómez and Arche, 1993a,b; Arche and López-Gómez, 1999a,b).

The base of the Cedrillas and Corbalán sections is faulted, and the Cañizar and the lower part of the Eslida Fm. are not represented. The base is similar in the Montán and Gátova sections for the Eslida Fm.; however, the Cañizar Fm. is wholly represented, and its subunits can be distinguished and correlated. In the latter sections, the subunits of the Eslida Fm. are less developed than in the Corbalán section because the Gátova–Montán sector was located near the basin boundary. A

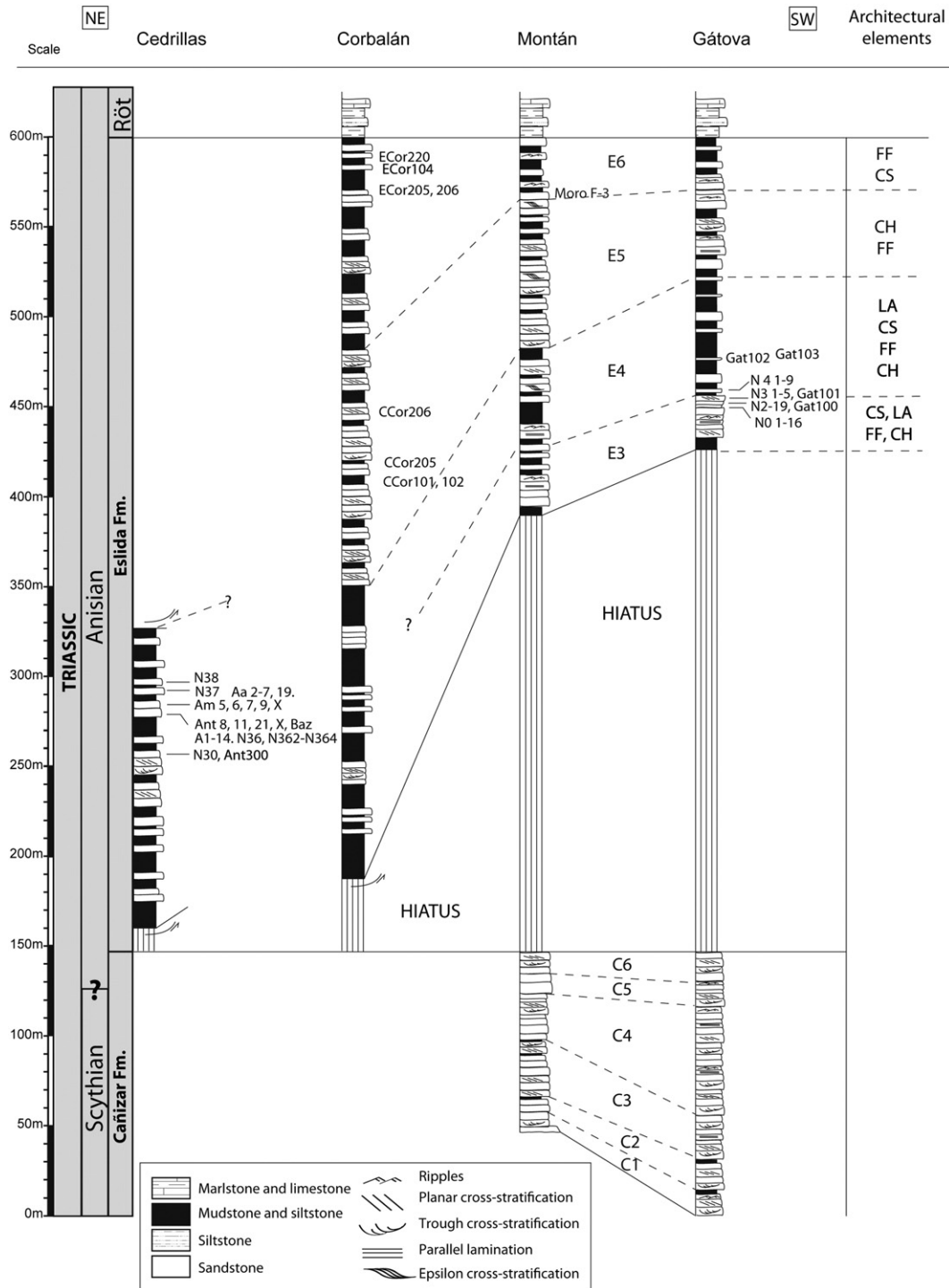


Fig. 3. Studied stratigraphy sections and location of the fossil macroflora samples (e.g., N38, CCor206). C1 to C6 and E3 to E6 indicate differentiated subunits in the Cañizar and Eslida formations respectively (Arche and López-Gómez, 1999a). Dominant lithologies are muds and silts (black) and sandstones (white). See Fig. 1 for the location of the sections.

more detailed study of the location of these subunits in the different sections is shown in Arche and López-Gómez (1999a,b).

3. Material and methods

In the studied sections, one of the largest associations of plant remains for the early Anisian (Middle Triassic) of the Iberian Peninsula has been found. Each horizon was examined in vertical and lateral

(spatial) contexts for plant-fossil assemblages. Although these remains are poorly preserved and generally represented by stem fragments, there are a few exceptions in which the preservation is sufficient for identification.

Each stratigraphic section was measured and described using conventional parameters (e.g., body geometry, grain size, Munsell colour, primary sedimentary structures, palaeontological attributes). In addition, there has been a detailed sedimentological study of fossiliferous

levels, including performance of facies analysis, definition of architectural elements and interpretation of the depositional environment in which the plants were deposited.

The field descriptions of the sediments and their sedimentological interpretation are based on facies, facies associations and architectural element differentiation, and they mainly follow the Miall, 1978, 1996, 2014 classification, with some modifications by the authors.

The taphonomic study follows Krassilov's (1975) criteria, as modified by Allen and Gastaldo (2006) and included thickness of the plant-bearing unit, relationships between plant material and sediments, the arrangement of axes in sediment (prostrate or erect, flat-lying or dispersed three-dimensionally), the aggregation of assemblages (concentrated or dispersed), the size of the remains (heteromeric versus isomeric), ordered (plants have a "dynamic" orientation; e.g., parallel arrangement) versus disordered (plants are oriented randomly on bedding planes), the concentration of debris, and mode of preservation.

Measurements were taken using Adobe Photoshop, and angles were measured with ImageJ. The angles between plants at each level were plotted and analysed statistically (Bateman, 1999) using Oriana v. 2.02 (Kovach Computing).

4. Sedimentology of the Eslida Fm.

The study of the Eslida Fm. is based on the differentiation of facies, facies associations and the definition of architectural elements. Facies are classified on the basis of the primary depositional attributes of the beds, notably bedding, grain size, texture, and sedimentary structures. Facies associations will result from the most common lateral and vertical combination in the rocks of the defined facies. The combination of the facies will constitute the main architectural elements of the Eslida Fm. Previous studies related to facies description and interpretation were published in Arche and López-Gómez (1999a,b, 2005).

4.1. Facies

A total of eight facies related to sandstones and mudstones and, punctually, siltstones have been differentiated in the Eslida Fm. (Table 1). Sandstones range from fine to very coarse and show colours ranging from pink to dark red. The thickness of the sandstone facies varies from 0.1 to 0.9 m, and they are mostly related to lower–upper flow regime bedform development. The plants and plant remains are basically related to these sandstone facies. These facies are St, Sp, Sh, Sr and Se.

Facies constituted by mudstones show colours ranging from dark pink to dark red, and their thickness may reach up to a few metres. A

total of five facies have been differentiated within the dominant mudstone lithology, and they are normally related to overbank deposit development. These facies are Fm, Fl and Ff. Some facies associations are constituted by the interaction of both sandstone and mudstone facies.

Facies St: sandstones with trough cross-stratification

These normally show fining-upward tendency, such as those described by Cant and Walker (1978) in the South Saskatchewan River. Isolated poorly sorted sand with siltstones and plant remains may be present as a lag at the base of the trough. Clay chips and, occasionally, reactivation surfaces can appear. This facies is interpreted as the result of the migration of sandstone dunes with sinuous crests of linguoid type in shallow waters.

Facies Sp: sandstones with planar cross-stratification

These normally show a fining-upward tendency and a cross-bedding angle ranging from 15 to 30°, with sharp and angular upper and lower terminations indicating avalanching on the foresets. Small reactivation surfaces are common, such as those described in the Tana River by Collinson (1970). Little evidence of scouring is common in the upper and lower bounding surfaces. This facies is interpreted as resulting from the migration of small-scale two-dimensional dunes, linguoid or transverse bars, and sand waves (lower flow regime) in shallow water. Sand is transported up the flank of the bedform by traction and intermittent suspension and is deposited at the crest, sometimes forming a carpet of small-scale current ripples. Occasionally, small current ripples are preserved at the toe of the avalanche slope.

Facies Se: sandstones with epsilon cross-stratification

These show cross-cutting erosion surfaces within macroforms that dip at a low angle and may truncate underlying cross-bedding at a low angle cutting through more than one cross-bed set. These surfaces also represent Miall (1996) third-order surfaces and indicate a form of large-scale reactivation in the sense of Collinson (1970).

Facies Sh: sandstones with parallel lamination

These commonly show parting lineation occurring on bedding planes, such as those described by Nyambe (1999) in the Lower Karoo Group, Zambia. This facies is interpreted as a planar bed flow in the upper-stage phase (upper flow regime). This facies may be deposited during a single dynamic event, such as a flash flood, when flow conditions may remain in the critical stage for short periods of time.

Table 1

Facies codes and sedimentary environment interpretation used in this work. Most of them are modified from Miall (1978, 1996), with some newly added codes.

Code	Facies	Colour	Sedimentary structures	Interpretation
St	Sand, medium to very coarse	Red–pink	Solitary or grouped trough cross-beds	Sinuuous-crested 3-D dunes
Sp	Sand, medium to very coarse	Red–pink	Solitary or grouped planar cross-beds	Linguoid and transverse bedforms 2-D dunes
Se	Sand, medium grain size	Red	Solitary or grouped epsilon cross-beds	Point bars
Sh	Sand, fine to medium grain	Dark pink	Horizontal lamination, parting or streaming lamination	Planar bed flow
Sr	Sand, fine to medium grain	Pink	Ripple cross-lamination	Ripples
Fm	Mud, silt	Red–brown	Massive, desiccation cracks (sporadic roots)	Overbank, abandoned channel, drape deposits
Fl	Mud to fine grain sand	Red–brown	Fine lamination and very small ripples	Overbank or waning flood, punctual traction currents
Ff	Mud to fine grain sand	Brown–pale green	Flaser bedding	Overbank with tidal influence
Architectural element		Facies association		Thickness
CH Channel		FA1: Sp, St, Sr		5th order finning-upwards <1.5 m thick <14 m long
LA Lateral accretion		FA2: Se, Sp, St, Fm		3rd order finning-upwards <1.5 m thick <20 m long
CS Crevasse splay		FA3: Sp, St, Sr, Sh, Fm, Fl		2nd order finning-upwards <0.5 m thick 100 s m long
FF Overbank fines		FA4: Fm, Fl, (Ff)		– 10 s m thick 100 s m thick

Facies Sr: ripple cross-laminated sand

It shows different types of asymmetric ripples that will depend on the flow velocity and the rate of sediment supply, as described by Allen (1984). This facies is interpreted as sedimentation during low-stage phase bed movements. Trains of ripples are occasionally mutually erosive or partially erosive when sediment is added from suspension during ripple migration, leading to partial preservation of the stoss sides of the ripple and constituting the so-called climbing ripples, related to settings where the river carries a large load of very fine sand (Jopling and Walker, 1968).

Facies Fm: massive mudstones or fine-grained sandstones

This facies shows vertically oriented root casts, and it represents the deposits from standing pools of water during low-stage channel abandonment (Miall, 1978). It may show carbonaceous nodules, plant roots, and desiccation cracks. These mudstones and sandstones normally conform their bottom with the shape of any underlying bedforms. This facies is interpreted as a distal floodplain facies, although Rust (1978) included this facies in other alluvial sedimentary settings.

Facies Fl: mudstones or fine-grained sandstones with fine lamination and very small ripples

Ripples mostly appear in the sand beds. Scattered bioturbation, including footprints and halite pseudomorphs, may also be present. This facies is interpreted as overbank or waning flood deposits and represents deposition from suspension and from weak traction currents. This facies may appear punctually in more-energetic floodplain traction currents, such as crevasse splay deposits (Miall, 1996).

Facies Ff: mudstones and fine-grained sandstones with flaser bedding, bioturbation and punctually asymmetric and symmetric ripples

This facies is restricted to the uppermost part of the Eslida Fm., in the transition with the Marines Fm. (Röt facies), and is interpreted as fine-grained floodplain deposits interbedded with tidal-influenced estuarine deposits, similar to the present-day San Simon Estuarine Complex described by Nombela et al. (1995) and Allen and Fielding (2007).

Lateral association and vertical succession of facies in the field allow us to separate different sedimentary sequences representing different sedimentary types (Morrison and Hein, 1987; Nyambe, 1999; Allen and Fielding, 2007).

4.2. Facies associations

Four main facies associations have been recognized among the differentiated facies: FA1, FA2, FA3 and FA4 (Table 1). FA1 is entirely represented by sandstone facies. It normally constitutes fining-upwards sequences 1–1.5 m thick, where St facies is located in the lower part on an erosive surface and Sp facies is above, with Sr facies in the uppermost part. This facies association is commonly stacked, forming sedimentary successions that may reach tens of metres. Present-day examples have been described by Cant and Walker (1978) in the South Saskatchewan River, Canada.

FA2 is mostly represented by sandstone facies and Fm. facies (Table 1). It normally constitutes fining-upwards sequences 0.8–1.3 m thick, where Sp facies laterally passes to Se facies in the lower part, both disposed on fine sediments by an erosive surface, and Sp and St facies together with Fm facies are above or lateral to the two previous ones. Similar examples have been described by Jackson (1981) and in the present-day Beaver River, Canada, by Burge and Smith (1999). This facies association is commonly isolated between mudstones, although sometimes these mudstone beds are very thin and sandstone bodies are in contact.

FA3 is represented by both mudstone and sandstone facies (Table 1). It constitutes successions up to 0.5 m thick, that may be fining-upwards and is represented by Sp and St facies in the lower part and Sr, Sh, and Fm or Fl at the top, all of which may rapidly change laterally. This

association is normally isolated into mudstones. Similar examples were described by Ramos et al. (1986) in Triassic red beds of Central Spain.

FA4 is entirely represented by mudstone facies (Table 1). It constitutes sheets that may reach more than 1 km in lateral dimensions and are tens of metres thick. Fm and Fl are the most representative facies of this association, and they normally appear alternatively in vertical succession, such as those described by Willis and Behrensmeyer (1994) in the Miocene overbank deposits of Pakistan. Ff facies is occasionally represented in this succession.

4.3. Architectural elements

The alluvial architecture is the geometric response to the different alluvial styles in terms of the stacking of sediments, so facies associations constitute the base for defining architectural elements. Hence, a body type is a channel, laminated sand sheet or sandy bedform with particular facies and facies association, and the characteristics of the body type groups could give rise to characteristic fluvial architectural bodies (Miall, 1985; Eberth and Miall, 1991; Fielding, 1993; Miall, 1996, 2014) or body geometries.

The vertical evolution of architectural elements in the Eslida Fm. mostly consists of channel (CH) and lateral accretion (LA), as architectural elements formed within channels, and crevasse splay (CS) and overbank fines (FF) related to overbank environments outside the channels. The latter is the most representative in the vertical succession of the Eslida Fm., while those related to channels appear intercalated within the FF element (Fig. 4). Deposits formed outside the main fluvial channel may include ephemeral sheet floods and more permanent floodplain ponds. These elements are bounded by different Miall (1996) order surfaces.

The architectural element CH appears in subunits E3, E4 and it is very common in subunit E5 and mainly consists of facies association FA1, with internal erosional and reactivation surfaces (rs) and an erosional base (eb). Major channels are bounded by fifth-order surfaces. These represent a channel-fill complex of sandstones with defined margins and show a concave-up erosional base and internal reactivation surfaces (rs), similar to examples described by Gibling (2006). The channels may reach a thickness of 1.5 m and a width of approximately 14 m, with plant remains and trunks normally located at the base or in the internal reactivation surfaces (Fig. 5a, b). The architectural element represents channel-fill sandstone bodies deposited during important lateral shifts. As a result, there are frequent internal erosive surfaces in the mesoforms that make it difficult to find outcrops showing channel margins. Minor channels may include partially to completely abandoned channels as well as other channels crossing sandflats that are generated in falling water (Bristow, 1987). The CH architectural elements are related to braided fluvial systems in proximal and medial areas and show concave-up fills deposited mainly by vertical or oblique aggradation during progressive or sudden abandonment, similar to examples described by Hopkins (1985) and Okolo (1983). Channels filled by simple vertical aggradation commonly show fining-upwards successions reflecting a progressive abandonment as a result of upstream avulsion, so the thicknesses of these channels do not exceed the depth of the channel (Miall, 2014). The measured palaeocurrents are always unidirectional, and most of them trend towards the east, always spreading at less than 35°.

The architectural element LA is constituted by facies association FA2, with reactivation surfaces (rs) and erosive boundaries (Fig. 4). The presence of these facies varies markedly depending on the sediment load and the discharge variability (Jackson, 1981; Smith, 1987). This architecture can be interpreted as a lateral accretion of sand mesoforms or point bars that may have preserved abandoned channel deposits, where plant remains may appear accumulated between fine sediments (Fig. 5c, d). The point bar would result from lateral growth of a compound, bank-attached macroform. Deposits of LA elements reflect the

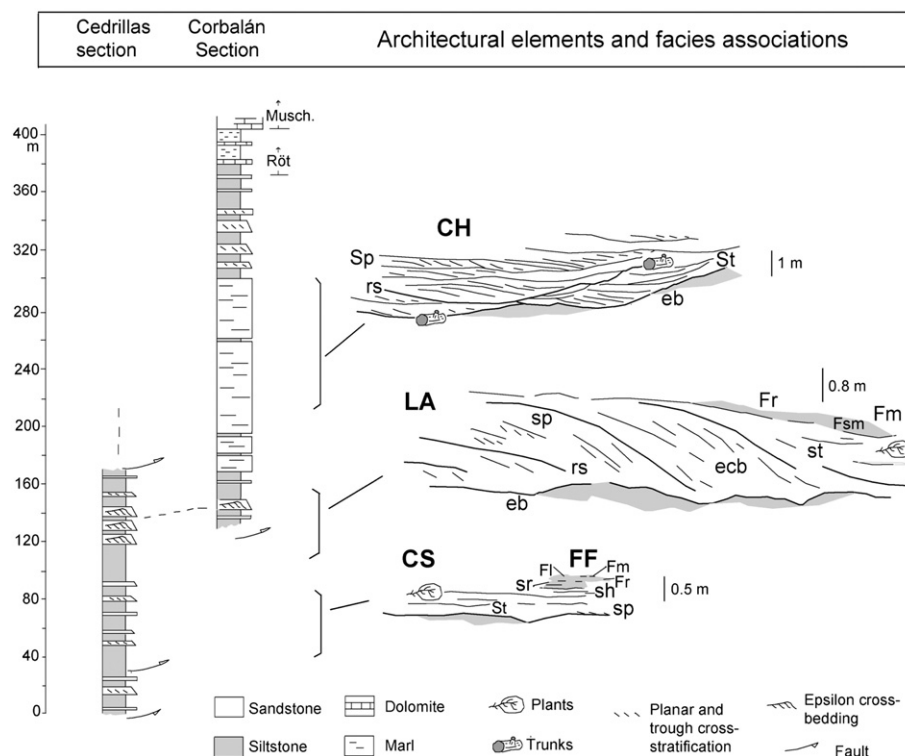


Fig. 4. Facies associations (St, Sp... for more information about this facies, see Table 1) and architectural elements (CS, LA, CH and FF) differentiated in the Eslida Fm. These examples are described in the Cedrillas and Corbalán sections but can also be observed in the Montán and Gátova sections (Arche and López-Gómez, 1999a,b).

long-term behaviour of large-scale vortices affecting the entire turbulent boundary layer (Crowley, 1983). These mesoforms are common in subunits E3 and E4 and may reach a thickness of 2 m and a length of 25 m separated by a pile of sediments represented by FF architectural element. Their lower termination downlaps onto the channel floor by means of third-order surfaces. This architectural element can be vertically connected with other similar elements or isolated and bounded by a FF architectural element, as in the examples described in the Miocene Ebro Basin by Donselaar and Overeem (2008). The LA architectural element is up to 20 m long and up to 1.5 m thick. The height or thickness of the element approximates the bankfull depth of the channel. The spread of the measured palaeocurrents reaches up to 105°, trending NW–SE.

The architectural element CS is constituted by an FA3 facies association in lens-shaped bodies less than one metre thick but hundreds of metres across (Fig. 4). The assemblages are characterized by thin bedding and abundant surfaces of non-deposition and small-scale erosion of a second-order surface. This architectural element is interpreted as a non-channelized crevasse splay deposited into the floodplain and adjacent to the margins of the main channels, representing short-lived structures where the plant remains are located on the top (Fig. 5e, f). This architectural element shows fourth-order bounding surfaces and is a result of flow expansion and loss of flow power as discharge leaves the confines of the channels and spreads out as sheet floods. Examples in ancient rocks were described by Gersib and McCabe (1981) from the Carboniferous of Nova Scotia and by Allen and Williams (1982) from the Devonian of South Wales. This element is interbedded with sediments represented by the FF element and is common in all subunits except E5.

The architectural element FF is represented by fine sediments and is constituted by an FA4 facies association. This element consists of sheet-like beds many hundreds of metres in lateral extent and tens of metres thick (e.g., Willis and Behrensmeier, 1994). It represents deposits of

overbank sheet flow that may include floodplain ponds. It is common throughout the subunit and normally separates CH, LA and CS elements (Figs. 4, 5e). In subunit E6, at the top of the Eslida Fm., Ff facies may be present together with Fm and FI facies, already indicating a marine influence.

The general vertical location of the architectural elements in the subunits and their sedimentary characteristics indicate long periods of floodplain development with isolated fluvial channels crossing huge areas where plants and soils were developed. This situation was predominant during the deposition of subunits E3 and E4 but suddenly changed at the beginning of subunit E5, when the broad development of channel systems with important lateral shift impeded floodplain sediment accumulation (Arche and López-Gómez, 1999a, 2005). A new sudden change appears in subunit E6, where the appearance of Ff facies may indicate the beginning of the marine transgression, leading to Röt facies and the appearance of Muschelkalk-type rocks (López-Gómez and Arche, 1992).

5. The plant assemblages

5.1. Cedrillas

Most plant remains at the Cedrillas section correspond to casts or impressions of the vascular bundles of sphenophytes. The stem fragments are up to 22 cm long and 7 cm wide and show clear nodes and impressions of vascular bundles (e.g., N37a, N362, N38a, N36, N38b; Fig. 6f). The leaf sheets are not preserved, as is typical in one of the most common sphenophyte taxa of the Buntsandstein, *Equisetites mougeotii* Brongniart, 1828–37, based on impressions of thick sphenophyte stems (e.g., Brongniart, 1828–37; Wills, 1910; Grauvogel-Stamm, 1978). Therefore, the axis fragments of the stems found in this section are attributed to *Equisetites mougeotii* as well. Several leaf fragments belong to *Pelourdea vogesiaca* (Schimper et Mougeot) Seward 1917



Fig. 5. The architectural elements, facies (St, Sp... for more information about this facies, see Table 1) and bounding surfaces differentiated in the studied sections. (a) Architectural element CH. (b) Plant remains in architectural element CH. (c) Architectural element LA. (d) Plant remains in architectural element LA. They are located in the abandoned channel, at the end of the picture, and covered with shrubs. (e) Architectural element CS. (f) Plant remains in architectural element CS.

(N30d, N36h). The lanceolate leaves are up to 170 mm long and 28 mm wide, with a slightly rounded apex and coarse, parallel veins. This taxon is one of the most common conifer taxa of the Middle Triassic of Europe (e.g., Schimper and Mougeot, 1844; Wills, 1910; Schlüter and Schmidt, 1927; Grauvogel-Stamm, 1978; Kustatscher and Van Konijnenburg-van Cittert, 2005; Kustatscher et al., 2012).

Additional conifer remains are represented by impressions of shoot fragments of the *Albertia* and *Voltzia* types. The shoot fragments and isolated leaves of *Albertia latifolia* Schimper and Mougeot 1844 are up to 35 cm long and 2.5 cm wide (N37a, Aa2, Aa5, Fig. 6c). The lanceolate to ovate leaves (10–15 × 2–6 mm) have a slightly rounded apex and are attached in a loose helix and with a constricted basis to the axis (2 mm). The leaves decrease apically in leaf width and are inserted more closely. The genus *Albertia* is known from the Anisian flora of France (e.g., Schimper and Mougeot, 1844; Grauvogel-Stamm, 1978), Spain (e.g., Díez et al., 2010) and Italy (e.g., Broglio-Loriga et al., 2002) as well from the Ladinian of Germany (Kelber and Hansch, 1995).

A first *Voltzia*-type of conifer is characterized by up to 30-mm-long and 6-mm-wide shoot fragments. The leaves are attached to 1 mm-wide axis in width in a close helix. They are distinctively falcate,

1.5–3 mm long and less than 1 mm wide. Even if the fragments are very small and the attachment of the lateral shoots to the primary axis is not preserved, the general morphology of the leaves (delicate, narrow and strongly falcate), suggests an attribution to *Voltzia walchiaeformis* Fliche 1910 (N30c, Fig. 6k); better preserved specimens need to be found to confirm this attribution. *Voltzia walchiaeformis* has been described from the Buntsandstein of France (Fliche, 1910; Grauvogel-Stamm, 1978) and perhaps from the late Anisian of the Dolomites (Broglio-Loriga et al., 2002).

Other impressions belong to *Voltzia heterophylla* Brongniart, 1828–37 (Ant 300, N362, N36g, Aa19, Fig. 6a, b). The shoot fragments are up to 120 mm long and 30 mm wide. From the axis, with a width of 2–3 mm arise, elongated to slightly falcate leaves with a length of 10–16 mm and a width of 1–2 mm and with a pointed apex at an acute angle. Apically, the leaves are elongated and sometimes occur only as a colouring of the sediment (Aa19, Fig. 6a). *Voltzia heterophylla* is typical for the late Buntsandstein of Germany (e.g., Blanckenhorn, 1886; Sander and Gee, 1994) and France (e.g., Brongniart, 1828–37; Schimper and Mougeot, 1844) but has most likely also been found in the Anisian of the Dolomites (Broglio-Loriga et al., 2002).

Dispersed in the sediment are also scale fragments of obovate shape (11–14 × 9–11 mm) with an elliptical to ovate fertile area

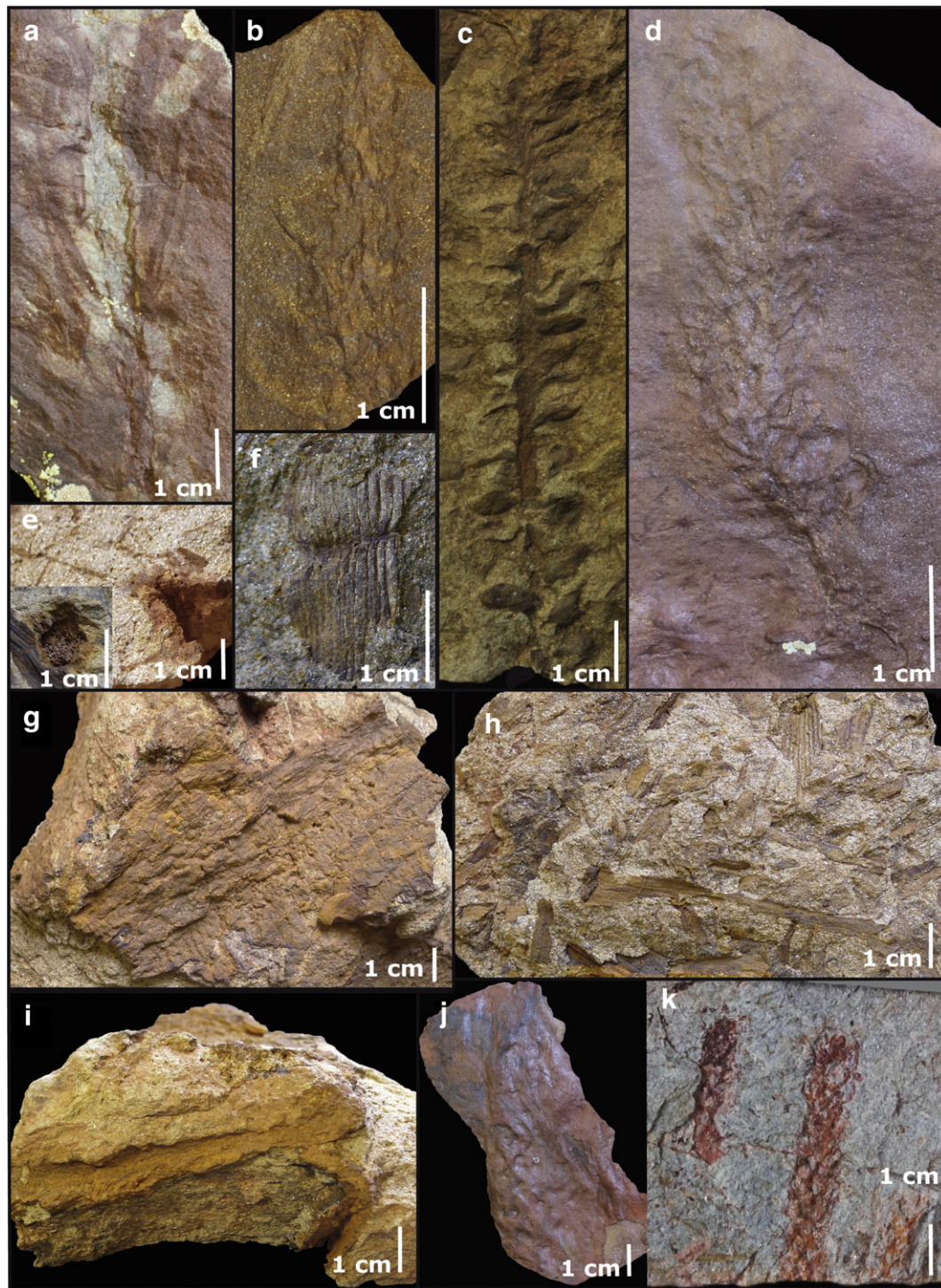


Fig. 6. Plant remains. (a, b) *Voltzia heterophylla* Brongniart, 1828. (c) *Albertia latifolia* Schimper et Mougeot 1844. (d) Female cone. (e) Three-dimensional hole interpreted as in situ root systems of sphenophytes. (f) Sphenophytes, most likely *Equisetites mougeotii* Brongniart 1828. (g) Shoot fragment of conifer. (h) Casts or impressions of indeterminate stem fragments and to vascular bundles of sphenophytes. (i) Three-dimensional shoot fragment. The fragment is the same as that in Fig. 6g. (j) *Pleuromeia sternbergii* (Münster) Corda ex Giebe, 1853. (k) Probable *Voltzia walchiaefornis* Fliche 1910.

(6–10 × 3–6 mm, e.g., N36c, N37a). The preservation is insufficient for any specific attribution, but these scales could well belong to lycophytes such as *Pleuromeia*. Similar fragments have recently been described from the Middle Buntsandstein (Solling Fm.) of Germany (Kustatscher et al., 2014). Also dispersed in the sediment are small root fragments, called in the literature *Radicles* (see also Kelber and Hansch, 1995; Kustatscher and Van Konijnenburg-van Cittert, 2008).

5.2. Corbalán

The plant assemblage of Corbalán is much less diversified; most remains are represented by small to medium-sized undeterminable stem fragments. So far, only two remains are identifiable.

One fragment is represented by a 52-mm-long and 15-mm-wide female cone (ECOR104, Fig. 6d). The cone is preserved only as a counterpart

of an impression; thus, there is little information regarding the general structure. The ovuliferous complexes are inserted in a close helix on the 3-mm-wide axis; each ovuliferous scale seems to bear one seed of 2–3 mm diameter. The preservation is unfortunately insufficient to determine the morphology of the ovuliferous scales; thus, a generic or specific attribution is not possible.

The second specimen is an impression of a stem fragment 10 cm in length and 5 cm in width (ECOR220, Fig. 6j). Roundish rootlet traces of 5×3 mm are arranged on the stem. This fragment can be putatively attributed to *Pleuromeia sternbergii* (Münster) Corda ex Giebe 1853, the most typical lycophyte of the Early–early Middle Triassic of Europe (e.g., Mägdefrau, 1931; Fuchs et al., 1991; Grauvogel-Stamm, 1993, 1999; Sander and Gee, 1994; Grauvogel-Stamm and Lugardon, 2001).

5.3. Montán

The plant remains in Montán are much scarcer than in the previous two sections. Most of them are indeterminable stem impressions. The stem fragments are up to 33 cm long and 1.5 cm wide. One specimen shows a roundish structure of 20–25 mm diameter with a central depression of 5 mm that could correspond to a *Peltaspermum*-like ovuliferous structure (e.g., Morof-3b). The specimen is too badly preserved to permit any certain attribution.

5.4. Gátova

The most abundant plant remains from Gátova correspond to casts or impressions of indeterminate stem fragments and to vascular bundles of sphenophytes. The stem fragments are up to 27.8 cm long and 8.3 cm wide (e.g., N0–10, N2–4, N3–5, N4–9, Fig. 6h). The sphenophyte fragments are up to 9 cm long and 4 cm wide and show clear nodes (e.g., N0–1, N0–11, N0–16, N2–10, N3–2, Fig. 6f). As in the Cedrillas section, the axis fragments could belong to *Equisetites mougeotii* Brongniart, 1828–37 (Brongniart, 1828–37; Wills, 1910; Grauvogel-Stamm, 1978), although it cannot be excluded that they belong to *Neocalamites* or *Schizoneura* because the stem fragments are in most cases very narrow.

The conifers are represented by impressions of shoot fragments. The thickest shoot fragment is 11.3 cm long and 8.1–4 cm wide and is preserved three-dimensionally in the sediment. Although the rough surface (bark?) is typical to the conifers, it is not possible to determine a genus due to the lack of diagnostic features (N0–6, Fig. 6g). One of the shoot fragments has poorly preserved leaf impressions, which may correspond to *Albertia* or *Voltzia* (N4–6). The best-preserved specimen of

this outcrop most likely belongs to *Albertia latifolia* Schimper and Mougeot 1844 (Gat100-1b). The shoot fragment is 25 cm long and 1.3 cm wide. The leaves are lanceolate, up to 5 mm long and 0.5 mm wide (although they are partially inserted in the sediment and thus the width is more like the thickness of the leaf) and decrease apically in leaf length and are inserted more closely. The axis is 1.5 mm thick.

Three-dimensional holes are observed in some of the samples (N0–5, Fig. 6e). These are cylindrical (1.3 cm diameter) and are positioned perpendicular to the channel bed through several layers of sediment. Kelber (1990, p 55–56, text-fig. 96) documented similar structures and interpreted them as in situ root systems of sphenophytes. These layers containing root traces were colonized by vegetation at some point and could represent poorly developed palaeosols.

6. Taphonomy

The plant remains of the Eslida Fm. occur in both channel- and floodplain-related deposits. An important aspect of their presence is the relation of the sedimentological and taphonomical processes that contributed to their preservation. A detailed description of the different architectural elements with plant remains is shown in the following sections.

6.1. Architectural element LA

In the Cedrillas section (subunits E3 and E4), plant remains were collected with a noticeable difference between the different levels of the section. The plant remains collected from architectural element LA (170 specimens collected in this architectural element) are the widest specimens that have been found. Most specimens are casts or impressions of undeterminable stem fragments (116), but sphenophyte stem fragments are also abundant (45). Several shoot fragments (6) belong to the conifers, of which three could be classified as *Voltzia heterophylla* and one as *Pelourdea vogesiaca*, while two remains could not be assigned to any conifer genus due to the bad preservation. Additionally, there are two scales most likely belonging to a *Pleuromeia*-type of lycophyte and root fragments (Table 2).

The stem sizes are highly variable; most fragments are small (7 cm \times 2.6 cm and 2 mm \times 0.7 mm). Nevertheless, in this architectural element larger trunks up to 22.5 cm in length and 8.8 cm in width are found. The average size of the fragments in the LA architectural element is 3 \times 1 cm (Fig. 7). The larger fragments are found at the base of the channels and on the reactivation surfaces, while the smaller fragments

Table 2
Relationship of plant remains with the lithofacies and the localities in which they were found.

	Cedrillas		Corbalán		Montán	Gátova
	E3, E4 subunits		E5 subunit	E6 subunit	E6 subunit	E3, E4 subunits
	Architectural element	Architectural element	Architectural element	Architectural element	Architectural element	Architectural element
	LA	CS	CH	CS	CS	CS
	Facies Se	Facies Sp	Facies Sp	Facies Sp	Facies Sp	Facies Sp
<i>Voltzia heterophylla</i>	3	3				
<i>Voltzia walchiformis</i>		1				
<i>Voltzia</i> or <i>Albertia</i>						1
<i>Albertia latifolia</i>		5				1
<i>Pelourdea vogesiaca</i>	1	1				
Conifer indet.	2					
<i>Pleuromeia</i>	2			1		
<i>Peltaspermum</i>					1?	
Sphenophytes	45	35				57
Female cone			1			
Stem fragments	116	21	16	1	7	585
<i>Radixites</i> sp.	1					
Roots						1

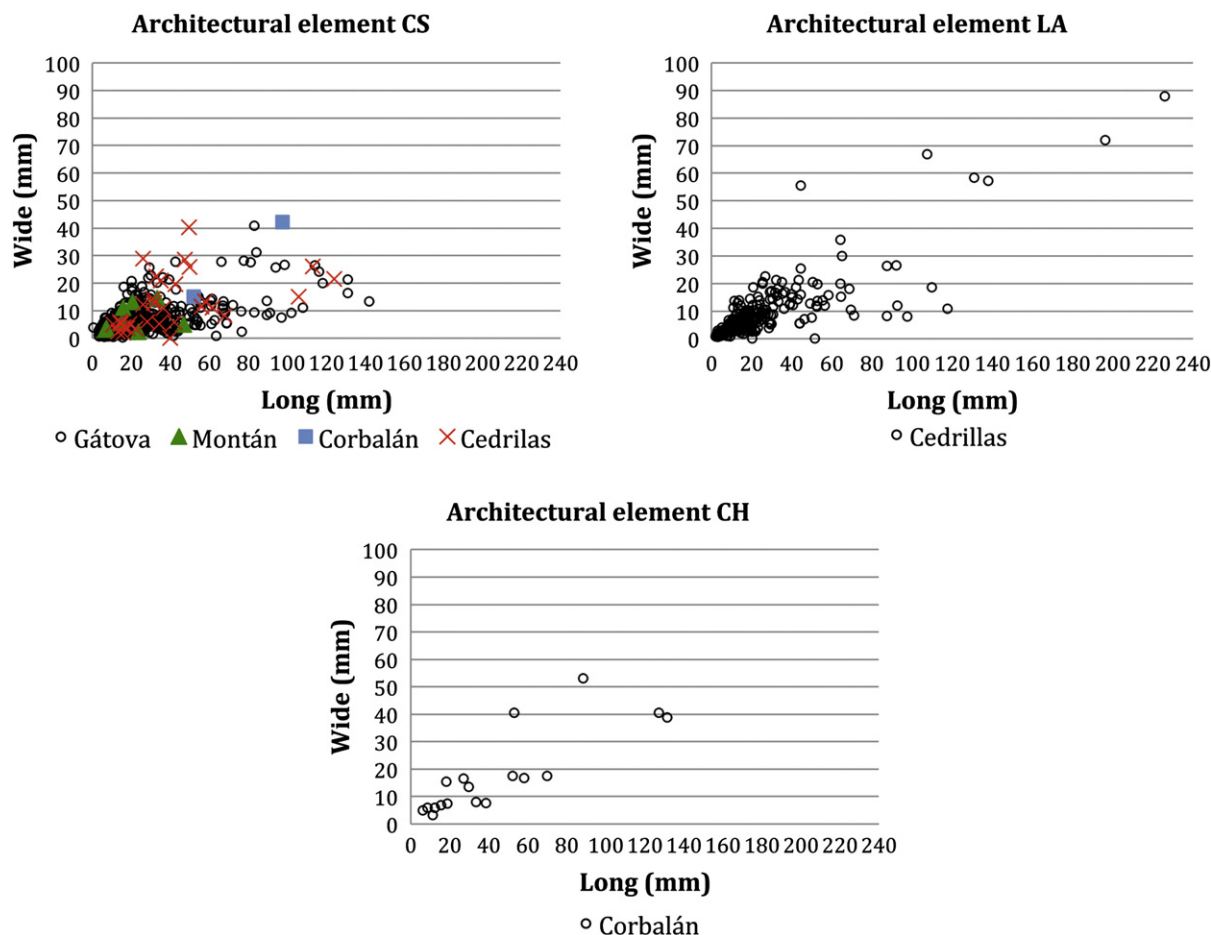


Fig. 7. Diagrams of the dimensions, long and width, of plant remains found in the different architectural elements and sections (plant remains in the architectural element CS = 721, LA = 170, CH = 17).

are normally located at the top of the architectural elements. At the top of some levels, and associated with finer sediments, impressions of leaves and conifer fragments were also found as well as the putative lycophyte scales.

The plant remains are dispersed in the matrix parallel to the bedding. The angles the plants form to each other vary between 0° and 180° , although some orientation is observed; 33% of these remains are orientated at angles between 0° and 20° (Fig. 8).

6.2. Architectural element CH

The plant remains found in the Corbalán section are mostly related to the architectural element CH located in subunit E5. This architectural element is characterized by fewer plant fossils than the others. Only 17 plant remains have been collected, and most of them are very poorly preserved stem fragments. Only a poorly preserved female cone has been found (Table 2).

The stems have a maximum length of 13 cm and width of 5.3 cm (Fig. 7) and a minimum length of 6 mm and width of 3 mm, with an average of 4.5×1.8 cm. The stems are scattered parallel to the bedding without a predominant direction (Fig. 8). They are preserved generally at the base of the channels and constitute part of the lag deposit related to erosive surfaces. The fact that the plant remains are at the base just above the erosive surfaces of the channels indicates that they were transported in high-energy stages, related to the reactivation of the alluvial system.

6.3. Architectural element CS

Most of the plant fragments of the Gátova and Montán sections, those of subunit E6 in the Corbalán section and some of the subunits E3 and E4 in the Cedrilas section are related to the architectural element CS. The plant remains (721 fragments collected in this architectural element) are dominated by impressions of indeterminable stems (614 specimens), followed by stem fragments of spenophytes (92 specimens) and conifer shoot fragments (11 specimens), of these, most remains belong to *Albertia latifolia* (6 Fig. 6h), followed by *Voltzia heterophylla* (3), *Voltzia walchiformis* (1) *Pelourdea vogesiaca* (1), and one specimen that could be attributed to *Albertia* or *Voltzia*. Furthermore, one specimen could correspond to a *Peltasperum*, and a fragment can be putatively attributed to *Pleuromeia* (Table 2).

The plant remains found at the top of these architectural elements are associated with finer sediments and they have the largest number of plant remains per cm^2 . They are scattered in the matrix parallel to the bedding and show a very small orientation because 32.17% of the angles of each plant vary from 0° to 20° (Fig. 8). The plant remains are the smallest found in the three architectural elements (14.2×4.2 cm and $1 \text{ mm} \times 0.5 \text{ mm}$; Fig. 7). The average of the measurements of these fragments is 2.5×0.6 cm. The small size of the plant remains and preservation of leaf impressions, indicate that the transport energy must have been low, thus disallowing the mobilization of larger fragments.

A level with vertically oriented structures was found in this architectural element. It is small in size, positioned perpendicular to the stratification, and passes through several layers of sediment, with a maximum

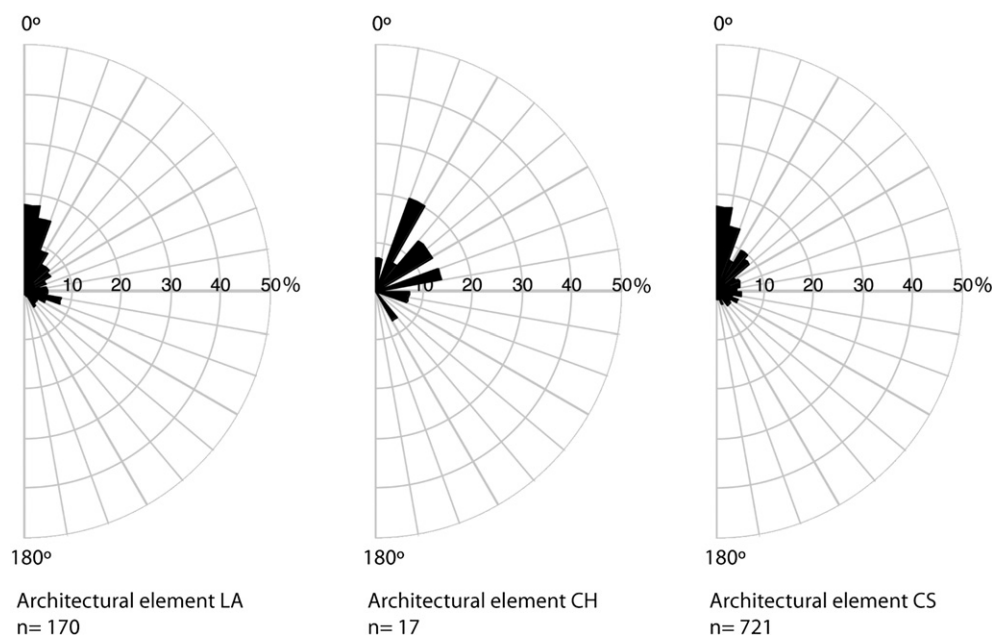


Fig. 8. Rose diagrams of the angles between plants (0° and 180° parallel plants and 90° perpendicular plants) at the same architectural element, at the 95% confidence interval calculated using Oriana v. 2.02.

length of 2 cm (Fig. 6e). These are interpreted as rooting structures, being the only location where possible autochthonous (primary) rooting is observed. In this level, a large shoot fragment ($11.3 \times 8\text{--}4$ cm) that is three-dimensionally preserved in the sediment (Fig. 6g, i) has been collected. This level also presents desiccation cracks.

7. Discussion

Sediment discharge into a basin and the geometry of the basin itself are the main controls on the basin's fluvial style. Heller and Paola (1996) stated that the magnitude of discharge, the nature of the sediments and the relative importance of longitudinal vs. transverse fault systems are of fundamental importance in the alluvial successions. Tectonic, geomorphic and climatic factors are, however, the main basic mechanisms controlling the nature of the sediments delivered to the basin.

Studies of the tectonic control on the Eslida Fm. indicate a series of half and full-grabens interconnected by transfer faults (Arche and López-Gómez, 1999a) and extension during sedimentation of this formation was not continuous, but most likely took place by pulses. During the beginning of a pulse, rapid extension led to the creation of accommodation, preserving most of the sediments delivered to the basin (Vargas et al., 2009). This period of basin evolution led to LA, CS and FF architectural elements developed in subunits E3 and E4. However, the sediments were partially reworked when accommodation diminished. At that time, the basin became oversupplied, and sandstone bodies evolved towards amalgamation, as mainly shown in the CH architectural element development and during the subunit E5 deposition, similar to the examples described by Bourquin et al. (2006) in the Lower Triassic of the Germanic Basin. The cessation of active extension led to lateral shifting and abandonment of the fluvial systems during the period of sedimentation of subunit E6 and the first connection with marine environments.

The plant taphonomic data indicate that almost all of the plant assemblages are allochthonous. The poor quality of preservation, degree of fragmentation, and arrangement of the fragments, normally parallel to the bedding, are characteristic of transported plant assemblages (Bateman, 1991; Behrensmeyer and Hook, 1992; Gastaldo et al., 1995, 2005; Allen and Gastaldo, 2006). However, in some CS elements there is evidence of vegetated surfaces and development of soils: occasionally, root traces are preserved in situ, crossing several layers of sediments.

Furthermore, a three-dimensional shoot fragment larger than all other plant remains has been found in this architectural element, indicating that this fragment is parautochthonous. Kelber (1990, 1999) and Kelber and Hansch (1995) described similar facies of layers crossed by root traces and interpreted them as a result of the development of several generations of plants. In these cases, the younger generation perforates the "fossils" of the older sediment-covered organic remains (Kelber, 1990), and this could also be the situation observed in the CS facies. On the other hand, the subaerial exposition of some CS elements is evidenced by desiccation cracks. Unfortunately, the vertical relation between the roots and the desiccation cracks cannot be reconstructed.

Roots have also been found in the architectural element LA, punctually these roots that were washed in and deposited parallel to the bedding plane, indicating they are not in situ but allochthonous.

Most of the plant-bearing horizons are laterally continuous. Plant assemblages are dominated by stem fragments mobilized within both channels and overbank settings during high-flow events. The orientation of plant material is normally parallel to the bedding.

Larger plant fragments occur at the base of the assemblages in the architectural elements LA and CH and decrease in size upwards. The architectural element LA (Cedrillas section) corresponds to the deepest channels of the Eslida Fm. These channels carry a greater volume of water, thus allowing the transport of the remains of larger plants. On the other hand, in element CH (subunit E5 of the Corbalán section) the active channels would be smaller and shallower, but with important periodical reactivations and energy stages that could mobilize large fragments. Because of these stages in the CH architectural element, the plant remains correspond to the most resistant plant parts that have a greater fossilization potential, such as stems and shoots. The relatively high energy of transport as well as the general coarse sediment explains why the material is poorly preserved and difficult to identify. Conversely, plant remains are better preserved and leaf impressions can be found in the element LA. This is because the plants were trapped in the low-energy shallowest areas, which tend to be abandoned, allowing better preservation.

The plant remains are smaller in the architectural element CS (Gátova, Cedrillas and Montán sections and subunit E6 of the Corbalán section) because they are associated with flood stages of the fluvial systems, but here the macroflora is preserved slightly better in the fine sediment.

In all architectural elements, the plant remains are highly fragmented and disarticulated, indicating a medium-long transport and/or a long period of residence in water. If plants were buried in place, the plant material would be expected to be much more articulated, even in growing position (upwards stems and downward projecting roots anchoring them in place), and to show a reduced dimensional selection of the fragments in each bedding plane. The fact that the plant remains are allochthonous is also supported by the preservation of plants as casts because the axes underwent a syndimentary decay followed by an early infilling with coarse silt and mud (e.g., [Gastaldo et al., 1989](#)). Decay is consistent with deposition in channels and overbank deposits ([Kosters, 1989](#); [Alexander et al., 1999](#)). According to [Allen and Gastaldo \(2006\)](#), plant remains of the floodplain would be swept away by flood waters into the channel. At first they would be

transported as a suspended load in the channel, but after decomposition, the axes are transported as bed-load and void hollow would be filled by sediment. Under high-discharge, these small sediment-filled axes could be re-entrained and transported to the lobes overflow and flood plain.

7.1. Palaeoenvironmental reconstruction

In the architectural elements CS and LA of subunits E3 and E4, sphenophyte fragments (most likely *Equisetites*) and conifers (*Voltzia*, *Pelourdea*) have been found. In the LA elements, *Albertia* and a lycophyte remain have also been found ([Table 2](#)). Thus, it can be considered that the flora found in these architectural elements was similar.

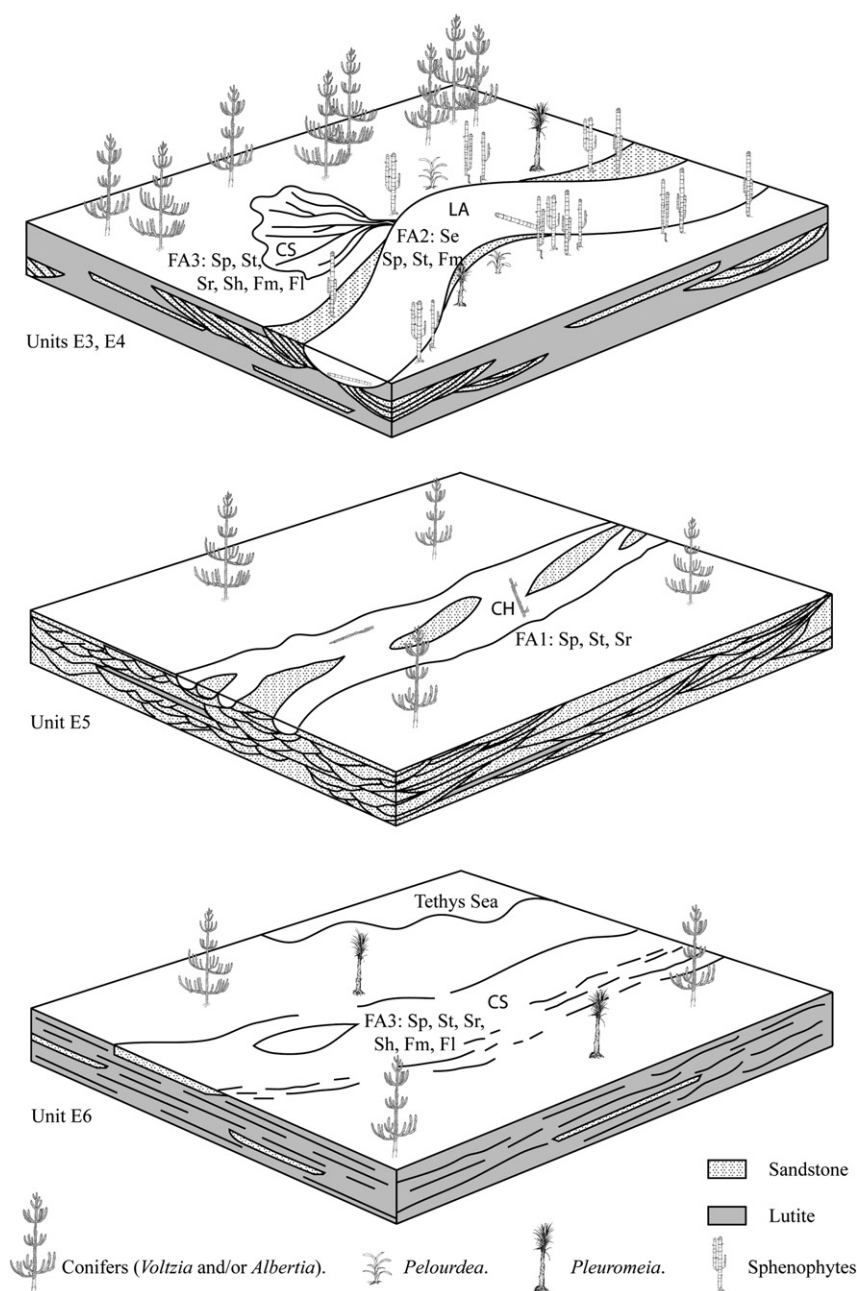


Fig. 9. Palaeoenvironmental reconstruction from sedimentology and plant remains of the subunits of the Esilda Fm. (LA, CS and CH: architectural elements. FA1, FA2, FA3: facies associations, for more information, see [Table 1](#)).

In these subunits, the plant associations also allow the recognition of riparian vegetation, represented by plants living near the water body (permanent floodplain ponds or river) and bearing periodical floods. The vegetation around the water bodies is composed of semiarborescent lycophytes (*Pleuromeia*), sphenophytes (at least *Equisetites*, perhaps also *Schizoneura*) and more hygrophytic conifers such as *Pelourdea* (see also Kustatscher et al., 2014). Farther from the water body, the vegetation of the lowlands is characterized by drier conditions, where various species of arboreal conifers developed, such as *Voltzia* and shrubby ones such as *Albertia* as well as, putatively, seed ferns (?*Peltaspermum*) (Fig. 9). The possible hinterland vegetation (permanent ground or seasonally dry) consists of conifers with shrubs (*Albertia*) and trees (*Voltzia*). Furthermore, in these subunits there are calcareous soils (nodular, massive or laminated), indicating rainfall between 200 and 600 mm/yr, with evaporation that exceeds precipitation (Tucker, 1991). As also halite pseudomorphs appear in the same levels, a seasonal climate with alternating wet and dry seasons is inferred affecting this subunit.

In the architectural element CH of subunit E5, large indeterminate fragments of putative conifers have been found, as they are the most resistant to transport during that time. As previously described, the subsidence during the deposition of this subunit may have been very slow, preventing the accumulation of fine-grain-size sediment, as floodplains had little or no development and there was an increasing reworking of the river body. Such channels did not have lateral barriers (Fig. 9), were able to easily mobilize all plant debris, booting the few that there were on the increased energy steps, and transporting them as basal lag. However, this could be also due to a more sparse vegetation that does not retain soils and they are eroded easily. On the other hand, the presence of conifers only, could be due to a shift to more arid conditions, to taphonomic selection or a combination of both processes.

Therefore, during the deposition of this subunit, the climate should be drier than in previous subunits, with very little vegetation (Fig. 9). However, plant remains are poorly preserved, and it is difficult to determine the vegetation due to the high energy of the channels.

In the architectural element CS of the subunit E6, very few plant remains have been found. Only a *Pleuromeia* fragment and other possible *Peltaspermum* have been identified. This is striking because in the same architectural element in subunits E3 and E4 there is a large number of specimens (Table 2).

In the subunit E6, more abundant halite pseudomorphs have been observed, which indicate a higher rate of evaporation. On the other hand, oscillation ripples and flaser lamination are also observed, indicating a marine influence. The sea made occasional forays into this subunit, indicating a progressive transgression of the Tethys that culminated in upwards Muschelkalk units (Fig. 9). Therefore, this subunit was deposited in an arid climate next to the sabkhas that would be installed with the overlying rocks of the Röt facies.

Although *Pleuromeia* is normally a hygrophytic plant (Krassilov and Zakharov, 1975; Retallack, 1975) and lycopod lifecycles rely on free water for reproductive success, many modern lycopods can withstand seasonally dry conditions, and some are adapted to extremely arid climates (e.g., *Selaginella* resurrection plants) because heterosporous lycopods are free sporing plants, being dependent on infrequent wet periods for growth and reproduction (Taylor et al., 2009). Furthermore, Retallack (1975) suggested the pleuromeids were facultative halophytes that could cope with high and variable salinities and formed specialized coastal associations. Therefore, *Pleuromeia* could survive under the extreme conditions deduced for subunit E6, with arid conditions near the sabkhas, in which there could be seasonal avenues.

7.2. Comparison with other Anisian plant localities of Iberia

Our plant associations resemble those of other Anisian localities of Iberia, where a predominance of conifers and sphenophytes is observed. However, it is noteworthy that in the Eslida Fm. there are no

fern remains, and the seed ferns are represented only by possible *Peltaspermum* remain.

This aspect is especially striking, considering that during the Middle Triassic, ferns were widespread on both hemispheres and ferns are generally typical for the Buntsandstein floras of the Germic Basin (e.g., Grauvogel-Stamm, 1978; Fuchs et al., 1991). Most modern leptosporangiate fern families appeared during the Middle–Late Triassic (Skog, 2001) while other families existed or appeared in the Permian, both in the Northern and Southern Hemispheres (Yao and Taylor, 1988; Tidwell and Ash, 1994; Wang et al., 1999; Skog, 2001).

In addition, in the Pyrenees a fragment of *Anomopteris mougeotii* has been found in the Shale Unit at Maya del Baztán, Navarra (Díez, 2000), a frond fragment of *Pecopteris sulziana* has been described from Catalan Coastal Range (Almera, 1909) and a small frond fragment of *Cladophlebis ruetimeyeri* (Heer) Leonardi, 1953 from the Spanish Buntsandstein is stored at the Museo Nacional de Ciencias Naturales-CSIC (MNCNV-08553b). This indicates that ferns were also present in the Buntsandstein of Spain even if perhaps as rare elements.

The comparison of the floral associations of this study with the Iberian Peninsula shows a great similarity to the flora described in the Aragonian Branch of the Iberian Range (Díez et al., 1996; Díez, 2000), which is composed of conifers and sphenophytes. In addition to the genera of conifers described in our association, those authors documented male conifer cones *Willsiostrobus* and *Darneya*. These conifer cones have also been described in the Pyrenees (Díez, 2000), but not in the Catalan Coastal Range. *Aethophyllum* remains have been found in the Catalan Coastal Range (Calzada, 1987), while *Pelourdea* leaves have been described, in all of the plant associations (Table 3).

The sphenophytes remains found in the Pyrenees belong to the genus *Neocalamites* (Müller, 1969; Díez, 2000). In the Aragonian Branch, both *Neocalamites* and *Equisetites* were found (Díez et al., 1996; Díez, 2000), while in the Catalan Coastal Range only *Equisetites* was reported (Calzada, 1987). In the flora described herein, remains of *Equisetites* have been identified, although some of the fragments could belong also to *Neocalamites* (Table 3).

The main difference between the flora studied and the one of the Aragonian Branch of the Iberian Range and the Pyrenees is the presence of lycophytes because no lycophyte remains have been reported in these areas during Anisian times. In Triassic sediments in the Castilian Branch, one specimen of *Pleuromeia sternbergii* was described by Schmidt (1937), in Dobruskina (1994), but unfortunately, without any precise stratigraphic or geographic position. However, in the Catalan Coastal Range Galán-Abellán (2011) and Galán-Abellán et al. (2013) describe the presence of a putative *Pleuromeia* remain in the upper part of the Eramprunyá unit that is late Spathian early Aegian in age, equivalent to the upper part of the Cañizar Fm.

The coeval floras of the Pyrenees and the Catalan Coastal Range are also composed of conifers and sphenophytes. The main difference to the Iberian Range is, as discussed above, the presence of ferns (Almera, 1909; Müller, 1969; Calzada, 1987; Díez, 2000) and, with our floral association, the absence of lycophytes, except for a putative *Pleuromeia* remain in the Catalan Coastal Range (Table 3).

The only pollen assemblage described in the Eslida Fm. (Boulouard and Vilallard, 1982) is composed of conifers, ferns and seed ferns (*Podocarpeapollenite*, *Minutosaccus*, *Platysaccus*, *Succintisporites* and *Cristatitriletes*; Table 4).

In the Aragonian Branch of the Iberian Range, two palynomorph assemblages have been described in Calcena Fm. (Arribas, 1984), equivalent to the upper unit of the Eslida Fm. The first assemblage (Díez et al., 1996, 2007) is dominated by conifers and ferns. It is characterized by *Alisporites*, *Chordasporites*, *Triadispora*, *Verrucosporites* and *Voltziaceasporites* (Table 4). The second assemblage (Díez et al., 2007) was collected in the upper part of the Calcena Fm. from the transition to the upper Muschelkalk dolomitic facies. The association is characterized by conifers, ferns and lycophytes (*Alisporites*, *Bhardwajispora*, *Calamospora*, *Chordasporites*, *Deltoidospora*, *Densoisporites*, *Endosporites*,

Table 3
Compilation of the Anisian macroflora of the Iberian Peninsula.

PYRENEES	IBERIAN RANGES		CATALONIAN COASTAL RANGES
	ARAGONIAN BRANCH	CASTILIAN BRANCH	
SHALE Unit. <i>Albertia</i> sp., <i>Pelourdea vogesiaca</i> , <i>Neocalamites</i> sp., <i>Schizoneura</i> sp. (Müller, 1969) <i>Anomopteris mougeotii</i> , <i>Darneya</i> sp., <i>Neocalamites</i> sp., <i>Pelourdea</i> sp., <i>P. vogesiaca</i> , <i>Willsiostrobus</i> sp., <i>Albertia</i> sp., <i>Voltzia</i> sp., <i>Voltzia heterophylla</i> . (Díez, 2000)	TRASOBARES Fm. CALCENA Fm. <i>Darneya</i> sp., <i>Darneyapeltata</i> , <i>Equisetites</i> sp., <i>Neocalamites</i> sp., <i>Neocalamites</i> cf. <i>carrerei</i> , <i>Willsiostrobus</i> sp., <i>Willsiostrobus rhomboidalis</i> , <i>Pelourdea vogesiaca</i> , <i>Albertia</i> sp., <i>Voltzia</i> sp., <i>Voltzia heterophylla</i> , <i>Voltzia walchiaeformis</i> . (Díez et al., 1996 and Díez, 2000)	EL MAS Fm. LANDETE Fm. MARINES Fm.	MIDDLE MUSCHELKALK LOWER MUSCHELKALK LUTITE CARBONATE EVAPORITE UNIT
CONGLOMERATE, SANDSTONE AND SHALE Unit.	TIERGA Fm. Debris plant (Díez et al., 2007)	ESLIDA Fm. <i>Equisetites mougeotii</i> , <i>Voltzia</i> sp., <i>Voltzia heterophylla</i> , <i>Voltzia walchiaeformis</i> , <i>Albertia latifolia</i> , <i>Radicites</i> sp., <i>Pelourdea vogesiaca</i> , obovate shape, ? <i>Peltaspermum</i> , <i>Pleuromeia sternbergii</i> , female cone (This work)	UPPER BUNTSANDSTEIN <i>Albertia</i> sp., <i>Calamites</i> sp., <i>Voltzia heterophylla</i> , <i>Pecopteris sulziana</i> , <i>V. heterophylla</i> . (Almera,1909) <i>Aethophyllum</i> sp. and <i>Equisetites</i> cf. <i>mougeotti</i> . (Calzada, 1987)
		CAÑIZAR Fm.	LOWER BUNTSANDSTEIN putative <i>Pleuromeia</i> (Galán-Abellán et al., 2013)

Hexasaccitesmuelleri, *Illinites*, *Leiotriletes*, *Microcachrydites*, *Platysaccus*, *Protohaploxylinus*, *Punctatisporites*, *Retusotriletes*, *Triadispora*, *Vitreisporites*; Table 4).

In the Anisian macroflora of the Iberian Range, no remains of ferns have been found, even if their spores are present in the palynological samples. Therefore, the fact that no ferns have been found, except for a possible *Peltaspermum*, is most likely due to taphonomic selection.

The *Pleuromeia*-like fossils and the lycophyte spored in the palynological assemblages, show that *Pleuromeia* may have survived into the Anisian in the Iberian Range. Moreover, as shown by Grauvogel-Stamm and Ash (2005), lycophytes played an important role in the recovery of the land plants in the Early Triassic and could have adapted to unfavourable arid conditions. Indeed, Wang (1996) described how this plant settled in the deserted environments during the Induan in North China and how it developed and diversified.

The pollen data from the Iberian Range and the macrofloral association described in this work, dominated by conifers and sphenophytes, is similar to that of the “Grès à *Voltzia*” Fm. of north-eastern France (Grauvogel-Stamm, 1978). Although in the “Grès à *Voltzia*” ginkgophytes occurred (Grauvogel-Stamm and Grauvogel, 1983), no specimens have been found in this study.

It is very likely that the plants of the “Grès à *Voltzia*” that occur already in the *Pleuromeia* flora (Mader, 1990; Fuchs et al., 1991; Grauvogel-Stamm, 1999) escaped the end-Permian life crisis and lived in refugia of extrabasinal areas. The replacement of the *Pleuromeia*

flora by the conifer-dominated flora or *Voltzia* flora may be due to a change in climatic and growth conditions, enabling the *Voltzia* flora to invade basal lowlands (Grauvogel-Stamm and Ash, 2005).

8. Conclusions

The studied Anisian flora is the first to appear after the Permian–Triassic crisis in the Castilian Branch of the Iberian Range.

This flora has been collected in alluvial deposits of the Eslida Fm., in three types of architectural elements: CH (channel deposits), LA (of lateral accretion), and CS (of crevasse splay).

The largest plant fragments occur at the base of the assemblages in the architectural elements LA and CH, while the best-preserved ones are included in the architectural element CS and in the low-energy shallower areas of the architectural element LA.

The plant taphonomic data indicate that all plant assemblages are allochthonous and they had medium-long transport and/or a long period of residence in water.

Four subunits (E3 to E6, from base to top) with different characteristics, both sedimentological and palaeobotanical, have been recognized. They show a trend of aridification and a decrease in floral diversity.

Subunits E3 and E4 (constituted by the architectural elements CS, LA and FF), were deposited in a seasonal climate with an alternation of wet and dry seasons with high evaporation rates. The following plant remains have been recognized in these subunits: 1) plant associations of

Table 4

Compilation of the microflora described in the Iberian Range in the Eslida Fm. and their equivalents.

IBERIAN RANGES	
ARAGONIAN BRANCH	CASTILIAN BRANCH
TRASOBARES Fm.	EL MAS Fm.
CALCENA Fm. <i>Alisporites</i> , <i>Bhardwajispora labichensis</i> , <i>Calamospora tener</i> , <i>Chordasporites</i> , <i>Deltoidospora</i> , <i>Densoisporites</i> , <i>Endosporites papillatus</i> , <i>Hexasaccites muelleri</i> , <i>Illinites</i> , <i>Microcachryidites doubingeri</i> , <i>Platysaccus</i> , <i>Protophloxypinus</i> cf. <i>microcorpus</i> , <i>Punctatisporites</i> sp., <i>Retusotriteles</i> sp., <i>Triadispora</i> , <i>Vitreisporites</i> sp. (Díez et al., 2007)	LANDETE Fm.
<i>Alisporites</i> , <i>Chordasporites</i> cf. <i>voltziaformis</i> , <i>Triadispora</i> , <i>Verrucosisporites</i> sp., <i>Voltziaceasporites heteromorpha</i> (Díez et al., 1996, 2007)	MARINES Fm.
TIERGA Fm.	ESLIDA Fm. <i>Podocarpeapollenites thiergartii</i> , <i>Minutosaccus potonieii</i> , <i>Platysaccus papilionis</i> , <i>Succintisporites</i> , <i>Cristatitriteles baculatus</i> . (Boulouard and Viallard, 1982)
	CANÍZAR Fm.

riparian vegetation: semiarborescent lycophytes (*Pleuromeia*), sphenophytes (at least *Equisetites*, perhaps also *Schizoneura*) and more hygrophytic conifers such as *Pelourdea*; 2) vegetation of the lowlands, characterized by drier conditions, with various species of arboreous conifers such as *Voltzia* and shrubby ones such as *Albertia*; and 3) upland/hinterland vegetation (permanent ground or seasonally dry) consists of conifers with herbaceous or shrubby habit (*Pelourdea*), shrubs (*Albertia*) and trees (*Voltzia*).

In the subunit E5, dominated by the architectural element CH, only conifer remains have been found. This subunit represents a stadium with a decreased subsidence, drier climate and sparse vegetation.

Subunit E6 consists of the architectural element CS and FF. It would have a similar aridity to subunit E5, but with a marine influence. Few plant remains have been collected: a *Pleuromeia* fragment, a possible *Peltaspermum* and indeterminate fragments, possibly from conifers.

The studied flora of the Eslida Fm. is similar to that described in the Aragonian Branch of the Iberian Range and differs from the Pyrenees and Catalan Coastal Range, in the absence of ferns. It is also the only association in which lycophyte macrofossils have been described so far in the Eslida Fm. and its equivalent units.

The pollen assemblages of Anisian age in the Iberian Range show the presence of ferns and lycophytes, so their (near) absence is due to taphonomic criteria.

The studied flora resembles that of the “Grès à *Voltzia*” Fm. of north-eastern France (Grauvogel-Stamm, 1978), although the one of the Iberian Range is slightly less diversified.

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