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Systematic palaeontology (Palaeobotany)

Late Permian plant remains in the SE Iberian Ranges, Spain: Biodiversity and palaeovegetational significance

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Abstract

The present study focuses on the diversity and paleovegetational significance of the floristic record of the Late Permian continental Alcotas Formation, in five sections of the southeastern Iberian Ranges, central Spain. This unit, of Upper Tatarian or Lower Lopingian (Upper Permian) age, can be subdivided into three parts, represented by sediments originating from sandy and gravely braided, high-sinuosity, and sandy-braided fluvial systems developed in wide floodplains, from bottom to top respectively. Five zones, referred to as A to D, have been differentiated after correlation of the four studied sections, based on sedimentary and stratigraphical criteria. The study of megaremains recovered from the levels placed within each zone indicates changes in both biodiversity and population density. The oldest assemblage comprises impressions of leafy shoots and caules of gymnosperms. The poor preservation of some megaremains hinders their classification. A significant increase in diversity and population density is evident in the next and younger association, which shows reproductive structures and remains of leaves, trunks, and indeterminate caules of sphenopsids, cordaitales, and conifers. The next assemblage is dominated by conifers. The specimens collected mainly correspond to silicified trunk fragments, highly carbonized. A total absence of fossilised plant and trunk remains is the main characteristic of the upper part of the Alcotas Fm. The occurrence of these fossil floras is significant, due to the paucity of the fossil record of megafloras of identical or similar geological age, which has made it difficult to acquire knowledge on the development of flora and vegetation in the Upper Permian of Europe. The evolution of the biodiversity of the megafloras allows us to infer paleoecological changes for a time interval close to the end-Guadalupian biotic crisis. ***To cite this article: C. Diéguez et al., C. R. Palevol 6 (2007).***

Résumé

Restes végétaux du Permien terminal dans la chaîne Ibérique sud-orientale, Espagne : biodiversité et signification paléovégétale. La présente étude est focalisée sur la diversité et la signification paléovégétale de l'enregistrement floristique du Permien terminal de la formation continentale Alcotas, dans quatre coupes de la chaîne Ibérique sud-orientale, en Espagne centrale. Cette unité, d'âge Tatarien supérieur à Lopingien inférieur (Permien supérieur), peut être divisée en trois parties, représentées par

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des sédiments issus de systèmes fluviatiles à bras multiples sableux et graveleux de grande sinuosité, et sableux développés dans de vastes plaines inondées, de la base vers le haut, respectivement. Cinq zones, dénommées de A à D, ont été différenciées après corrélation des données des quatre coupes étudiées, sur la base de critères sédimentaires et stratigraphiques. L'étude des mégarestes des niveaux localisés au sein de chaque zone indique des changements, à la fois dans la biodiversité et la diversité de population. Le plus ancien assemblage comporte des impressions de pousses de feuilles et de coiffes de gymnospermes. La mauvaise conservation de certains mégarestes empêche toute classification. Une augmentation significative de la diversité et de la densité de population est évidente dans l'association suivante, plus jeune, qui montre des structures de reproduction et de restes de feuilles, troncs et coiffes indéterminées de sphénopsides, cordaïtales et conifères. L'assemblage suivant est dominé par les conifères. Les échantillons récoltés correspondent principalement à des fragments de troncs silicifiés, très carbonisés. Une totale absence de restes fossiles de troncs et de végétaux caractérise la partie supérieure de la formation d'Alcotas. La présence de ces flores fossiles est importante, en raison de la pauvreté de l'enregistrement fossile de mégaflores d'âges géologiques identiques ou similaires. Cela a, pour une large part, rendu difficile l'acquisition de connaissances sur le développement de la flore et de la végétation au Permien supérieur en Europe. L'évolution de la biodiversité des mégaflores permet de rapporter les changements paléoécologiques à un intervalle de temps proche de la crise biotique de la fin du Guadalupien. ***Pour citer cet article : C. Diéguez et al., C. R. Palevol 6 (2007).***

Keywords: End-Guadalupian; Plant remains; Iberian Ranges; Permian; Flora

Mots clés : Fin du Guadalupien ; Restes végétaux ; Chaîne Ibérique ; Permien ; Flore

1. Introduction

The end-Permian extinction is the largest of all times. An estimated 57% of all the families and 95% of all species of marine animals became extinct. Some recent researches suggest a relatively sudden, possible catastrophic event, perhaps of duration 50,000 years or less [14,15]. Plant extinctions were less striking elsewhere in the world; nevertheless, they were more notable than earlier or later in the Permian and Triassic. A replacement of palaeophytic with mesophytic floras [18] was considered for this interval, and although a prolonged duration is thought for this changeover, the palynostratigraphic record has long hinted at more dramatic changes. More local studies should be done, as both regional and diachronous characters were important factors of this extinction.

The present study focuses on the diversity and palaeovegetational significance of the flora and microflora record of the Late Permian in the SE Iberian Ranges, central Spain (Fig. 1). The Permian, at the lower part of the Middle Triassic rocks of the Iberian Peninsula, is of continental origin [23]. In the southeastern Iberian Ranges, the subdivision of the continental Permian–Triassic sediments into formations is well established [2,3,5,21], and is represented by major sedimentary cycles separated by angular unconformities and/or hiatuses (Fig. 2).

The Late Permian sedimentary succession in the Iberian Ranges, southeastern Spain, shows a very interesting plant and palynostratigraphic record. This succession is represented in this area by the Boniches Conglomerates and the Alcotas Siltstones and Sandstones Formations, from base to top respectively. Different palynological assemblages found in these units indicate a Thuringian (Upper Permian) age [13] or Tatarian, as the Thuringian can be reasonably correlated with this age of the Russian Platform based on palynological data [17,29]. A more recent study of these palynological associations [22] indicates a Lower Tatarian or Upper Guadalupian age (Middle Permian) and an Upper Tatarian or Lower Lopingian (Upper Permian) age for the Boniches and Alcotas Formations, respectively.

2. Geological setting

The Iberian Basin was an intracratonic basin during the Mesozoic and experienced several extensional periods during the Mesozoic and Cenozoic [24]. The tectonic inversion of the Iberian Basin took place in several compressive phases during the Alpine orogeny, since the Latest Cretaceous to the Early Miocene [8,9], resulting in several folded and thrust linear structures that constituted the present-day Iberian Ranges.

As the rest of the Permian-Triassic basins in the Iberia microplate, the Iberian Basin started its development under an extensional tectonic regime, with several synrift–postrift phases that prolonged during almost 100 Myr, from the Early Permian to Late Triassic–Early Jurassic [4].

Ordovician and Silurian slates and quartzites of very low-grade metamorphism forming kilometre-size structures with NW–SE trend represent the Hercynian basement of the Iberian Basin where the Early Permian sediments were deposited [7]. Most of the extensional basin boundary faults were reactivated Hercynian

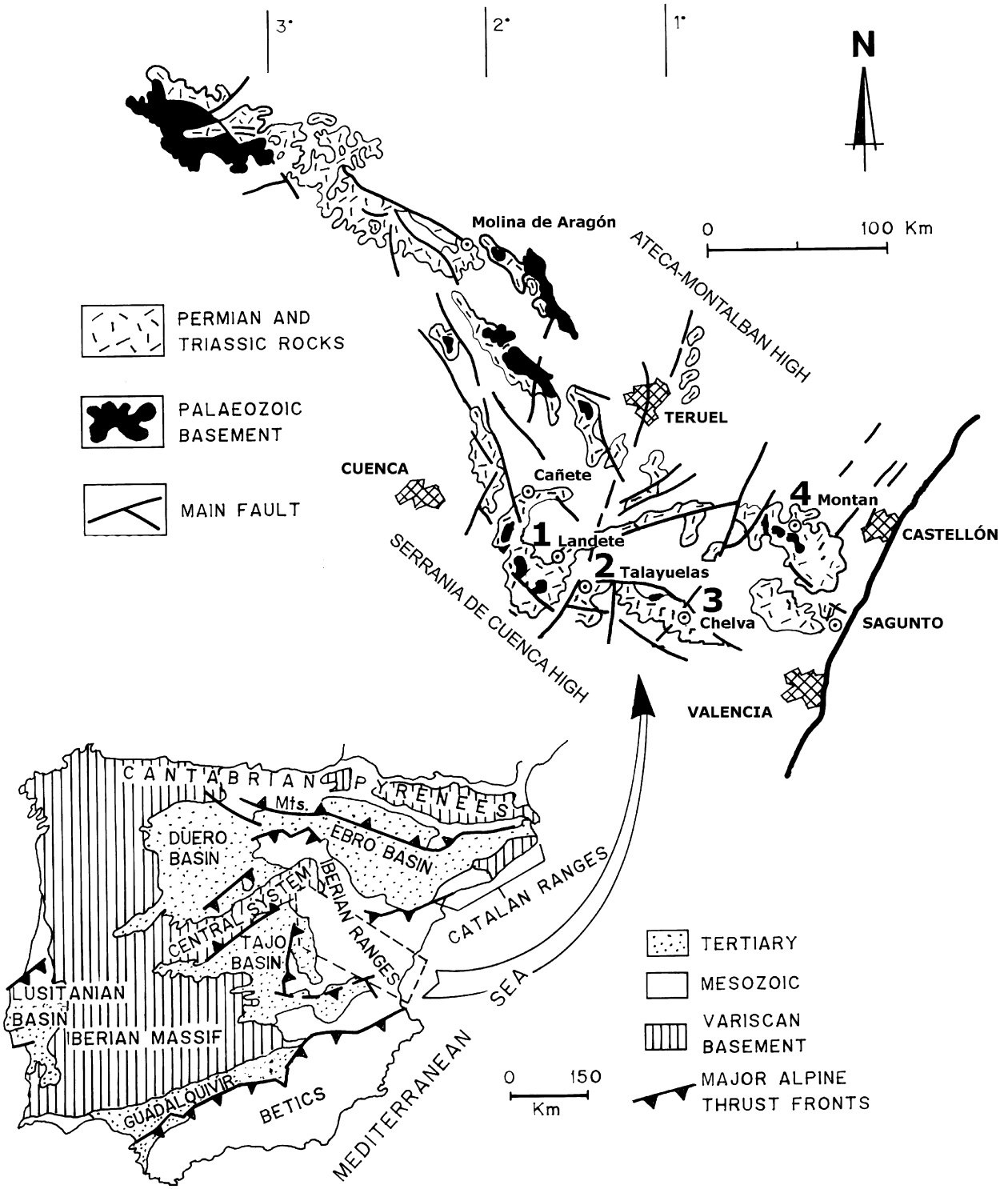


Fig. 1. Present-day geographical location of the studied area with superimposed studied sections: (1) Landete (2) Talayuelas, (3) Chelva, (4) Montan.
Fig. 1. Localisation géographique actuelle de la zone étudiée avec superposition des coupes étudiées : (1) Landete (2) Talayuelas, (3) Chelva, (4) Montan.

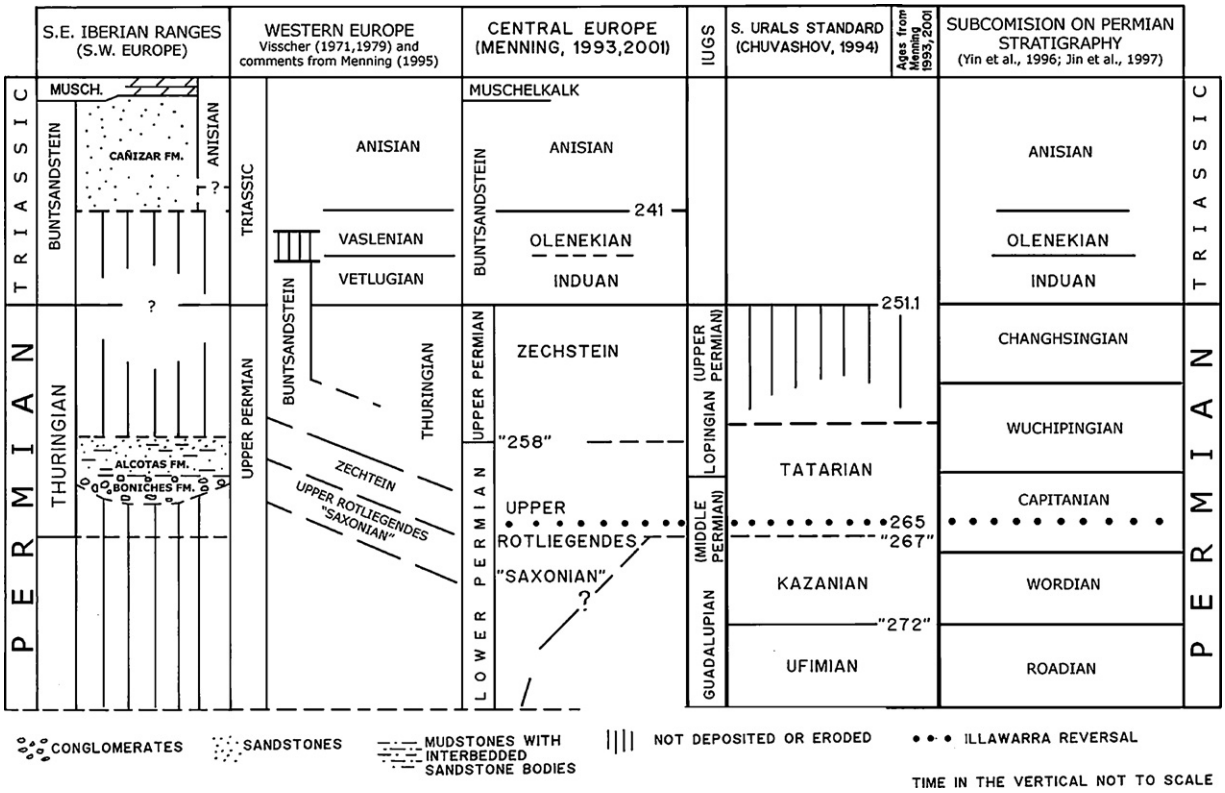


Fig. 2. Permian–Lower Triassic stratigraphic scheme of Iberia, western and central Europe, and southern Urals, with the assay of their possible unit equivalence accepted by the Sub-commission of Permian Stratigraphy. Based on López-Gómez et al., 2005 [22].
Fig. 2. Schéma stratigraphique au Permien et Trias inférieur de l'Espagne, de l'Europe centrale et occidentale et du Sud de l'Oural, avec essai d'équivalence possible des unités, acceptée par la sous-commission de stratigraphie du Permien. D'après [22].

or older lineaments, trending NW–SE and north–south [12,24].

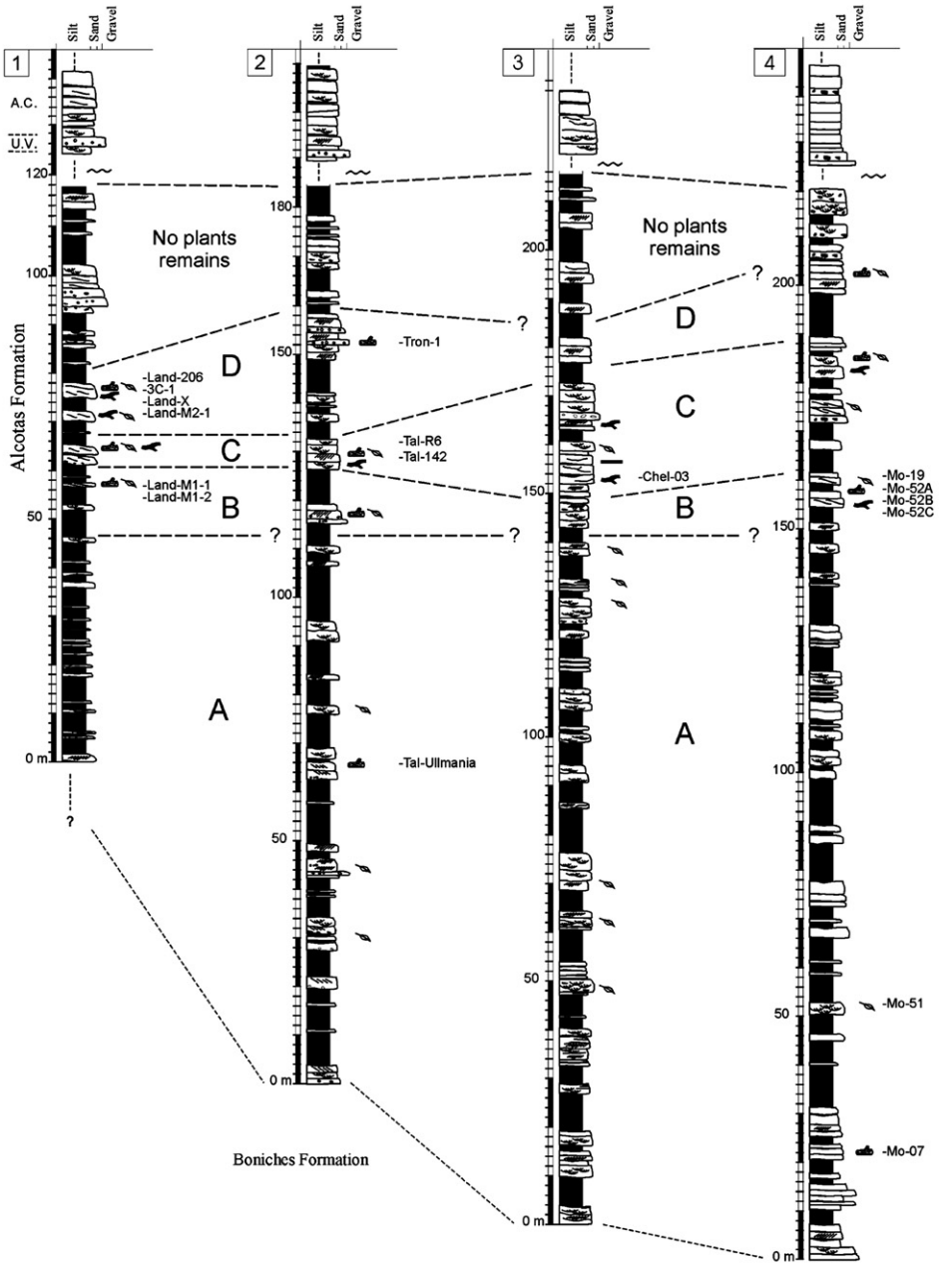
The Iberian and the Ebro Basins were separated during the Permian and Early Triassic by a narrow and longitudinal Palaeozoic high, the so-called Ateca-Montalbán High. On the other hand, to the southwest, another ill-defined Palaeozoic high, the so-called Serranía de Cuenca High, separated the Iberian Basin from the Cuenca–Valencia Basin (Fig. 1) [4]. Thus, the present-day configuration of the Iberian Ranges presents two Palaeozoic–Mesozoic chains, the Aragonese and Castilian Branches, that roughly mimic the Permian–Triassic basin and its bounding Palaeozoic highs.

Small and isolated extensional basins were present in the Iberian Basin during the beginning of the Late Permian. Later on, a new subsidence regime allowed the connection between most of these small basins; during the Early Triassic, it had exceeded most of the highs that were separating them. During this mature phase, other different basins of the Iberian microplate, which was located close to the equatorial eastern part of Pangea [16,21,30–32], were also connected.

3. The sediments

A closer look at the Permian sedimentary record in the SE Iberian Ranges reveals a much more complex facies and large thickness variations due to differential rates of extension during the synsedimentary extensional tectonics [4,12,18,21,25–28]. The sedimentary record has been subdivided into different tectono-sedimentary cycles, not always present in every location, and separated by angular unconformities and hiatuses. For the study area, the Late Permian sediments are represented by the Boniches Conglomerates and the Alcotas Siltstone and Sandstone Formations (Fig. 2) [3,20], both consisting of continental alluvial sediments, but only the latter will be studied in this paper.

The Alcotas Formation consists of red siltstones and sandstones, with minor presence of conglomerate lenses. In the study area, it lies apparently conformably on



Association	Representative Macroflora Samples
D	Land-X; Land-206; 3-C-1; Tron-1
C	Tal-142; Tal-R6; Chel-03
B	Land-M1-1; Land-M1-2;Mo-19; Mo-52A; Mo-52B; Mo-52C; Land-M2-1.
A	Mo-51; Mo-07; Ant-301; Ant-302; Ant-303; Tal-Ullmania.

Key to Simbols

Unconformity
Planar lamination
Trough cross bedding
Planar tabular cross bedding
Epsilon cross bedding
Clay rip up clasts
Pollen and spores asociation
Poorly preserved plant remains
Siltstone
Sandstone
Conglomerate / Pebbles
Logs
Coalified wood
Coal bed

Fig. 3. Studied stratigraphic sections and location of the fossil macroflora samples. See Fig. 1 for the location of the sections.
Fig. 3. Coupes stratigraphiques étudiées et localisation des échantillons de macroflore fossile. Voir la Fig. 1 pour la localisation des coupes.

the Boniches Formation or unconformably on the Hercynian basement, and it is unconformably overlain by the Cañizar Formation, although other possible contacts also occur in neighbouring areas [21]. Thickness reaches 220 m in the Montán section, although some of the studied sections are not complete. This unit crops out along the entire Iberian Ranges, except for some isolated highs.

Detailed studies on the petrological composition of the Alcotas Formation are found in López-Gómez [19] and Alonso-Azcárate et al. [1]. They showed red siltstone to be the dominant lithology (of about 70%), composed of quartz, of illite, of kaolinite, and of minor amounts of feldspars and hematite. Subrounded quartz and feldspar grains and mica flakes with clay matrix and quartz cements constitute the red to pink sandstones. A general increase in the quartz content is clearly observed towards the Southeast of the Iberian Ranges.

Five detailed sections have been used for the study of the plant assemblages of the Alcotas Formation in this work (Fig. 3). Most of these sections were previously studied from the sedimentological and petrological points of view [1,5,6,19]. The location of these sections shows a general NW–SE trend in the southeastern Castilian Branch of the Iberian Ranges (Fig. 1). Although punctual characteristics differentiate each one of the sections, a general study shows common features for all of them in the whole study area. These sections have been called: Landete, Talayuelas, Chelva, Montán, and Barranco del Rubio (referred to as 1 to 5, respectively).

The Alcotas Formation can be subdivided into three different units, referred to as 1 to 3 from base to top, respectively [5] (Fig. 3). Unit 1 is up to 150 m high and consists of lensoidal sandy and conglomerate bodies that reach 120 m in width and less than 8 m in thickness. They can be isolated or amalgamated, but in any case, they mostly show multi-storey internal structure. Siltstone facies are usually massive and they show carbonate palaeosoils of nodular and laminar horizons [6]. This unit is interpreted as the evolution of sandy and gravely braided fluvial systems with huge floodplains where carbonate palaeosoils were developed.

Unit 2 ranges from 45 to 55 m. It marks a clear change in lithofacies and fluvial style, where conglomerates disappear and sandstones represent almost 70% of the total lithology. They normally show single-storey sandstone bodies with tabular geometries and abundant lateral accretion surfaces littered by comminuted plant remains. Scarce large silicified trunks and wood fragments also appear at the base of some of the sandstone bodies [11]. This unit can be interpreted as a transition from distal sandy braided rivers to high sinuosity meandering rivers. The banks were probably vegetated by tree-like plants, sometimes uprooted and transported downwater.

Unit 3 reaches 45 m in thickness. A new drastic change is noticed with respect to the previous unit. It now consists of red siltstones (about 85%), which contain lenticular pink sandstone bodies up to 25 m wide and 1.5 m thick. No carbonate palaeosoil or macro- or microflora has been found up to now in this unit. Fining-upwards sequences with planar cross-stratification at their base constitute most of the sandstone bodies. This unit is interpreted as the development of distal very low energy braided fluvial systems within extensive floodplains.

4. Plant megaremains

As described previously, detailed sedimentological analysis of the differentiated zones has been recently described by Arche and López-Gómez [5]. This analysis shows abrupt changes that mainly consist in variations of the alluvial style. Zone A is represented by sandy braided fluvial systems that abruptly change to meandering systems in zones B, C, and D. Finally, a new braided fluvial style conditions is installed in the uppermost zone.

4.1. Zone A

Outcrops in zone A are scarce, and the number of megaremains per level is correlatively low. Specimens recovered from the fossiliferous levels of Talayuelas and Montan sections mainly correspond to cordaitalean (Fig. 4) and utrechtiacean axes as well as to well-preserved vegetative shoots, accompanied by highly carbonized fragments of axes. The preservation state of

Fig. 4. Distal part of a Cordaitalean axis. Scale bar: 1 cm.
Fig. 4. Partie distale de l'axe d'une cordaïtale. Barre d'échelle : 1 cm.

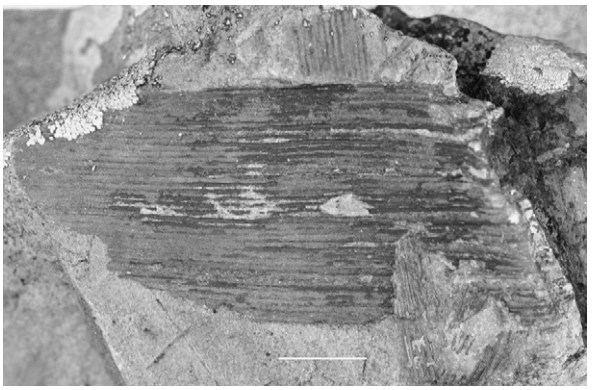


Fig. 5. Fragments of medullar moulds of sphenopsids stems. Scale bar: 5 cm.
Fig. 5. Fragments de moules de moelle de tige d'une sphénopside.

the latter hinders their classification, but their size and shape could allow us to attribute them to conifers.

The uppermost part of the Chelva section presents levels with tiny poorly preserved fragments of leaves.

4.2. Zone B

A significant increase in diversity and population density is evident in this zone, which shows reproductive structures and remains of leaves, trunks, and indeterminate axes of sphenopsids (Fig. 5), cordaitales, and conifers.

The collected material includes leave remains and scales (Fig. 6), of uncertain affinity, mainly due to their poor state of preservation.

The palaeovegetation could be interpreted as a forest with an undercanopy of sphenopsids.

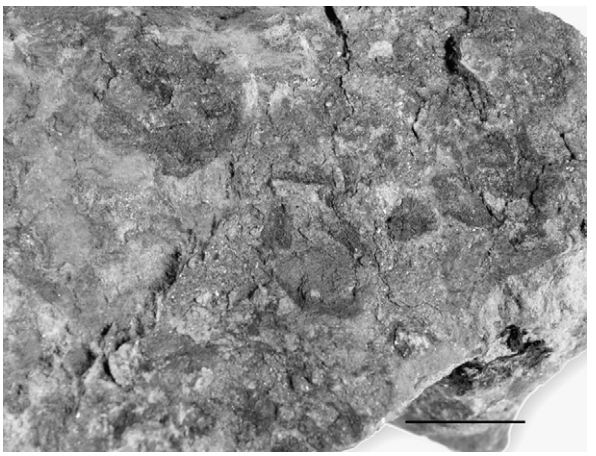


Fig. 6. Leaves and scales. Scale bar: 1 cm.
Fig. 6. Feuilles et écailles. Barre d'échelle : 1 cm.

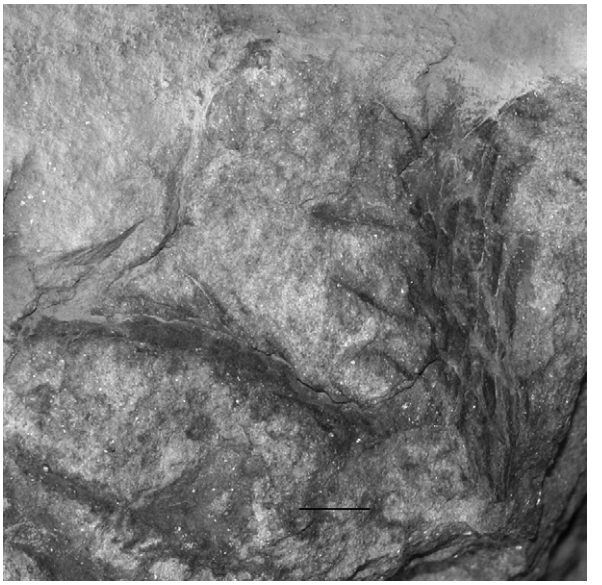


Fig. 7. Conifer axis and shoot. Scale bar: 5 cm.
Fig. 7. Axe et pousse de conifère. Barre d'échelle : 5 cm.

4.3. Zone C

This zone shows a great decrease in the number of megaremains, and the scarce specimens collected mainly correspond to silicified conifer trunk fragments, some of them being highly carbonized.

4.4. Zone D

In this zone, the number of fossiliferous levels and plant megaremains that correspond to silicified trunks and vegetative shoots of conifers (Majonicaceae) decreases (Fig. 7). Fossiliferous levels are restricted to the Landete.

The total absence of plant megaremains is the main characteristic of the upper part of the Alcotas Fm. (zone F).

In general terms, the evolution of palaeovegetation coincides with that obtained through palynological studies [10].

5. Conclusions

The occurrence of fossil plant remains recovered from the Alcotas Formation is significant, due to the paucity of the fossil record of megafloras of identical or similar ages in western Europe, which has made it difficult to acquire knowledge on the development of flora and vegetation in the Upper Permian of Europe.

In general terms, and due to the dominance of coniferous remains, the vegetation fits in well with Alpine Permian floras, but we have observed significant changes in the biodiversity and population density within each outcrop and defined zone. The patterns of changes and vegetation dynamics are similar to those described after the study of the palynological assemblages of the Alcotas Formation. The observed changes with respect to zone A are an increase of the megaremain levels, of the biodiversity, and of the population density in zone B, followed by a general decrease of these features in zone C. A new increase happened in zone D, and a significant decrease occurred in zone E, ushering in the lack of plant remains noticed in zone F. This pattern allows us to infer paleoecological changes for a time interval close to the biotic crisis of the end-Guadalupian.

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