



## Palynological and sedimentological implications of the sauropterygian Upper Triassic site of El Atance (Central Iberian Peninsula)

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### ABSTRACT

This study presents new palynological and sedimentological data concerning the Upper Triassic outcrop El Atance (Guadalajara province, Spain). This fossil site has provided a unique and unprecedented concentration of reptile skeletons from the Late Triassic in the Iberian Peninsula, which are almost complete, articulated and preserved in three dimensions. It is the type locality of the simosaurid nothosauroid *Paludidraco multidentatus* and the henodontid placodont *Parahenodus atancensis*, being the only species of these clades represented with some certainty in the Iberian record.

Although these reptiles are often linked to shallow marine environments, little is known about the sedimentary environment where they became fossilized. Furthermore, to compare these remains with those from other areas of Europe, greater precision in their age assignment is necessary.

The new palynological data provided in this study allows us to assign a precise age, in addition to other data such as a probable plant community, palaeoecology, and palaeoclimatic conditions. This information together with the geological and sedimentological data and the new isolated sauropterygian remains studied, allow a better understanding of the local palaeogeography and the evolutionary history of the vertebrates found in the El Atance fossil site.

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### 1. Introduction

The Upper Triassic of the Western Neotethys domain is characterized by an extensive carbonatic and evaporitic sedimentation under generally warm, arid to semiarid climatic conditions (Ortí et al., 2017). As in many other Upper Triassic basins of Western Europe, this sedimentary record has been assigned in Iberia to the Muschelkalk (carbonate platforms) and Keuper (evaporitic mudflats) facies (López-Gómez et al., 2002). Located in a marginal zone between continental and shallow marine environments, El Atance is the only Upper Triassic Iberian fossil site where several partial skeletons of reptiles, preserved in three dimensions, have been recovered (de Miguel Chaves et al., 2018c). The site is the type locality of two recently described sauropterygians, the placodont *Parahenodus atancensis* (de Miguel Chaves et al., 2018a) and the eosauroptrygian *Paludidraco multidentatus* (de Miguel Chaves et al., 2018c). *Paludidraco*

*multidentatus* is interpreted as a bizarre and highly pachyostotic nothosauroid Simosauridae, and one of the two species of this lineage currently recognized, the other being *Simosaurus gaillardoti*, known in the Ladinian of an area including northeastern France and southwestern Germany (de Miguel Chaves et al., 2018b). It shows a highly specialized trophic adaptation, being interpreted as a filter-feeding form (de Miguel Chaves et al., 2018c). Thus, the description of this taxon increased the ecological disparity of the Triassic marine reptiles. *Parahenodus atancensis* is the second known representative of the clade Henodontidae. It shares highly derived characters with the German lower Carnian placodont *Henodus chelyops* but also retains some primitive states concerning this form, shared with other cyamodontoid placodonts (de Miguel Chaves et al., 2018a). *Parahenodus* provides information on the acquisition process of the exclusive and highly specialized morphology of the skull of the Henodontidae and consequently of its specialized way of life within Placodontia. The information relative to the age of El Atance was extremely limited so far, being located in an imprecise time in the Carnian-Norian range of the Late Triassic (de Miguel Chaves et al., 2018a, 2018c). The lack of greater temporal

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precision makes difficult to interpret the evolutionary history of Simosauridae and Henodontidae. In addition, the two sauropterygians from El Atance have been related to shallow marine environments (de Miguel Chaves et al., 2018c), but little was known about the specific sedimentary environment. However, the El Atance site stands out for the important implications that can be drawn from its fauna content. For this reason, greater precision in assigning its age and type of sedimentary environment is necessary.

Based on the first study of the palynological record of El Atance, recognized as diverse, and on a bibliographic review of the palynology in the area of confluence between the Iberian Ranges and the Central System, a precise age is assigned to the site. The dating, the first geological and sedimentological characterization of the site, and the study of some new isolated eosauroptrygian remains contribute to understanding the local palaeogeography, palaeoecology, and evolution history of the vertebrates found in the Upper Triassic El Atance site.

## 2. Geological and stratigraphic setting

The study area is located north of the Province of Guadalajara (Autonomous Community of Castilla-La Mancha, Spain), on the border between the Central System and the northwestern margin of the Iberian Ranges. The region is characterized by the interaction of alpine tectonic structures of NW-SE and SW-NE directions (Fig. 1). In fact, the Iberian Ranges is the result of the compressive tectonic evolution in the Cenozoic of the Iberian Basin, a rift-related basin with a complex evolution from the Ciszurialian (i.e., early Permian) to the Early Cretaceous (Sopeña et al., 1988; Salas and Casas, 1993; Arche and López-Gómez, 1996; Vergés and Fernandez, 2006; López-Gómez et al., 2019).

The sedimentary record corresponding to the Triassic consists of continental, coastal, and marine rocks, deposited in three main transgressive-regressive cycles (López-Gómez et al., 2002; Sánchez-Moya and Sopeña, 2004). These cycles have been commonly described as a variation of the classical Germanic-type Triassic, differentiated into three main lithostratigraphic terms: the most basal corresponding to continental and siliciclastic deposits, composed of red sandstones and conglomerates of the Buntsandstein facies; the intermediate, represented by the marine and carbonatic Muschelkalk facies; and the upper one, composed by the mudstones and evaporites of the Keuper facies

(López-Gómez et al., 2002; Sánchez-Moya and Sopeña, 2004). Due to the presence or absence of carbonate Muschelkalk units, different Triassic areas have been described (Sopeña, 1979). El Atance fossil site region is located in the limit between the “Iberian Triassic” at the East, and the “Hesperian Triassic” to the West (García-Gil, 1990). The “Iberian Triassic” is characterized by the presence of a single carbonate term in Muschelkalk facies, not present in the “Hesperian Triassic”, which is mainly composed of siliciclastic facies.

Muschelkalk and Keuper facies are linked to the westward propagation of the Tethys Sea on the Iberian plate during the Middle and Late Triassic (López-Gómez et al., 2002). As the transgression was heterochronic, the oldest marine sediments were deposited in southeastern areas of the basin during Anisian, but the first representation of the marine incursion was in the Ladinian in the region where El Atance is located. In addition, minor transgressive-regressive cycles produced lateral facies changes between continental-influenced siliciclastics units and marine carbonates, which are described since the Anisian in the intra-basinal correlations (Arche et al., 2004; Sánchez-Moya and Sopeña, 2004). As the study area was located in the northwestern margin of the Iberian Basin (Fig. 1), the lateral relationships between coastal and marine facies are more evident than in the depocenters of the Basin. The final phases of the Middle Triassic and the beginning of the Upper Triassic in this region correspond to facies belts where terrestrial materials of continental influence alternate with coastal facies of carbonated and evaporitic tidal plains. This fact was described in the essential works of Sopeña (1979), Hernando (1977a), and García-Gil (1990), and can be observed in Fig. 2, that summarizes the stratigraphy of the region.

The Muschelkalk cycle in the area starts with the Torete Fm., composed by siltstone and sandstone intercalations with minor presence of conglomerates and dolomitic beds (García-Gil, 1995), dated as upper Fassanian (Dinarès-Turell et al., 2005). This siliciclastic unit is representative of the regression phase of the first main Triassic incursion of the Tethys Sea in the southeastern areas (Arche et al., 2004). The second marine incursion is more extensive to the northwest, being recorded in the region by the dolomitic carbonates and marls of the Tramacastilla and Royuela formations. These units laterally pass to the siliciclastic Cuesta del Castillo Fm. (Fig. 2), attributed to the Longobardian (García et al., work in progress).

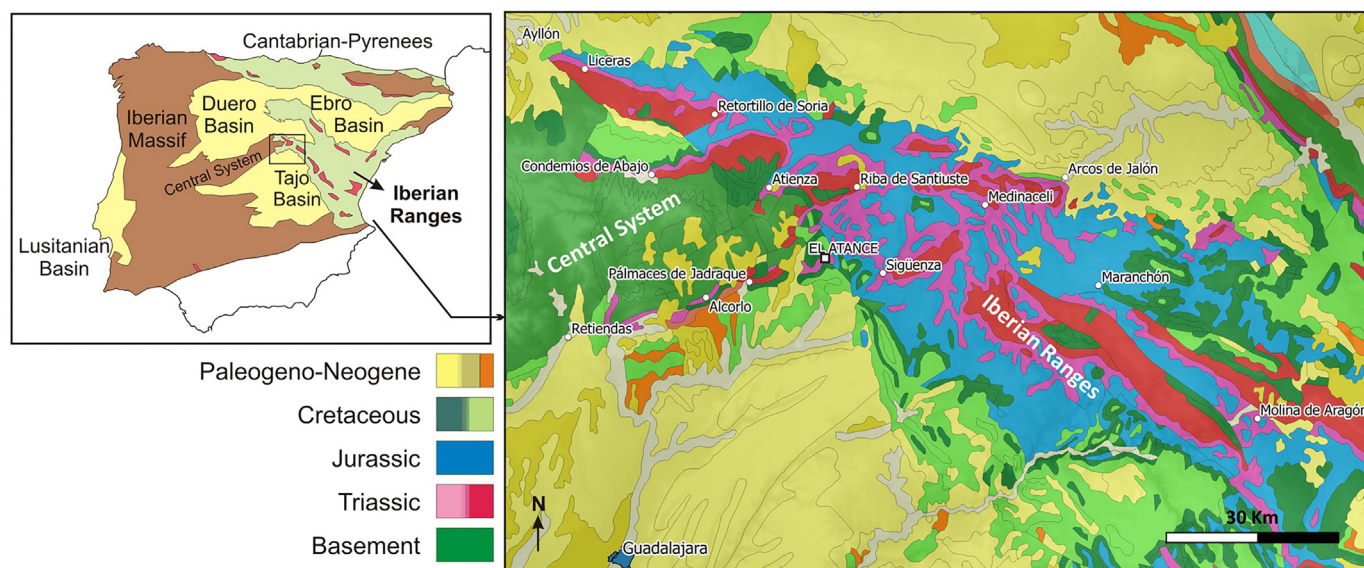


**Fig. 1.** A) Location of the study area in the confluence between the Iberian Ranges and the Central System, Spain. B) General geological map with the location of El Atance fossil site and localities of studied sections. Rocks of the Precambrian to Silurian basement are represented in dark green color. Modified from Servicio GEODE (2020).

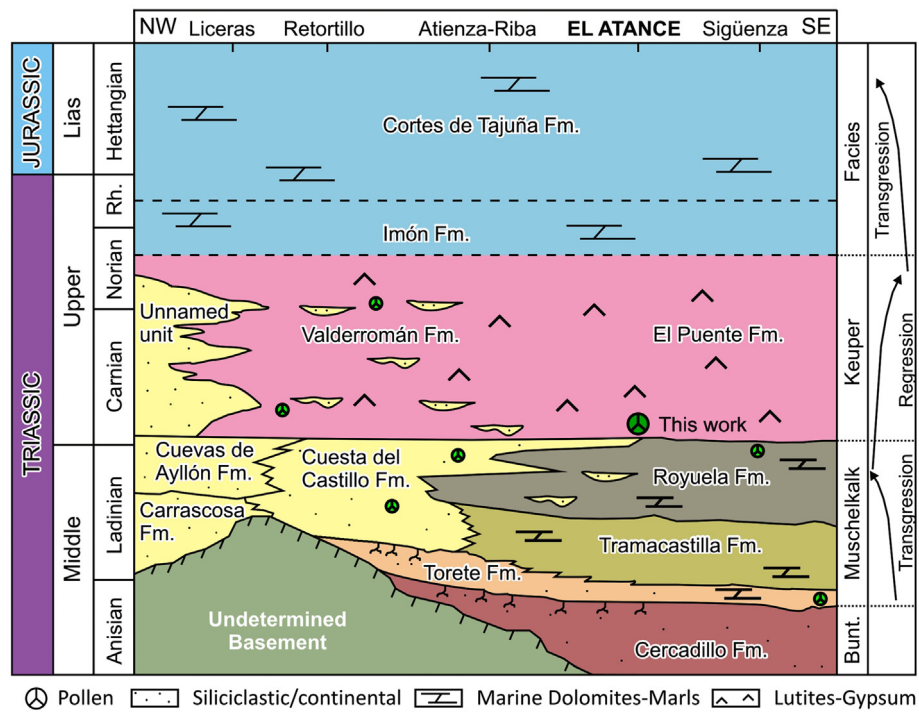


**Fig. 2.** Middle Triassic–Lower Jurassic stratigraphic framework of the study area. See text for further information about previous palynological samples (small green symbols). The stratigraphic location of the palynological data of El Atance studied in this work is represented by a bigger symbol.

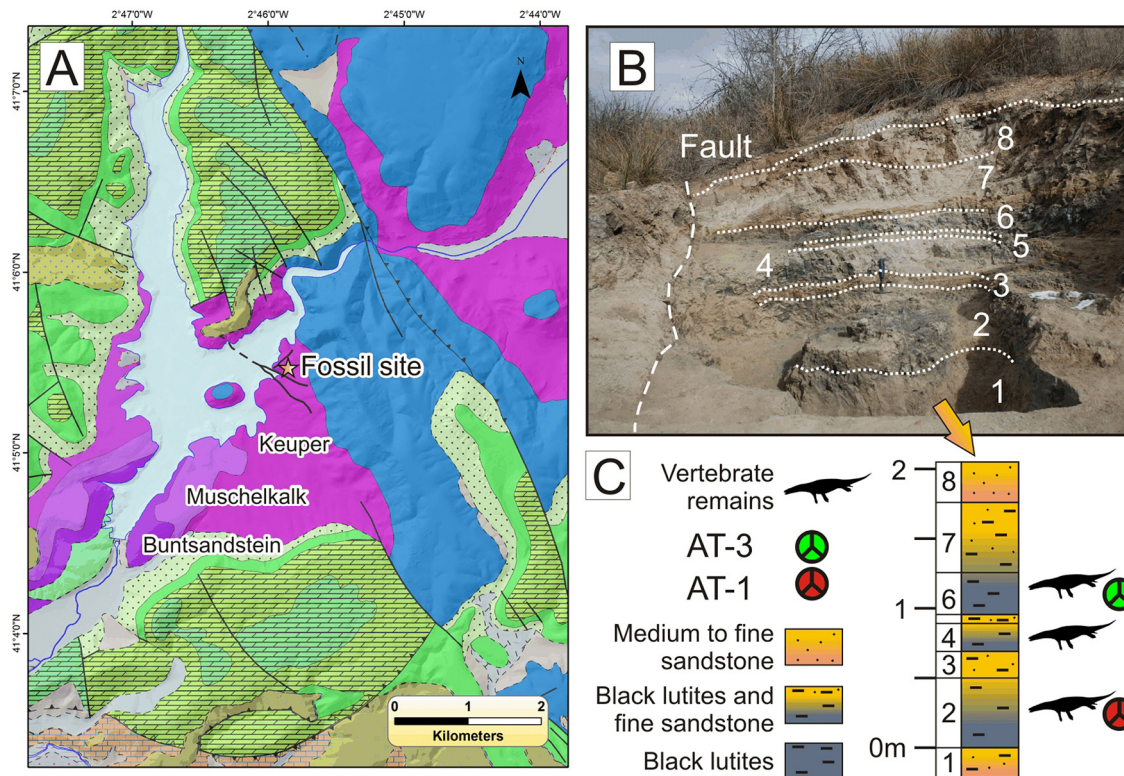


**Fig. 3.** A) Location of El Atance fossil site in Keuper facies. Modified from ArcGis Online (2020). Triassic: purple to pink; Jurassic: blue; Cretaceous: yellow and green. B) Palaeontological excavation at El Atance fossil site and levels identified in the field. Continuity of strata to the west is interrupted by a fault. C) Stratigraphic log with the location of palynological samples and vertebrate remains.

The Keuper corresponds to the main regressive pulse previous to the more extensive end-Triassic-Jurassic transgression (López-Gómez et al., 2002; Sánchez-Moya and Sopena, 2004; Arche et al., 2004). In central areas of the Iberian Basin, the Keuper Group is subdivided into five members (K1–K5) grouped in two evaporitic sequences of red, green, and gray mudflats separated by one of siliciclastic character (Ortí, 2004). However, due to the palaeogeographic location of the study area, away from the depocenters, the Keuper in the region is composed of a gray basal term of lutites, gypsum, sandstones, and carbonates, and an upper term of red lutites and gypsum. Therefore, it is convenient here to assign the Keuper facies to local units: El Puente and Valderromán formations (see in Fig. 2), that passes laterally to unnamed siliciclastic units to the northwest (Hernando, 1977a, 1977b; García-Gil and Sopena, 1987); and to the Los Gavilanes Fm. to the West (Sopena, 1979).

The sauropterygian fossil site studied here is located on the eastern slope of El Atance reservoir, in Keuper facies with a hitherto undefined location within the Carnian-Norian temporal range (de Miguel Chaves et al., 2018a, 2018c). In general terms, the Triassic materials in the study area are arranged on a Cambrian basement in a small anticline SW–NE oriented (Fig. 3A). The site is located in the basal gray term of the Keuper, but bad exposition and presence of faults hinder the strata continuity. In detail, the fossil site is composed by thin levels of pale yellow sand with wave ripples intercalated with gray to black and green muds (Fig. 3B). Overlying the fossil site, there is a ~50 m thick succession of gray and greenish marls with intercalations of sandstones. The Keuper ends with ~60 m of red marls with gypsum and characteristic authigenic minerals as aragonites and bipyramidal quartz.

The Keuper facies gradually pass into a transition unit 2–3 m thick of clayed limestone below the Imón Fm., which in the area reaches 20 m of thickness, to finally reach the Cortes de Tajuña Fm. that possibly record the Triassic-Jurassic transition (IGME, 1981b; Fig. 2). These latter authors suggest an imprecise Carnian-Norian age for the Keuper of the

region, based on palynological samples obtained 4 km east from the fossil site.

### 3. Materials and methods

This study is based on nine representative stratigraphic sections examined in the field to assess the sedimentological characteristics and obtain the facies scheme of the study area. Locations of the outcrops are showed in Fig. 4. The detailed revision of the bibliography of the area included the 1:50.000 geological maps of the National Geological Mapping Program (MAGNA Plan. IGME, 1981a, 1981b, 1981c, 1982a, 1982b, 1991a, 1991b, 2005, 2007) and their accompanying reports (Spanish Geological Survey IGME, [www.igme.es](http://www.igme.es)). The palaeogeographic maps obtained in this study were produced by integrating cartographic, sedimentological, and palynological data.

Fieldwork in El Atance fossil site included sample collection for pollen and spores determination, as well as the vertebrate macroremains. Three samples for palynological analysis were taken in El Atance fossil site, including the marly levels where the vertebrate remains were found. They were initially processed in the Faculty of Geology, Complutense University of Madrid. Only the two samples corresponding to the marly levels were productive (AT-1 and AT-3; Fig. 3) and sent to the Geosciences Department, University of Vigo. In this laboratory, carbonate and silicate minerals were removed with hydrochloric acid (HCl, 10%) and hydrofluoric acid (HF 40%), and then samples were stirred with 10% hydrochloric acid for 45 min to remove the secondary compounds produced during the hydrofluoric acid attack (Wood et al., 1996; Traverse, 2007). Finally, a dispersing agent was added to facilitate filtering and sieving at 10 µm. The prepared slides were examined with a Leica DM 2000 LED microscope, and the photomicrographs were taken with a Leica ICC50 W camera at a magnification of ×1000. The slides are housed in the Geosciences Department

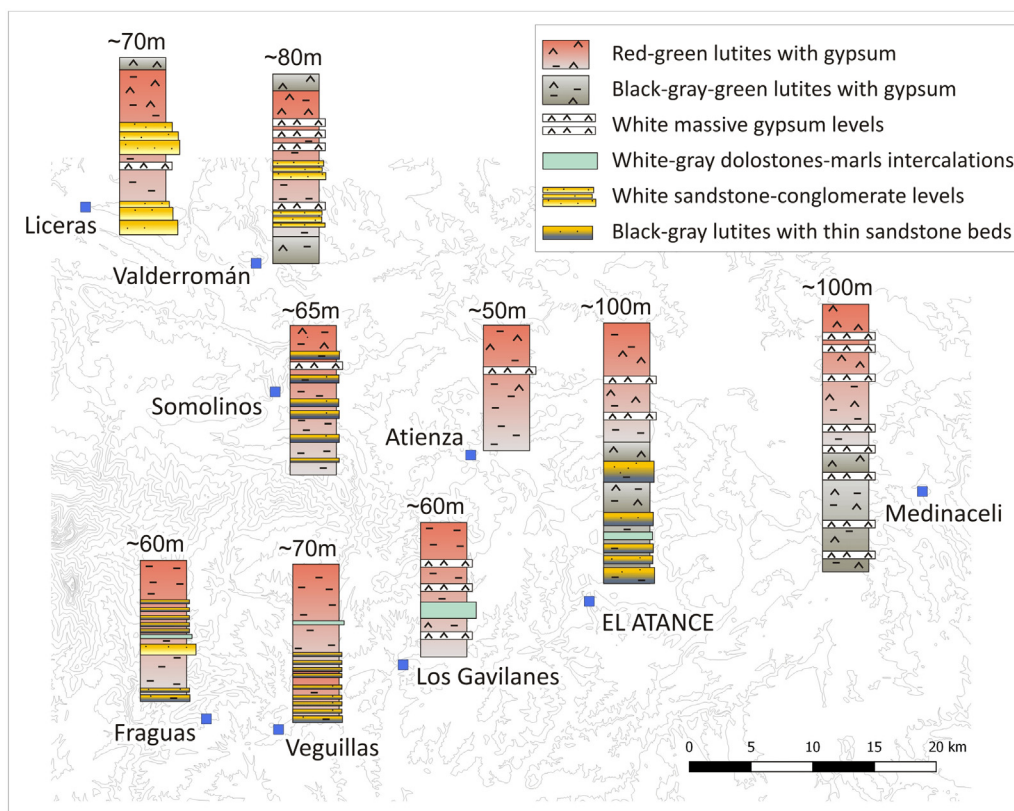


Fig. 4. Location of the simplified stratigraphic logs involved in this study and main facies associations. See text for more details.

Laboratory (University of Vigo). Specimen locations are referred by England Finder coordinates.

During the bibliographic review, a method was followed to analyze, validate, and discriminate the palynological data provided in previous works. The palynological data have been considered valid if a complete and correct figuration accompanied them or if the identified taxa were correctly illustrated. Data from different geographical locations, litho-stratigraphic formations, or levels presented together in a single palynological association have been rejected since they should have been presented independently.

## 4. Results

### 4.1. Facies associations

The Keuper Group is a complex phase that is not generally studied in detail because of dissolution of evaporitic intervals and because it was very tectonically deformed during the Alpine compression (Arche and López-Gómez, 1996; López-Gómez et al., 2002). There are only a few outcrops that allow studying the clayey-evaporitic materials in detail (Fig. 4). Located to the west, the stratigraphic columns of Fraguas, Camino de Veguillas, and Los Gavilanes were first studied by Sopeña (1979). In northwestern areas, the sections of Licerías, Valderromán, Somolinos, and Atienza were described by Hernando (1977a, 1977b) and Aracil and Hernando (1988). Finally, the stratigraphic log of El Puente (García-Gil and Sopeña, 1987) is located near Medinaceli in the east.

Mainly based on the interpretations of previous works and new visits to key stratigraphic locations, the sedimentological analysis can be summarized in four main facies associations: siliciclastics-rich to the west, fine siliciclastics and evaporites to the east, central black to gray lutites, and extensive red fine siliciclastics and evaporites (Fig. 4).

#### 4.1.1. Siliciclastic-rich facies association (west)

In the northwest (Licerías-Atienza sector, Fig. 4), the basal part of the Keuper is characterized by 1.5 to 2 m thick channelized sandstone levels with conglomeratic basal lags and overbank fines with lenticular, flasher, and wavy laminations, desiccation cracks, and iron coated levels (Hernando, 1977a, 1977b; Aracil and Hernando, 1988). Other sequences with sandstones are interpreted as crevasse splay and unconfined sheet-flood sandstones. These sedimentary features are related to meandering-channel sandstones and overbank sediments deposited by splaying and avulsion processes in the floodplain. Similar characteristics are observed in the Los Gavilanes Fm. of Sopeña (1979) in locations west of Fraguas (Fig. 4).

#### 4.1.2. Fine siliciclastics and evaporites facies association (east)

Towards the east, levels of sandstone decrease and gray lutites with gypsum beds are more common. In the Medinaceli area (Fig. 4), the sandstone beds are absent (García-Gil and Sopeña, 1987), and the lower part of the Keuper is constituted by gray and green lutites with intercalated gypsum levels. The common presence of sedimentary structures of sub-aerial origin are indicative of supratidal to intertidal flats, and the gypsum beds are probably related to a shallow sulfate lagoon with marine influence. Similar characteristics are observed by Ortí et al. (2018) in the Camposines Gypsum unit of the Middle Triassic in the Catalan Basin.

A similar lateral relationship between siliciclastic and evaporitic environments is described in a marginal-marine system of the Upper Triassic in the Dolomites (Breda and Preto, 2011).

#### 4.1.3. Black lutites facies association (central area)

This facies association characterizes El Atance fossil site, but it is also observed in Somolinos, Fraguas, and Veguillas locations (see Fig. 4;

Hernando, 1977b; Sopeña, 1979, this study). This association is characterized by gray to black lutites intercalated by layers of fine-grained sandstone of 6 to 35 cm in thickness and wave-ripple cross-laminations. In those mud-dominated layers, other sedimentary structures have been observed, as lenticular, wavy, and flasher laminations, vertical burrows, mud-cracks, and iron-hydroxide crusts located at the top of some layers. High contents of organic matter are inferred by these sedimentological features, dark colors, and microremains. All those features are indicative of low-energy conditions and alternating periods of traction and decantation, shallow waters, and periods of sub-aerial exposition (Reineck and Singh, 1980). Intertidal flats typically display those features; however, the black lutites facies association does not include other sedimentary structures of higher energy processes as thick subtidal channel fills or sand-bar complexes. Probably, the area of sedimentation of this facies association was sheltered from open marine and higher energy settings (Daidu, 2013).

#### 4.1.4. Extensive fine siliciclastics and evaporites

In the upper part of all the sections, gray and green colors decrease, and red colors dominate. This facies association is composed by red mudstones and gypsum beds with abundant pseudo-hexagonal aragonites and euhedral quartz crystals. The alternation of evaporite levels with gray to red mudstone beds is interpreted as desiccation of hypersaline shallow waters in mudflats, probably related with salinas and peripheral sabkhas in a clayey coastal plain environment (Ortí et al., 2017).

### 4.2. Palynological data

#### 4.2.1. Revision of previous works

In this section, we present a bibliographic review of the palynological works carried out previously in the area of confluence between the Iberian Ranges and the Central System (Fig. 1; and Supplementary material, Table 1). The Triassic rocks in the Aillón-Atienza region (Fig. 1) were studied by Hernando (1977a) and Hernando et al. (1977). In Hernando et al. (1977), samples obtained from Muschelkalk and Keuper facies offered a Carnian age due to the abundance of Circumpolles (*Paracirculina*, *Praecirculina*, and *Duplicisporites*) and specifically *Camerosporites secatus*. In the upper part of the Keuper, a Norian age was suggested due to the “absence of *Camerosporites secatus*” and the significant relative frequency of *Enzonalasporites*, *Patinasporites*, and *Inaperturopollenites*.

In Sopeña et al. (1977) and Doubinger et al. (1978), two palynological assemblages were obtained from gray-green clays and marls with dolomitic levels interbedded in the surroundings of Alcorlo (Fig. 1). These authors suggested a Carnian age due to the presence of *Camerosporites secatus*, *Duplicisporites granulatus* and *Praecirculina granifer*, and a late Carnian age due to the presence of *Circulina granulata* (Geiger and Hopping, 1968). In the area between Licerías, Somolinos and Retortillo (Fig. 1), Doubinger et al. (1978) presented a palynological assemblage obtained in Muschelkalk facies and suggested a Carnian age due to the abundance of circumpolles group and specially of the high presence of *Camerosporites secatus*. In the Somolinos section, located some kilometers east of Condemios (Fig. 1), another two samples were obtained at the top of the Triassic section and dated as Norian age due to the “absence of *Camerosporites secatus*” and the high relative frequency of *Patinasporites*, *Enzonalasporites*, and *Inaperturopollenites*.

Sopeña (1979) suggested a Carnian age for the dark clayey levels intercalated with dolomitic beds in the Riba de Santiuste and Camino de El Robledo sections (Fig. 1) due to the abundance of circumpolles grains, especially *Camerosporites secatus*. In the area of Veguillas, Fraguas, and Los Gavilanes (Fig. 4), a late Carnian age was suggested as the described assemblage was very similar to palynological assemblages obtained in the *Tropites subbullatus* ammonites zone of the late Carnian of the northern Austrian Alps (table IV, Dunay and Fisher, 1978), and to the

assemblage described in layers dated by ammonites (*Anatropites*) of the late Carnian of Sicily (table I, [Visscher and Krystyn, 1978](#)).

[Besems \(1981\)](#) analyzed the ages proposed by [Hernando et al. \(1977\)](#). He suggested that a Carnian age would be plausible for the upper Muschelkalk facies of the Somolinos section, through an investigation whose results were presented in an unpublished internal report ([Besems, 1977](#)) for the Laboratory of Palaeobotany and Palynology (Utrecht). In this internal report, this author reported the presence of *Patinasporites densus*, *Vallasporites ignacii* and *Duplicisporites quadruplicis* in the Somolinos section, and the assemblage obtained was attributed to the *Camerosporites secatus* - *Patinasporites densus* palynoflora. The upper part of the Somolinos section (Keuper), previously dated as Norian by [Doubinger et al. \(1978\)](#), was assigned to the *Camerosporites secatus* - *Patinasporites densus* palynoflora due to the presence of *Patinasporites densus* and *Duplicisporites quadruplicis* ([Besems, 1977](#)) and a Carnian age was proposed.

[Besems \(1981\)](#) also reviewed the Termancia assemblage of [Doubinger et al. \(1978\)](#) and the two palynological assemblages obtained in Alcorlo and described in [Sopeña et al. \(1977\)](#) and [Doubinger et al. \(1978\)](#). Through assemblages presented in [Besems \(1977\)](#), he proposed a Carnian age for the Termancia assemblage in this area by the presence of *Patinasporites densus* and *Duplicisporites quadruplicis* in combination with *Ovalipollis pseudoalatus* and *Triadispora* spp., and the Carnian age of the Alcorlo assemblages by the presence of *Patinasporites densus*, *Vallasporites ignacii* and *Duplicisporites quadruplicis*, placing them in the *Camerosporites secatus* - *Patinasporites densus* palynoflora.

[IGME \(1981b\)](#) indicated a palynological assemblage obtained from Carabias (about 4 km north of El Atance fossil site) in the memoir associated with the leaf map 461 of MAGNA 1:50,000, suggesting a later Triassic age (Carnian–Norian).

Finally, the palynological study of [Sopeña et al. \(1995\)](#) identified twelve palynological assemblages from Permian and Triassic rocks of the central area of Spain. Among them, three assemblages are discussed below. A late Ladinian age is proposed for the upper part of the Royuela Fm. and from the lower part of Keuper facies of the Noguera Fm., a lateral equivalence of El Puente Fm. ([Fig. 2](#)). This assemblage is characterized by the coexistence of Ladinian forms together with abundant circumpolles such as *Paracirculina scurrilis*, *Paracirculina tenebrosa*, *Praecirculina granifer*, and *Duplicisporites granulatus*. A late Ladinian age was suggested due to the presence of *Camerosporites secatus* and the “absence of *Patinasporites densus*”. The next assemblage was assigned to the lower Carnian, identified in samples from the Arrabal de Santa Barbara series (Teruel) in Keuper facies. Although this assemblage is taken far from our study area, [Sopeña et al. \(1995\)](#) compare it with those described in [Sopeña \(1979\)](#) located in the Robledo, Fraguas, and Riba de Santiuste ([Figs. 1 and 4](#)). They justify this age for the similarity with other assemblages (e.g., *Trachyceras aon* zone, [Dunay and Fisher, 1978](#)). The third assemblage was assigned to the late Carnian and was obtained from the upper part of the Keuper facies that outcrops at the Pálmaces de Jadraque section, located 12 km away from El Atance fossil site ([Fig. 1](#)). The palynological association is characterized by the presence of the Circumpolles group with a great variety of *Patinasporites*, *Inaperturopollenites varians*, and *Inaperturopollenites orbicularis*. *Paracirculina quadruplicis* also appears, and it is considered characteristic of the upper part of the Keuper ([Visscher and Brugman, 1981](#); [Van der Eem, 1983](#)). [Sopeña et al. \(1995\)](#) compare this assemblage with the described by [Hernando et al. \(1977\)](#) at the edge of the Central System, with the assemblage described by [Dunay and Fisher \(1978\)](#) in the late Carnian (Tuvalien) *Tropites subbulatus* ammonite zone of the Northern Austrian Alps, and with the assemblage identified by [Visscher and Krystyn \(1978\)](#) dated by ammonites (*Anatropites*) of the late Carnian of Sicily (Monte Triona).

In this review, some deficiencies have been found in identifying and presenting the palynological data: inaccurate identifications, lack of figure or illustrations, and data from different levels or stratigraphic sections grouped into a unique palynological assemblage. Furthermore,

the similarity between the Muschelkalk and Keuper facies in some sections has added an additional problem in the identification of the units. However, based on the validated information provided in [Hernando et al. \(1977\)](#) and by the lower and late Carnian associations provided by [Sopeña et al. \(1995\)](#), the age of El Atance fossil site would range between the upper Ladinian to the lower Carnian, as it will be discussed below.

#### 4.2.2. New Palynological results

The samples AT-1 and AT-3 contain 33 different taxa ([Table 1](#); [Plates I, II, and III](#)). The composition of both samples is very similar, so they have been considered as the same assemblage. The palynological assemblage is composed for spores: *Calamospora* sp., *Densoisporites* sp., *Verrucosporites* sp., and indeterminate trilete spore; pollen grains: *Alisporites opii* Daugherty 1941, *Alisporites* sp., *Camerosporites secatus* Leschik 1956, *Chordasporites* sp., *Cycadopites* sp., *Duplicisporites granulatus* (Leschik 1956) [Scheuring, 1970](#), *Enzonasporites vigens* Leschik 1956, *Ephedripites* sp., *Infernopollenites* sp., *Lunatisporites acutus* Leschik 1956, *Lunatisporites* sp., *Microcachrydites fastidioides* Klaus 1964, *Microcachrydites* sp., *Ovalipollis cultus* [Scheuring, 1970](#), *Ovalipollis ovalis* (Krutzsch 1955) [Scheuring, 1970](#), *Ovalipollis pseudoalatus* (Thiergart 1949) Schuurman 1976, *Paracirculina scurrilis* [Scheuring, 1970](#), *Paracirculina* sp., *Patinasporites densus* (Leschik 1956) [Scheuring, 1970](#), *Platysaccus papilionis* Potonié and Klaus 1954, *Platysaccus* sp., *Praecirculina granifer* (Leschik 1956) Klaus 1960, *Staurosaccites quadrifidus* Dolby and Balme, 1976, *Striatoabieites* sp., *Triadispora plicata* Klaus 1964, *Triadispora suspecta* [Scheuring, 1970](#), *Triadispora* sp., *Vallasporites ignacii* (Leschik, 1955) [Scheuring, 1970](#); and algae: *Plaesiodyctyon mosellanum* Wille 1970.

**Table 1**

List of species recorded from the study area.

|                                                                              | Samples |     |
|------------------------------------------------------------------------------|---------|-----|
|                                                                              | AT1     | AT3 |
| <b>Pollen grains</b>                                                         |         |     |
| <i>Alisporites opii</i> Daugherty, 1941                                      | •       | •   |
| <i>Alisporites</i> sp.                                                       | •       | •   |
| <i>Camerosporites secatus</i> Leschik, 1956                                  | •       | •   |
| <i>Chordasporites</i> sp.                                                    | •       |     |
| <i>Cycadopites</i> sp.                                                       | •       |     |
| <i>Duplicisporites granulatus</i> (Leschik) <a href="#">Scheuring, 1970</a>  | •       | •   |
| <i>Enzonasporites vigens</i> Leschik, 1956                                   | •       | •   |
| <i>Ephedripites</i> sp.                                                      |         | •   |
| <i>Infernopollenites</i> sp.                                                 | •       |     |
| <i>Lunatisporites</i> sp.                                                    | •       | •   |
| <i>Lunatisporites acutus</i> Leschik, 1956                                   |         | •   |
| <i>Microcachrydites fastidioides</i> Klaus, 1964                             | •       | •   |
| <i>Microcachrydites</i> sp.                                                  | •       | •   |
| <i>Ovalipollis cultus</i> <a href="#">Scheuring, 1970</a>                    | •       |     |
| <i>Ovalipollis ovalis</i> (Krutzsch 1955) <a href="#">Scheuring, 1970</a>    | •       | •   |
| <i>Ovalipollis pseudoalatus</i> (Thiergart) Schuurman, 1976                  | •       | •   |
| <i>Paracirculina</i> sp.                                                     | •       | •   |
| <i>Paracirculina scurrilis</i> <a href="#">Scheuring, 1970</a>               |         | •   |
| <i>Patinasporites densus</i> Leschik, 1955                                   | •       | •   |
| <i>Platysaccus</i> sp.                                                       |         | •   |
| <i>Platysaccus papilionis</i> Potonié and Klaus, 1954                        | •       | •   |
| <i>Praecirculina granifer</i> (Leschik) Klaus, 1960                          | •       | •   |
| <i>Staurosaccites quadrifidus</i> Dolby and Balme, 1976                      | •       |     |
| <i>Striatoabieites</i> sp.                                                   |         | •   |
| <i>Triadispora plicata</i> Klaus, 1964                                       | •       | •   |
| <i>Triadispora</i> sp.                                                       | •       | •   |
| <i>Triadispora suspecta</i> <a href="#">Scheuring, 1970</a>                  | •       | •   |
| <i>Vallasporites ignacii</i> (Leschik, 1955) <a href="#">Scheuring, 1970</a> | •       | •   |
| <b>Spores</b>                                                                |         |     |
| <i>Calamospora</i> sp.                                                       | •       | •   |
| <i>Densoisporites</i> sp.                                                    | •       |     |
| Indeterminate trilete spore                                                  | •       |     |
| <i>Verrucosporites</i> sp.                                                   | •       | •   |
| <b>Algae</b>                                                                 |         |     |
| <i>Plaesiodyctyon mosellanum</i> Wille, 1970                                 | •       | •   |

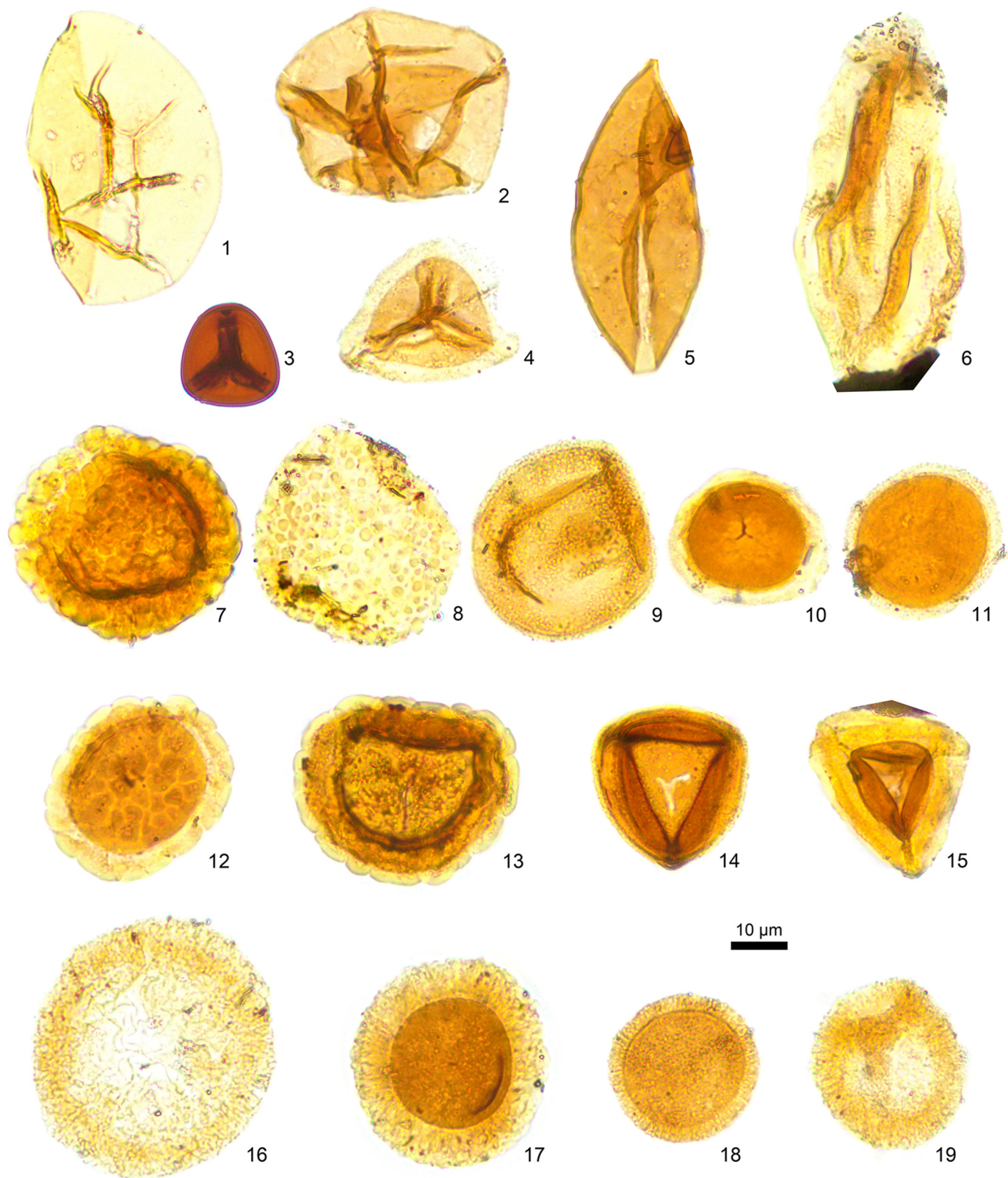


**Plate I.** Palynological assemblage AT-1, AT-3. **1.** *Calamospora* sp. AT-1\_3\_R532, **2.** *Calamospora* sp. AT-1\_1\_O441, **3.** Indeterminate trilete spore AT-1\_2\_Z452, **4.** *Densoisporites* sp. AT-1\_1\_L523, **5.** *Cycadopites* sp. AT-1\_2\_K112, **6.** *Ephedripites* sp. AT-3\_2\_T253, **7.** *Verrucosiporites* sp. AT-1\_2\_R340, **8.** *Verrucosiporites* sp. AT-3\_2\_J231, **9.** *Praecirculina granifer* AT-3\_2\_E500, **10.** *Paracirculina* sp. AT-3\_1\_N102, **11.** *Paracirculina scurrilis* AT-3\_1\_H490, **12.** *Camerosporites secatus* AT-3\_2\_N080, **13.** *Camerosporites secatus* AT-1\_3\_E410, **14.** *Duplicisporites granulatus* AT-3\_1\_G264, **15.** *Duplicisporites granulatus* AT-3\_1\_O091, **16.** *Patinasporites densus* AT-3\_3\_E274, **17.** *Patinasporites densus* AT-1\_1\_057\_H143, **18.** *Enzonasporites vigens* AT-3\_2\_N342, **19.** *Vallasporites ignacii* AT-1\_1\_G494.

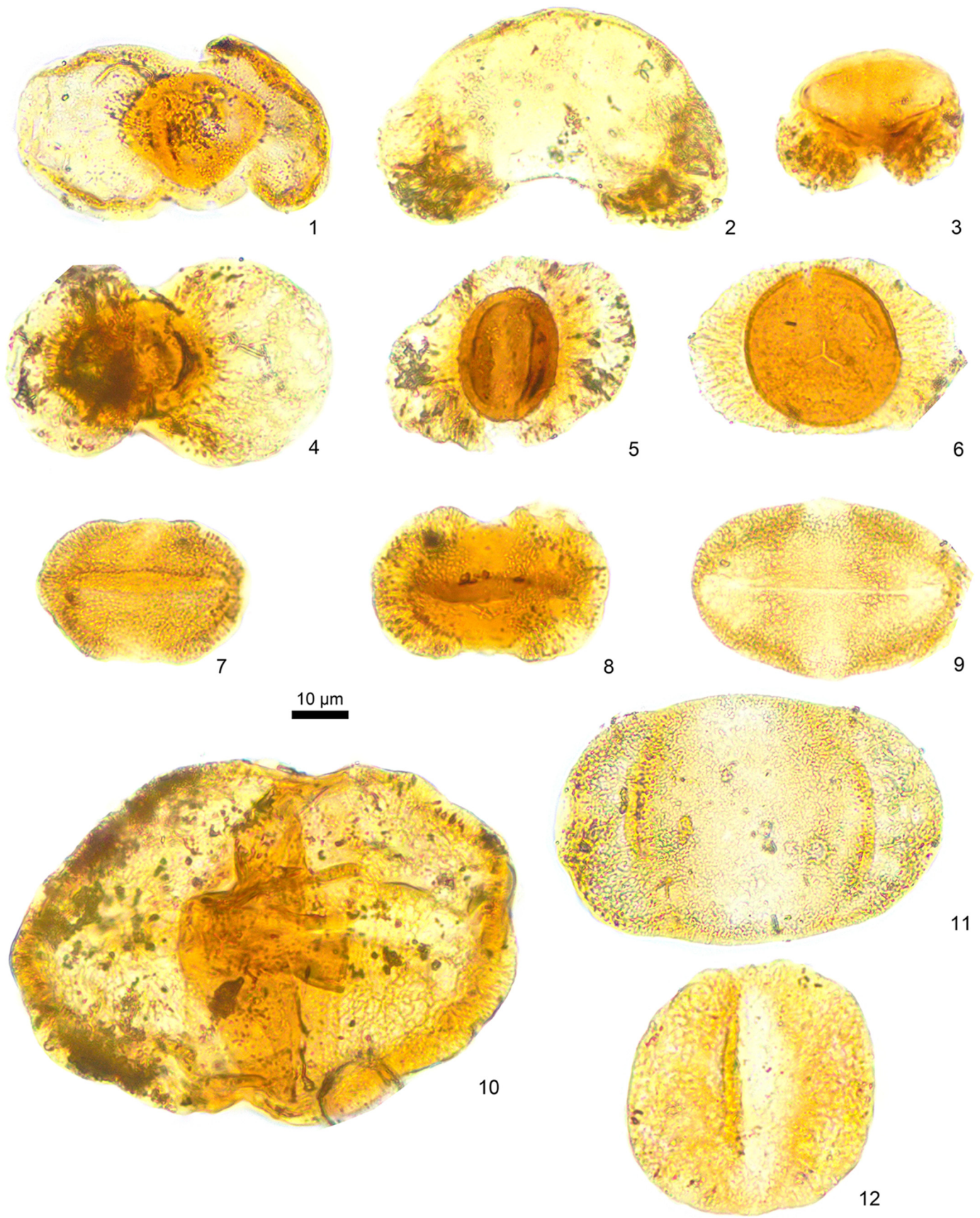


**Plate II.** Palynological assemblage AT-1, AT-3. **1.** *Platysaccus* sp. AT-3\_4\_E103, **2.** *Microcachrydites fastidioides* AT-3\_2\_M420, **3.** *Microcachrydites* sp. AT-1\_2\_P152, **4.** *Platysaccus papilionis* AT-1\_2\_H181, **5.** *Triadispora suspecta* AT-1\_2\_K113, **6.** *Triadispora plicata* AT-3\_1\_T461, **7.** *Ovalipollis ovalis* AT-3\_2\_P460, **8.** *Ovalipollis cultus* AT-1\_2\_N250, **9.** *Ovalipollis pseudoalatus* AT-1\_2\_P264, **10.** *Staurosaccites quadrifidus* AT-1\_1\_M512, **11.** *Alisporites* sp. AT-3\_4\_E291, **12.** *Alisporites opii* AT-1\_1\_C130.

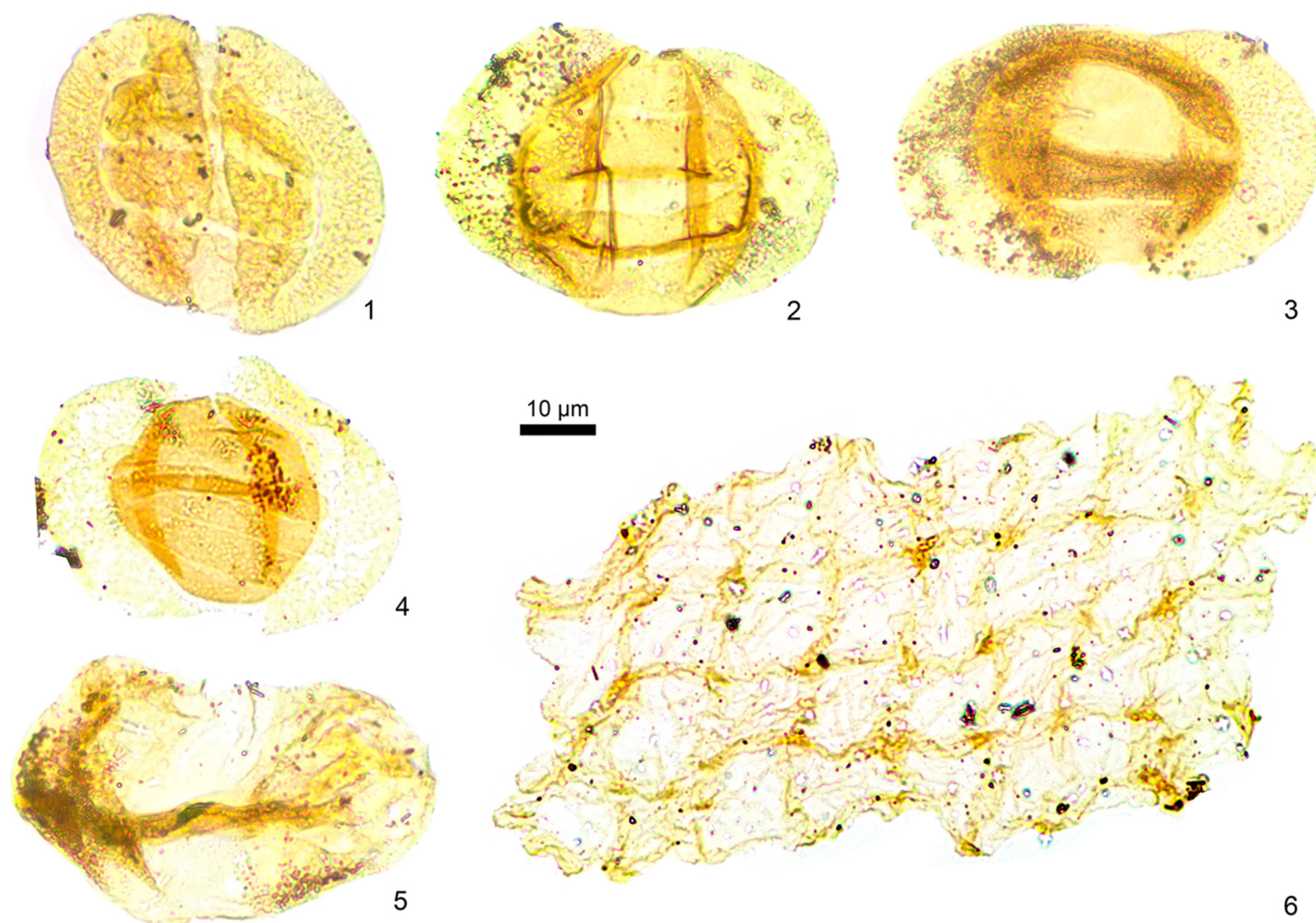


**Plate III.** Palynological assemblage AT-1, AT-3. 1. *Infernopollenites* sp. AT-1\_1\_P552, 2. *Lunatisporites acutus* AT-3\_2\_X531, 3. *Lunatisporites* sp. AT-3\_3\_H340 4. *Striatoabieites* sp. AT-3\_1\_R170, 5. *Chordasporites* sp. AT-1\_2\_R360, 6. *Plaesiodyctyon mosellanum* AT-1\_1\_M280.

#### 4.3. Vertebrate remains from El Atance fossil site

All vertebrate remains so far described from El Atance fossil site belong to sauropterygians: the simosaurid *Paludidraco multidentatus* (Plate IV, 1) and the henodontid *Parahenodus atancensis* (Plate IV, 2,3) (de Miguel Chaves et al., 2018a, 2018c). Both species are exclusively known from El Atance. *Parahenodus atancensis* has been identified as a member of Henodontidae (de Miguel Chaves et al., 2018a), a clade of cyamodontoid placodonts that traditionally only included the species *Henodus chelyops*, a sauropterygian of brackish lagoonal waters. The simosaurid *Paludidraco multidentatus* could have been an eosauroptrygian up to 4 m long that fed by filtering small and soft plants and animals (de Miguel Chaves et al., 2018c).

In this work, we present some isolated eosauroptrygian remains, from the same levels where the other vertebrate remains were found, never figured or described in detail so far. These remains included three small dorsal vertebral centra and a single tooth (Plate IV, 4–7), which we identified here as belonging to small indeterminate nothosaurs. The vertebral centra (Plate IV, 4–6), with around 10 mm in length, are not notochordal, and they are platycoelous or very slightly amphicoelous, opposite to the marked amphicoelous centra of *Paludidraco multidentatus* (de Miguel Chaves et al., 2018c). They present a butterfly-shaped articular surface, which is autapomorphic of the members of Eosauroptrygia (Rieppel, 1994). Two of them (Plate IV, 4 and 6) are dorsal centra, because they lack

intercentra or articular heads for the ribs (Rieppel, 2000). The other one (Plate IV, 5) presents articular heads for the ribs, and therefore probably belongs to a cervical vertebra. In addition, they lack the ventral constriction of the centrum present in *Paludidraco multidentatus* (de Miguel Chaves et al., 2018c), which is exclusive of the simosaurs within the clade Nothosauroida (de Miguel Chaves et al., 2018c, 2019). The morphology of these vertebral centra is clearly different from those of *Paludidraco multidentatus* and therefore indicates the presence of a second eosauroptrygian in El Atance site. The platycoelous morphology and the lack of a ventral constriction are shared by the members of Nothosauria (Rieppel, 2000), and therefore we determine the centra as belonging to this clade. The tooth is also identified as belonging to a nothosaur (Plate IV, 7). It is broken and incomplete, lacking the apex and the root. It is around 5 mm in length. It is pointed, conical and slender, and slightly curved, opposite to the sickle-like teeth of *Paludidraco multidentatus* (de Miguel Chaves et al., 2018c). It is circular in section, while teeth of *Paludidraco multidentatus* are mesiodistally compressed (de Miguel Chaves et al., 2018c). Tooth enamel is ornamented by numerous longitudinal ridges separated by narrow depressions. The presence of these ridges is a product of the folding of the enamel, being a character shared by most of the Triassic eosauroptrygians (Sanz, 1980; Alafont, 1992). The morphology of this tooth is similar to that of nothosaurs (Sanz, 1980, 1983; Alafont, 1992), this element being assigned to the Nothosauria clade.

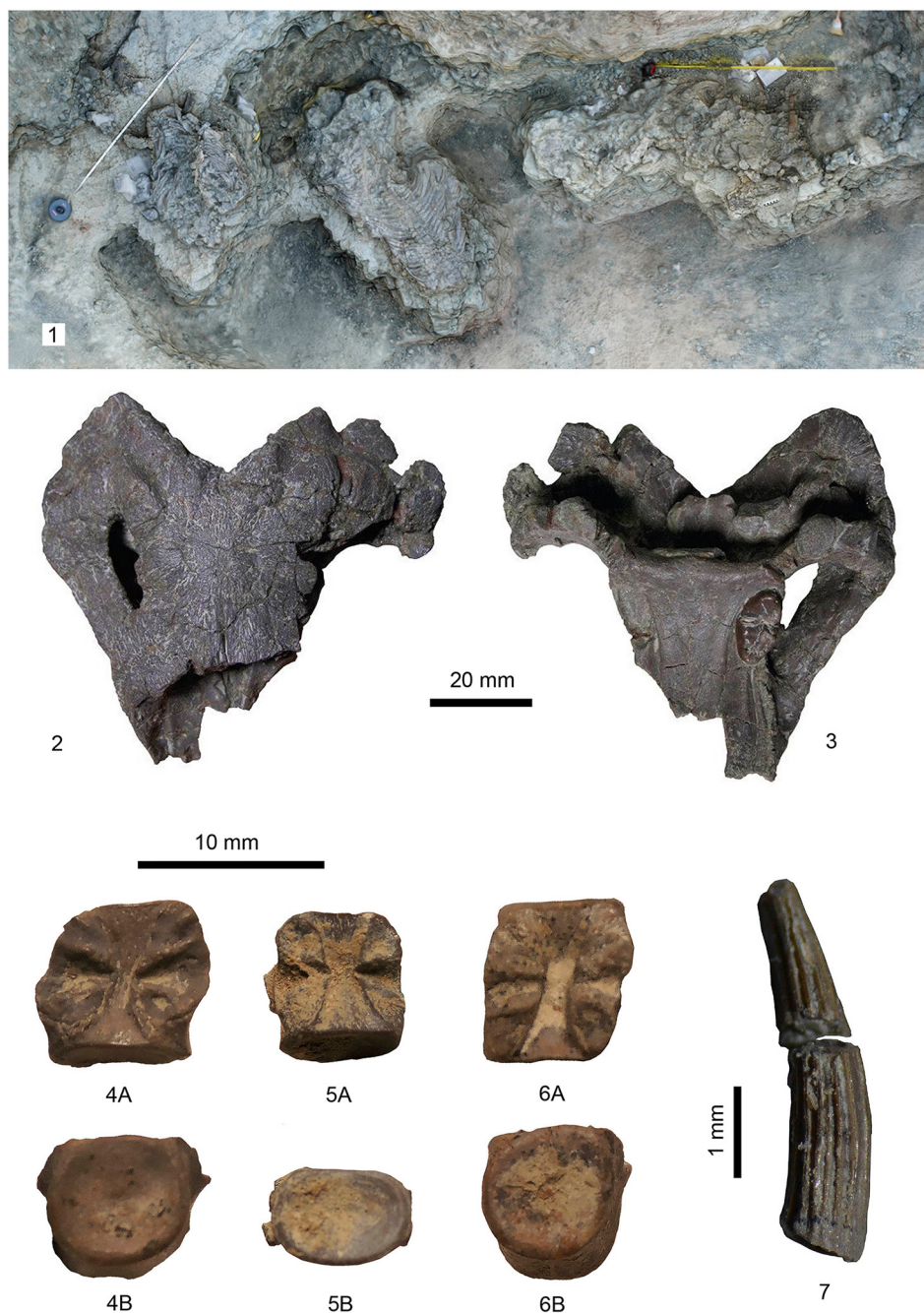


**Plate IV. 1:** Aerial view of El Atance fossil site during the fieldwork in 2015, in which three skeletons of the simosaurid *Paludidraco multidentatus* are exposed. The holotype of the taxon being that located on the right side. **2–3:** Views of the partial skull corresponding to the holotype of the placodont *Parahenodus atancensis*; dorsal (2) and ventral (3). **4–7:** vertebrae (4,5,6) and tooth (7) of a third member of Sauropterygia from El Atance, corresponding to an indeterminate nothosaur, of relatively small size. 4A, 5A, 6A: dorsal view; 4B, 5B, 6B: articular surfaces.

## 5. Discussion

### 5.1. Depositional systems

In this study three palaeogeographic reconstructions are presented (Fig. 5). The Keuper phase begins its deposition on top of the upper Ladinian (Fig. 5A) that is represented by homoclinal carbonate ramps in the east corresponding to the Royuela Fm. and a lateral change to the intertidal siliciclastic flats and fluvial environments of the Cuesta del Castillo Fm. (Fig. 2; García-Gil, 1990, 1995). Similar mixed carbonate-siliciclastic sedimentation in shallow and tide-influenced

basin is described by Tānavsuu-Milkeviciene et al. (2009) in the Middle Devonian Baltic Basin. In the SE Iberian Basin, the Keuper facies are generally interpreted as coastal sabkhas and shallow marine hypersaline inner shelf facies (e.g., López-Gómez et al., 2002). However, the beginning of the Keuper sedimentation in the study area during the lower Carnian (Fig. 5B) is characterized by a siliciclastic input coming from southwestern and northwestern areas and a lateral facies change from siliciclastics to evaporitic mudflats (Hernando, 1977b; Sopeña, 1979; Aracil and Hernando, 1988). In a broad west to east direction, an alluvial plain with coastal influence passes to mudflats and coastal sabkha evaporites. The black lutites facies association shows features of low-energy

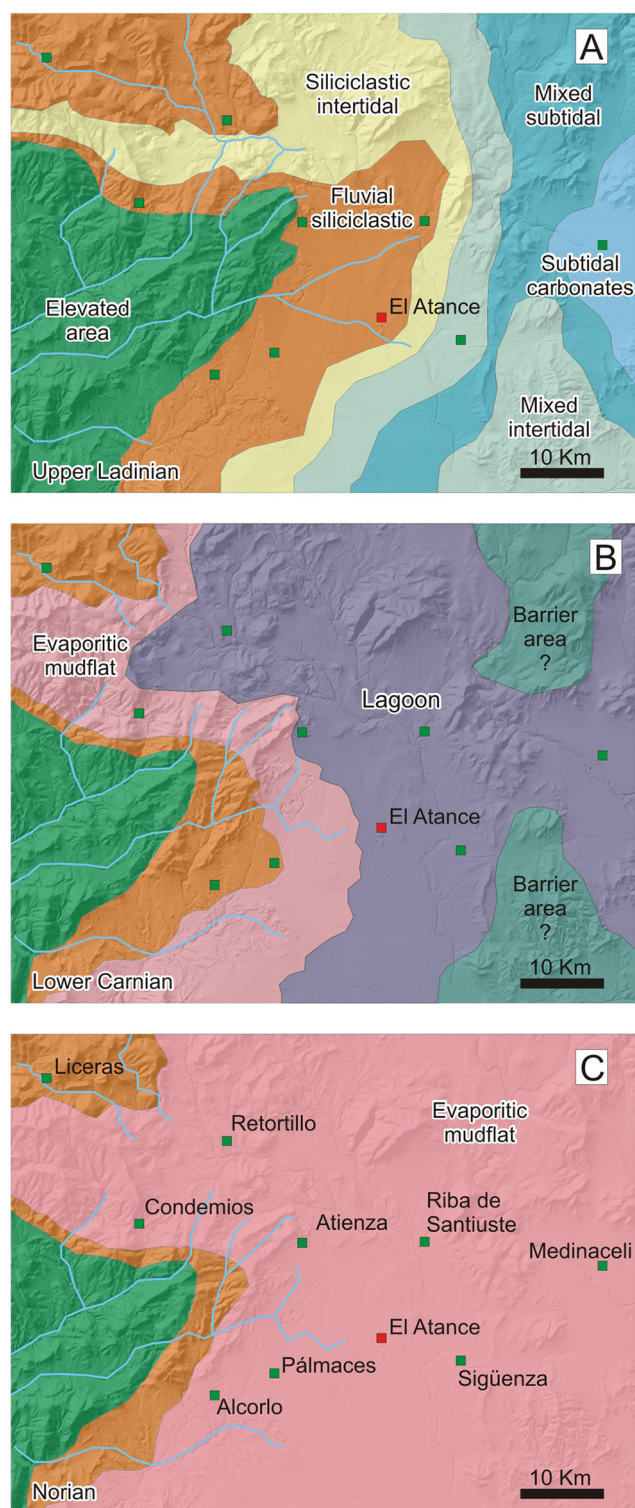


**Fig. 5.** Regional palaeogeography of the study area during the upper Ladinian (A), lower Carnian (B), and Norian (C). The palaeogeographic maps are based on previous studies (Hernando, 1977b; Sopeña, 1979; García-Gil, 1995) and new cartographic, sedimentological and palynological data. Green squares correspond to localities showed in Fig. 4.

submerged conditions, and it is related to restricted shallow marine environments with bad communication with the open sea (Hernando, 1977b). The palaeotopography of the region was very flat (Sopeña, 1979) and small variations on the base level, sedimentation rates and

marine fluctuations probably generated barrier areas to the east that favored extensive lagoonal conditions. Similar environments have been described in Sicily for the Carnian-Rhaetian interval by Martini et al. (2007). Finally, large areas of evaporitic mudflats were generated during the upper Carnian to Norian times (Fig. 5C).

## 5.2. Age determination

The two productive samples are very similar and were located in the outcrop within 1 m of vertical distance (Fig. 3C). Therefore, they can be grouped into a single assemblage and assign them the same age.

*Microcachrydites doubingeri* and *Microcachrydites fastidioides* are characteristic of the Early-Middle Triassic, and its appearance is scarce in the early Carnian assemblages: e.g., Doubinger and Bühmann, 1981 (Germany); Doubinger and Adloff, 1983 (Mediterranean area); Orłowska-Zwolińska, 1983, 1985 (Poland); Eshet, 1990 (Israel); Kürschner and Waldemaar Herengreen, 2010 (Central and Northwestern Europe). Kürschner and Waldemaar Herengreen (2010) placed the Last Appearance Datum (LAD) of *Protodiploxylinus fastidioides* (= *Microcachrydites fastidioides*) in the middle Longobardian (upper Ladinian) in central and northwestern Europe.

*Camerosporites secatus* was usually considered a species whose First Appearance Datum (FAD) is located in the Carnian. However, Visscher and Brugman (1981), Besems (1981), Van der Eem (1983), Roghi (1995), Diez (2000), and Stockar et al. (2012) place the FAD of *Camerosporites secatus* in the early Fasnian (lower Ladinian) of the alpine Domaine of Europe. The LAD of *Camerosporites secatus* is located at the Carnian–Norian boundary (Cirili, 2010 in the northern hemisphere; Kürschner and Waldemaar Herengreen, 2010 in Central and Northwestern Europe).

The FAD of *Patinasporites densus* corresponds to the base of the early Carnian: (*Enzonasporites vigens* - *Patinasporites densus* phase, Van Der Eem, 1983 in Wester Dolomites (Italy); Scheuring, 1970 in Solothurner Jura (Switzerland); and Kürschner and Waldemaar Herengreen, 2010 (Central and Northwestern Europe). In addition, *Vallasporites ignacii* appears in both samples. Its FAD at the base of the Carnian is commonly associated with the FAD of *Patinasporites densus* (e.g., Visscher and Brugman, 1981; Van Der Eem, 1983; Bledinger, 1988; Broglio Loriga et al., 1999; Warrington, 1996; Roghi, 2004; Cirili, 2010; Kürschner and Waldemaar Herengreen, 2010; Juncal et al., 2018).

According to this, the palynological assemblage from El Atance clearly indicates a Carnian age, although the presence of the genus *Microcachrydites* suggests that the sedimentation may have taken place in a time close to the Ladinian. Therefore, the palynological assemblage composed by samples AT-1 and AT-3 indicates the base of the Julian age, the basal term of the two-substage organization of the Carnian.

This age corresponds to the base of Phase 1 of Schuurman, 1977, 1979; the base of *Camerosporites secatus*–*Patinasporites densus* sub-phase of Besems, 1982, 1983; the base of *Enzonasporites vigens*–*Patinasporites densus* phase of Van Der Eem, 1983, the base of the GTr-12 zone of Heunisch, 1999, the base of *Porcellispora longdonensis* zone of Orłowska-Zwolińska (1983, 1985, 1988) and the base of *Camerosporites secatus* zone of Kürschner and Waldemaar Herengreen, 2010.

## 5.3. Palaeoecological data derived from the palynological analysis

The remains of sauropterygians recovered from El Atance fossil site are indicative of marine settings. However, the palynomorphs found in samples AT-1 and AT-3 suggest a continental contribution, with several genera of pollen grains and a poor representation of spores and aquatic forms. There is a predominance of anemophilous pollens. In areas of high concentration of tree species with anemophilous pollination, they would be able to form pollen clouds that could often travel considerable distances. Of terrestrial origin, a predominantly anemophilous assemblage will often be parautochthonous or allochthonous and sedimented

in the marine environment (Düringer and Doubringer, 1985). In El Atance palynological samples, there are palynomorphs of continental origin belonging to the Circumpolles Group (*Camerospores*, *Duplicisporites*, *Paracirculina*, and *Praecirculina*), related to the Cheirolepidiaceae family (Scheuring, 1970; Scheuring, 1978; Visscher et al., 1994; Roghi, 2004; Zavialova and Roghi, 2005; Buratti and Cirilli, 2007), and monosaccates related to conifers (*Enzonasporites*, *Patinasporites*, and *Vallasporites*) (Scheuring, 1970; Visscher et al., 1994; Balme, 1995; Roghi, 2004; Zavialova and Roghi, 2005; Roghi et al., 2006; Breda et al., 2009; Roghi et al., 2010; Césari and Colombi, 2016; Lindström et al., 2017) that could represent xerophytic coastal pioneer vegetation (Roghi et al., 2010), and indicate a drier and/or saline influence (Kustatscher et al., 2018). Although scarcer, other xerophytic elements such as the *Triadispora* genus related to Voltziales (Balme, 1995; Looy et al., 1999; Kustatscher et al., 2012; Lindström et al., 2017) indicate an influx of hinterland elements with saline mudflats (Brugman et al., 1994; Roghi et al., 2010).

On the other hand, hygrophytic vegetation associated with more humid environments in the hinterland is inferred by the presence of spores like *Verrucosporites*, related to small and larger sized ferns, lycopsids, and cycads; *Calamospora*, related to Equisetales sourced from wetter areas or along small rivers; and *Densoisporites*, which is linked to lycopsids of ground cover on coastal muds (Supplementary material, Table 2).

In aquatic environments, as in modern lagoons, the algal contribution to the organic debris could represent a significant amount in the final sediments. Generally, its presence is related to episodes of marine influence (Torres et al., 2014), which is consistent in this case with the marine macro-remains of the fossil site and the presence of alternating lithologies of mudstone and sandstone beds, interpreted as shallowing-upward small cycles deposited in a lagoonal environment. The gray-black lutites probably are related to reducing conditions, very favorable for the palynomorphs preservation, and high biological productivity. This high productivity could have favored the presence of nectonic animals, such as the eosauroptrygians and the placodonts discovered in the fossil site (de Miguel Chaves et al., 2018a, 2018c). In fact, *Paludidraco multidentatus* has been interpreted as a dweller of shallow waters that acquired its food by filter-feeding on soft plant material or small and soft animals (de Miguel Chaves et al., 2018c). The algal content observed in the mudstones of El Atance fossil site is composed by abundant fragments, including well-preserved specimens of the green algae *Plaesiodyctyon mosellanum*. The occurrence of this brackish to freshwater colonial microalga (Lindström et al., 2009) suggests that the sedimentation zone could be located in the supratidal zone of marginal coastal settings (Lindström et al., 2017), coastal marshes (Düringer and Doubringer, 1985), and marine environments with freshwater influx (Hauschke and Heunisch, 1990; Vigran et al., 2014).

The sedimentological features of the black lutites facies association that characterizes the Atance fossil site are indicative of low-energy conditions and restricted shallow marine environments, as well as the algal content and the sauropterygians remains, which are typically associated with brackish lagoonal waters. In summary, according to the new and restudied sedimentological and palynological data, we can propose an approximate palaeoenvironmental reconstruction of the study area, which would be related to a large shallow water lagoon. This lagoon would be surrounded in some areas by meandering channels and hypersaline lakes. The palynological assemblage, very similar to the pre Carnian Pluvial Event palynological assemblages in the UK (Baranyi et al., 2018), suggest arid palaeoclimatic conditions and a predominance of xerophytic plants, that is, those adapted to surviving with little water and capable of tolerating periods of severe droughts. This generally arid climate is coherent with the Julian (early Carnian). Near the coast, we would find conifers producing palynomorphs of the Circumpolles group (*Camerospores*, *Duplicisporites*, *Paracirculina*, and *Praecirculina*), bisaccate (*Microcachrydites*), and monosaccate pollen grains (*Enzonasporites*, *Patinasporites*, and *Vallasporites*). Also, on coastal

areas, cycads would grow producing palynomorphs of *Cycadopites*, while lycopsids, covering the ground in the wetter areas of the landscape, are interpreted by the presence of *Densoisporites*. In higher areas located further inland, different types of conifers and pteridosperms of well-drained soils would produce *Triadispora*, *Striatoabietites*, *Ovalipollis*, and *Lunatisporites*. Under those prevailing palaeoclimatic arid conditions, we also find equisetales producing *Calamospora*, which would be found in wet and muddy areas of rivers and lakes, and ferns and other groups of plants producing *Verrucosporites* (Fig. 6).

#### 5.4. Chronostratigraphic implications for the sauropterygian record

Two new aquatic reptile taxa that provide important information on two poorly known clades of Triassic sauropterygians have been described in El Atance (de Miguel Chaves et al., 2018a, 2018c). However, the hitherto absence of an accurate dating for this fossil site prevented adjusting some hypotheses about the evolutionary history of both lineages.

One of the sauropterygians described from El Atance is *Parahenodus atancensis* (de Miguel Chaves et al., 2018a), exclusively found in this site. *Parahenodus atancensis* was proposed as a Henodontidae (de Miguel Chaves et al., 2018a), a clade of cyamodontoid placodonts previously composed just by *Henodus chelyops*.

Its remains have only been recovered from the uppermost Gipskeuper (Estheriensichten, lower Carnian) of Lustnau (Tübingen, Germany) (Huene, 1936). *Parahenodus atancensis* presents some of the derived features of *Henodus chelyops*, but it also retains several plesiomorphic conditions for cyamodontoid (de Miguel Chaves et al., 2018a). The Estheriensichten are dated in the Julian (lower Carnian) (Bachmann and Kozur, 2004). The recognition of El Atance as a Julian site shows that *Parahenodus atancensis* and *Henodus chelyops* lived at the same time in different areas of the Occidental Tethys, implying a divergence of these two taxa anterior to this period.

Most of the placodonts were inhabitants of shallow marine waters (Rieppel, 2002; Scheyer et al., 2012; Neenan and Scheyer, 2014), but the levels where *Henodus chelyops* was found indicate a brackish lagoon with influxes of freshwater (Reif and Stein, 1999; Rieppel, 2002; Naish, 2004). This is consistent with the environment where *Parahenodus atancensis* inhabited, since the results of the present paper suggest a restricted shallow-marine environment with freshwater influence.

Our new palynostratigraphical data allow confirm that *Parahenodus atancensis* is one of the youngest placodonts from the Iberian Peninsula since most of the Iberian remains of this clade have been found in Middle Triassic levels (de Miguel Chaves et al., 2020a, 2020b), although other cyamodontoids survived until the Rhaetian (e.g., Rieppel, 2000).

The most abundant taxon in El Atance is *Paludidraco multidentatus*, being so far exclusive to this site. It has been identified as a member of Simosauridae, being the sister taxon of *Simosaurus gaillardoti* (de Miguel Chaves et al., 2018c), from the Ladinian (Middle Triassic) of southwestern Germany and eastern France (Rieppel, 1994; de Miguel Chaves et al., 2018b); other indeterminate simosaurid remains are also known (de Miguel Chaves et al., 2019). Thus, the fossil record of the Simosauridae ranges from the Anisian-Ladinian boundary (Middle Triassic) to the Middle-Upper Triassic, and material attributed to this clade has been found in France, Spain, Italy, Germany, Austria, Hungary, Israel, and Saudi Arabia (Haas, 1981; Rieppel, 1994, 1996, 2000; Vickers-Rich et al., 1999; Dalla Vecchia, 2008; Kear et al., 2010; de Miguel Chaves et al., 2015, 2019; Berrocal-Casero et al., 2018; Segesdi and Ősi, 2021). The stratigraphically youngest remains of simosaurids were found in the Italian Alps, near Dogna (Friuli), in Julian (early Carnian) levels (Dalla Vecchia, 2008), and near the municipality of Manzanera (Teruel, Spain), in early-middle Carnian levels (de Miguel Chaves et al., 2015), but none of them apparently belonging to *Paludidraco multidentatus* (de Miguel Chaves et al., 2019). Thus, *Paludidraco multidentatus* is recognized as synchronic with the last

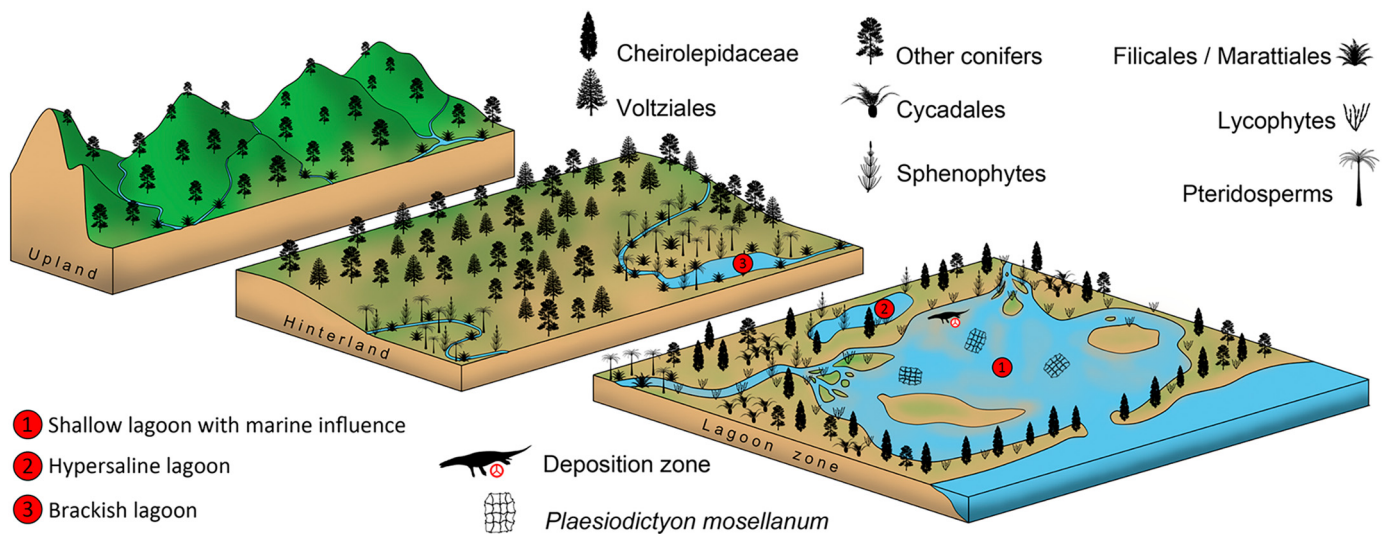


**Fig. 6.** Palaeoenvironmental reconstruction according to the sedimentological and palynological data. Based on the presence of the black lutites facies association, algal content, and sauropterygians remains, a large lagoonal area has been interpreted. Also, the approximate distribution of the different types of elements is shown schematically.

known members of the clade Simosauridae, two simosaurid taxa being identified at the same time in the lower Carnian of the Iberian Peninsula. In addition, an isolated rib from the Ladinian (Middle Triassic) of the Sierra de Lújar (Granada Province, Spain) has been suggested as belonging to *Paludidraco multidentatus* (Reolid and Reolid, 2020). If new remains confirm this attribution, this would be the oldest record of the species.

According to de Miguel Chaves et al. (2018c), *Paludidraco multidentatus* was an organism with very restricted maneuverability that would swim slowly near the sea bottom in shallow coastal waters while searching for food in the substrate, which is consistent with the palaeoenvironmental reconstruction presented here (Fig. 6).

The nothosaurs compose a well-known group from the Middle and lower Upper Triassic of Europe, North Africa, Middle East, and China (Rieppel, 2000). Iberian remains of nothosaurs have been found in fossil sites and outcrops of several Spanish regions (see de Miguel Chaves et al., 2020a for a compilation). However, the nothosaur remains recovered from El Atance implies one of the youngest fossil records in the Iberian Peninsula.

## 6. Conclusions

The coexistence of *Camerosporites secatus*, *Patinasporites densus* and *Vallasporites ignacii* clearly indicates a Carnian age. However, the presence of *Microcachrydites fastidioides* suggests that the sedimentation may have taken place in a time close to the Ladinian. Therefore, the palynological assemblage from El Atance fossil site indicates the base of the Julian age, the basal term of the two-substage organization of the Carnian.

A large lagoonal area of shallow water has been proposed as an approximate palaeoenvironmental reconstruction of the Atance fossil site, based on sedimentological data, sauropterygians remains, presence of the green algae *Plaesiodictyon mosellanum*, and identification of different types of continental palynomorphs of xerophytic and xerophytic coastal pioneer vegetation, together with other of more humid environments.

The placodont from El Atance, *Parahenodus atancesis*, is recognized here as a synchronous species with the other known representative of Henodontidae: the German *Henodus chelyops*. The biostratigraphic distribution of Henodontidae is identified here as restricted to the base of the Julian. The bizarre *Paludidraco multidentatus* is identified here as a form younger than the central European Ladinian *Simosaurus gaillardoti*.

The highly specialized lifestyles of *Parahenodus atancesis* and *Paludidraco multidentatus* are consistent with the palaeoenvironmental reconstruction presented here for El Atance fossil site.

## Declaration of Competing Interest

Authors declare that they have no competing interest.

## Acknowledgments

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.revpalbo.2021.104541>.

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