Review of Palaeobotany and Palynology 162 (2010) 341–361

Contents lists available at ScienceDirect

Review of Palaeobotany and Palynology

journal homepage: www.elsevier.com/locate/revpalbo

Cretaceous diversification of angiosperms in the western part of the Iberian Peninsula

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ARTICLE INFO

Article history:
Received 22 September 2009
Received in revised form 19 November 2009
Accepted 23 November 2009
Available online 2 December 2009

Keywords:
angiosperm flowers
Araceae
Chloranthaceae
Early Cretaceous
eudicots
Late Cretaceous
Lusitanian Basin
monocots
Normapolles complex

ABSTRACT

The classic leaf fossil floras from the Cretaceous of the Lusitanian Basin, Portugal, which were first described more than one hundred years ago, have played an important role in the development of ideas on the early evolution of angiosperms. Insights into the nature of vegetational change in the Lusitanian Basin through the Cretaceous have also come from studies of fossil pollen and spores, but the discovery of a series of mesofossil floras containing well-preserved angiosperm reproductive structures has provided a new basis for understanding the systematic relationships and biology of angiosperms at several stratigraphic levels through the Cretaceous. In the earliest mesofossil floras from the Torres Vedras locality, which are of probable Late Barremian–Early Aptian age, angiosperms are surprisingly diverse with about 50 different taxa. In slightly later mesofossil floras, which are of probable Late Aptian–Early Albian age, the diversity of angiosperms is still more substantial with more than hundred different kinds of angiosperm reproductive structures recognized from the Famalicão locality alone. However, this early diversity is largely among angiosperm lineages that produced monoaperturate pollen (e.g., Chloranthaceae, Nymphaeales) and early diverging monocots (Alismatales). Eudicots are rare in these Early Cretaceous mesofossil floras, but already by the Late Cenomanian the vegetation of the western Iberian Peninsula is dominated by angiosperms belonging to various groups of core eudicots. The Normapolles complex is a particularly conspicuous element in both mesofossil floras and in palynological assemblages. In the Late Cretaceous mesofossil floras from Esgueira and Mira, which are of Campanian–Maastrichtian age, core eudicots are also floristically dominant and flowers show great organisational similarity to fossil flowers from other Late Cretaceous floras described from other localities in Asia, Europe and North America.

1. Introduction

Numerous well-preserved plant fossils discovered in Cretaceous sediments from the Lusitanian Basin of western Portugal provide a unique insight into the initial radiation of angiosperms during the Early Cretaceous and their rise to ecological dominance during the Late Cretaceous. The earliest detailed report of Cretaceous floras from the region was by Saporta (1894), who described the now classic Early Cretaceous leaf floras of Cercal, Buarcos-para-Tavarede and Nazaré as well as several other floras from the Late Cretaceous. This work, together with the classic studies of the Early Cretaceous Potomac Group leaf floras published at approximately the same time (e.g., Fontaine, 1889), was especially influential in early discussions of angiosperm origin and diversification. It has also been used as key reference for correlation and comparison of Early Cretaceous floras from other areas.

The Portuguese leaf floras were later investigated by Teixeira, who published a series of studies on fossil assemblages from both the Early and Late Cretaceous (Teixeira, 1945, 1946, 1947, 1948, 1950, 1952). These studies provide a broad framework for understanding vegetational changes in the Iberian region during the Cretaceous and show a clear pattern of turnover similar to that seen elsewhere in the world. Earliest Cretaceous floras, are dominated by ferns and non-angiospermous seed-plants, while Late Cretaceous floras, are dominated by angiosperms. Unfortunately, however, the detailed information that can be obtained from these floras is limited by their typical preservation as impressions or thin compressions, and they have not been recollected or restudied using modern techniques.

Since the early studies of leaf floras, palynological investigations have added important new information on broad patterns of vegetational change through the Portuguese Cretaceous. Most of these studies focus on palynofloras from Upper Cretaceous strata (e.g., Diniz, 1967; e.g., Kedves and Diniz, 1967; Diniz et al., 1974; Kedves and Pittau, 1979; Medus et al., 1980; Medus, 1981; Batten, 1986), but there are also several studies of palynofloras from Lower Cretaceous deposits (e.g., Groot and Groot, 1962; Medus and Berthou, 1980; Hasenboehler, 1981;

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doi:10.1016/j.revpalbo.2009.11.009

Pais and Reyre, 1981; Trincão, 1990; Heimhofer et al., 2005, 2007). These palynological investigations provide important information on aspects of vegetational change that complement inferences based on leaf floras, but palynological studies using light microscopy also confront significant challenges in determining the systematic affinities of isolated pollen grains. Taxonomic resolution is often not possible at a level below orders and families and the composition of the palynofloras to a large extent reflects those components of the vegetation that are either most abundant or have wind dispersed pollen and spores, such as seed plants with wind-pollination.

Rich mesofossil floras recently discovered from the Lusitanian Basin in western Portugal are more informative about the systematic relationships of early angiosperms than either leaf floras or assemblages of fossil pollen. They also provide information on those plants, such as herbaceous and insect-pollinated forms, that are usually not well represented in leaf and pollen floras. Mesofossil floras often include diverse assemblages of small plant fragments, and are particularly important for their well-preserved flowers, fruits, seeds and stamens of angiosperms (e.g., Friis et al., 1992, 1997, 1999, 2000b, 2006a; Pedersen et al., 2007; Friis et al., 2009b). They also comprise informative fossil remains of other plant groups, including many seeds and other reproductive structures assigned to the Bennettitales–Erdtmanithecales–Gnetales (BEG) group (Friis and Pedersen, 1996; Rydin et al., 2006; Friis et al., 2007; Mendes et al., 2008; Friis et al., 2009a; Mendes et al., 2010).

The mesofossil floras from Portugal occur at several stratigraphic levels from the earliest Cretaceous (Berriasian) to the Late Cretaceous (Campanian–Maastrichtian). The earliest angiosperms occur in mesofossil floras that date from about the Late Barremian–Early Aptian. Excellent preservation of many of the reproductive organs from both Early and Late Cretaceous mesofossil floras allows detailed comparison with extant taxa and well-founded systematic analyses. It also facilitates inferences about aspects of reproductive biology in Cretaceous angiosperms, including floral function and probable modes of pollination and dispersal. In this account we review the Cretaceous radiation of angiosperms in the western part of the Iberian Peninsula based mainly on an overview of the evidence from mesofossil floras in the context of earlier work on fossil leaf floras and palynological assemblages.

2. Materials and methods

Mesofossil floras have been recovered from numerous samples collected at several different localities in the Lusitanian Basin. These localities span a range of stratigraphic levels through the Cretaceous. Mesofossils were recovered mainly from unconsolidated sands, silts and clays of lacustrine or fluviatile origin that contain dispersed organic material. Typically several samples were collected at each locality, both vertically and horizontally. Sediments were sieved in water in the laboratory over a 125 μm mesh. Organic material collected on the sieves was treated with 40% HF and 10% HCl to remove adhering mineral matter. The organic remains were then thoroughly washed in water and dried in air.

The plant fossils were sorted using a binocular microscope. Details of morphology and anatomy were studied using a Hitachi S-4300 field emission scanning electron microscope at 1–2 kV and a Philips 515 scanning electron microscope at 15 kV. Specimens studied in early work prior to around the year 2000 were coated with gold for about 7 min, while specimens studied later were coated only for about 60 s. Many specimens were also analysed for internal features and organisation using synchrotron-radiation X-ray tomographic microscopy (SRXTM and PCXTM) at the TOMCAT beamline of the Swiss Light Source at the Paul Scherrer Institute, Villigen, Switzerland. Imagining was made at 10 keV using a 4×, 10× or 20× objective following the technique outlined by Donoghue et al. (2006) and Friis et al. (2007). Reconstructions based on the slice data derived from the scans were made using Avizo™ www.tgs.com software. Black backgrounds for SEM micrographs were made using Adobe Photoshop CS2.

All specimens figured are deposited in the collections of the Swedish Museum of Natural History, Stockholm (S).

3. Occurrences of Cretaceous floras in Portugal and their stratigraphic position

Cretaceous deposits mainly occur in southern (Algarve region) and western (Estremadura and Beira Litoral regions) Portugal. In southern Portugal these deposits occur in a narrow zone along the coast. They are mainly marine in origin and are Early to mid-Cretaceous in age (Rey, 1983). Leaf floras or mesofossil assemblages have not been recognized in these strata, but recently well-preserved palynological assemblages with angiosperms have been described (Heimhofer et al., 2007). In western Portugal Cretaceous strata include both terrestrial and marine sediments deposited in the Lusitanian (Western Portuguese) Basin. The sequence ranges from the earliest Cretaceous (Berriasian) to latest Cretaceous (Maastrichtian) and plant fossils have been collected from many localities (Fig. 1). Terrestrial sediments with floras of Early Cretaceous age are exposed in the southern and central part of the basin. Most of the classic leaf floras described by Saporta (1894) and Teixeira (1947, 1948), as well as several rich mesofossil floras, are from this part of the basin. Especially informative are the Early Cretaceous mesofossil floras collected in the areas around Torres Vedras and Runa, around Cós-Juncal-Nazaré-Leiria, and around Figueira da Foz. Terrestrial sediments of Late Cretaceous age that contain well-preserved plant fossils also occur in the northern part of the Lusitanian Basin. Mesofossil floras are particularly common in an area that extends from about Mira and Presa to around Aveiro and Esgueira (Fig. 1).

The mesofossil floras on which our studies have been based were collected most intensively during fieldwork from about 1989 to about 2000 and in many cases the outcrops that were sampled are no longer available for collection. For example, extensive outcrops exposed by major road construction in the area around Esgueira yielded rich Late Cretaceous mesofossil floras, but are now covered by motorways and city development. The most productive horizons for Early Cretaceous mesofossil floras (Buarcos, Famalicão, and Torres Vedras) are also no longer available for collection, some have been covered by urban development, while others have been lost as the old clay pits have been filled.

The geological development of the Lusitanian Basin is manifested in extensional rift phases and extensive regional subsidence closely associated with the opening of the North Atlantic Ocean (Rasmussen et al., 1998). This resulted in fluctuation of the Cretaceous coastline across the area and the deposition of a range of terrestrial near-shore and marine sediments. Detailed geological and palaeontological studies of the Lower Cretaceous sequence in the Lusitanian Basin have been carried out for the Estremadura region (Rey, 1972, 1979, 1982, 1992, 1993; Rey et al., 2006), and investigations have been initiated for Cretaceous sediments further north in the Lusitanian Basin (Dinis and Trincão, 1995; Dinis, 2001; Dinis et al., 2002, 2008; Rey et al., 2006). Marine conditions predominate in the southern and western parts of the basin, while conditions were mainly terrestrial towards the eastern and northern margins of the Basin. Despite the presence of marine sediments in some places precise dating of the fossil floras from the Cretaceous of Portugal is problematic, mainly due to the lack of marine control in the areas where plant fossils are most abundant. These difficulties are further exacerbated by the fragmentation of the depositional basin caused by tectonic activity and the paucity of well-dated floras from other areas that can be used as a stratigraphic reference points. In addition, most outcrops are rather small and regional correlation is difficult because it is rarely possible to trace horizons laterally over longer distances.