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Article *in* Palaeogeography Palaeoclimatology Palaeoecology · October 1998

DOI: 10.1016/S0031-0182(98)00075-3

ELSEVIER

Palaeogeography, Palaeoclimatology, Palaeoecology 143 (1998) 135–158

PALAEO

Middle Bathonian floras and phytocoenoses of France

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Received 11 September 1997; accepted 2 April 1998

Abstract

In the Causses Basin (SE France), a continental lignitic deposit yields a diverse middle Bathonian megaflora, until now almost unstudied. The floristic data include megafloras, palynology and data from woods and leafy shoots. The palaeoecology of this flora is quite unique, representing backswamps, fens, and freshwater ponds in a carbonate domain. There is little evidence of vegetation from brackish environments. Elsewhere in France, contemporaneous floras are known, with different ecologies. These include a flora of low undulating tracts on shell sand in Normandy and a mangal assemblage in Franche-Comté. New palaeobotanical and palynological data are given for both floras. The floristic composition of the three floras is compared and discussed together with additional coeval data. This set of floras is of interest as they grew mainly on calcareous soils, whereas most Middle Jurassic floristic associations described previously were mainly from siliciclastic environments. Because of their contemporaneous nature, asserted with an accuracy rarely reached for continental biota, these floras can be used to estimate the climatic gradient of the middle Bathonian.

Keywords: France; Bathonian; Jurassic; palaeobotany; palaeoclimatology

1. Introduction

In the middle Bathonian of France, terrestrial plant remains are relatively common, sometimes found in their original growth-sites (Parent, 1944). From a previous investigation of this stage in the Causses Basin, we discovered that the flora is indicative of freshwater environments in a carbonate area (Thévenard et al., 1993). It is a depositional setting that is different from most of those described up to now for the Middle Jurassic of Western Europe. To document the palaeoecology of this level, we now review a large but scattered set of literature, revise previously described material, and add new field data from various localities in France. Despite being much less well documented than the contemporaneous siliciclastic assemblages from England, it appears that these middle Bathonian floras represent poorly known, although widely distributed, phytocoenoses, established on carbonate sand and mud. These assemblages include mangal, freshwater ponds, and dunes.

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PII S0031-0182(98)00075-3

We will first report the data for the three main floras we studied: Causses, Mamers, and Franche-Comté. Systematical descriptions will not be given as our new data mostly concern well known and widespread species. Each time a sample or a set of samples set a problem, we let it in open nomenclature. Palaeoecological inferences will be drawn for each main flora (Causses, Mamers and Franche-Comté). Then, other floras from France will be briefly presented.

Afterwards, as the stratigraphical setting is quite accurate, the whole data set will be used for floristic comparisons and a realistic evaluation of the climatic gradient over Western Europe at that time.

2. The Causses Middle Bathonian flora

2.1. Geological setting

Lignite deposits of the Causses Plateaux, and especially those from Larzac, have been long known, for they have been reportedly excavated as early as the Palaeolithic (Théry et al., 1995). Most mining occurred from the sixteenth to the beginning of the twentieth century, then stopped (Bleicher, 1872; Rouire, 1928). Mining resumed for a while during World War Two, allowing new geological studies to be conducted (Rouire, 1946; Bergounioux and Doubinger, 1948; Maubeuge, 1949; Cox and Maubeuge, 1950). Recent studies include an attempt to integrate the lignite deposits in a sequence stratigraphic framework (Charcosset et al., 1996) and investigations on aquatic biocoenoses (Fürsich et al., 1995) and microvertebrate remains (Kriwet et al., 1997).

As a whole (Rouire, 1928), the lignite-bearing calcareous formation (or so-called ‘Calcaires à Stipites’) lies atop a regional unconformity above several hundred metres of Aalenian to Bajocian shallow-water marine limestones (Fig. 1). It is overlain by a very thick dolomitic formation (‘Dolomies Ruiniformes’) of late Bathonian age. The thickness of the lignite-bearing formation may reach 170 m but it thins to a few metres towards the south (Charcosset et al., 1996) on the Cevennes swell, which forms the transition to the deep marine subalpine basin. Maximum thickness of the coals occurs in the central part of the basin (Rouire, 1928) where most mining took place. The thickness of the main coal beds may reach one metre or more, but are usually thinner. The word ‘stipites’ (made of trunks), a term formerly proposed by Brongniart (Rouire, 1928), is inappropriate here because large woody debris is a minor component of the organic-rich layers. The limestone beds between the lignite layers are either shallow to marginal marine, lacustrine, or palustrine. Lignite beds and associated clays have preserved freshwater or, rarely, brackish floras (see below). The abundance of in-situ rooting horizons, as well as their large extent, characterizes Causses lignites as continental deposits. However, terrestrial animal remains are uncommon, with the exception of freshwater bivalves (Fürsich et al., 1995). Cox and Maubeuge (1950) mentioned Coleoptera and pulmonate Gastropoda. Various vertebrate remains are reported: *Lepidotus* scales, small teeth of Saurian and Pterodactyles by Bleicher (1872); urodelan and anuran amphibians by Seiffert (1969a,b); fishes, crocodilians and theropods by Kriwet et al. (1997). Nevertheless, the majority of data for terrestrial biota is from the plant realm.

The age of the lignite-bearing formation is poorly constrained. In a first attempt at regional correlation, Rouire (1928) gave miner names (such as ‘la Principale’ or ‘la Bâtarde’) to the different coal beds. In fact, it is hard to correlate the sections that originate from the different outcrops, pits, and mines without definitive stratigraphic data. The ‘Calcaires à Stipites’ have long been considered as early Bathonian (Rouire, 1928) but, as rightly pointed out by Alabouvette (1988), there is hardly any hard evidence for this.

The age of the formation lies somewhere between the late Bajocian to late Bathonian. The last Bajocian limestones below the basal unconformity are oolitic. They preserve a brachiopod fauna of late Bajocian age (Alméras et al., 1990). A study of ostracods from the basalmost carbonates resulted in an early Bathonian age (Rohr, 1976). A late Bathonian ammonite fauna was once found (Gourret, 1885) in the upper part of the formation, below the upper Bathonian ‘Dolomies Ruiniformes’. Brachiopods are the only marine component that have recently provided some biostratigraphic clues. According to Charcosset et al. (1996), three successive faunas of middle to late Bathonian age have been found. But new findings (J.P. Garcia, pers. commun., 1997) provide evidence

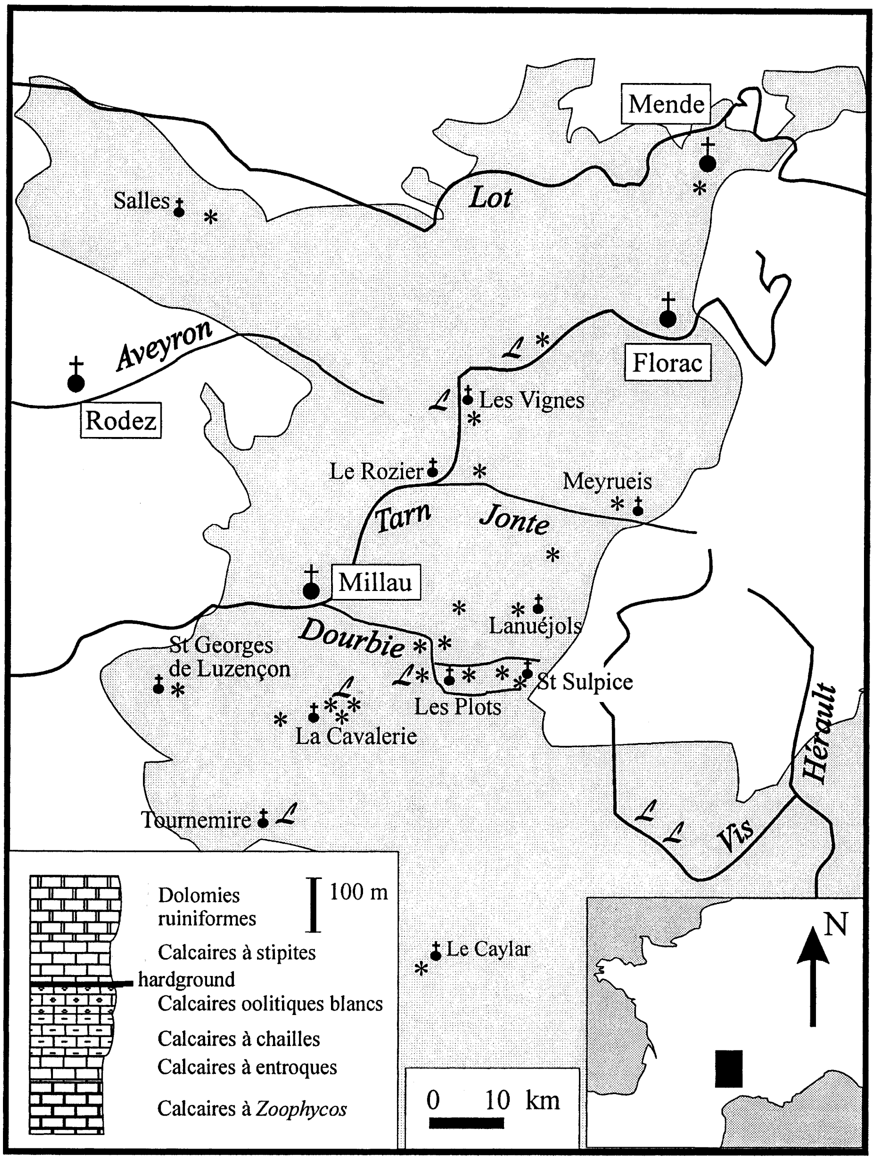


Fig. 1. Sketch of the location, simplified lithological column, and localities (*) in the Causses Basin (stippled area indicates Jurassic deposits). * = locality with allochthonous material; $\mathcal{L}$ = locality with autochthonous material.

of an early Bathonian age in at least some places for the very base of the formation. So, given both the kind of depositional environments encountered and the biostratigraphic data, it is possible that only the maximum flooding episodes of successive 3rd-order depositional sequences (sensu Vail, Haq and others) are recorded and amalgamated into this particular formation in a basin insulated from the subalpine sea by the Cevennes shoal. These flooding episodes are only represented here by marginal marine to freshwater deposits according to Charcosset et al. (1996). These authors recognized four R/T depositional sequences in the entire formation. Hence, as a whole, most of the lignite layers seem to have been deposited over a period beginning in the mid Bathonian and extending into the earliest part of the late Bathonian.

Depositional environments of this interval are still poorly studied. The lignite-bearing unit is made up of thin depositional cycles whose thickness may reach ten metres or so, but usually is much less, sometimes only several decimetres. The thinnest sequences are composed of a 'transgressive' lignite overlain by subaerial palustrine limestones bioturbated by roots. Marine bioclastic and/or oolitic limestones are in the thickest sequences within which the lignitic marls then appear as 'regressive' deposits. In the Millau section, along the road 'Route Nationale 9', the formation begins with a transgressive conglomerate made of well-rounded fossil debris. This is overlain by marls with some storm layers indicative of an open marine environment. However, a few kilometres away, the 'Millau section' (actually drawn at La Cavalerie, cf. Fig. 1) of Charcosset et al. (1996) starts with lignitic marls. Thus there is evidence for a changing very low relief landscape which probably prevailed throughout the deposition of the whole formation. This complicates lithostratigraphic correlations. In this kind of depositional setting it may be difficult to identify emersion surfaces to correctly place these into a hierarchy of sequence boundaries in different sections. Palaeogeographic reconstructions (Peybernès and Pélissié, 1985) also suggest that the Grand Causses Basin may have been at times a corridor between the Aquitaine Basin and the Subalpine basin across the so-called 'Haut-fond occitan'. This, a very shallow seaway, may have funnelled tidal currents from the Atlantic to the Alpine basin during the strongest sea-level highstands, but did not have enough accommodation space to accumulate thick deposits. This may explain the relatively abrupt superposition of marine and freshwater deposits in thin sequences over such a long a period of time.

2.2. Palaeobotanical data

2.2.1. Palynology

Palynological investigations have been carried out by Doubinger (1961) and Alabouvette (1988). The palynomorphs found in the Causses lignites are listed in Table 1, from a compilation of these works. As there is no consensus among palynologists to ascribe every taxon to a major group, we prefer not to indicate systematical relationships, even tentatively.

Berger and Taugourdeau (1965) studied the palynology of lignites from three localities in the Tarn Valley, all said to belong to the Calcaires à Stipites. However, new biostratigraphical data based on Foraminifera (P. Charcosset, pers. commun., 1995) suggest a Bajocian age for the sample taken in Les Vignes, one of their localities. As results are given as a whole for their three localities, we did not include Berger and Taugourdeau's data.

The palynoflora is characterized by a strong diversity of fern spores, including all major groups of Pteridophyta. The other groups are also well represented. However, there are strong lateral variations. In typical Larzac lignites, conifers are abundant and diverse, always with high percentages of *Tsugaepollenites* (= *Cerebropollenites*) *mesozoicus* (Doubinger, 1961). On the other hand, *Corollina* is rather rare.

2.2.2. Leafy rests and fossil wood

Previous data are few and limited. Bleicher collected the first fossil plants (fern fragments, cycadean pinnules, and a horsetail species) which were determined by de Saporta (1873). Nicklès (1907) described a cycadean leaf from the Le Caylar outcrop (Fig. 1), now housed in Maubeuge's collection in Nancy. Gérard (1936) added *Lycopodites* sp. to this first systematic list, and Maubeuge (1949) identified *Phlebopteris polypodioides*. According to our review, the specimens described as *Laccopteris fabrei* by de Saporta (1891, Pl. 285, fig. 3) from the Bathonian of Lanuejols (Gard) are *Phlebopteris* sp. Some plant remains from the Causses named *Microdictyon woodwardianum* by de Saporta (1891) are probably conspecific. Moreover, de Saporta (1873) also described some sterile and fertile pinnules as *Microdictyon rutenicum*, which is actually a synonym of *Phlebopteris dunkeri* (Harris, 1961).

In our own investigations we have identified seven genera and ten species that had not been recorded previously for this area (Table 2). As a matter of fact, few localities yielded good impressions or cuticles (Le Rozier, Saint-Georges-de-Luzençon, Les Plots, Salles and mainly Saint-Sulpice outcrops, Fig. 1). As a rule, plant fossils in lignitic levels are poorly preserved. Nevertheless, overlying clay-rich sediments have sometimes yielded well preserved cuticles and twigs that have been extracted using Schulze's method. All the investigated fossil woods are tracheidoxyls. They always lack pith or bark. Seventeen wood samples were well enough preserved for anatomical investigations. They have been studied using Collodion casts and a scanning electronic microscope. Detailed description of these fossils will be given elsewhere. The full systematic list is given in Table 2.

Horsetails (*Equisetum duvalii*) may be found in dense growth in places. However, we collected mostly subterranean axes with roots. Fern remains are locally abundant, mainly with *Phlebopteris* sp. Specimens related to this genus are never fusainised, but found as impressions. *Brachyphyllum crucis* is the most frequently observed conifer. It represents approximately 80% of the remains. *Pagiophyllum maculosum* is well represented in Saint-George-de-Luzençon, whereas it represents only a few percent of the material in Saint-Sulpice. Material of *Elatides williamsoni*, *Brachyphyllum* cf. *trautii*, and *Pagiophyllum araucarinum* is encountered much less frequently.

Although five species of conifer foliage have been recognized, only four species of wood have been found. This discrepancy may be due to one or two causes as wood is exposed to a different taphonomic process and as wood-based form-species usually do not fit leave-based ones. *Agathoxylon desnoyersii* was originally described (Lemoigne, 1968) as the wood of *Brachyphyllum desnoyersii*. However, it now has been demonstrated that this wood taxon, as so far delimited, corresponds to a variety of different foliage (Philippe, 1995). *Brachyoxylon* also has been related to various types of foliage. Although sometimes recognized as the wood of *Cheirolepidiaceae*, its relationship with this family is still unclear. *Protopodocarpoxylon* is recognized for the first time with absolute certainty in the Jurassic of France. The other occurrences of *Protopodocarpoxylon araucarioides* are from the early Malm of Westfalia (Müller-Stoll and Schultze-Motel, 1989) and the Bathonian of Angren in Uzbekistan (Gomolitzky et al., 1981). In the Causses, *Prototaxodioxylon* has only been found in Saint-Sulpice, but it is common there. The find of a *Prototaxodioxylon* is interesting as *Elatides williamsonii*, a putative Taxodiaceae, has been collected at the same locality, together with its pollen, *Perinopollenites elatoides*. It is worth noting that this wood has also been found in the Paris Basin, at the base of the middle Callovian (Philippe, unpublished data, 1995). These occurrences demonstrate that this species was widespread, at least in coastal areas.

Generally strongly flattened, the wood samples rarely allow growth-ring measurements. In radial view, growth-rings are clearly marked. They seem to be rather regular, although a quantification is not realistic because of preservation.

2.3. Causses Bathonian phytocoenoses and their environment: a preliminary discussion

Despite the fact that different lignitic layers are slightly diachronous, lateral floristic variation is higher than vertical variation. There are no clues to indicate that an environmental shift occurred during the deposition of the lignite. The same plant species are found throughout the series and, thus, we will discuss the floristic data as a whole.

Three related taxa, the wood *Prototaxodioxylon* sp., the foliage *Elatides williamsonii*, and the pollen *Perinopollenites elatoides*, all have different frequencies of occurrence. The relationships between wood, foliage, and pollen abundance are, thus, intricate. The microflora is more diverse than the megaflora. Indeed, nineteen spore and sixteen pollen taxa have been documented in the Causses lignites (Table 1), whereas our census lists only seventeen taxa (impressions and wood) for megafossils (Table 2). If we accept Doubinger's systematical attribution for palynomorphs (1961), the palynology almost only confirms the occurrence of Ginkgoales, Bennettitales, Caytoniales, and Pteridospermales in the area. Either these were not preserved as megafossils, or allochthonous pollen grains were transported into the basin by wind or water. According to Batten (1982) and Mussard et al. (1994), the association of bisaccates with numerous *Corollina* sp. and other diverse gymnosperm pollen characterizes influx from the hinterland. As there was occasional water influx (Fürsich et al., 1995), water transport and deposition of palynomorphs is quite plausible.

Palaeoecological inferences can be drawn from plant megafossils. As ferns, the species of *Phlebopteris* may be interpreted to indicate conditions of appreciable humidity. However, as they are commonly found as fusain (Harris, 1961; Van der Burgh

Table 1
Palynological data for the middle Bathonian of France

Taxa	Causses 1	Causses 2	Champlitte	Chemaudin[a]	Anteuil[a]	Alsace	
Pollens							
Abietinaepollenites microalatus Potonié	1.9						
Alisporites microsaccus (Couper) Pocock	0.8						
Alisporites robustus Nilsson						X	
Araucariacites australis Cookson	8.3		X			X	
Callialasporites dampieri (Balme) Sukh-Dev	X		X		X		
Callialasporites microvelatus Schulz				9	2	X	
Callialasporites minus (Tralau) Guy			X			X	
Callialasporites segmentatus (Balme) Srivastava					2	X	
Callialasporites trilobatus (Balme) Sukh-Dev	X	X	X	10		X	
Callialasporites turbatus (Balme) Schulz			X			X	
Cerebropollenites macroverrucosus (Thiergart) Schulz			X				
Cerebropollenites mesozoicus Nilsson	22					X	
Chasmasporites hians Nilsson			X				
Classopollis torosus (Reissinger) Couper et C. sp.	16.5	X	6				
Corollina sp.				20		X	
Cryptomeriapollenites sp.	0.4						
Ephedripites menendezii Volkheimer						X	
Eucommiidites minor Groot and Penny			X				
Eucommiidites troedsonii Erdtmann	0.6	X	X	15	8	X	
Excesipollenites scabrosus Norris					14		
Excesipollenites tumulus Balme			11		6	X	
Excesipollenites sp.		X			11		
Inaperturopollenites giganteus Goczan						X	
Monosulcites carpentieri Delc. et Sprum.	X	X					
Monosulcites minimus Cookson	X	X					
Monosulcites sp.					10	X	
Perinopollenites elatoides Couper	4.7				12		
Piceites latens Bolkhovitina						X	
Podocarpidites sp.			X			X	
Spheripollenites subgranulatus Couper	X		X				
Spheripollenites scabratus Couper	X						
Vitreisporites pallidus (Reissinger) Nilsson	0.5	X	X	20			
Spores							
Calamospora mesozoica Couper	2.3					X	
Calamospora tener (Leschik) Mädler			X	10			
Circularesporites cerebroides Danzé and Laveine			X				reworked from Liassic
Converrucosisporites sp.			X				
Contignisporites dunrobinensis (Couper) Schulz						X	
Cyathiidites australis Couper	X		X			X	
Cyathiidites concavus (Bolkhovitina) Dettmann			X				
Cyathiidites minor Couper	X		X				
Deltoidospora toralis (Leschik) Lund			X	16			
Deltoidospora sp.					5	X	
Densoisporites perinatus Couper	0.1						
Densoisporites erdtmanii Guy-Ohlson			X				
Densoisporites velatus Weyland and Kreiger			X			X	reworked
Dictyophyllidites harrisii Couper		X	X			X	
Distalanulisporites punctus Klaus						X	
Foveotriletes irregularis Couper						X	
Gleicheniidites conspiciendus (Bolkhovitina) Krutzsch			X				
Gleicheniidites senonicus Ross	4.4		X		10	X	

Table 1 (continued)

Taxa	Causses 1	Causses 2	Champlitte	Chemaudin[a]	Anteuil[a]	Alsace	
Intrapunctisporis toralis (Leschik) Lund			X				
Ischiosporites crateris Balme			X				
Ischiosporites granulosus Tralau			X				
Ischiosporites variegatus (Couper) Schulz	0.3	X	X				
Leptolepidites equatibosus (Couper) Tralau			X				
Leptolepidites macroverrucosus Schulz			X				
Leptolepidites major Couper	0.9					X	
Lycopodiacidites rugulatus (Couper) Schulz					2	X	
Lycopodiumsporites austroclavatidites (Cookson) Hiltman					4		
Lycopodiumcidites cerniidites (Ross) Delc. et Sprum.	X						
Lycopodiumsporites gristhorpensis Couper	X						
Lycopodiumsporites sp.					10	X	
Marattisporites scabratus Couper	3.8	X			3		
Matonisporites equiexinus Couper	X						
Matonisporites phlebopteroides Couper	X						
Monolites sp.	0.9						
Neoraistrickia truncata (Cookson) Potonié						X	
Neoraistrickia sp.			X				
Osmundacidites wellmanii Couper	1.3				1	X	
Cf. *Porcellispora longdonensis* (Clarke) Scheuring			X				reworked from Triassic
Punctatisporites globosus (Leschik) Lund			X				
Staplinisporites pseudoalveolatus (Couper)	0.1						
Todisporites major Couper	X		X			X	
Todisporites minor Couper	X						
Trilites bossus Couper	1.9						
Uvaesporites argentaeformis (Bolkhovitina) Schulz						X	
Valatisporites sp.						X	

[a] New data.

Causses 1 from Doubinger (1961), 1000 counted; Causses 2 from Alabouvette (1988); Champlitte from Médus and Mojon (1996); Chemaudin from M. Roche (pers. commun.) and new data, 102 counted; Anteuil, new data, 150 counted; Alsace from Schmitt (1987). Names have been updated according to Schmitt (1987) and Courtinat (1989) in the case of nomenclatural synonymy. However, to avoid confusion, original names have been kept if, subsequently, only taxonomic synonymy has been proposed. When known, percentages are given.

and Van Konijnenburg-Van Cittert, 1984), they are usually seen rather as plants from inland heaths (Van Konijnenburg-Van Cittert and Van der Burgh, 1996). Ziegler et al. (1994) indicate a rather mesic position for this genus. *Equisetum* is perhaps the most common genus, although it is rarely well preserved. Typical horsetails are hygrophytic plants, some species resisting a low degree of salinity and others temporary drought. *Equisetum duvalii* is found associated with a freshwater fauna (Maubeuge, 1949) and was, hence, probably a rather typical horsetail, growing in lentic zones. The bulk of the flora is represented by the taxon *Brachyphyllum crucis*. This taxon is known in Great Britain in 25 localities associated with marine horizons and 19 localities in which there is no marine influence (Harris, 1979). The majority of the specimens (including cones), however, comes from marine localities (J.H. Van Konijnenburg-Van Cittert, pers. commun., 1997). In the Hasty Bank Formation, *B. crucis* is associated with *Pachypteris papillosa*, a typical mangrove (Harris, 1964). Because it has a broad ecological spectrum, *B. crucis* is unfortunately a poor palaeoenvironmental indicator. According to Harris (1979) its shoots were caducous. *Elatides williamsonii*, a widespread species in the western Tethys, was probably a deciduous tree, growing adjacent to lagoons (Harris, 1979). *Pagiophyllum maculosum*, a common species in the

Table 2
Palaeobotanical data for the Middle Bathonian of France

Taxa	Causses	Mamers	Franche-Comté	Pas-de-Calais	Other localities
Pteridophyta	*Equisetum duvalii*	*Equisetum mamertinus*	*Equisetum* sp.		*Equisetum hommeyi*
	Phlebopteris dunkeri	*Equisetum sarthensis*			*Equisetum* sp.
	Phlebopteris polypodioides	***Phlebopteris* sp.**			*Phlebopteris woodwardi*
	***Phlebopteris* sp.**				
	Lycopodites				
Prespermatophyta	*Cycadites* sp.	*Cycadites delessei*		***Cycadopteris moretiana***	
		Cycadopteris moretiana			
Bennettitales	*Otozamites* sp.	*Otozamites brevifolius*	***Bucklandia* sp.**	*Otozamites beckei*	*Otozamites* sp.
	Sphenozamites sp.	*Otozamites bucklandii*	**cf. *Otozamites* sp.**	*Pterophyllum hortensiae*	*Zamites* sp.
		Otozamites lagotis	*Zamites dubisensis*	*Zamites* sp.	Cycadean stems
		Otozamites major			
		Otozamites marginatus			
		Otozamites pterophylloides			
		Otozamites rechini			
		Otozamites reglei			
		? *Pterophyllum* sp.			
		Sphenozamites brongniartii			
		Zamites moreaui			
		Zamites approximatus			
		Zamites confusus			
Coniferae	***Brachyphyllum crucis***	*Brachyphyllum desnoyersii*	***Brachyphyllum trautii***	***Brachyphyllum* cf. *mamillare***	*Brachyphyllum desnoyersii*
	Brachyphyllum* cf. *trautii	*Brachyphyllum* sp.	***B.* cf. *desnoyersii***	*Brachyphyllum* sp.	*Brachyphyllum* sp.
	Elatides williamsonii	*Pagiophyllum* sp.	***B.* cf. *mamillare***	*Pagiophyllum uncifolium*	***Agathoxylon* sp.**
	Pagiophyllum araucarinum	*Conites pontisgirardi*	***Araucarites* sp.**	*Protophyllocladus* sp.	***Brachyoxylon* sp.**
	Pagiophyllum maculosum	***Brachyoxylon* sp.**	*Brachyoxylon trautii*	***Brachyoxylon* sp.**	***Cupressinoxylon* sp.**
	Agathoxylon desnoyersii				
	***Brachyoxylon* sp.**				
	Protopodocarpoxylon* cf. *araucarioides				
	***Prototaxodioxylon* sp.**				

The new data reported in this work are in boldface. The data from the literature are from Lignier (1911), Dutertre (1930, 1938, 1939), and others (see text).

Middle Deltaic Series, “grew near enough to river channels and to *Equisetum* swamps ... to provide many separate leaves and occasional intact shoots” (Harris, 1979). This is exactly what we observed in Saint-George-de-Luzençon, where *P. maculosum* has been collected at the top of ‘in situ’ horsetail rhizome levels. However, in Saint-Sulpice, *P. maculosum* has also been collected, along with two other conifers (*Brachyphyllum crucis* and *Pagiophyllum araucarinum*), in a lenticular argillaceous bed that occurs between two calcareous rooting horizons without horsetails. According to Harris (1979), *Pagiophyllum araucarinum* might be an element of an ‘upland’ flora, usually washed into a depositional basin as fragments.

The mangrove *Brachyphyllum trautii* (Barale et al., 1991) may have been part of this assemblage, as rare isolated leaves have been found in one locality. The exact identification is not positive, however, owing to inadequate preservation. The corresponding wood, *Brachyoxylon trautii*, has not yet been found. If present, patches of mangal were rare and local. The occurrence of *Prototaxodioxylon* can not be used to interpret a wetland setting. Indeed, the occurrence of Taxodiaceae is no proof of a swamp biota, as is unfortunately too frequently noted (e.g., Giraud, 1988). *Agathoxylon desnoyersii*, on the other hand, is usually associated with sites of unequivocal emersion. It is also noteworthy that the floristic elements of the coastal/deltaic forest described by Bateman and Morton (1994) from the Middle Jurassic of the United Kingdom are not represented.

As a whole, the megaflora characterizes a freshwater swamp setting in a carbonate regime. Few data exist to interpret a more brackish vegetation on one hand, and of a more ‘upland’ vegetation on the other. The lateral variations in the composition of both micro- and megaflora may be related to edaphic differences. This hypothesis is reinforced by the occurrence, in the central part of the Causses, of a contemporaneous lava flow (Baubron et al., 1978), with a palaeosol at its top, the vegetation of which was probably different than the one supported by the carbonate backswamps, fens, and ponds.

Evidence to support an interpretation that significant rainfall occurred during this time includes the quantity of biomass trapped in the lignite, the abundance of horsetails, the density of roots in rooting horizons, the apparently regular growth-rings of the woods, the relatively high biodiversity, and the leaf cuticles with no outstanding xerophytic adaptations (except perhaps for the poorly represented *Pagiophyllum araucarinum*). This was probably seasonal, as trees were, at least partly, deciduous and as growth-rings are marked. However, because of the abundance of pteridophytes and hygrophytic conifers, this seasonality can not have been strong. This view of a rather mesic climate should be tempered if the poor record of Bennettitales, Caytoniales and Cycadales is not due to a bias (i.e. if the corresponding pollens are allochthonous), as these taxa are typical of temperate warm and rather wet areas (Vakhrameev, 1991).

According to Fürsich et al. (1995), at this time the Causses climate was semi-arid with occasional influxes of fresh-water, changing to arid conditions with very low freshwater influxes later in the Bathonian (Fechner, 1987). Inferences from plants fit with the results from bivalves, but indicate a somewhat wetter climate. With less exhaustive studies of the malacofauna, Rouire (1928) suggested an estuary in the Philippine Islands as a modern analogue.

3. Other middle Bathonian floras in France

3.1. Mamers

At the borders between Maine and Normandy (Fig. 2), Mamers (Sarthe) has long been known for its Bathonian flora, which is rich and diverse. It was studied by Desnoyers (1824), Brongniart (1825), de Saporta (1873, 1884, 1891), Crié (1878, 1885) and Lignier (1911). Unfortunately, the strata yielding this flora are no longer well exposed (Juignet and Lebert, 1986). Moreover, the rich private collection, mentioned in a letter by Crié (Lignier, 1913) has apparently been lost (M. Rioult, pers. commun., 1997). Crié’s collection itself has also been lost, and finally, the collection studied by Lignier was destroyed during World War Two (M. Rioult, pers. commun., 1997).

In Mamers, Bathonian deposits began (Juignet and Lebert, 1986) with ten regressive sequences (with emersion clues and vascular plant remains; M. Rioult, pers. commun., 1996) of sublithographic

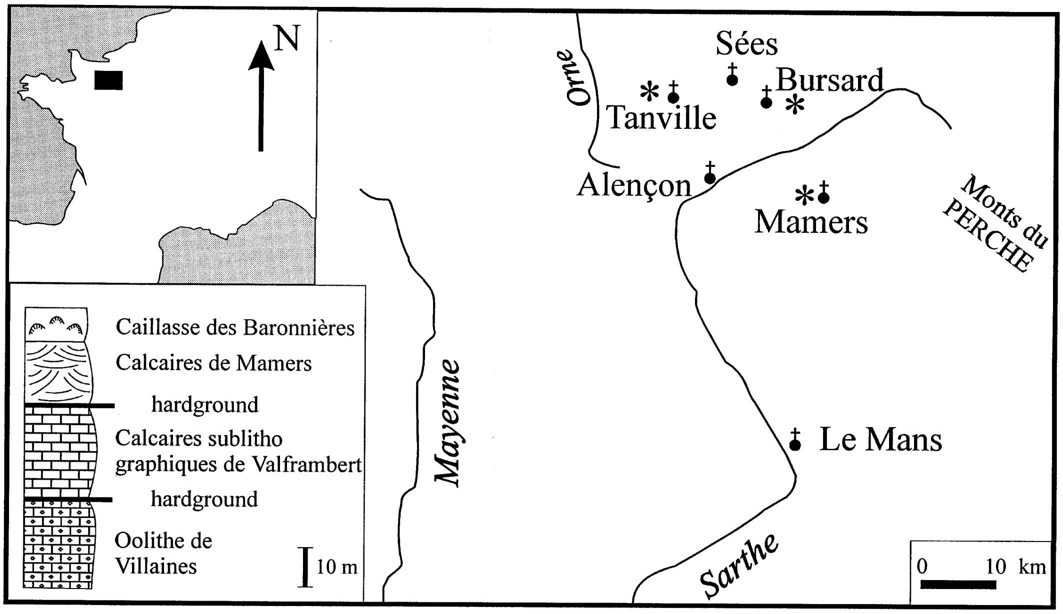


Fig. 2. Sketch of the location, simplified lithological column, and localities in the Mamers area.

limestone, a set known as the 'Calcaires sublithographiques de Valframbert' and dated as middle Bathonian. Then sedimentation stopped and a hardground developed, bored by deep galeries and decimetric gullies. On this surface the 'Calcaires de Mamers' were deposited (formerly known as the 'Oolithe de Mamers'), dated as the base of the Retrocostatum zone (Rioult, in litt., 1997). These shoreface calcarenites are a local marine deposit, disappearing rapidly eastwards and northwards. Trough and cross stratification is typical in the lower part, and gradually changes into flat bedding upwards. Salient rocks (Rioult, 1985) and conglomerates with Palaeozoic elements (Fily, 1975) are known throughout the region. The latter demonstrate the existence of islands and salient rocks with Palaeozoic basement. As there is very little silica in the calcarenites and as the continental influence is limited (Juignet and Lebert, 1986), these landscapes do not seem, however, to have been a source of the plant megafossils found in the Calcaire de Mamers. As for palaeontological content, this deposit is fossil-rich, with a mixture of marine organisms (brachiopods, bivalves, crinoids, occasional selacians and crocodilian teeth) and terrestrial plants (Table 2). The latter are mainly floated woody fragments and are mostly found in plant debris-rich lenses, where they accumulated after being transported over some distance and sorted by currents. There is no evidence of in-situ roots. Despite that the plant assemblage is allochthonous, it cannot have been transported far from its source as it is systematically diverse and well preserved.

On the Calcaire de Mamers came the 'Caillasse des Baronnières', dated as the summit of the Retrocostatum zone (Rioult, in litt., 1997). This Caillasse is made up of coral reef fragments and sea-shore organisms and does not show any plant fossil.

The megafloral systematics for the Calcaires de Mamers have not been reviewed since Lignier's work. A rigorous revision of this flora is difficult, as there is no preserved cuticle and most of the reference collections have been lost or destroyed. However, some remarks about Lignier's floral list are worth noting. *Equisetum laevis,* described by Lignier (1911), has been subsequently renamed *Equisetum sarthensis,* the first name being a junior synonym (Lignier, 1913). *Linopteris mamertiana* is actually a *Phlebopteris* sp., as is clearly shown by the shape and venation of the described specimen pinnules. Furthermore, the two *Cycadopteris* species are both closely similar to *C. moretiana. Pagiophyllum cirinicum* is, in our opinion, only determinable

Table 3
Mean sensitivities and growth-ring features for seven wood specimens from the middle Bathonian of France

Sample origin	Rings counted	Mean sensitivity	Growth-ring width (mm)			Preservation
			minimum	maximum	average	
Franche-Comté	8	0.510	0.24	1.41	0.74	lignite
Franche-Comté	4	0.431	0.21	1.02	0.55	lignite
Franche-Comté	6	0.649	0.23	1.66	0.58	lignite
Franche-Comté	4	0.610	0.25	1.57	0.60	lignite
Franche-Comté	7	0.378	0.31	0.97	0.62	lignite
Franche-Comté	24	0.324	0.07	0.55	0.25	charcoal
Mamers	16	0.387	0.50	3.50	1.71	mineralized
		Average = 0.470			Average = 0.72	

A caveat is necessary about ring widths as sample preservation is variable, frequently involving allometric transformations. Mean sensitivity $= 1/(n-1)\sum_{t=1}^{t=n-1}[2(X_{t+1}-X_t)/(X_{t+1}+X_t)]$, where n is the number of rings in the sequence, t is the number of the ring, and X is the ring width (any unit).

at the generic level. Finally, the several species of *Otozamites* can probably be grouped into no more than four taxa. However, this is not certain due to the lack of cuticles. Synonymies are highly probable and the nomenclature is not at all reliable. Thus, the list in Table 2 is given with some reservations. Anyhow, this list clearly shows a high quantity of Bennettitales and varied conifers, with the Pteridophyta limited to a *Phlebopteris* and an *Equisetum* species.

A piece of silicified wood has also been found, which we have identified as a *Brachyoxylon*. This is now housed in the Palaeobotanical Collection of Museum National d'Histoire Naturelle in Paris (No. 6855). It is much more abietinean in its radial pitting than the *Brachyoxylon* found in the Causses. The sample shows several insect borings, some being probably due to sawflies (Scott, 1992). Results from growth-ring analyses are given in Table 3. Growth-rings are marked, with a narrow late wood (three to five cell layers).

As there are no palynological data available from Mamers, the one described from a late-middle Bathonian (Girardin, 1982) deposit in Champlitte (Haute-Saône, Fig. 3) by Médus and Mojon (1996) has been used as an approximation for this deposit. This palynoflora (Table 1) is associated with an unfortunately unstudied flora that was mentioned by Etallon (1864) in a bottom-page note as "a rich flora, similar to the Mamers one, and consisting of ferns and conifers with *Brachyphyllum desnoyersii*". In the palynological assemblage the contribution of pteridophyte spores is significant, whereas *Corollina* is poorly represented (Fig. 5).

Let us now discuss briefly the palaeoecology of the Mamers flora. It was deposited on skeletal sand in low undulating tracts, sheltered from the open sea (Fily, 1989) and isolated from continental alluvia. The systematic composition of the Mamers flora is similar to that of Etrochey (Côte d'Or), a Callovian flora with similar palaeoecology (Lemoigne and Thierry, 1968). Both floras are dominated by *Brachyphyllum desnoyersii*. We interpret the Mamers flora as a coastal one, probably subject to sea-spray, but not 'saline-stressed'. Amazingly, this flora is composed of rather hygrophytic plants (horsetails and ferns) together with rather xerophytic ones (several cycadophytic species). Such a contrast in a coastal vegetation is usually encountered in areas where low dunes interfinger with humid interdunes. To maintain the necessary watertable, the rainfall has to be significant (higher than 1 metre per year) and not strongly seasonal. In fact, this phytocoenosis can be compared with a tropical version of a Scottish machair.

3.2. Franche-Comté

A middle (late-middle/early-late) Bathonian flora is also known in Franche-Comté. Following a *Teleosaurus* find in Picarreau (Jura), Parrandier (1891) noted a widespread level with a terrestrial flora in the middle part of this stage. However, some other Bathonian floras in the area may be slightly

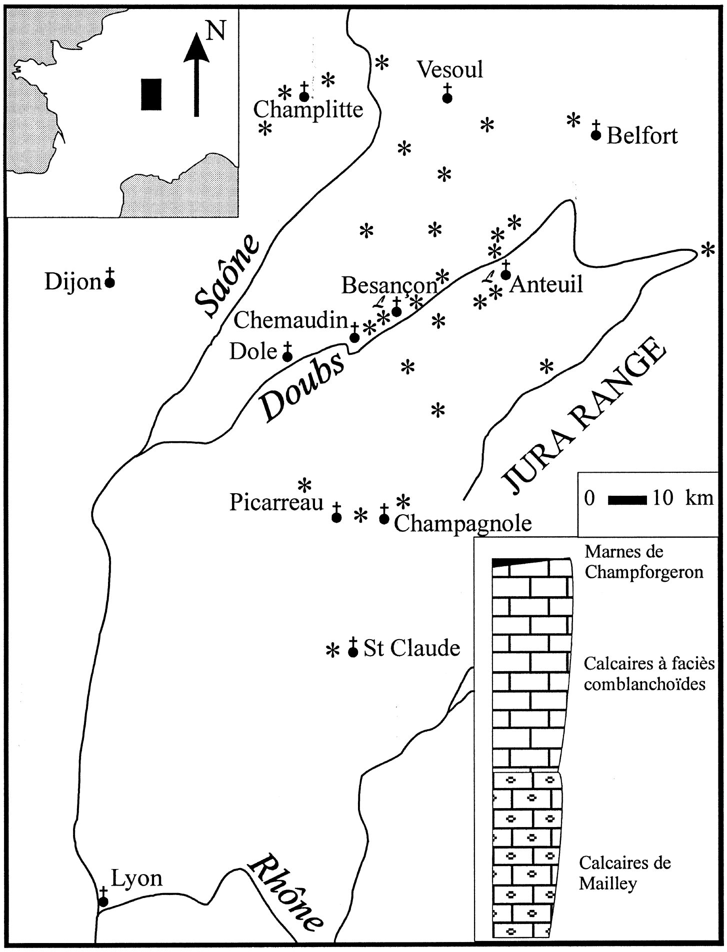


Fig. 3. Sketch of the location, simplified lithological column, and localities in the Franche-Comté. * = localities with allochthonous material; $\mathcal{L}$ = localities with autochthonous material.

younger or older. Indeed, lignites and a ramified *Equisetum* have been found (Girardot, 1893) in the 'Oolithe du Vaudioux (Jura)', Discus zone (see Table 4 for stratigraphy).

However, the bulk of fossil plants for the Bathonian of this region originate from a marine level at the transition from a group of bioclastic and oolithic calcarenites to a group of sublithographic limestones (Fig. 3). This level is documented in 27 localities (Table 5), distributed all over northern Franche-Comté (Fig. 3). In Champagnole, Girardot (1893) placed this level into the Retrocostatum zone. New sedimentological (F. Gaumet, pers. commun., 1997) and brachiopod-based palaeontological (J.-P. Garcia, pers. commun., 1997) investigations assigned this main level to the Hodsoni zone and highlight that the different localities are slightly diachronous. In every locality, plant remains are encountered in marine sediments, without any brackish fauna. Nevertheless, Charophytes have been found sporadically (Girardin, 1982). Rooting horizons are present locally, and are usually dense (e.g. with a vertical root every 12.5 cm in average, $n = 9$, on a bed section at La Cocotte quarry, Doubs). In Crozey (Doubs) we found two in-situ stumps, both roughly 20 cm in diameter. Although these rooting structures may not be exactly synchronous, according to these observations trees may have formed a continuous canopy.

With M. Roche, we have performed a palynological analysis of this level on an organic-rich clayey

Table 4
Stratigraphical framework. Bathonian stratigraphy is much debated. Bathonian ranges roughly from 166 Ma to 160 Ma (Harland et al., 1990; Odin and Odin, 1990)

	Pomerol, 1974		Harland et al., 1990	Mangold and Rioult, 1997				
	zones	subzones	zones	submediterranean province		subboreal province		
				zones	subzones	subzones	zones	
Late Bathonian	Discus	Discus	Discus	Discus	Discus	Discus	Discus	Late Bathonian
		Hollandi	Aspidoides		Hollandi	Hollandi		
	Retrocostatum	Retrocostatum	Hodsoni	Retrocostatum	Hannoveranus	Hannoveranus	Orbis	
		Blanazense			Blanazense	Blanazense		
Middle Bathonian	Subcontractus	Morrisi	Morrisi	Bremeri	Fortecostatum	Hodsoni	Hodsoni	
					Bullatimorphus			
				Morrisi	Morrisi	Morrisi	Morrisi	Middle Bathonian
		Subcontractus	Subcontractus	Subcontractus	Subcontractus	Subcontractus	Subcontractus	
			Progracilis	Progracilis	Progracilis	Progracilis	Progracilis	
					Orbignyi			
Early Bathonian	Zigzag	Zigzag	Tenuiplicatus	Aurigerus	Tenuiplicatus	Tenuiplicatus	Tenuiplicatus	Early Bathonian
					Recinctus	Yeovilensis		
			Zigzag	Zigzag	Macrescens	Macrescens	Zigzag	
					Parvum	Convergens		

Table 5
Localities with middle Bathonian fossil plants in Franche-Comté (northeastern France)

Locality	Departement	Reference	Locality	Departement	Reference
Clerval	Doubs	Parrandier, 1891	Epeugney	idem	idem
Lavigny	Jura	Girardot, 1893	Hyemondans	idem	idem
Syam	idem	idem	Romain	idem	idem
Forêt de la Joux	idem	Weber, 1961	Saraz	idem	idem
Dole	idem	Pernin, 1978	Villers-le-Lac	idem	idem
Mamirolle	Doubs	Bulle et al., 1968	Bougnon	Haute-Saône	Chanson, 1967
Anteuil	idem	Laffly, 1973	Tresilley	idem	Dreyfuss and Kuntz, 1970
L'Hôpital St.-Lieffroy	idem	Barale, 1981	Gy	idem	Girardin, 1982
Chalezeule	idem	Girardin, 1982	Leffond	idem	idem
Besançon–Tarragnoz	idem	idem	Mailley	idem	idem
Marchaux	idem	idem	Les Belles Baraques	idem	idem
Chemaudin	idem	Philippe, 1991	Champlitte	idem	Philippe, 1991
Crozey-le-Grand	idem	idem	Argiesans	Territoire de Belfort	idem
Deluz	idem	idem	St.-Ursanne	Vaud, Switzerland	idem

The swiss locality is close to the border with the Doubs. Mamirolle, given as Oxfordian by Bulle et al., 1968, is actually Bathonian in age (J. Bulle, pers. commun., 1989). A 'département' is one of the 95 main administrative divisions of France.

level (Fig. 3) from Chemaudin (Doubs). The palynofacies is sapropelic, with abundant (95%) amorphous organic matter and acanthomorph acritarchs (M. Roche, pers. commun., 1990). *Botryococcus* is also found (M. Roche, pers. commun., 1990) and its association with acritarchs suggests a middle mesohaline environment (Hudson et al., 1995). Our results for spores and pollen are included in Table 1. Pteridophyte spores are quite diverse. *Corollina* appears uncommonly. Furthermore, we investigated palynologically a lignitic marl (Fig. 3) from Anteuil (Doubs). Palynomorphs are more diversified (Table 1), again with a significant contribution from pteridophyte spores. Amazingly, *Corollina* is absent from this locality. This pollen, which has been said to be characteristic of a mangal palaeoenvironment (Plaziat, 1995), mainly on the basis of its distribution is, hence, poorly represented here.

The megaflora (Table 2) is almost exclusively composed of various-sized wood fragments, all determined as *Brachyoxylon trautii* (ca. 200 samples studied, more than 50 determined, some exceeding 1 m in length). They all show clear growth-rings, though most are narrow. False rings are common. Six samples are suitable to calculate mean sensitivities (Fritts, 1976). The results are given in Table 3. The late wood is always narrow, limited to one to four cell layers.

Leafy twigs and isolated leaves are rarely found. Most of them are assignable to *Brachyphyllum trautii*, whereas some isolated leaves have been tentatively determined as *Brachyphyllum* cf. *desnoyersii* and *Brachyphyllum* cf. *mamillare*. Some other taxa have also been identified. A cycadophytic plant found near Champagnole (Jura) comes from a level placed within the Retrocostatum zone (Girardot, 1893). This sample is now housed at the Musée d'Archéologie in Lons-le-Saunier (Jura), where we reviewed it. Because of its bad preservation, we cannot determine it more accurately than cf. *Otozamites* sp. Roche (1947) described the base of a cycadophytic plant as *Fittonia* sp. (an inappropriate synonym for *Bucklandia*) from Saint-Claude (Jura). Roche thought that the fossil belonged to the early Bathonian, but Mangold, who studied the outcrop, assigned it to the Morrisi zone (C. Mangold, pers. commun., 1980). In 1981, Barale described *Zamites dubisensis*, along with short undeterminable conifer leafy twigs from l'Hopital-St.-Lieffroy (Doubs). In Chemaudin (Doubs) badly preserved horsetails have been observed.

It would be useful to have a preliminary discussion about this flora. Despite the fact that the different plant remains are probably not exactly synchronous, they all represent a stable biotope, with an unchanging flora, almost limited to *Brachyphyllum trautii*. This tree was a low mangrove (Barale et al., 1991). *Brachyoxylon*-dominated wood assemblages are typical of low, sedimentologically isolated islands, with a halophytic flora (Garcia and Philippe, 1995; Garcia et al., 1998). The flora studied here inhabited lime muds in the intertidal zone, in a sheltered environment with a low tide amplitude (Fily, 1989). Its biodiversity is low. However, as in the Causses, there is a discrepancy between micro- and megafloral assemblages. Médus and Mojon (1996), studying the palynology of this level, in Champlitte (Haute-Saône, Franche-Comté), found Triassic and Liassic reworked palynomorphs. This demonstrates that, although there were few typical continental sediment supplies (i.e., fluvial quartz grains), plant microfossils found may be allochthonous. The low abundance of *Corollina*, which is amazing because several authors have related this pollen to mangals (Plaziat, 1995), may be due to tidal flushing. Nevertheless, it must be noted that the hypothesis of its relationship with mangal is poorly documented. The thickest lignite lenses are rich in pyrite. This supports the interpretation that these were local organic matter accumulations possibly in blocked tidal channels (Phillips and Bustin, 1996). The hypothesis that strong streams ran through the mangal area is also supported by the existence, as in Anteuil (Laffly, 1973), of lens-like lignitic claybanks, which are as thick as 1 m. The proposed palaeoecological setting fits with the reported occurrence of crocodilians, mostly Teleosauridae (Parrandier, 1891; Buffetaut and Thierry, 1977; Médus and Mojon, 1996).

3.3. Other middle Bathonian floras

Poorer middle Bathonian megafloras are known in many other French localities. Most of them are poorly dated, but may be roughly related to the second-order minimum known for the Morrisi subzone (Graciansky et al., 1993). Additionally many other continental (in the broad sense) features have been reported from France (Table 6 and Fig. 4), from conglomerates with Palaeozoic pebbles (Klein, 1960) to terrestrial vertebrates (Lorenz, 1989). Incidentally, many of these features of temporary emersion have been related to a single middle Bathonian event (Parent, 1944), whereas, at least in the Paris Basin, emersions and fossil plant levels range from the base (Fliche and Bleicher, 1882) to the top of the Bathonian stage (Bruet, 1933; Lemoigne and Thierry, 1968; Garcia, 1993). Caution is, thus, necessary when dating and establishing the relationships between these data.

According to sedimentological data, the late Bathonian palaeoclimate seems to have been slightly different from the middle Bathonian (Fechner, 1987; Lorenz, 1989; Garcia, 1993). In order to avoid too much bias in the palaeofloristic interpretation, we have decided to consider only those floras whose age falls within the former Subcontractus and Retrocostatum zones (present Subcontractus, Morrisi, Bremeri and Retrocostatum zones, see Table 4).

Bathonian lignites are known (Durand-Delga, 1958) in the Grésigne (Tarn-et-Garonne). They are intercalated within marine marls or sublithographic limestones and associated with a marine or brackish fauna. The age of these lignites is dubious, but the associated fauna fits with a middle Bathonian age. In fact, there are two levels with Charophytes and brackish fauna in the area. In the upper one, dated as late-middle Bathonian (Fabre, 1971), we found *Brachyphyllum* sp. and horsetail root beds with Charophytes in Nidauzel (Tarn-et-Garonne).

In the neighbouring area of Quercy we have found *Brachyphyllum* sp. near Saillac (Lot) and Saint-Projet (Tarn-et-Garonne), and Charophytes in Cajarc (Lot). The Quercy lignites are sometimes supposed to be middle Bathonian in age (Astruc, 1988); recent founds of brachiopods clearly assign them to the Bajocian (T. Pélissié, pers. commun., 1997). Also in Quercy, the woods noted from Cressensac (Lot) by Grambast (1953) and Koeniguer (1980) as Bathonian in age, actually belong to the Tertiary (Astruc, 1988). However, near to this locality, several *Otozamites* fronds have been found (Monteil, 1977) in basal upper Bathonian strata. Lacustrine deposits of the same age have been characterized (Mouret, 1968).

Aside from the Mamers flora, other floras have been mentioned from the middle Bathonian in Normandy. At La Ferrière-Béchet (Orne), *Phlebopteris woodwardi* has been reported (Lignier, 1913). A sandy rooting horizon with *Equisetum hommeyi* has been described in Aunou (Orne; Lignier, 1913). However, several other fossil plants that were previously assigned to the Bathonian are, in fact, much younger (Rioult, 1966).

From boreholes in the Paris Basin, we have identified some woods: *Cupressinoxylon* sp. from the

Table 6
Evidence of continental biota in the Middle Jurassic of France

Reference	Locality or area	Age	Type of continental evidence
Etallon, 1864	Champlitte (Haute-Saône)	Middle Bathonian	Fossil flora with ferns and conifers
Douvillé and Roland, 1885	Poitiers (Vienne)	Bathonian	Cycadean stems
Schlippe, 1888	Haut-Rhin	Retrocostatum	Fossil wood
Bigot, 1891	Bursard (Orne)	Bathonian	Palaeosols with horsetails
Glangeaud, 1895	Thiviers (Dordogne)	Middle Bathonian	Marls with brackish fauna
Benoist, 1900; Garde, 1904	St.-Gaultier (Creuse)	Middle Bathonian	Brackish bivalve fauna
Lignier, 1913	Tanville (Orne)	Middle Bathonian	Fossil ferns
Debelmas, 1950	Champcella (Haute-Alpes)	Dogger	Coals
Pelletier, 1952	St.-Rambert (Ain)	Hodsoni zone	Lignites
Durand-Delga, 1958	Grésigne (Tarn-et-Garonne)	Late-middle Bathonian	Lignites, charophytes and brackish fauna
Klein, 1960	Normandie and Maine	Early-late Bathonian	Conglomerate and roots
Magniez et al., 1960	Dijon (Côte d'Or)	Late-middle Bathonian	Charophytes
Fischer, 1962	Argenton (Indre)	Middle Bathonian	Lignites, palaeosols and vertebrates
Mouret, 1968	Brives area (Corrèze)	Aspidoides zone	Lacustrine deposits
Mangold, 1970	Southern Jura Mts. (Ain, Jura)	Late-middle Bathonian	Lignitic marls
Fily, 1975	St. Germain le vieux (Orne)	Late-middle Bathonian	Conglomerate with Palaeozoic elements
Monteil, 1977	Cressensac (Lot)	Middle Bathonian	Cycadomorphic frond, ?*Otozamites*
Dardeau, 1983	Tinée (Alpes Maritimes)	Middle Bathonian	Plant remains
Peybernès, 1984	Durban (Aude)	Middle Bathonian	Lignitic marls with ostracods and charophytes
Cavelier and Médioni, 1987	Amiens (Somme)	Middle Bathonian	Lignitic debris
Elmi, 1987	Crussol (Ardèche)	Late-middle Bathonian	Palaeosoil on palaeokarst
Cubaynes et al., 1989	Quercy (Lot)	Middle Bathonian	Synsedimentary breccia and evaporites
Fily, 1989	Perche (Orne)	Middle Bathonian	Palaeosols with kaolinite and illite
Lorenz, 1989	St. Gaultier (Creuse)	Middle Bathonian	Continental vertebrates
Peybernès, 1991	Western Pyrénées	Middle Bathonian, ante Hodsoni	Lignitic marls with charophytes and ostracods
See text	Causses	Middle Bathonian	Lignites, fossil flora, brackish fauna etc.
See text	Mamers	Base of Aspidoides zone	Fossil continental flora
See text	Franche Comté	Late-middle/early-late Bathonian	Lignites, fossil flora, in situ stumps and roots
See text	Marquise (Pas de Calais)	early-late Bathonian	Fossil flora
Olivero, pers. commun., 1989	Digne (Alpes de Hte. Provence)	Morrisi zone	Large floatted logs
new data	Nidausel (Tarn et Garonne)	Middle Bathonian	Horsetail root beds, *Brachyphyllum*
new data	Toul (Meuse)	Morrisi Zone	Floated wood
new data	Ancerville (Meuse)	Middle Bathonian	Floated wood
new data	Soudron (Marne)	Hodsoni zone	Floated wood

For localities, the corresponding 'département' is given between brackets.

middle Bathonian and *Brachyoxylon* sp. from the Hodsoni zone. In Burgundy, the Bathonian flora described by Bruet (1932), and said to be middle Bathonian in age (Stchépinsky, 1953), is actually assigned to the Discus zone based upon brachiopod evidence (J.-P. Garcia, pers. commun., 1992).

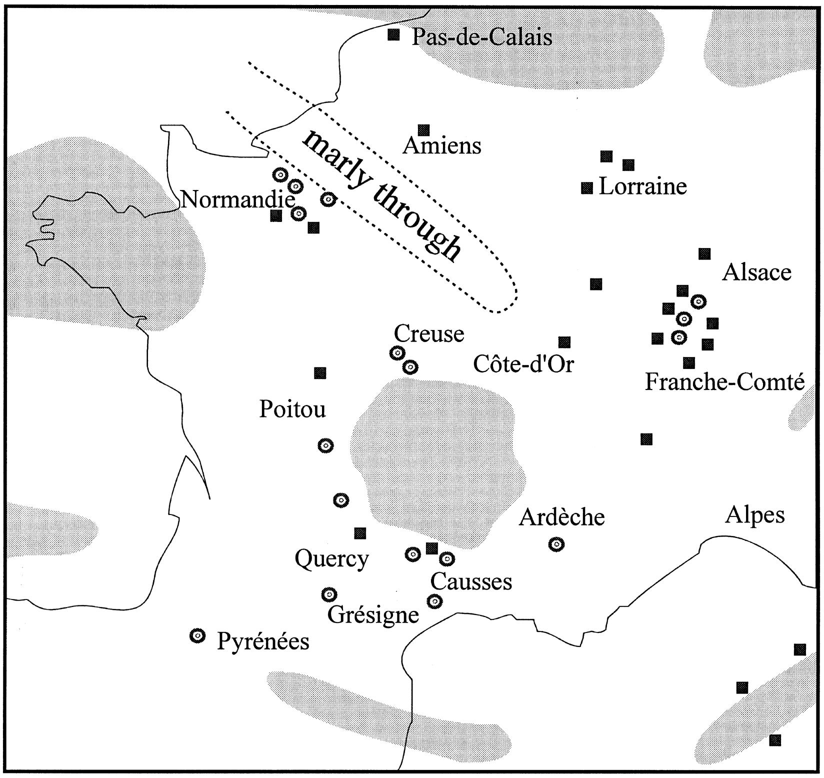


Fig. 4. Localities where evidence was found for continental biota in the Middle Jurassic of France. Palaeogeography from Yilmaz et al. (1996); data from Table 6. Stippled areas are presumably emergent zones. Squares indicate allochthonous data such as plant remains in marine sediments. Circles represent in-situ evidences such as rooting horizons or lacustrine deposits.

B. Laurin collected a piece of fossil wood in Lorraine, north of Toul (Meurthe-et-Moselle) and dated as middle Bathonian Morrisi zone. We determined it to be *Agathoxylon* sp. As it is associated with offshore deposits, it was probably allochthonous and is, thus, of low palaeoecological value.

A middle Bathonian flora has been found in Pas-de-Calais (northern France) and described (Zeiller, 1912; Dutertre, 1930, 1938, 1939; Corsin et al., 1962). It occurs in the 'Oolithe de Marquise', dated within the Retrocostatum zone (Vidier et al., 1995). We investigated woods from this level and found that they all belong to *Brachyoxylon*. The sedimentological character is quite close to that at Mamers, that is an oolitic shoreface with tidally influenced sheltered areas. Despite the absence of horsetails, a fact probably related to the local absence of mires, this flora is systematically close to that at Mamers, with a significant proportion of cycadophytic plants.

4. Phytoecology during the late-middle/early-late Bathonian of France

4.1. Data from megafossils

The composition of the three main megafloras considered here are summarized in Table 2. Data from the other localities are used incidentally.

It is noteworthy that each flora yields a different *Brachyphyllum* species. *Brachyphyllum desnoyersii*, found in Mamers, is otherwise abundant, each time with an interpreted palaeoecology similar to that of Mamers, in the Etrochey area (Côte d'Or, early Callovian), Champlitte (Haute-Saône, late-middle Bathonian; Etallon, 1864), La Combe aux Serpents (near Dijon, early Callovian; Thierry, 1967; Garcia, 1993), and other localities (see review in Barale, 1981). The palaeoecology of *Brachyphyllum crucis*, which is widely encountered in the Causses backswamp deposits, seems to have been quite different, but the data from England are contradictory (Harris, 1979). The third species, *Brachyphyllum trautii*, has a limited geographical range (known with certainty only from Franche-Comté, from the Bajocian to the Oxfordian; unpublished data). It has always been found associated with back-reef deposits. *Brachyphyllum mamillare* has been tentatively determined from Franche-Comté and Pas-de-Calais, and is known to be an element of a coastal biota (Bateman and Morton, 1994).

The palaeoflora of the Causses Basin is more diversified than that of the Franche-Comté, but less than that of Mamers. *Agathoxylon desnoyersii* and the *Prototaxodioxylon* sp. have both been found outside the Causses (Philippe, 1995, and unpublished data). The leaf flora of the Causses lignites is not endemic, apart from *Equisetum*. Almost all the species found in Mamers have been found elsewhere in France, Germany, and the United Kingdom. Despite the archipelago palaeogeography of the Jurassic in Western Europe, there seems to have been low floristic endemism. This means that an efficient dispersal mechanism existed for these terrestrial plants. Moreover, the number of species shared by siliciclastic (e.g. in Yorkshire, see Harris, 1961, 1964, 1979) and carbonate regimes implies little edaphic preference of this vegetation.

Because of their particular ecology, present mangal stands tend to have a lower biodiversity than the coeval continental floras. In this respect, the Bathonian mangal of Franche-Comté looks to be a typical mangal association because it is relatively poor in species, with conifers almost limited to *Brachyphyllum trautii*. On the other hand, at our present state of knowledge, the distribution of this species is limited to eastern France. This is surprising because, at present, mangroves are among the most widespread species in the tropical belt.

4.2. Comparisons with palynological data

In the Causses' microflora, according to Doubinger's (1961) systematical attribution for palynomorphs, Ginkgoales, Bennettitales, and Cycadales are fairly well represented, whereas these groups are almost unknown in the megaflora. The taphonomy of the two types of assemblages is different (Barale and Courtinat, 1980; Pittet and Gorin, 1997). The case of the probably cycadalean pollen — *Eucommiidites troedsonii* — is of interest. This pollen is common in the Causses, while cycadalean fronds are rare. The situation is the complete opposite in Creys (Barale and Courtinat, 1980), a Late Jurassic back-reef deposit.

Callialasporites trilobatus and *Eucommiidites troedsonii* are the most common species in the record (Table 1). The former species may be a palaeoclimatological indicator (Courtinat, 1989), as in the Malm of the Jura Mountains, *Callialasporites*, a typical coastal element, is encountered in marine strata deposited under a climate with average humidity. It is worth noting that *Callialasporites* becomes much rarer in the upper Bathonian of the Causses (Fechner, 1987), wherein conditions changed to hypersaline or even schizohaline. According to Srivastava (1994), *Cerebropollenites* is typical of wet and cool temperate zones.

In all palynological assemblages (Fig. 5) there is a high proportion of pteridophyte spores. These spores are diverse and numerous. At the same time, *Corollina* contribution is always low. In diagrams of Vakhrameev (1991) such low *Corollina* percentages are usually encountered much further north. It may be possible that this relationship was the result of significant rainfall with a limited dry season. It must be noted that, for the late Middle Jurassic of the British Isles, Boulter and Windle (1993) noted a peak contribution of pteridophyte (and mainly ferns) spores (their group 2).

4.3. The Bathonian palaeoclimate in France as seen by fossil plants

Elements of the evoked floras (Causses, Mamers, Franche-Comté) are typical of an environment that experienced significant rainfall. Coniferous mangroves may have had a different physiology than angiospermous ones. The problem is that, to our knowledge, no recent coniferous halophytes are known. Thus we have to hypothesize that their growth requirements were not so different from those of angiosperms, noting that if they were able to survive in harsh haline conditions they would probably have survived until now. The eastern coast of Queensland demonstrates the influence of rainfall on mangal distribution particularly well (Hutchings and Saenger,

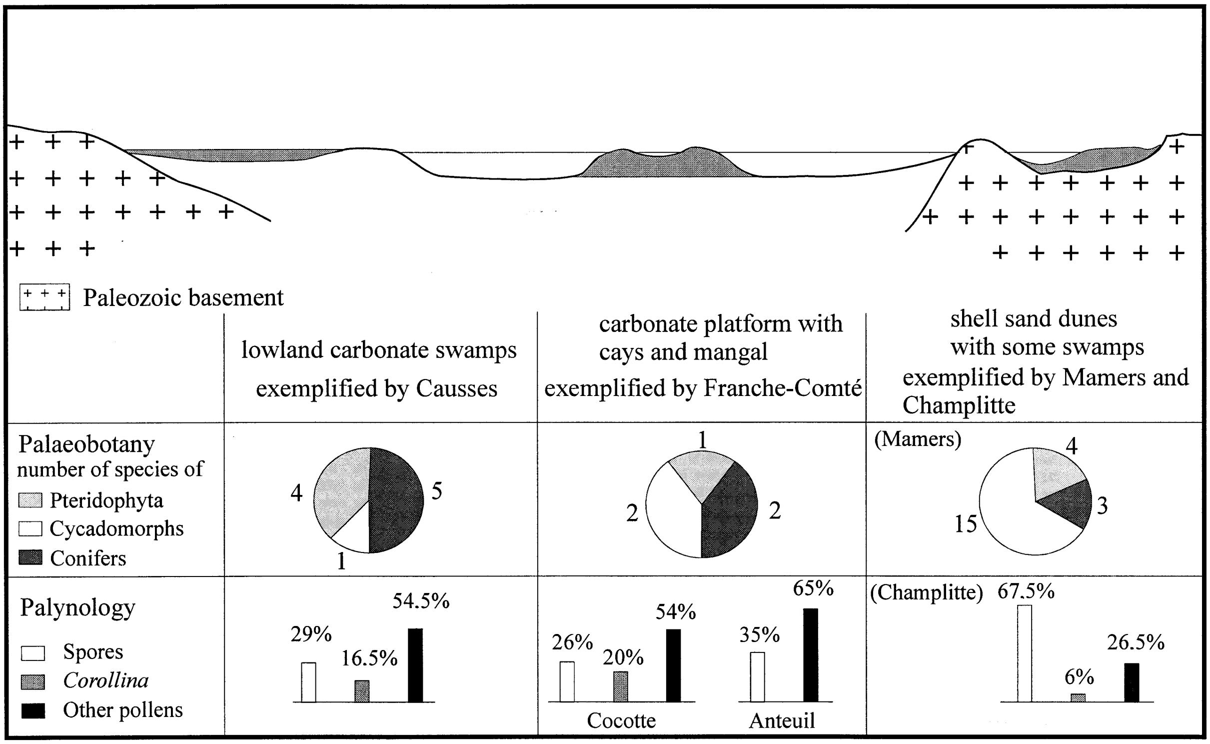
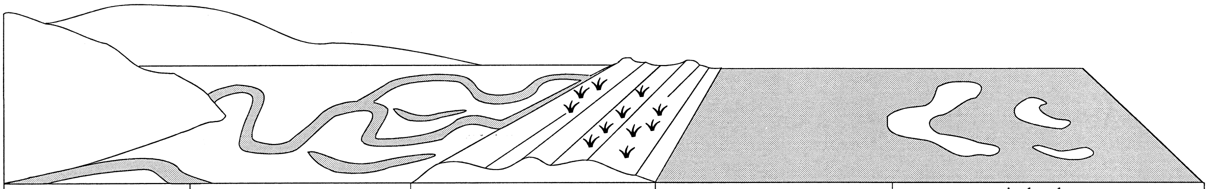


Fig. 5. Distribution of palynological and palaeobotanical remains over an idealized transect for the middle Bathonian of France. For data sources, see Tables 1 and 2. The number of cycadomorphic species for Mamers must be taken with care as Lignier's data (1911) cannot be checked; this number may have been smaller, though probably still considerable.

1987). There, mangrove forest is now at its best in an area with 3.5 m of annual rainfall, which is not highly seasonal. Where rainfall decreases to 1 m and is highly seasonal, mangroves are confined to stream banks or replaced by bare salt flats. The Franche-Comté palaeomangal was not dense, thick, or tall (Barale et al., 1991). However, if the mean annual temperature (MAT) was around 20–25°C (Donn, 1989; J.-P. Garcia et al., in prep.), then annual rainfall may hardly have been lower than 1 m and highly seasonal. This one-metre value is higher than the one simulated by climate models (Valdes, 1994). The genera of Table 2 mostly range in the middle part of the plots given by Ziegler et al. (1994), i.e. their biomes 4 (the midlatitude winterwet) and 5 (the warm temperate) (Fig. 6).

The commonness of *Equisetum* rooting horizons and the presence of *Calamospora* fitts well with an hypothesized sizeable rainfall and average humidity. Visscher et al. (1994) argued that horsetails may grow under arid conditions if there is enough freshwater influx. However, there are no sedimentological clues to verify this assertion in the localities studied here. Moreover, in each palynoflora, pteridophyte spores are diverse. At present, some extant ferns withstand drought, but diverse fern floras are always found in higher precipitation areas.

Nearby, in the British Midlands, the Bathonian palaeoclimate has been interpreted to have experienced seasonal rainfall, subject to anticyclonic weather which ensures high atmospheric humidity (Metcalf, 1995). The rainfall was probably seasonal, although not strongly so. The growth rings observed in the wood of the three main localities are all weakly marked, with a clear but narrow late wood, limited to two to five cell layers. In our opinion, this pattern of narrow late wood may be much more related to the wood systematics (i.e. genera) than to the climate (Philippe, 1991). False rings are common, probably due to anachronous droughts. According to the results of Table 3, the climate was quite variable. However, because of the low suitability of



Data used	lowland carbonate swamps (Doubinger, 1961)	shell sand dunes with some swamps (Médus & Mojon, 1996)	sea sediments with low continental influx (Schmitt, 1987)	isolated cays (Marc Roche pers. comm. and new data)	
				mangal	tidal channel
spores : number of species	19	20	16	2	7
number of genera	15	13	16	2	6
pollens : number of species	16	14	17	5	8
number of genera	13	10	12	4	5
% of spores (in number of species)	54	59	48	28	46
restricted genera of spores	*Matonisporites, Trilites, Staplinisporites.*	*Converrucosporites, Punctatisporites, Intrapunctisporis.*	*Contignisporites, Foveotrilites, Distalanulisporites, Uvaesporites, Valatisporites.*	none	none
restricted genera of pollens	*Abietinaepollenites, Cryptomeriapollenites.*	*Chasmasporites.*	*Ephedripites, Piceites, Inaperturopollenites.*	none	none

Fig. 6. Partition of spores and pollen in different environments recognized for the middle Bathonian of France. Data are given in Table 1. The two bottom rows indicate genera that have been presented in Table 1 from only one type of environment.

lignitic samples for growth-ring analysis, too often only a small number of rings were taken into account. This enhances variability. Compared to the Purbeck forests (Francis, 1984), where average mean sensitivities reached 0.57, the Bathonian wood samples studied here recorded a more stable climate. In our samples, growth-ring width is typically low and never exceeds 3.5 mm. The average ring width for all the samples considered in Table 3 is only 0.72 mm. This low value apparently infers that conditions were somewhat marginal for tree growth. As a matter of fact this value should be considered with care as wood usually shrinks when becoming lignite or charcoal. This also limits the comparisons with data from literature. The only mineralized sample is from Mamers, and its mean growth-ring width is 1.71 mm ($n = 16$ rings). It is slightly more than what Francis (1984) calculated for the Purbeck forest (i.e. 1.13 ± 0.46 mm, calculated for twenty trees), also with mineralized samples. As a whole, growth-ring data are not in contradiction to the hypothesis of a rather humid climate with seasonal rainfall.

Some of the conifers were probably deciduous, like *Brachyphyllum crucis* or *Elatides williamsonii* (Harris, 1979); others, like *Pagiophyllum araucarinum*, showed strong heterophylly. Drought avoidance may have been the cause for leaf deciduousness and heterophylly. Our observations fit quite well with the seasonal type of climate usually inferred for mid-latitudes. Otherwise, they also moderate Hallam's views of 'a strongly monsoonal climate' at that time (Hallam, 1994), fitting better with a lower seasonality. According to Francis (1994), the monsoon climate declined at the end of the Middle Jurassic. The other localities in which the plant species recognized here occur, are in the Paris Basin, Bourgogne, England, and Germany. If we assume that the climate was the main chorological factor at that time, we have to conclude that climatic differentiation around the Massif Central was small. There were possibly low floristic differences between southern France and northern England at that time. This is hardly compatible with the strong winter temperature gradient that has been calculated by various simulations for western Tethys (Valdes, 1994).

Acknowledgements

We thank the two reviewers R.A. Gastaldo and J. Van Konijnenburg-Van Cittert whose comments significantly enhanced the quality of the final manuscript. We are very much indebted to Michel Rioult for important information about the Mamers area and its palaeoflora. Jacques Bulle, Pierre Charcosset, Jean-Pierre Garcia, Fabrice Gaumet, Charles Mangold, David Olivero, Thierry Pélissié, and Marc Roche all contributed actively to this work by providing samples and during fruitful discussions. Thanks are due to Louize Hill for her critical review of the English text.

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