

# The palaeoxylological record of *Metapodocarpoxylon libanoticum* (Edwards) Dupéron-Laudoueneix et Pons and the Gondwana Late Jurassic–Early Cretaceous continental biogeography

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## Abstract

**Aim** Vertebrates, palynomorphs and leaf floras each give a different picture of continental biogeography of Northern Gondwana during the Middle Jurassic–Early Cretaceous interval. A new biogeographical marker is required to get a clearer picture.

**Location** Northern part of the Gondwana during the Middle Jurassic–Early Cretaceous interval.

**Methods** Comparisons and correlations of wood data from the literature and new material.

**Results** We have selected *Metapodocarpoxylon* Dupéron-Laudoueneix et Pons because it has a restricted distribution, temporally and geographically; it is a well-defined Mesozoic fossil wood monospecific genus, and there are wide-ranging data on its distribution.

**Conclusions** *Metapodocarpoxylon* distribution draws a clear latitudinal belt extending from Lebanon westward to Peru. Climate being the main factor of plant distribution at a global scale, the *Metapodocarpoxylon* area probably underlines a climatic belt. This has several implications, for example, choosing among different Global Circulation Models or discussing dinosaur distribution.

## Keywords

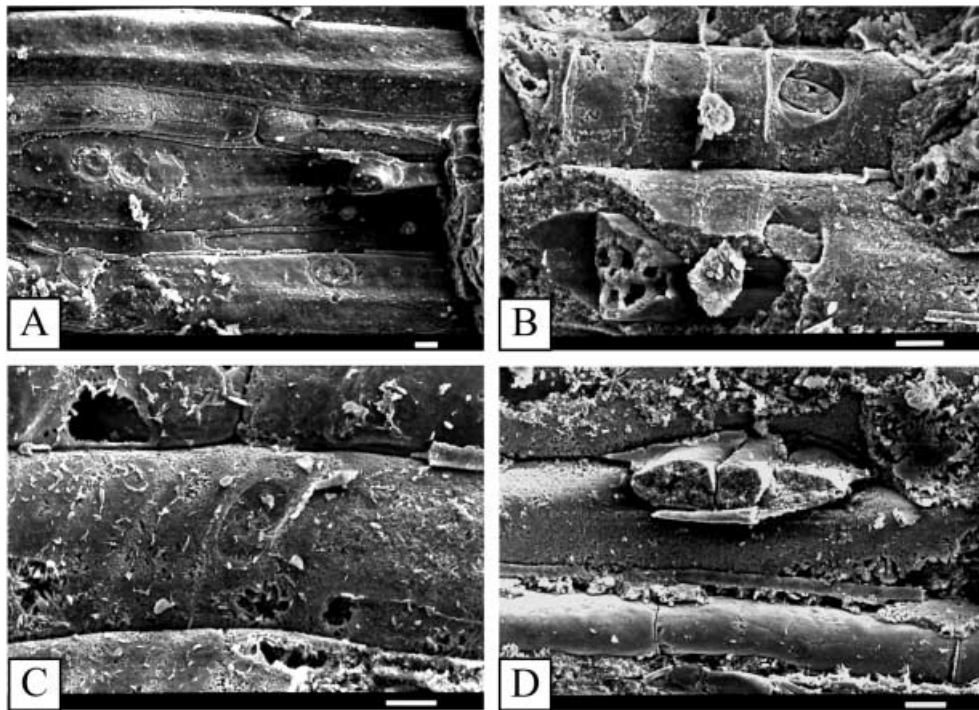
Palaeobiogeography, Gondwana, Mesozoic, fossil wood, conifers.

## INTRODUCTION

For a long time, the palaeobiogeography of the Jurassic–Early Cretaceous period has been considered as uniform, with little provincialism (e.g. Seward, 1903). Only in the 1960s did it become clear that various plant geographic provinces could be distinguished (Vakhrameev, 1964; Gócz

zan *et al.*, 1967; Hengreen, 1974). Hengreen & Chlonova (1981) proposed the microfloral provinces for the Cretaceous of Northern Gondwana. The West African–South American (WASA) microfloral province was succeeded by an African–South American (ASA) province, both of which have been well documented. However, the biogeography of Northern Gondwana for the Jurassic–Early Cretaceous interval is much less clear, if leaf imprints or dinosaurs are considered (Wolfen, 1979; Sereno *et al.*, 1994, 1998; Barale *et al.*, 2000; Chure, 2001). On the contrary, strong relationships with North America and Europe were, therefore,

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**Figure 1** *Metapodocarpoxylon libanoticum* xylological features in scanning electronic microscopy; sample MP860 from the Callovian of Oued Zefrat, Southern Tunisia; scale bar is 10 µm: (A) radial view – axial parenchyma, tracheid radial wall with araucarian and abietinean pitting; (B) radial view – ray with taxodioid oculipores in cross-fields; (C) radial view – ray with a large oopore; (D) tangential view – uniseriate low ray and axial parenchyma with smooth transverse wall.

evidenced. We decided to use fossil wood to tackle this question. Effectively, fossil wood is of interest insofar as it is much less mobile than pollen and vertebrates, and much more common and widely distributed in the geological record than leaf imprint floras. We chose the genus *Metapodocarpoxylon* because it is among the most frequently recorded wood for the area and time interval, it runs from the Bathonian up to the Albian, and its distribution is centred on Northern Gondwana (Dupéron-Laudoueneix & Pons, 1986; Dupéron-Laudoueneix, 1991a; Dupéron-Laudoueneix & Dupéron, 1995; Philippe, 1995). Moreover, it is suitable to address the question of the biogeography of Northern Gondwana in the Middle Jurassic–Early Cretaceous time interval.

The genus *Metapodocarpoxylon* was proposed by Dupéron-Laudoueneix & Pons (1986). It is based on a type previously determined as *Mesembrioxylon libanoticum* by Edwards (1929), a wood originating from the Neocomian of Lebanon. Together with the type-slides, Dupéron-Laudoueneix & Pons (1986) also reviewed several woods that had been previously published under various names, and concluded that they were building a taxon well enough characterized xylologically to deserve generic naming. All these woods were grouped under the same species name, *M. libanoticum* (Edwards) Dupéron-Laudoueneix et Pons. Despite a small nomenclatural problem, the genus and the species can be considered as validly published (Bamford & Philippe, 2001). In 1970, Lemoigne included the generotype

in his new morphogenus form-genus *Embergerixylon*. As no type was designed for his new genus (Lemoigne, 1968), it is nomenclaturally invalid (Philippe, 1993). *Embergerixylon* is not well supported by biogeographical evidence. To date, the genus *Metapodocarpoxylon* is monospecific. Its xylological features are illustrated in Fig. 1.

Further data (published and unpublished) have recently improved our knowledge of the distribution area of *M. libanoticum*. It has become clear that its distribution is of biogeographical interest. Therefore, we performed a survey and present the findings in this article. The inferences that come out are relevant in the discussion of biogeographic and palaeoclimatic maps of Northern Gondwana for the Middle Jurassic–Early Cretaceous period. The analysis questions the observed similarities between North American and North African dinosaur fauna for this period (Serenó *et al.*, 1994, 1998).

## DATA AND RESULTS

Data are compiled from literature. Furthermore, we include in this study a number of previously unpublished data that significantly improve knowledge of the distribution area for *Metapodocarpoxylon*. We are aware, however, that both Africa and South America are not well known as a whole from a palaeoxylological point of view. Another bias is that before the recognition of *Metapodocarpoxylon* in 1986, some

woods actually belonging to this taxon may have been assigned to other morphogenera like, e.g. *Protophyllocladoxylon* Kräusel. Amazingly, the generotype of the later genus itself is very similar to *Metapodocarpoxylon libanoticum*, a fact already underlined by Kräusel (1939, p. 18) and Dupéron-Laudoueneix (1991b, p. 395). A complete survey of all the Mesozoic gondwanan wood-type materials would be necessary to avoid the bias generated by incorrect generic attribution, but as these types are scattered world-wide this is almost an impossible task. With regard to this bias, as a precaution we performed a detailed bibliographical survey of all the Gondwana wood data for the Late Jurassic–Early Cretaceous period (Bamford & Philippe, 2001). The most troubling question is – does *Metapodocarpoxylon* occur in the India and Madagascar plates? For the latter the wood record is very limited (Fliche, 1900, 1905). For the former, however, despite a quite good wood record (Sahni, 1931; Bhardwaj, 1953; Jeyasingh & Kumarasamy, 1995), nothing clearly ascribable to *Metapodocarpoxylon* has ever been mentioned. In addition, special attention was paid to the southern Africa Early Cretaceous wood record (Bamford & Corbett, 1994; Bamford & Corbett, 1995; Bamford & Philippe, 2001; Bamford *et al.*, 2002; Bamford & Stevenson, 2002). Nothing has been found there that could be related to *Metapodocarpoxylon*.

As the geological framework is quite intricate, at least for the westernmost range of the distribution of the wood genus, and still a matter of debate, we prefer to refer to the classical synthesis given by Andrieux *et al.* (1989) and Delfaud & Zellouf (1995). The geology of our new data from Peru and Ecuador is described by Shoemaker (1982) and Jaillard *et al.* (1998). The age of the holotype is given as uncertain (may be Upper Jurassic or Lower Cretaceous; Edwards, 1929, p. 401). It probably belongs to the 'Grès lignitifères', which have been attributed to the Valanginian–Hauterivian (Bischoff, 1990; Noujaim Clark & Boudagher-Fadel, 2001). We have found the genus in this level in Beskintaa, Lebanon (see data MP1181 below). The geological context of most African data is described by Lefranc & Guiraud (1990).

Before considering the biogeography we had to sort out the taxonomy and type material. According to Paul Davis (pers. comm.), the holotype, presented by Prof. A.E. Day in October 1926, is still at the British Museum of Natural History, with seven slides instead of five as indicated by Edwards (LV20497d, b, c, g and f radial sections, LV20497a cross-section and LV20497e tangential section). The illustration by Edwards is limited (based on V20497a and c), but good illustrations of the type can be found in Lemoigne (1970, Plate 2, Figs 1–8), who erroneously attributed it to the Holden collection, Dupéron-Laudoueneix & Pons (1986, Figs 1–16) and Dupéron-Laudoueneix (1991b, Figs 1–4), all of them under light microscope. Scanning electronic microscopy of a Tunisian sample of *Metapodocarpoxylon libanoticum* is illustrated in Barale *et al.* (1998, Plate, Figs 5–8).

### Review of bibliographical data

*Metapodocarpoxylon* has been quoted from various localities. Bibliographical data are summarized in Table 1.

### New data

Investigations of numerous wood samples from Gondwana led to the recognition of several examples of *M. libanoticum*. Table 2 summarizes the presently unpublished data. While reviewing the syntypes for *Dadoxylon aegyptiacum* Unger 1858 in the Muséum national d'Histoire Naturelle in Paris (Unger 467–469), we found samples that could be related to *Metapodocarpoxylon*. Their preservation, however, is not quite good enough to challenge the present nomenclature.

Unfortunately, the age is not always accurately known for all these data. It is worth noting, on the other hand, that there is no field evidence suggesting that these undated samples may have originated from outside the Middle Jurassic–Early Cretaceous interval.

The data from France is surprising. The corresponding sample is a silicified piece of trunk found in a karstic resurgence, and thus completely exotic to its geological context. Moreover, this sample clearly displays the typical desert wind polishing. We, therefore, consider that this sample was displaced, probably a souvenir of former relationships between France and Northern Africa. The rest of the data are compiled in a distribution map (Fig. 2).

### Palaeoecological results

*Metapodocarpoxylon* is mostly found in coarse fluvial and estuarine deposits, more rarely in fine-grained sediments like black marls or continental red clays.

Field collection has allowed us to make some observations on *M. libanoticum* morphology and palaeoecology. At Merbah el Asfer, Tataouine area, Southern Tunisia, a trunk related to this species is 7 m long and 60 cm in girth at both tips. Similar sizes have been observed for trunks in the Bayuda desert, Sudan, and in Southern Libya. At Nekrif, south of Remada, Tunisia, a *Metapodocarpoxylon* trunk reaches 23 m in length and 75 cm in girth at its base. The tree had a slender trunk, which is rather typical of a forest tree. In most localities throughout its range, numerous *Agathoxylon* logs are associated with *Metapodocarpoxylon*, making it probable that this association is not only a taphonomical one. In these localities, *Agathoxylon* trunks reach 25–30 m in length and 55–80 cm in girth. These are hints of a forest-like phytocoenosis, with closed canopy. Such forests are not encountered today, in the tropical zone, in areas with less than 1500–2000 mm of annual rainfall. According to Frakes *et al.* (1994, Fig. 2), all *Metapodocarpoxylon* localities had a mean annual temperature higher than 25 °C.

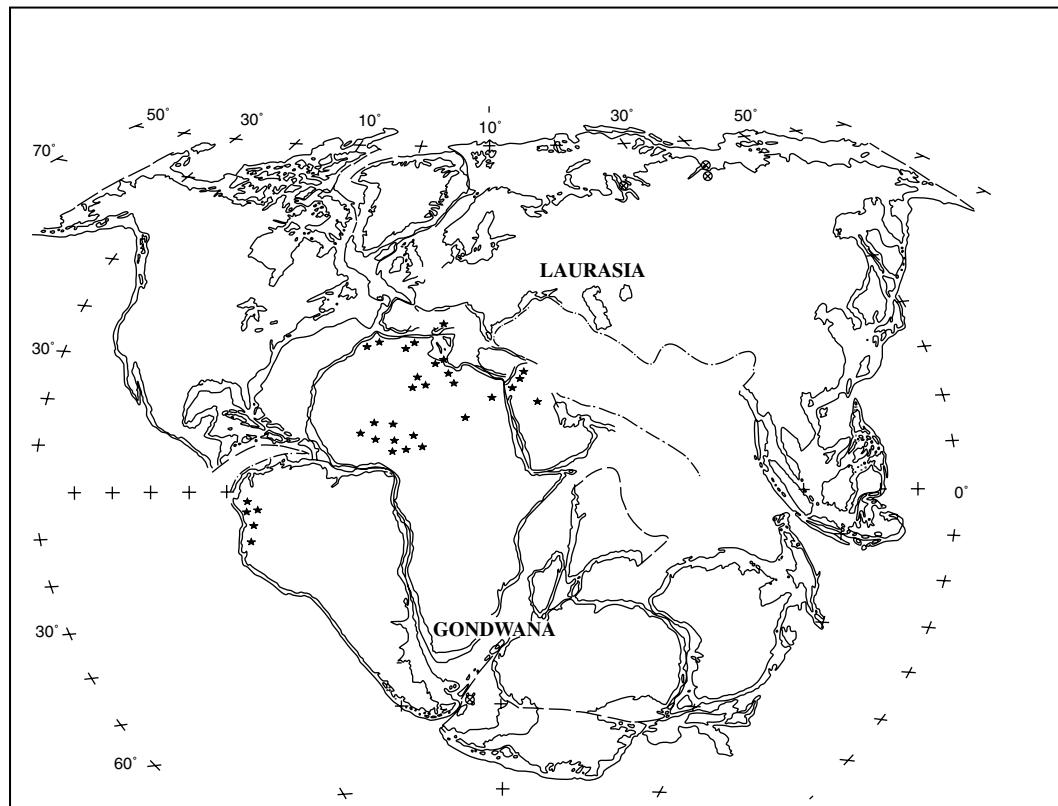
The growth rings have been analysed in samples from various origins. Their width ranges from 0.5–6 mm ( $n = 124$ ), which is quite low. Whilst the rings are always subtle with very small amounts of latewood (type E in Creber & Chaloner, 1984), this it is not always the case in the woods belonging to other genera encountered in the same localities. Skew values of the cumulative sum of deviations from mean radial diameter (CSDM) (Falcon-Lang,

**Table 1** Bibliographical data for *Metapodocarpoxylon libanoticum* Dupéron-Laudoueneix et Pons. Most synonymies are from Dupéron-Laudoueneix & Pons (1986)

Country	Age	References	Note
Algeria	Late Jurassic	Benest <i>et al.</i> (1998, 1999)	Identified by us
Cameroon	Early Cretaceous	Brunet <i>et al.</i> (1986, 1988, 1990), Flynn <i>et al.</i> (1987), Dupéron-Laudoueneix (1991a,b) and Dejax & Brunet (1995)	
Cameroon	Cretaceous	Dupéron-Laudoueneix (1976)	As <i>Protophyllocladoxylon subdiphthericum</i>
Colombia	Barremian/Aptian	Pons (1978, 1988)	As <i>Protophyllocladoxylon curitiense</i>
Colombia	Late Jurassic	Pons (1983, 1988)	As <i>Protophyllocladoxylon</i> sp.
Colombia	Aptian	Pons (1988)	
Egypt	Late Jurassic–Early Cretaceous	Youssef (2002)	As <i>Xenoxylon saadawi</i>
Italy	Aptian/Albian	Biondi (1980)	As <i>Protophyllocladoxylon aff. subdiphthericum</i>
Lebanon	Neocomian	Edwards (1929)	As <i>Mesembrioxylon libanoticum</i>
Mali	Early Cretaceous	Bamford <i>et al.</i> (2002)	Footnote, p. 164
Mali	Unknown	Dupéron-Laudoueneix & Pons (1986)	
Mali	Middle Jurassic–Early Cretaceous	Bellion <i>et al.</i> (1990)	
Morocco	Middle Jurassic–Early Cretaceous	Attims (1970)	As <i>Protophyllocladoxylon aff. libanoticum</i>
Morocco	Middle Jurassic	Gazeau (1970) and Gazeau & Koeniguer (1970)	As <i>Protophyllocladoxylon maurianum</i>
Morocco	Middle Jurassic	Dupéron-Laudoueneix & Pons (1986)	As <i>Protophyllocladoxylon chudeaui</i>
Nigeria	Early Cretaceous	Batton (1965)	
Tchad (Mayo-Kébbi)	'Middle' Cretaceous	Batton & Boureau (1965)	As <i>Protophyllocladoxylon diphthericum</i>
Tunisia	Late Jurassic	Barale <i>et al.</i> (1998)	
Tunisia	Early Cretaceous	Barale <i>et al.</i> (1998)	
Tunisia	Middle Jurassic	Barale <i>et al.</i> (2000)	

**Table 2** New data for *Metapodocarpoxylon libanoticum*

Sample number	Locality	Country	Age
MP651	Daïa Mountains	Algeria	Kimmeridgian
MP697	Makhtesh Ramon	Israël	Middle Jurassic
MP702	Makhtesh Ramon	Israël	Middle Jurassic
MP708	Makhtesh Ramon	Israël	Middle Jurassic
MP919	Messak	Lybia, 25°16'92/11°39'62	Middle Jurassic–Early Cretaceous
MP920	Messak	Lybia, 25°16'92/11°39'62	Middle Jurassic–Early Cretaceous
MP921	Messak	Lybia, 28°44'55/11°40'21	Middle Jurassic–Early Cretaceous
MP925	Hassi en Nahia	Lybia, 28°44'55/11°40'21	Middle Jurassic–Early Cretaceous
MP844	Sidi bel Abbès, Atlas	Algeria	Early Kimmeridgian
MP887	In'salha, NW of Tamenghest	Algeria	Unknown
MP990	Pont-d'Ain	France	Unknown
MP1032	Bir Miteur	Tunisia	Aptian/Albian
MP1038	Bayuda desert	Sudan, 17°30'/33°10'	Mesozoic
MP1050	Lancones	Peru	Early Albian
MP1073	Puyango	Ecuador	Early Albian
MP1076	Puyango	Ecuador	Early Albian
MP1077	Puyango	Ecuador	Early Albian
MP1085	Hoggar	Algeria	Mesozoic
MP1086	Hoggar	Algeria	Mesozoic
MP1087	Hoggar	Algeria	Mesozoic
MP1088	Hoggar	Algeria	Mesozoic
MP1089	Hoggar	Algeria	Mesozoic
MP1139	Road Agadez – Tahoua	Nigeria	Aptian/Albian
MP1181	Beskintaa	Lebanon	Neocomian
MP1202	Gombe	Nigeria	Early Cretaceous
MP1306	Ad Dahna	Saudi Arabia	Early Cretaceous



**Figure 2** Data distribution for *Metapodocarpoxylon* Dupéron-Laudoueneix et Pons. World palaeogeographic map during the Early Cretaceous (anomaly M7, redrawn from Owen, 1983). The data range from the Middle Jurassic to the Early Cretaceous.

2000a) curves have been calculated for ten rings (Table 3), one ring of the holotype and three consecutive rings in three samples from Tunisia (Middle and Late Jurassic, Early Cretaceous). The rings were chosen as normal and well preserved. The average percentage skew is important, typical for E-type rings, with a relatively high standard deviation. Bearing the limitations given by Falcon-Lang (2000a) in

mind, there is a high probability that *Metapodocarpoxylon* was an evergreen conifer with a leaf retention time bracketed between 3 and 10 years.

## DISCUSSION

Except for the curious data from France, obviously a displaced specimen, all data are distributed on the northern part of Gondwana (Fig. 2). The distribution area stretched over the South Atlantic area to reach Colombia and Peru. Eastward and Northward, *Metapodocarpoxylon libanoticum* reached some microplates, the position of which is a matter of debate (Stampfli *et al.*, 1991; Bosellini, 2002): Italy, Neguev, Lebanon, Saudi Arabia. *M. libanoticum* has never been found north of the Tethys, although areas like Alps, Iberian Peninsula or Central America were quite close to the northern Gondwana border according to most palaeogeographic reconstructions (Stephan, 1990; Nairn *et al.*, 1995). In the course of this study, we also paid special attention to the Jurassic–Cretaceous wood assemblages of these areas. For the Alps we analysed more than seventy-four new specimens, mostly from south-western Alps, ranging in age from the Middle Jurassic to the Early Cretaceous, plus a dozen samples of wood from the Upper Cretaceous of that region, and performed a bibliographical survey. According to this unpublished screening, *Metapodocarpoxylon* has never been

**Table 3** Some features of selected growth-rings for *Metapodocarpoxylon libanoticum*

Sample	Ring width (mm)	Cell number	Percentage skew
Lebanon, Early Cretaceous	0.785	19	57.89
Tunisia, Middle Jurassic	0.811	21	-4.76
Tunisia, Middle Jurassic	0.756	18	22.22
Tunisia, Middle Jurassic	0.803	23	39.13
Tunisia, Late Jurassic	0.784	19	68.42
Tunisia, Late Jurassic	0.829	24	50.00
Tunisia, Late Jurassic	0.615	15	73.33
Tunisia, Early Cretaceous	0.825	23	39.13
Tunisia, Early Cretaceous	0.818	20	50.00
Tunisia, Early Cretaceous	0.794	19	68.42
Average	0.782	20.1	46.38
Standard deviation	0.063	2.73	23.95

found in the Alps, today just 400 km north of its northernmost locality in Italy (but in the Early Cretaceous Central Italy could have been as much as 3000 km away from the Tethys northern margin). The Iberian Peninsula has quite a good wood record for the Late Jurassic and Early Cretaceous (Boureau, 1949, 1951; Lemoigne & Marin, 1972; Barale & Viera, 1991; Diez *et al.*, 1996; del Nido *et al.*, 1998; Valenzuela *et al.*, 1998; Gomez *et al.*, 1999; Muñoz Barragán, 1999; Philippe, unpublished data). The Iberian Peninsula would have been quite close to Morocco during the considered time interval, probably no more than 100–300 km. For this area we studied fifty-seven new specimens from the Early Cretaceous of the Iberian Ranges, and never once encountered *Metapodocarpoxylo*. Central America is poorly known from the point of view of fossil wood (Person & Delevoryas, 1982). Turning to the sub-saharian Gondwana, *Metapodocarpoxylo* is not known in the areas with a reliable Middle Jurassic to Early Cretaceous wood record: Namibia (Bamford & Corbett, 1994, 1995; Bamford, 2000; Bamford & Stevenson, 2002; Bamford *et al.*, 2002), Tanzania (Kahlert *et al.*, 1999; Süß & Schultka, 2001), Ethiopia (Beauchamp & Lemoigne, 1971; Lemoigne *et al.*, 1971; Lemoigne & Beauchamp, 1972; material reviewed), Southern Chile (Philippe *et al.*, 2000), and Antarctica Peninsula (Philippe *et al.*, 1993a,b, 1995; Torres *et al.*, 1982, 1994, 1997, 1998, 2000; Falcon-Lang & Cantrill, 2000, 2001). This should not eclipse the fact that affinities between Northern and Southern Gondwana floras have been shown for the Early Cretaceous on the basis of leaf floras (El Chair *et al.*, 1995; Barale *et al.*, 1997). The distribution of the wood genus clearly draws a latitudinal belt, sandwiched between the palaeolatitudes 30° North and 15° South. The lack of data makes the southern limit of this range quite vague. As a climatic boundary probably took place across Africa (see below), new finds will probably not extend the range as south as the southern boundary of the ASA microfloral province (Herngreen & Duenas-Jimenez, 1990).

Stratigraphically data range from the Middle Jurassic (Bathonian and perhaps even Bajocian as there is some uncertainty about the age of Israel locality) to the Aptian. The time range of *M. libanoticum* crosses the Jurassic/Cretaceous (J/K) boundary. It has been shown (Philippe *et al.*, 1999) that there is minimal floristic turnover in Northern Gondwana at the J/K limit, and the persistence of a Jurassic species through the Early Cretaceous is not surprising. As the older data for the occurrence of *Metapodocarpoxylo* is Middle Jurassic in age in Africa and Late Jurassic in South America, the genus crossed the proto-South Atlantic during the Jurassic. Towards the end of the Jurassic, the formation of the South Atlantic began with the separation of southern South America and Africa. Deserts developed to the North of this rift from the Kimmeridgian into the Neocomian. As they expanded towards the equator, these deserts probably created a filter limiting intercontinental dispersal of terrestrial vertebrates (Novas, 1997; Goodwin *et al.*, 1999). However, the distribution of freshwater fishes indicates that communication between the two continents was still poss-

ible in the Early Cretaceous as the freshwater coelacanth *Mawsonia* is found in the 'Neocomian' of both Brazil and Niger, and the freshwater amiid *Calamopleurus* is found in the 'Neocomian' of Brazil and the Cenomanian of Morocco (Maisey, 2000). The presence of the freshwater crocodile *Araripesuchus* in both the Aptian of Niger and Brazil (Buffetaut, 1982) was also used to infer a complete opening of the South Atlantic later than the Aptian. However, a revision of '*Araripesuchus wegneri*' from Niger has recently demonstrated that this crocodile does not belong to the genus *Araripesuchus* (Ortega *et al.*, 2000). It is, nonetheless, very close to *Araripesuchus* and probably shares a pre-Aptian Gondwanic common ancestor with *Araripesuchus*. So, although the communication was probably closed by Aptian time, vertebrate distribution supports the possibility of biological exchange between Africa and South America during the Neocomian. There are no xylogenetic hints that Early Cretaceous *Metapodocarpoxylo* of South America became somewhat different from the African ones, and thus, there is no evidence of an allopatric evolution.

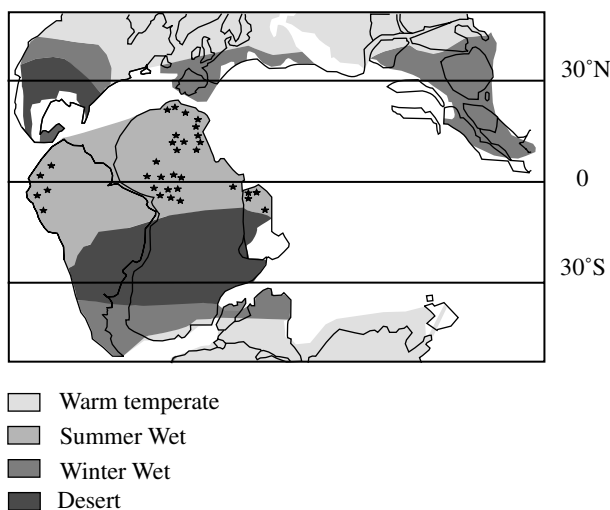
As *Metapodocarpoxylo* draws a clear latitudinal belt, and as climatic factors are the most determinant one for plant distribution at this scale, we make the hypothesis that the *Metapodocarpoxylo* distribution area fits with a climatic zone. Very few palaeoclimatic reconstructions, either from geological data or from general circulation models (GCM) (see, e.g. Moore *et al.*, 1992a,b; Valdes, 1993; Rees *et al.*, 2000; Sellwood *et al.*, 2000), draw a climatic belt that fits with the wood distribution. Even fewer reconstructions propose a palaeoclimatic map that could explain why *Metapodocarpoxylo* never managed to settle in North America and the Iberian Peninsula.

The problem is enhanced by the fact that other continental biotic components, i.e. dinosaurs or ferns, show a similarity between Europe, North America and North Africa during the Late Jurassic and Early Cretaceous. For example, the extreme similarity between *Suchomimus* from the Aptian of Niger and *Baryonyx* from the Barremian of Europe (Serenó *et al.*, 1998) favours a dispersal event across the Tethyan seaway during the Early Cretaceous. This is also supported by the similarity between the Nigerian theropod *Afrovenator* and the American *Torvosaurus* (Serenó *et al.*, 1994), the occurrence of the African theropod *Elaphosaurus* in the USA (Chure, 2001) or the recent find in the Albian of Morocco of the pelynomorph *Penetratites mollis*, previously known only from Southern USA (Bettar & Méon, 2001). The occurrence of the ornithischian *Valdosaurus* in the Lower Cretaceous of both Britain and Niger (Galton & Taquet, 1982) also supports this idea and Le Loeuff (1991) introduced an Afro-Euro-American palaeobioprovince for the Early Cretaceous. However, the sphenodontian and mammals described from the Berriasian of Morocco (Sigogneau-Russell, 1989, 1991a,b, 1992; Sigogneau-Russell *et al.*, 1990; Evans & Sigogneau-Russell, 1997) show peculiarities suggestive of a period of isolation from Euramerica, which would indicate that migrations between Euramerica and Africa were more difficult for small animals (sphenodontians, mammals) than for larger ones (dinosaurs).

However, the presence of the Euramerican lizard *Paramacellodus* in Morocco warns us against a too simplistic explanation. Eventually, another clue of biotic exchanges between North America and North Africa at this time is a fern, *Weichselia reticulata*, which has a large distribution encompassing both areas.

Relationships between Euramerica and Africa during the Early Cretaceous are suggested by numerous clues, but nevertheless show a complex pattern. The distribution of *Metapodocarpoxylon*, which indicates a climatic barrier between Africa and Euramerica in addition to a geographical barrier represented by the Tethys, suggests that biotic exchanges between these two landmasses during the Early Cretaceous were limited to taxa able to adapt themselves to various climatic conditions. The dinosaur faunas also show similarities between Africa, Europe and North America during the Late Jurassic with the presence of *Elaphrosaurus* in North America and Tanzania (Chure, 2001) and the presence of *Allosaurus fragilis* in North America and Portugal (Perez-Moreno *et al.*, 1999).

The different simulations of past climate with GCMs give quite different palaeoclimatological maps for the Mesozoic (Moore *et al.*, 1992a,b; Sellwood *et al.*, 2000). Among these, only a modelling experiment runs with Late Jurassic boundary conditions and, using the UK Meteorological Office GCM (UKMO) by Sellwood *et al.* (2000), gives maps on which all the *Metapodocarpoxylon* data are in the same climatic zone (i.e. same mean surface air temperature and same annual mean precipitation). The palaeoclimatological maps given by Rees *et al.* (2000), compiled from geological and paleontological data, are also of great interest. Effectively, these maps would also put the *Metapodocarpoxylon* data in one climatic zone only, described as summer-wet (Fig. 3). Interestingly, the Iberian Peninsula and part of Northern America are given as winter-wet, while a summer-wet climate is inferred for the *Metapodocarpoxylon* range. It



**Figure 3** *Metapodocarpoxylon* distribution on a palaeoclimatological map given by Rees *et al.* (2000).

could have been that not only the amount of annual rainfall, but also its distribution within the year influenced the distribution of *Metapodocarpoxylon*, whereas this might not have been the case for other biotic elements (e.g. dinosaurs or ferns) of this biocoenosis. Both autecological and synecological data assert that *Metapodocarpoxylon* was not a tree growing under arid climate. Hadley cell could have been a feature of atmospheric circulation of that time, determining the existence of a low-latitude climatic belt, but our data temper the aridity inferred by Fenner (2001).

*Metapodocarpoxylon* was probably a forest tree, growing in coniferous forest together with *Agathoxylon* trees. As large logs growing inland would have little probability of being deposited in fluvial systems in great numbers, we think that this forest type colonized alluvial plains. The usual narrowness of its growth rings indicates a slow growth. Such growth is encountered for trees growing in poor conditions (dry, cold) and for trees growing under strong competition (dense forests), but also sometimes for conifers growing with little stress (Brison *et al.*, 2001). Present-day riparian and hygrophytic coniferous trees, like *Taxodium distichum* and *Glyptostrobus pensilis* do not display particularly thick rings. It is, thus, difficult to interpret growth-ring width, the most defensible inference being that *Metapodocarpoxylon* was probably not a quick growing colonizer. *Metapodocarpoxylon* logs are rarely associated with leaf floras that could allow synecological inferences. In Tunisia, the wood is associated with the Merbah el Asfer flora (Barale *et al.*, 1998) and in Ecuador with the flora of Ciano Formation (Shoemaker, 1982). Both are diversified, with a mixture of ferns and conifers, with cycadeoids in Ecuador. According to Lefranc & Guiraud (1990), the silicification of wood, a common feature of *Metapodocarpoxylon*-related fossil woods, occurred mainly in trophile forests. The low growth ring markedness and strong right skew of CSDM curves are probably related to a long leaf-retention time (Falcon-Lang, 2000a,b). To sum up, *Metapodocarpoxylon* (Podocarpaceae?) probably built evergreen trophophilous forests in alluvial plains together with *Agathoxylon* (Araucariaceae) under a summer-wet climate.

## CONCLUSIONS

*Metapodocarpoxylon* is a wood morphogenus endemic of Northern Gondwana, ranging over the Middle Jurassic–Early Cretaceous period. There are few fossil taxa that are really endemic of the Northern Gondwana margin, and thus *Metapodocarpoxylon* is an interesting marker. Its distribution is also of biogeographical interest as it draws a clear latitudinal belt. This distribution fits with the northern part of WASA and ASA provinces proposed by Herngreen (1974) and Herngreen & Duenas-Jimenez (1990) on the basis of the palynological record. This is an important result as the meaning of these palynological provinces for continental biota as a whole was questioned by the data from dinosaurs and leaf imprints. *Metapodocarpoxylon* distribution points out that Jurassic–Early Cretaceous continental fauna and flora of Northern

Gondwana may have had different biogeographical histories. For the Mesozoic as for the Holocene (Birks & Birks, 2000), plant macrofossils can enhance the information from pollen analysis.

The distribution of this wood helps in the discussion of the biogeographical relationships of some microplates within the Tethys. Italy, Neguev and Lebanon had, at least for the Late Jurassic–Early Cretaceous interval, a typically North Gondwanan biota element. Further, *Metapodocarpoxyton* is also pertinent to the discussion of the palaeoecology of its distribution range. It belonged to a forest biota, and probably built a closed canopy together with *Agathoxyton* trees.

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## BIOSKETCHES

Integrating the fossil evidence from the different sections of the biosphere the authors have explored the continental biogeography of the Mesozoic. This is based essentially on plant macrofossils (fossil woods, **M. Bamford** and **M. Philippe**; leaf impressions and compressions, **G. Barale**, **F. Thévenard** and **M. Thiébaud**), as well as the vertebrates (**G. Cuny**). In order to reduce the bias from the nature of fossil preservation, and to increase the accuracy, the authors have included stratigraphic studies (**E. Jaillard**), biogeography (**P. von Sengbusch**), sedimentology (**M. Ouaja**) and taphonomy (**B. Gomez**). The ultimate aim is to produce a biogeographical model to understand the role of external forces in the evolution of continental plants.