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Are Mesozoic wood growth rings climate-induced?

Anne-Lise Brison, Marc Philippe, and Frédéric Thevenard

Abstract.—Growth rings of Mesozoic fossil woods have often been used for paleoclimatological inferences. Most of the studies, however, rest upon uniformitarian deductions based on the observation of conifers from the present boreal temperate realm, whereas warm climates dominated during the Mesozoic. We propose a new approach, based on the study of the distribution of growth ring types among 643 samples from the Jurassic–Cretaceous interval. A clear picture emerges from analysis, consistent with what is known of Mesozoic climates from other sources. Woods with no rings are encountered in a wide latitudinal zone, extending up to 75°N and 65°S during the Late Cretaceous. Woods with well-developed latewood do not occur at low latitude and disappeared from the Northern Hemisphere during the Late Cretaceous. Our data set also shows that the taxonomic distribution of growth ring types is not regular. Among the genera encountered, 40% can build only one type of ring. The genus *Agathoxylon* never displays thick latewood, although it ranges from 75°S to 70°N. This demonstrates that growth ring studies must include a taxonomic analysis.

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Introduction

For the Quaternary, growth ring analysis has proved to be a powerful tool in the field of paleoclimatology, at least in the cool temperate realm (Antevs 1916; Cook 1987; Ash and Creber 1992). However, wood anatomists concerned with xylogenesis in warm climates have long been puzzled by incoherent growth ring patterns (Jacoby 1989; Worbes 1995, 1999; Borchert 1999) and emphasize the role of genetic regulation (Tomlinson and Longman 1981; Savidge 1996). Even for the Mesozoic, fossil wood rings have been considered a reliable record of climatic variability (Hallam 1998), although “hothouse” conditions prevailed on Earth (Frakes et al. 1992; Rees, Rowley, and Ziegler at <http://plates.uchicago.edu/>). Most recent analyses of Mesozoic wood rings (e.g., Francis 1984, 1986; Parrish and Spicer 1988; Spicer and Parrish 1990; Yadav and Bhattacharyya 1994; Keller and Hendrix 1997; Brea 1998; Morgans 1999; Morgans et al. 1999) have applied the mean sensitivity method (Fritts 1976), yet its straightforward application to Mesozoic woods is inappropriate given what is known about both the growth of extant tropical trees (Jacoby 1989)

and the variability of tropical climates (Pfefferkorn 1995).

We have developed another method to analyze tree growth during the Mesozoic. For that we looked at the geographical and taxonomic distribution of the growth ring types defined by Creber and Chaloner (1984) and illustrated in Figure 1. We based this study on an analysis of a large wood assemblage in order to limit the possibilities of bias. We tried to make inferences only from distribution patterns on a global scale, with as few inductions as possible from the present.

Material and Methods

We analyzed growth rings of 643 samples, originating from 181 Mesozoic localities scattered on five continents (Fig. 2). The data were mainly taken from the literature, when the growth ring pattern was well enough described (the list of the 179 references used is available on request). In addition, 55 samples originated from a wood slide collection kept in the Laboratoire de Paléobotanique of Lyon-1 University. Within the Mesozoic only the Jurassic and the Cretaceous were considered, as the Triassic had quite a different paleogeography and paleoclimate. After the important

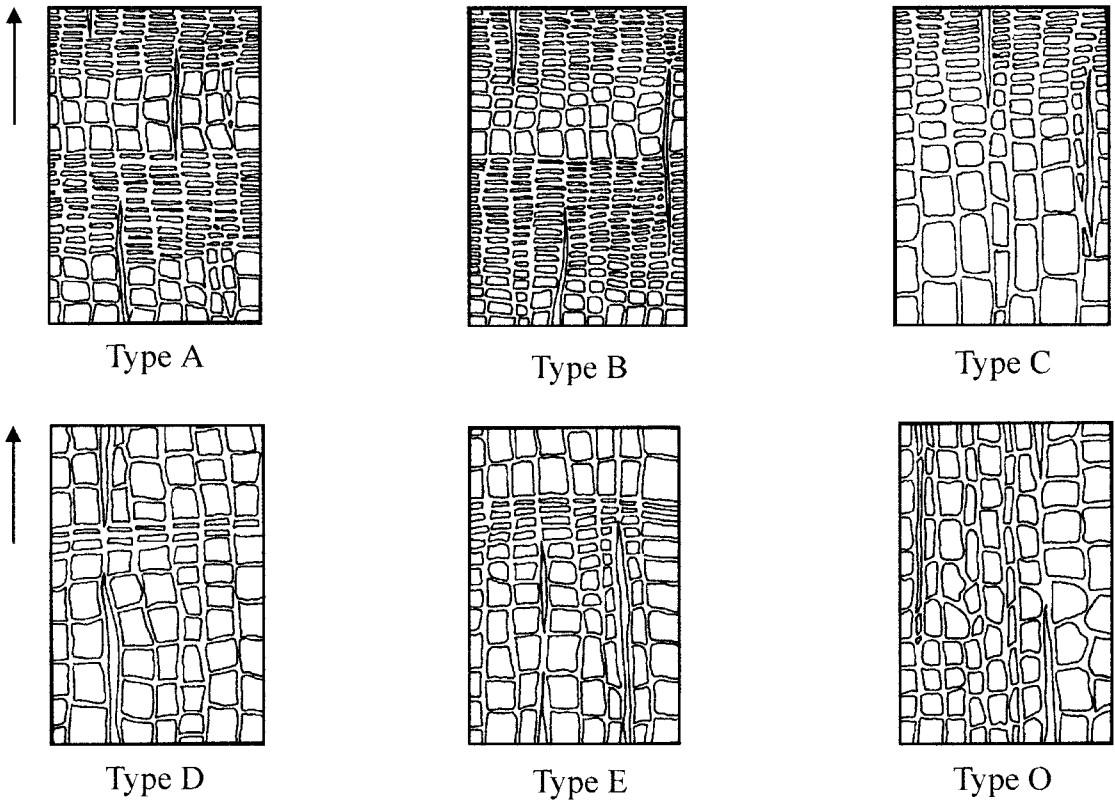


FIGURE 1. An illustration of the six growth ring types devised by Creber and Chaloner (1984) to categorize different earlywood/latewood relationships. Type A: rings without much earlywood; sharp transitions at the earlywood/latewood boundaries. Type B: rings with a wide band of latewood; the transition to latewood is more gradual. Type C: rings with a very gradual transition from earlywood to latewood; rings indicate growth in an environment with only gradual change during the growing season. Type D: rings with a thin band of latewood; earlywood/latewood boundary well marked. Type E: rings similar to type D, but the transition to latewood is not so sharp. Type O: rings resulting from a situation where all the requirements for growth are constantly present; no noticeable change in the tracheid diameter. The arrow indicates growth direction.

biotic crisis that occurred on land at the end of the Triassic (Philippe et al. 1999a), continents were colonized by new types of vegetation (Vakhrameev 1991), although the general distribution pattern in latitudinal zones was maintained (Krassilov 1994). With regard to trees, conifers of extant families dominated, together with trees of the now-extinct Cheirolepidiaceae (Alvin 1982). Prespermatophyta were also widespread at this time, but among them apparently only Ginkgoales had a thick wood. These, as far as we know, do not differ from conifers in their cambial activity (Schultze-DeWitz et al. 1988; Süß 1988).

For every sample the following was gathered: fossil identification at generic level, growth ring type, paleolatitude, presence/ab-

sence of false rings, and ring width. However, samples lacking only one of these elements were used when possible ($n = 80$).

For generic names, several published records have had to be taxonomically revised to integrate all data into a consistent taxonomic framework. Our taxonomical positions have been described in previous works (see, e.g., Philippe 1993, 1995; Philippe et al. 1999b; Bamford and Philippe 2001). For data from the literature, when there was a discrepancy between description and illustration in the type of growth ring, the latter was followed. In the rare cases where two types of growth rings were observed in the same sample, the most frequent one was used (it always represented more than 90% of the rings). Determining

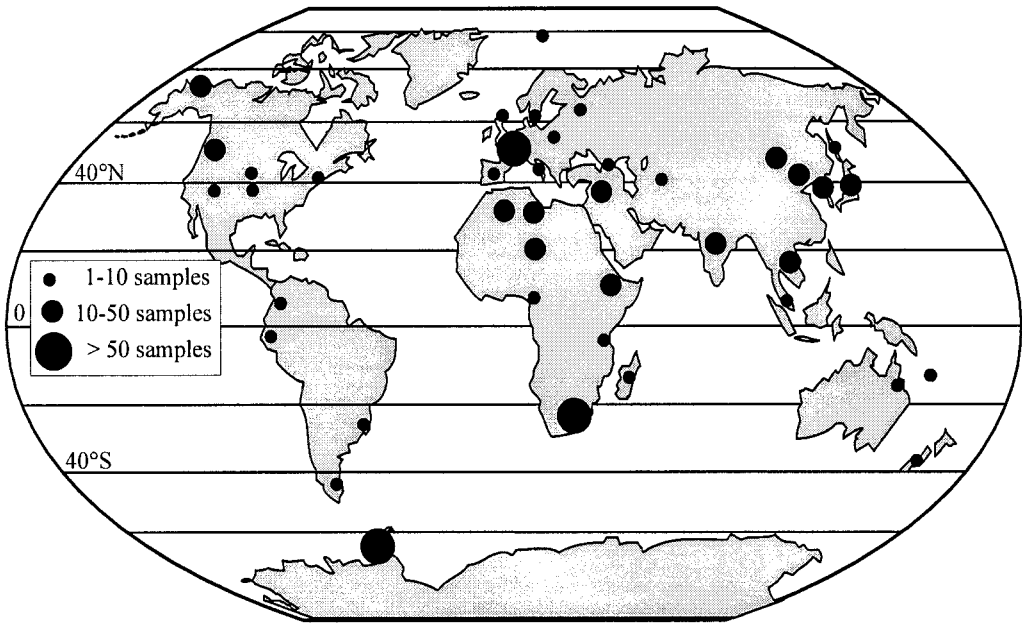


FIGURE 2. Map showing the distribution of the samples.

type O (growth rings absent) is difficult because the samples are sometimes quite small. We chose 200 cells without any significant radial-diameter variation as a threshold above which the sample is considered as belonging to the O type. Distinguishing between types E and D, and between types A, B, and C, regularly proved to be difficult. We thus clustered, for some analyses, the six basal types into three supertypes only, namely (A,B,C), (D,E), and O, on the basis of their latewood content. These supertypes cannot be used to consider the earlywood to latewood transition, because in this respect B, C, and E are grouped together.

Paleolatitude was determined from three

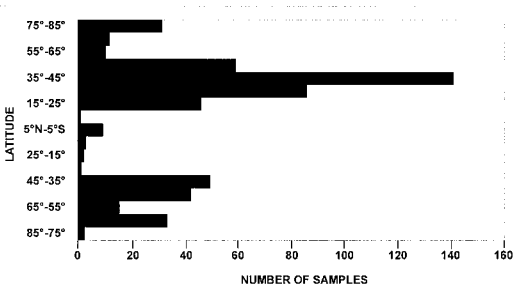


FIGURE 3. Histogram showing the number of samples per paleolatitudinal classes.

sources (Barron et al. 1981; Ricou 1994; Smith et al. 1994) and averaged. Paleolatitudes were placed in 17 classes, each spanning 10° , in order to minimize the bias induced by plotting error on maps, an error estimated to $\pm 2^\circ$, and the bias linked to postmortem transport. The samples we analyzed correspond to axes with a diameter ranging from 2 cm to 50 cm. We avoided smaller axes because rings in these can be quite atypical.

Results

Out of 643 samples, 555 were well enough preserved for taxonomic determination. These samples correspond to 30 morphogenera. The entire Jurassic–Cretaceous interval is covered, with data from the Hettangian to the Maastrichtian. Samples are regularly distributed in the periods considered, with 3.9 samples/Myr for the Jurassic, 4.6 samples/Myr for the Early Cretaceous, and 3.5 samples/Myr for the Late Cretaceous. The paleolatitudes extend from 85°S to 85°N , with two peaks centered on the middle latitudes of both hemispheres (Fig. 3).

Growth Ring Types versus Taxonomy.—To limit bias, we considered only the morphogenera represented by at least ten samples. Results are given in Table 1. Type O is displayed by

TABLE 1. Distribution (in number of samples) of the growth ring supertypes for the wood morphogenera considered. An asterisk indicates morphogenera with rings belonging to one supertype only.

Morphogenus	Growth ring type		
	(A, B, C)	(D, E)	O
<i>Agathoxylon</i> Hartig	0	70	45
<i>Brachyoxylon</i> Hollick et Jeffrey	0	14	3
<i>Cupressinoxylon</i> * Göppert	0	34	0
<i>Protocupressinoxylon</i> Eckhold	1	26	1
<i>Metapodocarpoxyton</i> Dupéron-L. et Pons	0	4	9
<i>Phyllocladoxylon</i> * Gothan	0	18	0
<i>Protopiceoxylon</i> Gothan	2	11	0
<i>Podocarpoxyton</i> Gothan	0	45	2
<i>Protopodocarpoxyton</i> * Eckhold	0	74	0
<i>Simplicioxylon</i> Andreanszky	0	9	4
<i>Taxodioxyton</i> * Hartig	0	13	0
<i>Xenoxylon</i> * Gothan	0	44	0
Total	3	362	64

only half the genera. Ring types D and E are dominant, and all the genera considered can produce them. Only *Protopiceoxylon* woods build a significant amount of (A,B,C) growth ring types, and only *Protocupressinoxylon* displays rings of all the three supertypes. Five out of 12 genera can build rings of only one supertype.

Growth Ring Types versus Paleolatitude.—When studying these relationships, we distinguished three different time periods, as the paleobiogeography in each case is quite different: the Jurassic, the Early Cretaceous, and the Late Cretaceous. For the Jurassic (Fig. 4) the absence of growth rings (i.e., the occurrence of type O) extended from 45°S to 55°N. The (A,B,C) supertype is encountered only south of 45°S or north of 25°N. During the Early Cretaceous the figure is quite similar (Fig. 5). Type O is more frequent, counting for more

than 70% of some low-latitude wood assemblages. The distribution of the (A,B,C) supertype is not obviously different from the one observed for the Jurassic. The Late Cretaceous shows quite a different pattern (Fig. 6). The (A,B,C) supertype disappears from the Northern Hemisphere and type O rings are encountered in a much wider latitudinal zone (65°S–75°N). For all three time periods considered, the (D,E) supertype is widely distributed.

Late Cretaceous data are too sparse to analyze the nature of the earlywood to latewood transition. For the Jurassic and Early Cretaceous results are similar and data from both periods have therefore been combined (Fig. 7). The “progressive” woods, i.e., those with a progressive transition from earlywood to latewood—types B, C, and E—are encountered at mid-latitudes for both hemispheres, occurring

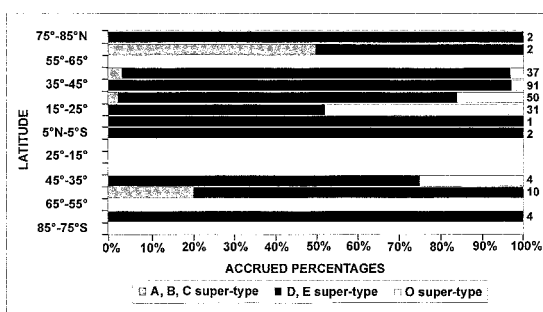


FIGURE 4. Distribution of the growth ring supertypes as a function of the paleolatitude during the Jurassic. Latitudinal bands with no bar: no data available. On the right, number of samples per latitudinal class.

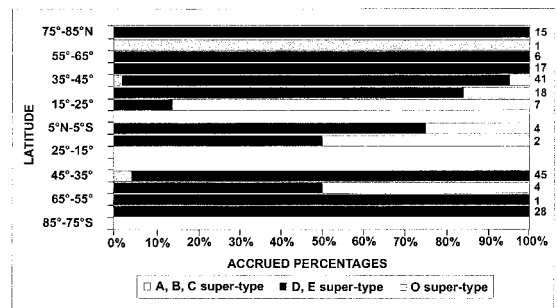


FIGURE 5. Distribution of the growth ring supertypes as a function of the paleolatitude during the Early Cretaceous. Latitudinal bands with no bar: no data available. On the right, number of samples per latitudinal class.

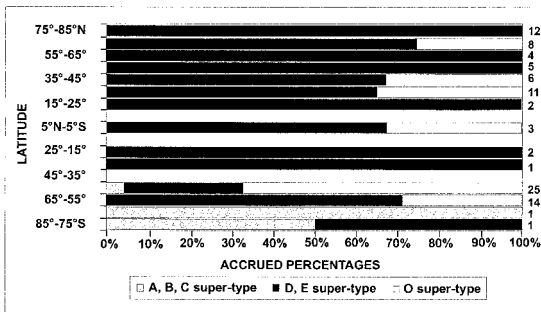


FIGURE 6. Distribution of the growth ring super-types as a function of the paleolatitude during the Late Cretaceous. Latitudinal bands with no bar: no data available. On the right, number of samples per latitudinal class.

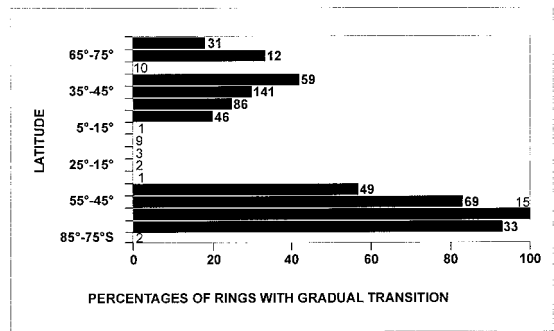


FIGURE 7. Percentages of rings with gradual transition from earlywood to latewood within well-marked rings as a function of the paleolatitude. Samples from Jurassic and Early Cretaceous are combined. Numbers indicate sample size.

with a higher frequency in the Southern Hemisphere.

To sum up, the data set clearly shows that (1) the O type is always encountered in a latitudinal band centered on the Equator, which is much broader in the Late Cretaceous; and (2) the (A,B,C) super-type is confined to the high latitudes and disappears from the Northern Hemisphere during the Late Cretaceous.

False Rings and Ring Widths.—False growth rings have been noted, but no clear trend arose from the analysis. They can occur with all growth ring types. The relationship between growth ring width and ring types is not clear, except in the trivial case of the O ring type. In environments with no apparent limiting factors, extant conifers may still build very narrow rings. For example, *Lagarostrobus franklinii* (Hook f.) Quinn from Tasmania has a slow growth despite an unlimited water availability (Enright and Hill 1995). On the reverse, in cold temperate regions trees such as *Pseudotsuga menziesii* (Mirbel) Franco may display rings thicker than 1 cm (Kort and Baas 1997). This suggests that growth ring width is not related to latitude in as simple a way as has been previously supposed (Creber and Chaloner 1985).

Discussion

A ring-type method might seem inappropriate for the analysis of growth rings, because within a given tree ring types are quite different at root, trunk, or branch level (Conwentz 1880; Felix 1882; Chapman 1994). The

analysis at a global scale of wood assemblages allows us to partially avoid the problem if a significant trend emerges from the data. If no clear picture comes out of the data set, however, samples have to be analyzed one by one. In this case it is almost impossible to split apart the environmental signal and the variance due to endogenous factors like systematic position, developmental stage, and position within the plant.

The distribution pattern of growth ring type at a global scale clearly shows here a climatic effect. Nevertheless, this distribution is also pro parte correlated with wood taxonomy. It is meaningless to draw inferences from the presence of E type rings, which are common in Mesozoic wood-ring studies (e.g., Keller and Hendrix 1997), if the considered wood morphogenera can only build this type of ring, as for example *Cupressinoxylon* or *Protodocarpoxydon*.

The distribution of growth ring type is consistent with what may be expected from a logical analysis. Continuous growth is absent from the polar regions, which always experienced long periods of darkness. Rings with a gradual transition from earlywood to latewood are logically encountered mainly in the middle latitudes of both hemispheres, where climatological models predict the occurrence of temperate climate (Valdes 1993).

Agathoxylon, the most common wood morphogenus in the Mesozoic record, is distributed from 75°S to 70°N latitude. In spite of its wide latitudinal distribution it never displays

rings of the (A,B,C) super-type, even when other woods from the same locality do. Extant Araucariaceae with *Agathoxylon*-type wood also never display these A, B, or C types (see, e.g., Seitz and Kanninen 1989), even when growing in clearly seasonal climates. Several species of Araucariaceae live under climates that are seasonal in temperature and/or rainfall. *Araucaria araucana* (central Chile and Argentina, ~40°S), *A. angustifolia* (Brazil and Argentina, 15°–30°S), *A. cunninghamii* (New Guinea–New South Wales, Australia), and *Wollemia nobilis* (New South Wales, 35°S) can withstand frost, and the first-mentioned species survives temperatures as low as –20°C. *Agathis ovata* (New Caledonia), *Araucaria angustifolia*, and *A. ruleii* (New Caledonia) grow in areas with a marked dry season. Some fossil Araucariaceae, such as *Agathoxylon* found in the Tertiary of South Shetland Islands at paleolatitude 65°S (Torres et al. 1984), must have lived in areas with strongly seasonal light. In spite of living under highly seasonal climates, none of these species has thick latewood. We hypothesize that this family lacks the ability to make rings of the (A,B,C) super-type and suggest that climatic and ecological conclusions should not be based on the absence of this supertype in *Agathoxylon*.

A circumpolar genus can never have continuous growth (type O), as the winter light minimum always induces a physiological stop (Chaloner and Creber 1989; Francis et al. 1994). The genus *Xenoxylon* gives only the (D,E) supertype of rings, but because of its circumpolar distribution (Philippe and Thévenard 1996), we cannot know if the lack of type O in this genus reflects genetically determined growth or environmental conditions.

The data set shows that during the Late Cretaceous the O type occurred over a much broader latitudinal band and the (A,B,C) supertype disappeared from the Northern Hemisphere. That means that the climatic belt with low seasonality was probably broader, and that the global climate was probably warmer. Previous authors have noted that the Late Cretaceous was relatively warmer (e.g., Frakes et al. 1992; Herman and Spicer 1996), but our data demonstrate this independently, with little uniformitarianism.

Impressive studies on extant conifers recently demonstrated that phylogenetic factors may be preeminent in controlling growth ring markedness and anatomy (Falcon-Lang 2000a,b) and that variables like ring width may show no significant relationships with climatic data (Wimmer and Grabner 2000). Falcon-Lang (2000a) found that the greater the leaf longevity (a parameter largely under genetic control), the more weakly developed are the growth rings in the wood. This finding ties in with our results and reinforces the idea that paleoecological studies should not deal with isolated samples.

Conclusion

Growth ring types in Mesozoic wood were not determined by environmental factors alone. The genera *Cupressinoxylon*, *Phyllocladoxylon*, *Protopodocarpoxylon*, *Taxodioxylon*, and *Xenoxylon* can build rings of only one type. The last is unique among these, being circumpolar, but the others are probably strongly genetically controlled in their growth. The common genus *Agathoxylon* never has thick latewood, and its growth rings should be interpreted with caution.

Our results show that a paleoclimatological analysis of the ring types has to be based on large and taxonomically diverse assemblages. Our method using growth ring type looks promising, and we can envisage applications at a more local scale, either geographic or temporal.

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