Silicified angiosperm wood from the Dangu locality (Ypresian of the Gisors region, Eure, France) – final part: the problem of palaeoclimate reconstruction based on fossil wood

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ABSTRACT

The systematic part of the study of the Dangu locality, dealing with angiosperm wood, is completed. In addition to three previously described types (two species), two others (*Dichrostachyoxylon* cf. *zirkelii* and *Anogeissus* sp.) are described. A new combination *Dichrostachyoxylon sahabiense* (Louvet) n. comb. is proposed. The locality as a whole reflects a specific climatic regime, corresponding approximately to the paratropical rain forest. Most broadleaved trees and palms grew on riverbanks under favourable microclimate. Conifers and *Anogeissus* were more distant from surface waters, probably on uplifted terrain, exposed to seasonal dry periods. Proximity of a lagoon is suggested. Regarding the palaeoclimate reconstruction based on fossil wood in general, two main problems have been encountered: intraspecific and individual variability of non-ecological significance, and insufficient number of fossil wood types necessary for statistical methods.

KEY WORDS
Paris Basin,
lower Ypresian,
silicified angiosperm wood,
palaeoclimate reconstruction.

RÉSUMÉ

Bois silicifiés d'angiospermes du gisement de Dangu (Yprésien de la région de Gisors, Eure, France) – dernière partie : le problème de la reconstitution paléoclimatique basée sur le bois fossile.

L'étude systématique du gisement de Dangu, traitant du bois d'angiospermes, est complétée. Aux trois types (deux espèces), décrits précédemment, deux autres sont ajoutés (*Dichrostachyoxylon* cf. *zirkelii* et *Anogeissus* sp.). Une nouvelle combinaison *Dichrostachyoxylon sahabiense* (Louvet) est proposée. Le gisement présente dans l'ensemble un régime climatique spécifique, similaire à celui rencontré en forêt paratropicale humide. Feuillus et palmiers poussaient sur les rives des cours d'eau, sous micro-climat favorable. Conifères et *Anogeissus* étaient plus éloignés de l'eau, probablement sur des reliefs exposés à un assèchement saisonnier. La proximité d'un lagon est suggérée. Concernant la reconstitution paléoclimatique basée sur le bois fossile en général, deux problèmes principaux sont mis en évidence : celui de la variabilité intraspécifique et individuelle de signification non-écologique et le problème du nombre insuffisant des types de bois fossiles nécessaires pour les méthodes statistiques.

MOTS CLÉS
Bassin de Paris,
Yprésien inférieur,
bois silicifié d'angiospermes,
reconstitution paléoclimatique.

INTRODUCTION

The present paper summarizes the main results of the Master's thesis of the author (Sakala 1998). On one hand, it completes the previously published descriptions of the angiosperm woods of Dangu (Koeniguer 1981; Sakala *et al.* 1999); on the other hand, it attempts to give a palaeoenvironmental reconstruction based on wood and other silicified remains. The reconstruction uses two approaches: traditional (intuitive) and statistical, using multivariate statistics, recently published by Wiemann *et al.* (1998). Both methods compare past phenomena to the present. Their advantages and risks with regard to the reconstruction of the palaeoenvironment and palaeoclimate are discussed. As a conclusion, a palaeoenvironmental reconstruction of the locality is given and the problem of the wood-based palaeoclimate reconstruction in general is discussed.

GEOLOGICAL SETTING

The Dangu locality is situated in the Paris Basin, 65 km NW from Paris, in the "Vexin normand" (Eure department), 7 km WSW from Gisors (Fig. 1). The fossils occur in sand (to conglomerate) with flint pebbles known as "galets avellanaires". It is a residual formation, which originated from an altered terminal level of the lower Ypresian (at the top of the "Sparnaciens" facies) deposited in a fluvio-marine regime (Kuntz *et al.* 1976). Generally, most pebbles associated with fossil wood are distributed approximately in the N-S direction, following a channel of detrital supply probably from the anticlinal of Bray to the North (Kuntz *et al.* 1976).

SYSTEMATICS

Five different entities of dicotyledons have been recognized in the Dangu locality on the basis of seven wood samples. They belong to the families Hamamelidaceae, Mimosaceae vel Caesalpiniaceae, Combretaceae and ?Rubiaceae. Besides dicotyledonous woods, palms and gymnosperms (Taxodiaceae) occur in this locality. They are mentioned by Koeniguer (1981) but are not studied in detail in the present paper.

The descriptions and affinities of three types (two species), with discussion about root wood, have

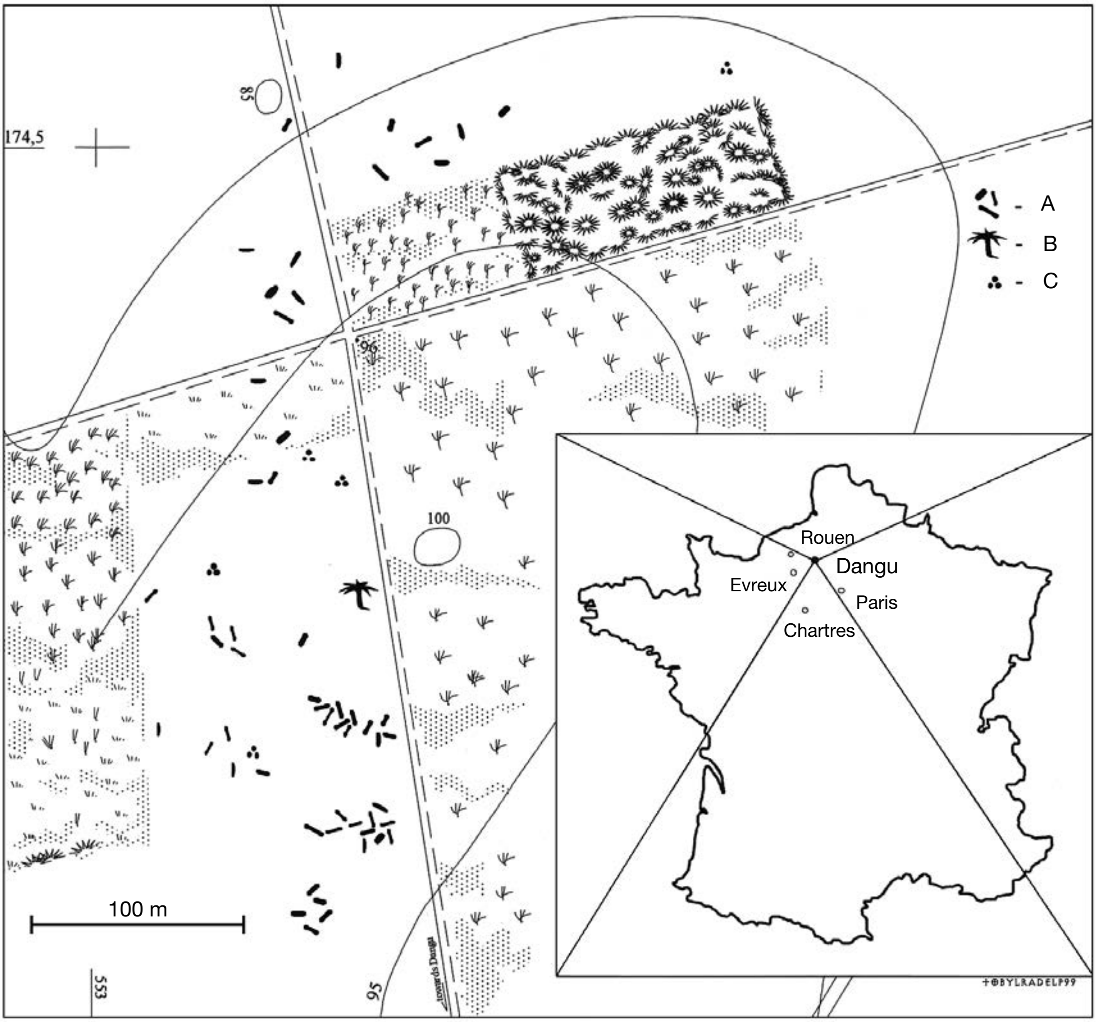

FIG. 1. — Location and overview of the Dangu locality; **A**, gymnosperm and angiosperm wood; **B**, palm wood; **C**, silicified peat, after Koeniguer (1981), modified.

been recently published by Sakala *et al.* (1999). The present work complements the flora by anatomical data of two other woods (including a photographic documentation of all five angiosperm woody taxa of Dangu) and gives an overview of the studied locality.

All studied specimens, described herein and previously in Sakala *et al.* (1999), will be housed in the palaeobotanical collections of the French National Museum of Natural History (Muséum national d'Histoire naturelle) in Paris. Every specimen has already got its preliminary catalogue number, i.e. W1, W2, W4, Wtourbe and SY7.

Division MAGNOLIOPHYTA
Family HAMAMELIDACEAE R. Brown
Genus *Liquidambaroxylon* Felix

cf. *Liquidambaroxylon* sp.
(Fig. 2F-H)

For description and discussion, see Sakala *et al.* (1999).

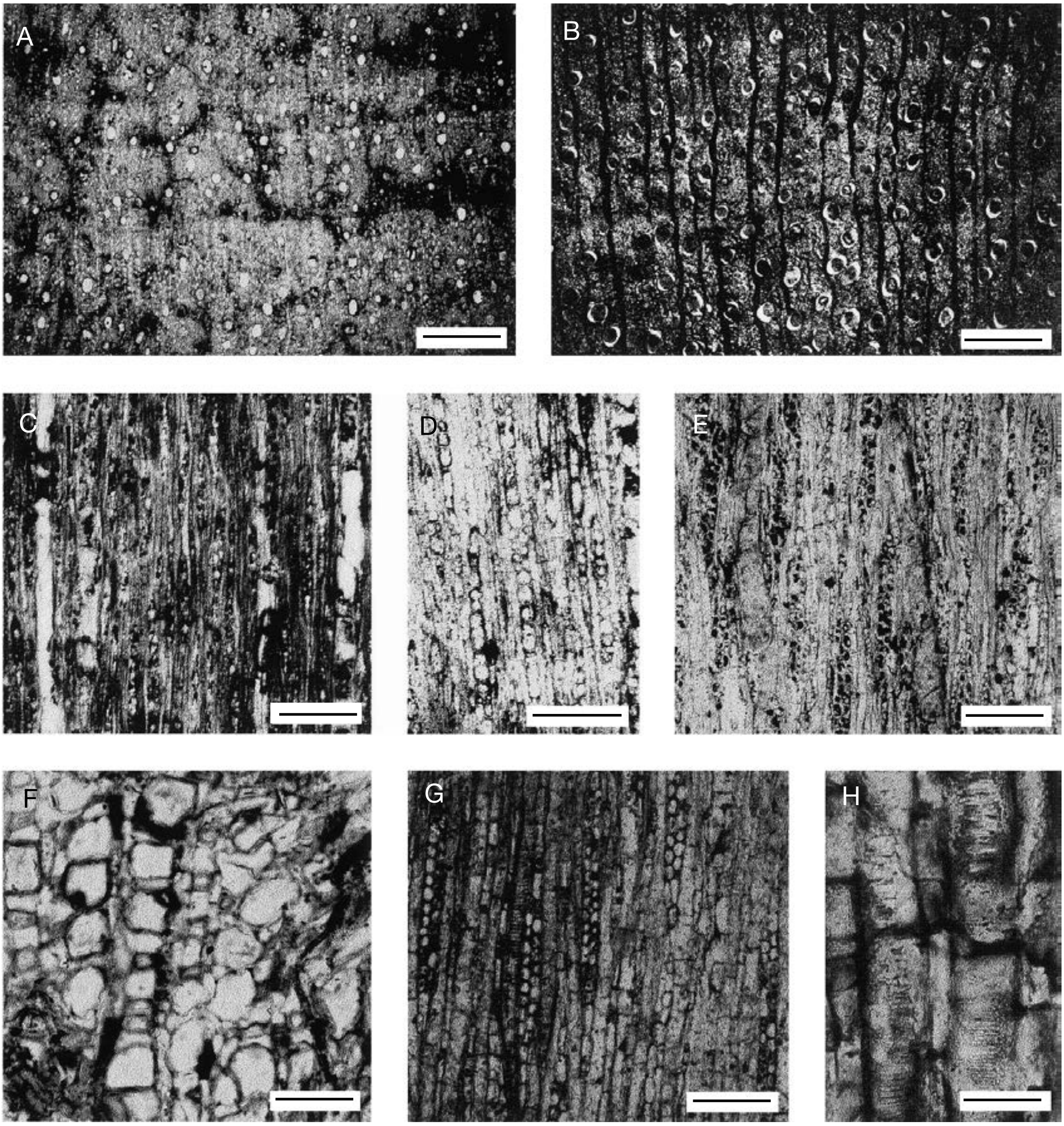

FIG. 2. — **A**-**E**, *Grangeonixylon danguense* (W1, W2); **A**, cross-section of the stem form (W2); **B**, cross-section of the root form (W1); **C**, stem form in tangential view (W2); **D**, stem form in tangential view, rays detail (W2); **E**, root form in tangential view (W1); **F**-**H**, cf. *Liquidambaroxylon* sp. (Wtourbe); **F**, cross-section (same part, vertically reversed, described in detail in Sakala *et al.* 1999: fig. 2a); **G**, tangential section; **H**, tangential section, detail of scalariform pitting. Scale bars: A, B, 500 µm; C, E, G, 200 µm; D, 150 µm; F, 100 µm; H, 50 µm.

Family MIMOSACEAE R. Brown vel CAESALPINIACEAE R. Brown

Genus *Dichrostachyoxylon* Müller-Stoll & Mädel

Dichrostachyoxylon* cf. *zirkelii (Felix) Müller-Stoll & Mädel

(Figs 3; 5A, C)

DESCRIPTION

The growth rings are slightly distinct to the naked eye (emphasized by secondary mineralization), but they are hardly noticeable under the microscope. The wood is diffuse porous.

The vessels are solitary (60%) and in radial multiples of 2 (23%), 3 (10%) or 4 (7%), 9 in number (13-14 pores) per mm^2, rounded to elliptical in section, very often deformed (radially elongated). The tangential diameter varies from 36 to 153 µm, with a mean of 83 µm; the radial diameter varies from 70 to 190 µm. The wall thickness varies from 7 to 12 µm. The vessel elements are 237-328 µm long, with simple perforation plates. The intervascular pits are bordered, alternate, quite dense, circular to elliptical, horizontally elongate, from 2.5 to 12 µm in diameter according to the longest axis, 2.5-4.5 µm in diameter according to the shortest axis and with an aperture from 1 to 8 µm in diameter. They appear to be vestured.

The fibres are quadrangular in cross section. They form regular radial lines of two to six fibres between two rays. Their mean tangential and radial diameters vary from 4.5 to 14 µm. Fibre pits are not visible. Two fibres types can be distinguished: 1) thin-walled (walls 1-2.5 µm thick) in which the lumen in cross section represents 75% of the fibre diameter; 2) thick-walled (walls about 4.5 µm thick) in which the lumen in cross section represents 20% of the diameter. The arrangement of both fibre types is irregular.

The axial parenchyma is apotracheal, forming tangential circummedullar bands and paratracheal (vasicentric, slightly aliform, very rarely confluent). The cell dimensions (tangential diameter × radial diameter × cell height) are: 7-21 µm × 6-46 µm × 35-51 µm.

The rays seem to be homogeneous (such as they appear in the tangential section, the radial section is not available) or slightly heterogeneous. They are uni- and multiseriate (type 1 or slightly 3 of Metcalfe & Chalk 1989: 23), one to four cells wide (mostly bi- to triseriate), with 12-19 rays per one horizontal mm in tangential section. The uniseriate rays are made up of weakly vertically elongate cells. These cells are also present at the extremities of the multiseriate rays, forming unicellular endings, while the body of the multiseriate rays is constituted of rather flattened cells. The height of the uniseriate rays varies from two to ten cells (48-231 µm), their width varies from 7.5-18 µm. The multiseriate rays are 15-40 µm wide, their height varies from 4 to 18 cells (66-333 µm). In tangential section, the cell dimensions (height × width) are 7.5-60 µm × 5.5-18 µm.

DISCUSSION

The most characteristic features of the studied wood are the following: wood diffuse porous; vessels solitary (60%) or in radial multiples of 2, 3 or 4 (very rarely of 5), composed of very short elements; small vessel pits (from 2.5 to 11.5 µm) which seem vestured; axial parenchyma vasicentric, slightly aliform, and very rarely confluent, or in tangential bands; rays homogeneous, 1-4 seriate, very short and thin. These features point to the Fabales, especially to the families Caesalpiniaceae and Mimosaceae (Louvet 1976). Storied rays, which would have placed the fossil wood nearer to the family Fabaceae or some Caesalpiniaceae (Metcalfe & Chalk 1950), are absent.

The first report of leguminous wood of Dangu appears in Koeniguer *et al.* (1985), although its affinity is not discussed. Based on the work done by Müller-Stoll & Mädel (1967), our fossil can be assigned to the genus *Dichrostachyoxylon* Müller-Stoll & Mädel (Müller-Stoll & Mädel 1967: 138). Among the species described within this genus (see the comparative table in Privé 1970: 200), two are very close: *D. zirkelii* (Felix) Müller-Stoll & Mädel and *D. royaderum* Privé. Unlike our fossil, *D. zirkelii* has more porous

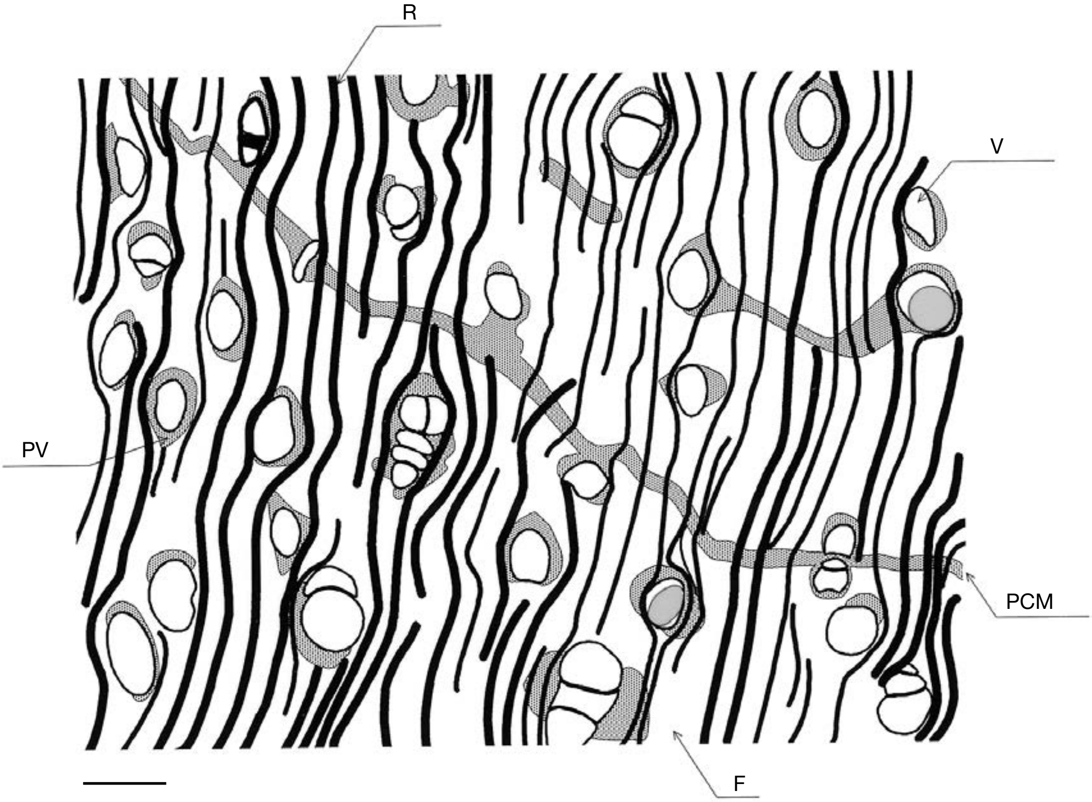

FIG. 3. — *Dichrostachyoxylon* cf. *zirkelii* (SY7), cross-section. Abbreviations: **F**, fibres; **PCM**, circummedullar parenchym; **PV**, vasicentric parenchyma; **R**, rays; **V**, vessels. Scale bar: 200 µm.

wood with larger vessels, whereas *D. royaderum*, described by Privé (1970), has fewer vessels, which are less frequently grouped. Another fossil species, described as *Leguminoxylon sahabiense* by Louvet (1976), is similar to both species of *Dichrostachyoxylon* mentioned above, and is in fact a species of the genus *Dichrostachyoxylon*. It is also similar to our fossil, except for its lower ray density and markedly bigger vessels.

Therefore we propose: 1) to transfer the species *Leguminoxylon sahabiense* Louvet to *Dichrostachyoxylon*, because its species diagnose (Louvet 1976: 82) fits entirely that of *Dichrostachyoxylon* (Müller-Stoll & Mädel 1967: 138): *Dichrostachyoxylon sahabiense* (Louvet, 1976) n. comb. (1976 – *Leguminoxylon sahabiense* Louvet, Actes 97e Cong. nat. Soc. sav., Nantes, 1972, sci. 4: 82, pl. 1, figs 1; 2, text-fig. 1 [basionym]) ; and 2) to call our fossil wood *Dichrostachyoxylon* cf. *zirkelii* (Felix) Müller-Stoll & Mädel, pointing to the species *D. zirkelii* as the nearest and most similar, but not identical species to the Dangu fossil.

Family COMBRETACEAE R. Brown
Genus *Anogeissus* Wallich

Anogeissus sp. (Figs 4; 5B, D, E)

DESCRIPTION

The growth rings are slightly distinct due to the presence of terminal parenchyma.

The wood is diffuse porous.

The vessels are solitary (15%) or in radial (rarely in tangential) multiples of 2 (25%), 3 (20%), 4 (15%), 5 to 10 (20%) or more than 10 (up to 21) (5%), in number of 25 vessels (100 pores) per

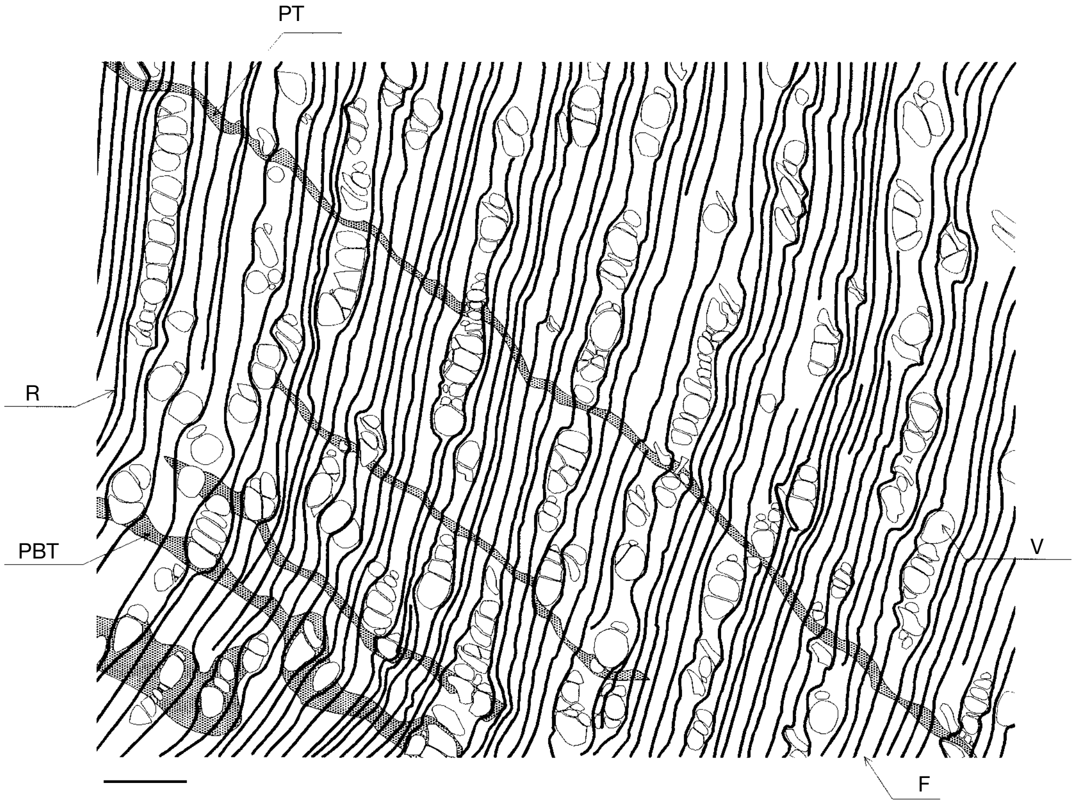

FIG. 4. — *Anogeissus* sp. (W4), cross-section. Abbreviations: **F**, fibres; **PBT**, parenchyma in tangential band; **PT**, terminal parenchyma; **R**, rays; **V**, vessels. Scale bar: 200 µm.

mm^2. The tangential diameter varies from 22 to 91 µm (mean 57 µm), the radial diameter varies from 22 to 109 µm. The vessel elements, from 85 to 445 µm (mean 180 µm) in length, have subhorizontal simple perforation plates. The walls of the pores are 3-8.5 µm thick. The intervascular pits are bordered, alternate, non-vestured, very dense and 1.5-3 µm in diameter.

The fibres are arranged in one to 15 radial, rather regular, series between the rays. They are at least 640 µm long and are sometimes septate. The tangential diameter reaches 14 µm, the wall thickness is about 4.5 µm. The pits are not visible.

The axial parenchyma is in three to five cells thick tangential bands and terminal. The cell dimensions (tangential diameter × radial diameter × height) are 6-18 µm × 3-21 µm × 58-85 µm. The cells have dark contents.

The rays are uniseriate or rarely biseriate in one to eight cells tall portions, heterogeneous (type 7 of Metcalfe & Chalk 1989: 23), 18-24 in number per horizontal tangential mm. They are 11-37 µm wide and 3-30 cells (100-930 µm) high. In the tangential section, the cell dimensions (height × width) are 44-64 µm × 12-23 µm. Examples of radial dimensions (height × length) of the different types of cells are: upright cells 44 × 21; 64 × 22... µm, square cells 29 × 32... µm and procumbent cells 29 × 66; 32 × 131... µm.

DISCUSSION

The studied wood, with its bands of terminal parenchyma and vessels in frequent radial multiples, shows affinities with some genera of the families Meliaceae, Rutaceae, Sapindaceae, Sapotaceae, Apocynaceae and Combretaceae.

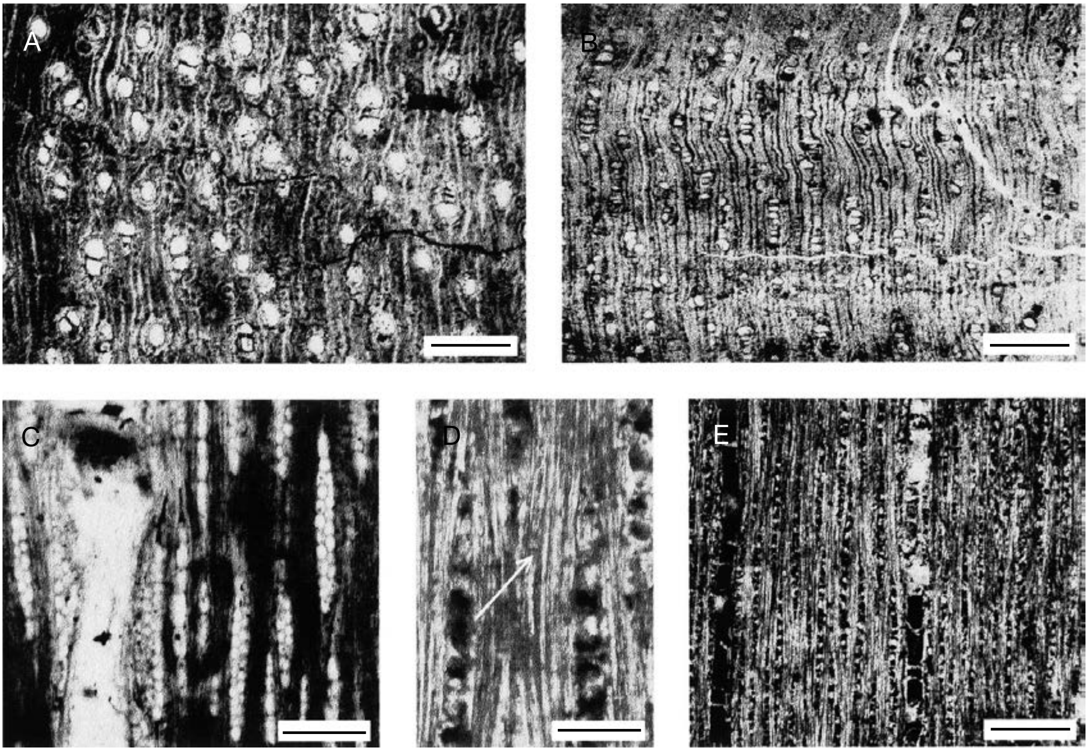

FIG. 5. — **A**, *Dichrostachyoxylon* cf. *zirkelii* (SY7), cross-section; **B**, *Anogeissus* sp. (W4), cross-section; **C**, *Dichrostachyoxylon* cf. *zirkelii* (SY7), tangential section; **D**, *Anogeissus* sp. (W4), tangential section, detail of a septate fibre (septum indicated by the arrow); **E**, *Anogeissus* sp. (W4), tangential section, general view. Scale bars: A, B, 500 µm; C, 100 µm; D, 50 µm; E, 200 µm.

Among these six families, there is no species that corresponds in all features to the fossil wood (Heimsch 1942; Metcalfe & Chalk 1950). The Sapotaceae family is the closest in general vessel arrangement, although unlike the fossil at hand, its representatives show regularly banded parenchyma and no septate fibres, when uni- (or rarely biseriate) rays are present. In Combretaceae, *Anogeissus* and *Lumnitzera* have vessels in radial multiples and uniseriate (rarely biseriate) rays (Metcalfe & Chalk 1950). Furthermore, some species of *Anogeissus* have septate fibres (Metcalfe & Chalk 1950). The absence of terminal parenchyma in the extant *Anogeissus* has probably no systematic importance; its presence in the fossil wood may be due to environmental conditions. This problem is discussed below (see below "Sedimentation pattern and climatic conditions based on wood anatomy observations").

The fossil is identified only to the genus. Because our wood does not fit the diagnosis of the fossil genus *Anogeissuxylon* (Louvet 1965: 295-296) and no other similar wood plan has been found in the fossil record, the living genus *Anogeissus* is proposed. Its characteristic of wood fits the Dangu fossil very well. The absence of terminal parenchyma in *Anogeissus* is not considered to be of systematic importance.

Family ?RUBIACEAE Jussieu
Genus *Grangeonixylon* Privé-Gill

Grangeonixylon danguense Sakala *et al.*
(Fig. 2A-E)

For description and discussion, see Sakala *et al.* (1999)

PALAEOENVIRONMENT OF THE DANGU LOCALITY

To reconstruct the palaeoenvironment of the Dangu locality, two approaches were applied: classical (intuitive) and statistical, using the multivariate statistical model recently published by Wiemann *et al.* (1998).

CLASSICAL APPROACH

The Dangu wood taxa were compared with their nearest living relatives and the sedimentation and climate conditions were reconstructed, both based just on fossil wood anatomy. Then, the silicified peat, its mode of fossilisation and general significance respectively, were taken into account. Finally, the Dangu locality as a whole was compared with other similar fossil localities.

Comparison of the fossil woods with the nearest living relatives

Five different dicotyledonous wood types were recognized in the Dangu locality on the basis of seven samples. They probably belong to the families Combretaceae, Mimosaceae vel Caesalpiniaceae, ?Rubiaceae and Hamamelidaceae.

The first of them, *Anogeissus*, includes at present 12 species and grows today in Asia and in tropical Africa (Louvet 1965). The fossil wood is rather similar to the species *A. pendula* Edgeworth (see in Ilic 1991), a small tree or shrub growing in the northwest of India and Rajputana (Louvet 1965).

The fossil leguminous wood, with affinities to the species *Dichrostachyoxylon zirkelii*, is similar to the living genera *Acacia*, *Dichrostachys*, *Guibourtia*, *Hardwickia* and *Hymenaea* (Privé-Gill 1985; Privé-Gill *et al.* 1992). The species *Acacia catechu*, presently growing in areas of India, Burma and Thailand with a marked dry season (seven to eight months), seems in particular very close to *Dichrostachyoxylon zirkelii* (Privé-Gill *et al.* 1992), and hence to our fossil wood.

The species from the ?Rubiaceae family (two forms of the same species, *Grangeonixylon danguense* Sakala *et al.*) presents affinities with several genera of Asia, Africa and America. Regarding the fact that at present there is not a single type exactly matching our fossil wood, we must confine our description to the general characters of the Rubiaceae. This family has quite a vast geographical distribution, but is mostly tropical (Metcalfe & Chalk 1950). However, because even affinity of the fossil to the family is uncertain (Sakala *et al.* 1999), the value of *Grangeonixylon* for this part is rather low.

The wood cf. *Liquidambaroxylon* sp. (see in Sakala *et al.* 1999) from the peat is close to several genera of the Hamamelidaceae family and also to the Cornaceae, of which only the genus *Nyssa* is somewhat similar. *Nyssa*, growing today in East Asia and in North America, is considered to be a good indicator of a swampy environment in warm Tertiary climates comparable to the "swamp forest" of southeastern North America (Mai 1995). Concerning the potential affinities with the Hamamelidaceae family, the genera *Altingia* and *Liquidambar* are the closest. Both genera grow in Asia (Koeniguer 1981), but *Liquidambar* is also dominant (*L. styraciflua* L.) in the alluvial forests in southern North America in association with oaks, hickories and ashes (Mai 1968). *Altingia* (e.g., *A. excelsa* Noronha) is spread in Assam, all along the rivers which drain the Himalayas in the formation of a "Tropical valley frost water swamp forest", associated with the genera *Machilus* and *Eugenia*. This type of formation is close to the fossil laurophyllous association, from which the forests of subtropical China or mountainous rainy forest of southeast Asia are the best analogues (Mai 1968).

Resuming this part of the systematic comparison, the described types indicate a warm climate, subtropical to tropical. The geographic distribution of the extant analogues is rather close to Asia and eastern North America. This fact matches well with numerous data about European Tertiary floras showing affinities with both regions. This similarity is due to the existence of land bridges (Bering and North Atlantic Land Bridges) in the Cenozoic between North America and Eurasia (Graham 1972; Tiffney 2000).

Sedimentation pattern and climatic conditions based on wood anatomy observations

The set of the broad-leaved trees, which are the subject of this paper, lacks very pronounced growth rings, although there is a slight zonation in the case of *Grangeonixylon* and *Anogeissus.* This suggests a regularly humid riparian forest as well as the influence of brackish water (for details see in Koeniguer 1981; Koeniguer *et al.* 1985). Because growth rings are not very clear, the trees probably grew in rather equable climatic conditions. The presence of terminal parenchyma in the fossil *Anogeissus,* unlike its extant analogue, can be linked to abrupt, perhaps seasonal, interruptions of the stable conditions, as it is often the case (Privé-Gill pers. comm.). The same interpretation has been given for the Dangu conifers, dealt with below.

The fossil Taxodiaceae of the Dangu site show, in agreement with Koeniguer (1981), very clear and narrow rings, sometimes false-rings and a dense wood structure. According to Koeniguer (1987), these features suggest a forest of a seasonal climate, locally drier, rather than a riparian, and constantly flooded one. The conifers probably grew on a sandy, uplifted littoral terrain, sensitive to short, periodic dry periods (Koeniguer 1981). Unlike the angiosperms, the gymnosperms as a whole point to periodical interruptions of the optimal conditions (e.g., dry, cold periods, etc.).

Formation and possible modification of growth rings are a very complex phenomenon (Zimmermann & Brown 1971). Diverse causes, that may occur simultaneously, can be responsible. Nevertheless, if we suppose that the conifers and the broad-leaved trees were growing more or less in the same place, the only cause, that could provoke these selective differences, is a periodical drying, linked to the surface and ground water fluctuation.

Mode of fossilisation and signification of the silicified peat

The silicified remains of the lignitic peat of Dangu were the subject of a study by Koeniguer (1981). He compared this fossil peat with the recent peats from Florida Everglades, based on the observations of Cohen & Spackman (1977, 1980). For the Dangu peats, Koeniguer (1981) comes to the following sedimentological and palaeoecological conclusions: the peat is slightly allochtonous, deposited in shallow water (1 to 2 m maximum depth), in a lagoon, within marine or brackish environment. It has been subject to the drainage actions of tidal currents, as well as to wetting, corresponding perhaps to emersion phases.

Regarding these facts and taking geological data into account (Kuntz *et al.* 1976), the deposition of the peat points to a shallow brackish lagoonal environment, sheltered from the direct influence of the sea, which was situated to the North (Kuntz *et al.* 1976). Rivers supplied the lagoon with fresh water from the South. These two agents, marine in the North and fluviatile in the South, were responsible for the allochtonous character of the silicified peat, deposited somewhere between.

Comparison of the Dangu locality with other localities

Koeniguer (1981) concluded that the Dangu locality had been subject to a warm and humid climate, subtropical of the northern tropical zone, with seasonal drying, due to the fact that the growth rings of the conifers were narrow and distinct. This conclusion, in spite of the fact that it is still discussed (e.g., Russell *et al.* 1990), agrees in general with the character of the early Ypresian (Sparnacian) climate in the Paris Basin: subtropical, seasonally dry, less warm and humid than the climate in the Cuisian (Ducreux *et al.* 1984; Koeniger 1987).

Among the other Lower Eocene palaeontological localities, the London Clay flora may chiefly be compared to Dangu to which it is analogous, both in floral composition and environment conditions. The London Clay flora is geographically close, very rich (250 species, 151 genera) and of comparable age (lower Ypresian). Collinson (1983) summarized the principal traits of this flora. There are 131 tropical genera, 86 subtropical genera, 60 temperate genera and 17 north-temperate genera, 30% of gymnosperms in the twig flora, considered as a more temperate group (50% in Dangu according to Koeniguer pers. comm.). The growth rings were observed in 31% of the twigs and larger blocks of fossil angiosperm wood, described by Brett (1960, 1972), present growth rings too. Finally, the London Clay flora has, in comparison with other Tertiary floras of Great Britain, the highest proportion of tropical taxa and the lowest proportion of temperate taxa: 18% of the taxa are allied to plants with a strictly tropical distribution (Collinson 1983).

From a temperature reconstitution based on the oxygen isotope ratio (20-27 °C), Collinson (1983) considers the vegetation of the London Clay close to the paratropical rain forest in Wolfe's (1979) sense. This type of forest is limited by the isotherms of 20 °C and of 25 °C MAT. The paratropical forest, replaced above 25 °C by the tropical rain forest, has a two-storied canopy, whereas the tropical rain forest canopy is three-storied. Nevertheless, there are some contradictions. First, there are some temperate taxa, indicated by palynological data, and the combination of plants in the macroflora that do not allow the London Clay flora to be called a paratropical rain forest. Second, the presence of growth rings and a high percentage of gymnosperms (up to 30%) in the twig flora are a little confusing. Finally, the fluctuation in insolation indicated by the palaeolatitude of the locality (41°N) and the absence of important elements (e.g., Dipterocarpaceae) must be noted. The result is that the paratropical rain forest is not identical to the "London Clay" vegetation, but it presents its best extant parallel. Collinson (1983) concludes in agreement with another work tackling this problem (Daley 1972), that in the case of the London Clay flora, a specific climatic regime, not known at present, must be assumed.

What conclusions can we extract from the flora of the Dangu locality? First of all, our vegetation was not tropical, although there are some similarities between the structures of our woods (mainly in *Grangeonixylon danguense* and *Dichrostachyoxylon* cf. *zirkelii*) and tropical woods. The model of Daley (1972) fits pretty well on our locality. The tropical types (in our case the set constituted by broad-leaved trees and palms) grew on riverbanks or on shores of some other water reservoirs, under a favourable microclimate (particularly sufficient humidity). To explain the existence of temperate plants among the tropical ones, we must anticipate more temperate types (conifers of the Taxodiaceae family in the case of Dangu) to be more distant from the water, perhaps on uplifted terrains. They were exposed to regional conditions, less humid and optimal, more confronted to the climatic fluctuations all along the year. *Anogeissus*, because of its terminal parenchyma, probably also grew on uplifted terrains, where it was exposed, together with the conifers, to the seasonal fluctuations of water availability.

STATISTICAL APPROACH

In order to get a fossil wood-based palaeoenvironment reconstruction, we applied the statistical, recently published model of Wiemann *et al.* (1998).

Wiemann *et al.* (1998) observed 50 ligneous anatomical features in the recent floras of 37 regions of North and South America, Africa, Malaysia and Pacific islands. The features were taken from the OPCN database of the GUESS software, version 1.1. This study focuses on the influence of six climatic variables (MAT, mean annual temperature; MART, mean annual range of temperature; CMMT, cold month mean temperature; MAP, mean annual precipitation; DMP, dry month precipitation; DRY, length of dry season in months) on the wood characters.

A preliminary correlation and regression analysis was used to determine the best correlated wood anatomical characters. Ten of them were chosen for the subsequent analyses by Wiemann *et al.* (1998), based on their consistent occurrence and simple recognition (Table 1, caption). Finally, five regression equations have been presented (see in Wiemann *et al.* 1998: 89; 91) to calculate the values of the climate variables.

If we calculate the percentages, which characterise the fossil Dangu assemblage (Table 1), we will get, using the regression equations, the following values of climate variables:

TABLE 1. — Wood characteristics of the fossil Dangu assemblage. Abbreviations: **mult**, vessels with multiple perforations; **spir**, spiral thickening present in the vessels; **< 100 µm**, vessel mean tangential diameter less than 100 µm; **sept**, septate fibres present; **> 10 ser**, rays commonly more than 10 cells wide; **het4+**, heterogeneous rays with four or more rows of upright cells; **stor**, rays storied; **abs**, axial parenchyma absent or rare; **marg**, marginal parenchyma present; **rp**, wood ring-porous; **0**, character absent; **1**, character present.

Dangu wood	mult	spir	< 100 µm	sept	> 10 ser	het4+	stor	abs	marg	rp
Grangeonixylon	0	0	1	0	0	1	0	0	0	0
Dichrostachyoxylon	0	0	1	0	0	0	0	0	1	0
Anogeissus	0	0	1	1	0	0	0	0	1	0
Liquidambaroxylon	1	0	1	0	0	1	0	0	0	0
Present/total (%)	25	0	100	25	0	50	0	0	50	0

MAT = 26.2 °C; MART = 10.0 °C; CMMT = 18.5 °C; MAP = 152.2 cm; DRY = - 0.9 month. The climate suggested by temperature and precipitation rates indicated above would be tropical humid, at present typical of the zone limited by two tropics. Among the sites where Wiemann *et al.* (1998) recorded climatic data, the TUX site, situated in southern Mexico (MAT = 24.4; MART = 7.6; CMMT = 20.5; MAP = 211) is climatically the most similar to the fossil Dangu site. Nevertheless, our results are easily contestable for the following reasons:

– according to our interpretation (Sakala *et al.* 1999), the wood of *Liquidambaroxylon* comes possibly from a root. Therefore, its structure might be modified. However, we included it in the analysis because we think that the 10 characters considered were most probably identical in the stem wood. The change in the abundance of parenchyma and vessel grouping in the root wood cannot modify the obtained values;

– the negative value in DRY (- 0.9) can be explained by the complete absence of a dry season, that is a climate with precipitation distributed throughout the year. Nevertheless, this problematics is discussed by the authors (Wiemann *et al.* 1998) and should still be verified;

– finally, the main problem is the low number of samples in our analysis. Wiemann *et al.* (1998) included only sites with at least 25 wood types to establish their model. In the case of the validation sites (sites which serve to verify the theoretical model), there were sometimes as few as eight wood types per site and these sites had large errors. It is clear that our locality with only four types is far from being ideal for a correct and convincing statistical analysis. However, it should be realised that it is difficult to obtain a sufficient number of different wood types in most palaeontological sites. Localities with more than several different wood types are rare (but they exist as shown by Wiemann *et al.* 1999). We can find a good example in the recently published paper of Figueiral *et al.* (1999) on the Miocene of the Lower Rhine basin in Germany: of 708 pieces of wood only 140 (19.5%) belong to angiosperms. These 140 pieces represent only 12 different dicotyledonous wood types.

THE PROBLEM OF THE FOSSIL WOOD-BASED PALAEOCLIMATE RECONSTRUCTION

Some of the problems of palaeoclimate reconstruction based on fossil wood, e.g., Baileyan trends of specialization *versus* climatically controlled changes in dicotyledonous wood, have been already discussed by Wheeler & Baas (1993). In the palaeoclimate reconstruction of the Dangu locality, we encountered two principal problems, which are inherent to any fossil wood-based palaeoclimate reconstruction: the intraspecific and individual variability of non-ecological significance and the number of fossil wood types necessary for statistical methods.

Intraspecific and individual variability of non-ecological significance

The problem of root wood, discussed in this paper and previously by Sakala *et al.* (1999), has a more general significance in palaeoxylology, especially in palaeoclimate or palaeoenvironment

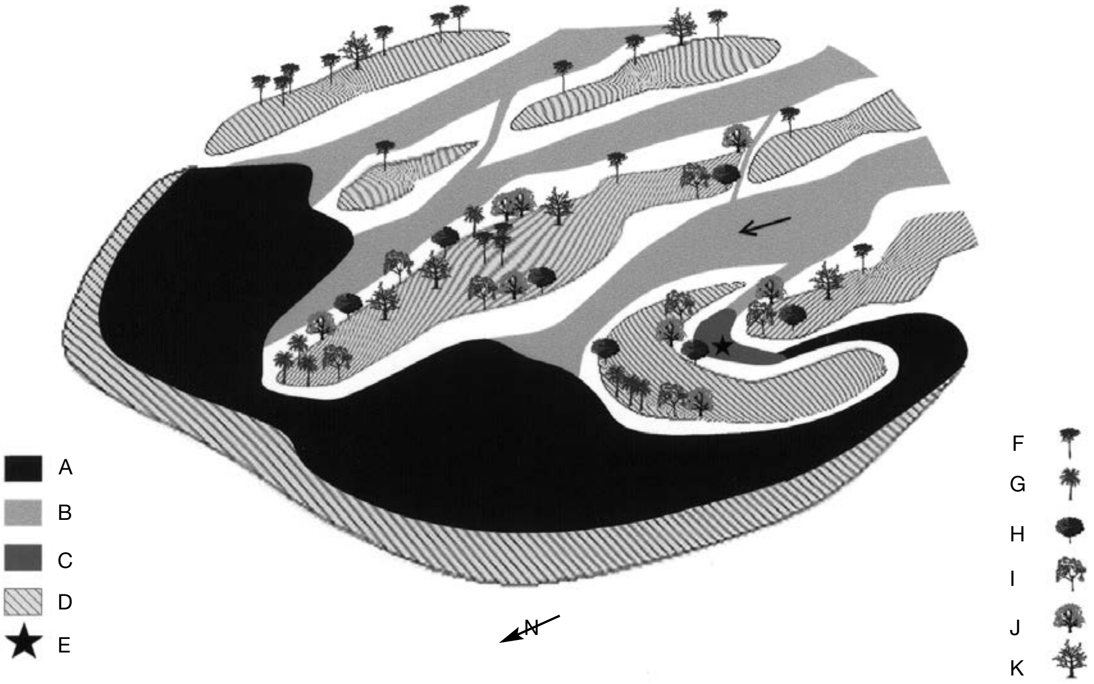

FIG. 6. — Reconstitution of the Dangu locality in the time of the sedimentation of the fossil peat (lower Ypresian, sparnacian facies); **A**, lagoon environment; **B**, fluvial environment; **C**, lagoon-fluvial environment; **D**, sandy-clay reliefs; **E**, environment of the peat deposition; **F**, *Taxodioxylon*; **G**, *Palmoxylon*; **H**, *Dichrostachyoxylon*; **I**, *Liquidambaroxylon*; **J**, *Grangeonixylon*; **K**, *Anogeissus*.

reconstruction based on the fossil wood. We have shown how much root wood can differ from normal trunk wood (Sakala *et al.* 1999). A good example of these differences is presented in the extant *Styrax camporum* Pohl by Machado *et al.* (1997). Their work demonstrates a major difference between the two types of wood. If one finds similar two woods in the fossil record, one would probably not attribute them to the same species. Therefore, someone working on the taxonomy of fossil woods must always keep this intraspecific and individual variability in mind. Moreover, because there are non-ecological differences, we must be very careful not to attribute ecological significance to this variability when making palaeoenvironment reconstruction.

Number of fossil wood types necessary for statistical methods

The statistical model recently developed by Wiemann *et al.* (1998) presents a very simple and effective tool to reconstruct past climate. However, the problem of sufficient numbers of fossil wood samples, even for the whole time intervals (e.g., Palaeocene, see in Wheeler & Baas 1993), remains the principal limiting factor for this method and for statistical methods in general. A possible solution might be the use of a set of ecologically similar and coeval localities.

CONCLUSIONS

First, we completed the systematic part of the Dangu locality. Besides palms and gymnosperms (Taxodiaceae) that are not studied in the present paper, five different angiosperm woody types (four species) in total are now recognized in the Dangu locality. They belong to the families Combretaceae, Mimosaceae vel Caesalpiniaceae, ?Rubiaceae and Hamamelidaceae. To the three types (two species), previously described by

Sakala *et al.* (1999), two others are added by this work (*Dichrostachyoxylon* cf. *zirkelii* and *Anogeissus* sp.). A new combination *Dichrostachyoxylon sahabiense* (Louvet) n. comb. is also proposed.

Second, based on the described woods, we tried to give a palaeoenvironmental reconstruction of the locality. For this purpose, we used two different approaches: classical and statistical. Summarizing the results, the Dangu flora probably reflects a specific climatic regime, not known at present, similar to the modern paratropical rain forest. Broad-leaved trees and palms grew on the water's edge, in conditions of a favourable microclimate (particularly sufficient humidity). The more "temperate" types (i.e. conifers and *Anogeissus*) were more distant from the water, on uplifted terrain, exposed to less favourable conditions, especially to a seasonal drying. The locality as a whole was situated near a brackish lagoon, sheltered from the direct influence of the sea in the North and supplied with fresh water from the South. The general palaeoenvironment overview of the locality, resuming the main results of the classical approach, is shown in the Fig. 6.

Third, from the sample of root wood from the Lower Eocene of France (Sakala *et al.* 1999), we showed intraspecific and individual variability of non-ecological significance. When making a palaeoenvironment reconstruction, one must be very careful not to attribute ecological significance to this type of variability. Observation and comparisons with recent structures are necessary to detect this type of variability and must precede the creation of new species, i.e. splitting of fossil taxa.

Fourth, we demonstrated the weakest point of any palaeoenvironmental reconstruction using statistical data based on fossil wood: insufficient number of wood types. A possible solution to this problem is to group several localities that are ecologically similar and coeval. Such a set allows to evaluate the general character of the climate in some period and region.

Finally, it must be noted that results based on palaeoxylology should be compared, if possible, to those from other palaeobotanical remains (foliage, seeds, fruits, pollen, etc.).

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REFERENCES

Brett D. W. 1960. — Fossil oak wood from the British Eocene. *Palaeontology* 3: 86-92.

Brett D. W. 1972. — Fossil wood of *Platanus* from the British Eocene. *Palaeontology* 15: 496-500.

Cohen A. D. & Spackman W. 1977. — Phytogenic organic sediments and sedimentary environments in the Everglades-Mangrove Complex. Part II: The origin, description and classification of the peats of southern Florida. *Palaeontographica* 162 (B): 71-114.

Cohen A. D. & Spackman W. 1980. — Phytogenic organic sediments and sedimentary environments in the Everglades-Mangrove Complex of Florida. Part III: The alteration of plant material in Peats and the Origin of coal macerals. *Palaeontographica* 172 (B): 125-149.

Collinson M. E. 1983. — *Fossils Plants of the London Clay*. The Palaeontological Association, London, 121 p.

Daley B. 1972. — Some problems concerning the Early Tertiary climate of southern Britain. *Palaeogeography Palaeoclimatology Palaeoecology* 11: 177-190.

Ducreux J.-L., Michoux D. & Wyns R. 1984. — Contrôle climatique de la sédimentation yprésienne (Éocène inférieur) en Brie et en Champagne (Est du Bassin de Paris, France). Conséquences stratigraphiques. *Comptes Rendus de l'Académie des Sciences, Mécanique, Physique, Chimie, Sciences de l'Univers, Science de la Terre, Paris* 299: 1283-1286.

Figueiral I., Mosbrugger V., Rowe N. P., Ashraf A. R., Utescher T. & Jones T. P. 1999. — The Miocene peat-forming vegetation of northwestern Germany: an analysis of wood remains and comparison with previous palynological interpretations. *Review of Palaeobotany and Palynology* 104: 239-266.

Graham A. (ed.) 1972. — *Floristics and palaeofloristics of Asia and Eastern North America*. Elsevier Publishing Company, Amsterdam; London; New York, 278 p.

Heimsch C. Jun. 1942. — Comparative anatomy of the secondary xylem of the "Gruinales" and "Terebinthales" of Wettstein with reference to taxonomic grouping. *Lilloa* 8: 83-198.

Ilic J. 1991. — *CSIRO Atlas of Hardwoods*. Springer-Verlag, Berlin, 525 p.

Koeniguer J.-C. 1981. — Tourbes ligneuses silicifiées dans le Cuisien du bassin de Paris, *in Comptes Rendus du 106^e^ Congrès national des Sociétés savantes, Perpignan, 1981. Sciences* 1: 41-53.

Koeniguer J.-C. 1987. — Paléoécologie de quelques gisements à végétaux fossiles du Bassin parisien. *Bulletin d'Information des Géologues du Bassin de Paris* 24 (2): 23-32.

Koeniguer J.-C., Laurain M., Mouton J., Plaziat J.-C., Wyns R. & Boureau E. 1985. — Sur de nouveaux gisements cénozoïques à végétaux fossiles dans le Bassin de Paris : végétations et paléoclimats. *Comptes Rendus de l'Académie des Sciences, Mécanique, Physique, Chimie, Sciences de l'Univers, Sciences de la Terre*, Paris 301: 509-514.

Kuntz G., Wyns R., Lautridou J. P., Panel R., Bournerias M., Lavergne D. & Verron G. 1976. — Geological map of France in 1/50 000, sheet of Gisors, BRGM, Orléans, 125 p.

Louvet P. 1965. — Sur une Combrétacée fossile nouvelle du Tinrhert (Algérie), *in Comptes Rendus du 89^e^ Congrès national des Sociétés savantes, Lyon, 1964. Sciences* 2: 281-301.

Louvet P. 1976. — Sur une Légumineuse fossile nouvelle du Miocène supérieur de Libye *Leguminoxylon sahabiense* n. sp., *in Actes du 97^e^ Congrès national des Sociétés savantes, Nantes, 1972. Sciences 4:* 79-83.

Machado S. R., Angyalossy-Alfonso V. & de Morretes B. L. 1997. — Comparative wood anatomy of root and stem in *Styrax camporum* (Styracaeae). *IAWA Journal* 18: 13-25.

Mai D. H. 1968. — Zwei ausgestorbene Gattungen im Tertiär Europas und ihre florengeschichtliche Bedeutung. *Palaeontographica* 123 (B): 184-199.

Mai D. H. 1995. — *Tertiäre Vegetationsgeschichte Europas*. Gustav Fischer Verlag, Jena, 691 p.

Metcalfe C. R. & Chalk L. 1950. — *Anatomy of the Dicotyledons*. Vol. 2. Clarendon Press, Oxford, 1 500 p.

Metcalfe C. R. & Chalk L. 1989. — *Anatomy of the Dicotyledons. Second Edition.* Vol. 2. Clarendon Press, Oxford, 276 + 297 p.

Müller-Stoll W. R. & Mädel E. 1967. — Die fossilen Leguminosen-Hölzer. Eine Revision der mit Leguminosen verglichenen fossilen Hölzer und Beschreibungen älterer und neuer Arten. *Palaeontographica* 119 (B): 95-174.

Privé C. 1970. — Sur un bois de Légumineuses du Stampien de Royat (Puy-de-Dôme), *in Comptes Rendus du 94^e^ Congrès national des Sociétés savantes, Pau, 1969. Sciences* 3: 191-205.

Privé-Gill C. 1985. — Sur la présence de *Dichrostachyoxylon zirkelii* (Felix) Müller-Stoll and Mädel au Burdigalien dans le Puy-de-Dôme, Massif Central français. *Comité des Travaux historiques et scientifiques, Bulletin de la Section des Sciences* 8: 213-223.

Privé-Gill C., Ginsburg L. & Gill G. A. 1992. — A leguminous fossil wood among vertebrate fauna in the Early Miocene Orléanais sands, Beauce, France. *Review of Palaeobotany and Palynology* 72: 317-323.

Russell D. E., Broin F. de, Galoyer A., Gaudant J., Gingerich P. D. & Rage J.-C. 1990. — Les vertébrés du Sparnacien de Meudon. *Bulletin d'Information des Géologues du Bassin de Paris* 27 (4): 21-31.

Sakala J. 1998. — *Étude des bois silicifiés du gisement de Dangu (Yprésien de la région de Gisors). Systématique, fossilisation et paléoenvironnement.* Master's thesis (DEA), University Paris 6, Paris; University Montpellier II, Montpellier, France, 48 p.

Sakala J., Privé-Gill C. & Koeniguer J.-C. 1999. — Silicified Angiosperm wood from the Dangu locality (Ypresian of the Gisors region, Eure, France): the problem of root wood. *Comptes Rendus de l'Académie des Sciences, Sciences de la terre et des planètes, Paris* 328: 553-557.

Tiffney B. H. 2000. — Geographic and Climatic Influences on the Cretaceous and Tertiary History of Euramerican Floristic Similarity. *Acta Universitatis Carolinae Geologica* 44 (1): 5-16.

Wheeler E. A. & Baas P. 1993. — The potentials and limitations of dicotyledonous wood anatomy for climatic reconstruction. *Paleobiology* 19: 487-498.

Wiemann M. C., Manchester S. R., & Wheeler E. A. 1999. — Paleotemperature Estimation From Dicotyledonous Wood Anatomical Characters. *Palaios* 14: 459-474.

Wiemann M. C., Wheeler E. A., Manchester S. R. & Portier K. M. 1998. — Dicotyledonous wood anatomical characters as predictors of climate. *Palaeogeography Palaeoclimatology Palaeoecology* 139: 83-100.

Wolfe J. A. 1979. — Temperature parameters of humid to Mesic forests of Eastern Asia and relations to forests of other regions of the Northern Hemisphere and Australasia. *Professional Paper Geological Survey (U.S.)* 1106: 1-37.

Zimmermann M. H. & Brown C. L. 1971. — *Trees Structure and Function*. Springer-Verlag, Berlin; Heidelberg; New York, 336 p.

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