



Systematic palaeontology (Palaeobotany)

How many species of *Araucarioxylon*?

Combien d'espèces d'Araucarioxylon ?

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ABSTRACT

Fossil wood, similar to that of modern Araucariaceae, has been known for a long time, and is usually called *Araucarioxylon*. More than 400 morphospecies have been described, whereas this wood type displays few characteristic features. This taxonomical profusion is compounded by nomenclatural problems, *Araucarioxylon* being an illegitimate name. The status of the wood morphogenus, the infrageneric structure and the names that apply to the taxa designated for fossil woods of the *Araucarioxylon*-type are discussed. A database with 428 morphospecies designated for *Araucarioxylon*-type of wood is analyzed. The name *Agathoxylon* Hartig seems to be the most appropriate for the corresponding morphogenus. Albeit theoretically several hundred morphospecies could be recognized within this group, it is at least as probable that only one should be retained.

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R É S U M É

Les bois fossiles semblables à ceux des Araucariacées modernes sont connus depuis longtemps, et usuellement nommés *Araucarioxylon*. Plus de 400 morpho-espèces ont été décrites, alors que ce type de bois montre peu de caractéristiques. Cette profusion taxonomique est aggravée par des problèmes nomenclaturaux, *Araucarioxylon* étant un nom illégitime. Le statut du morphogène, la structuration infragénérique et les noms qui s'appliquent aux taxa sont discutés pour les bois de type *Araucarioxylon*. Une base de données comprenant 428 morpho-espèces proposées pour des bois de type *Araucarioxylon* est analysée. Le nom d'*Agathoxylon* Hartig semble le plus approprié pour le morphogène correspondant. Même s'il est théoriquement possible de reconnaître plusieurs centaines de morpho-espèces dans ce groupe, il est au moins aussi probable qu'une seule doive être conservée.

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1. Introduction

One of the most common types of fossil wood is usually named *Araucarioxylon*. This name is widely

used in scientific literature since more than a century, while sometimes are preferred avatars like *Dadoxylon* or *Dadoxylon* (*Araucarioxylon*). Hundreds of wood species have been described with this type of anatomy, and provided with a binomial like, for e.g., *Araucarioxylon arizonicum* Knowlton. With the well known fossils from Arizona and Madagascar, the word

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“*Araucarioxylon*” is also in every fossil shop around the world.

In the same time, however, the use of the name *Araucarioxylon* and the interpretation of *Araucarioxylon* data are a matter of much confusion. From a taxonomical point of view, and according to the current version of the International Code of Botanical Nomenclature (ICBN, in McNeill et al., 2006), *Araucarioxylon* Kraus is a morphogenus, a taxon of debated status (Bateman and Hilton, 2009) and usually considered as a “holding bin”. From a systematic point of view, *Araucarioxylon* is often assigned to the Araucariaceae, a modern family of mainly austral conifers, whereas the fossil record for *Araucarioxylon* started in the Carboniferous, long before the Araucariaceae appeared (Renner, 2009). From an anatomical point of view, most *Araucarioxylon* species fall well within the xylogenical variability of one or two modern species of the Araucariaceae (Gondran et al., 1997; Greguss, 1955; Seward and Ford, 1906). Those problems are compounded by a nomenclatural imbroglio, *Araucarioxylon* being an illegitimate name according to the ICBN rules, most of its synonyms being also illegitimate, or invalid (Philippe, 1993). Even if the *Araucarioxylon* case is one of the most difficult, it questions the interest of fossil wood study as a whole.

For those wanting to go beyond the palaeoxylogenical names and understand which scientific information they carry, most prerequisites could be summarized here by the question: how many species of *Araucarioxylon*? Indeed, this apparently simple question cannot be addressed without previously tackling with three others: (1) what is *Araucarioxylon* as a fossil wood taxon? (2) is a subdivision of *Araucarioxylon* possible? (3) how to name these taxa? As trivial as they may appear, these three questions remain open. They arise mainly because of the shift among neobotanists from a purely morpho-anatomical species concept towards a more biological and phylogenetical concept, which orphaned palaeobotanical species of a general definition and plunged palaeobotanists into much questioning.

The Ariadne’s thread to sort this out is that fossil plant taxonomy must be character-based, in a bottoms-up approach (Bateman and Hilton, 2009; Frentzen, 1931). This principle is applied here to a data basis with 423 entries. It includes the wood species described within *Araucarioxylon* Kraus, as well as within genera usually considered as synonyms or closely related: *Agathoxylon* Hartig, *Araucariopsis* Caspary, *Araucarites sensu* Göppert, *Cordaites sensu* Penhallow, *Dadoxylon* Unger, *Dammaroxylon* Schultze-Motel and *Simplicioxylon* Andreanzsky. The database does not take into account the numerous data in open nomenclature (as *Araucarioxylon* sp., or *Dadoxylon* (*Araucarioxylon*) aff. *lugriense*), nor the data corresponding to a second (or more) description of a species on the basis of new material, nor the names resulting from a new combination. Fossil conifer-like woods are sometimes called tracheidoxyls, a convenient concept defined as an isolated piece of secondary xylem made of tracheids, with only a minor proportion of other cell types (Creber, 1972). For the following, the *Araucarioxylon*-type of wood is defined as tracheidoxyls displaying araucarian radial pitting (with no grouping on only portions of the walls, like in *Callixylon*), no or few

pitting on tracheid tangential walls, rays mostly uniseriate, araucarioid cross-fields, smooth and thin ray-cell walls, as well as lacking resin channels (see IAWA Committee, 2004 and Philippe and Bamford, 2008, for the definition of these terms; Fig. 1 illustrates a typical specimen).

2. What is *Araucarioxylon* as a fossil wood taxon?

As a matter of fact, fossil wood is mostly encountered as isolated pieces of secondary xylem. Primary xylem, pith and periderm are sometimes found in connection, but such situation is exceptional, and for the following “wood” will be understood as “secondary xylem”.

Fossil wood taxonomy was born while descriptive obsession and fixist views dominated palaeontology. Until at least the mid-twentieth century, palaeobotany’s main goal was to make a census of fossil diversity and to order it within a system which was designed for extant plants. “Genera” and “species” of fossil wood were described; binomials were used, which more or less implicitly hypothesised that the lowest taxonomical level fitted with that of the species recognised by the neobotanists. Such was satisfying as long as species were considered as morpho-anatomically determined units. The neobotanical and palaeobotanical species concepts, however, diverged as fast as the species concept integrated biological and genetical considerations.

This prompted palaeobotanists to have an appendix to the ICBN to accommodate the taxonomic challenges posed by fossil plants (Bateman and Hilton, 2009), and to distinguish, as an artificial taxon, the form-genus. The form-genus was “maintained for classifying fossil specimens that lack diagnostic characteristics indicative of natural affinity but which for practical reasons need to be provided with binary names” and conceived as a taxon “within which species may be recognized” (Lanjouw et al., 1956). At the same time, the somewhat parallel concept of organ-genus was proposed which, in 2000, was eventually merged with that of form-genus into the new concept of morphogenus, an evolution of which Bateman and Hilton (2009) remarkably discussed the ins and outs.

As for tracheidoxyls, the important fact is that the ICBN establishes a taxonomical unit, at the genus rank, within which species can be recognized. The choice of this ranking is purely arbitrary, however, even if it can be understood by the convenience of binomials and by the importance given formerly to the identification of fossil specimens at family level. It is clear, now that family diagnosis has shifted from morpho-anatomy to molecular phylogeny, that the former belief according which almost every isolated plant fossil could be assigned to a modern family is an utopia, rooted in times predating evolution theory. Even for extant conifers, a character-based xylogenical system of their woods does not fit with a phylogenetical system (see, for e.g., the similarity between the wood of some *Podocarpus* and that of some Taxodiaceae, Marguerier and Woltz, 1977). Morphotaxa being arbitrary ranked entities, they are not comparable. Although they may represent similar disparities, they do not necessarily encompass the same diversity (i.e. that of corresponding extinct biological species). Two morphogenera (resp.

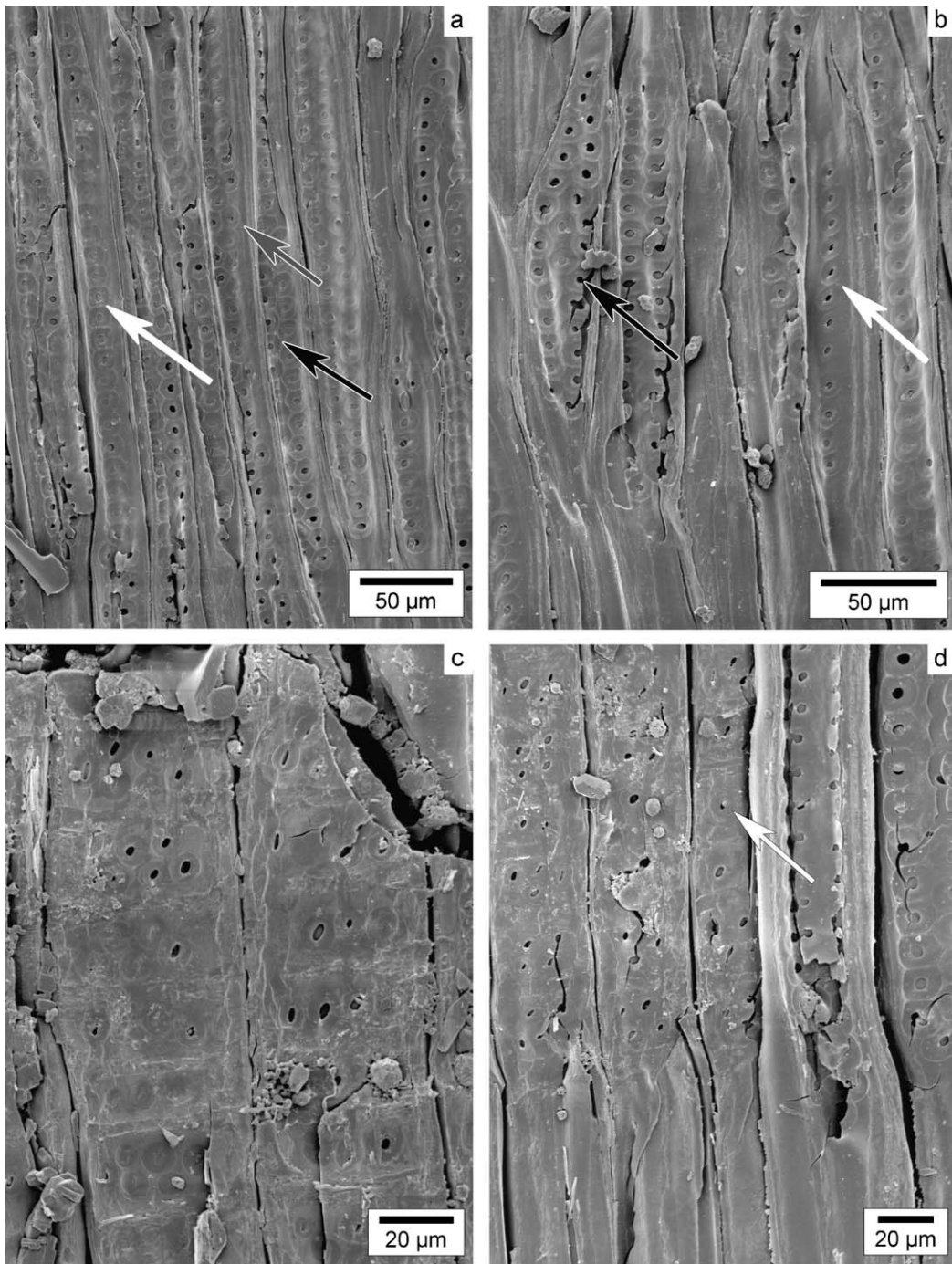


Fig. 1. *Agathoxylon desnoyersii* (Lemoigne) Philippe, Mid-Oxfordian, Voray-sur-l'Ognon (Haute-Saône, France), sample MP1789 in Laboratoire de Paléobotanique de l'Université de Lyon (France). Scanning electronic microscopy, radial view; a: view of the radial pitting, pits crowded, either uniseriate (white arrow) or biseriate alternate (black arrow), rare opposite pair of pits (grey arrow); b: view of radial pitting at tracheid tips, note the broadened tip with triseriate alternate pitting (black arrow) and the narrow area with some round and distant pits (white arrow); c: cross-field pitting, note the variable aspect, depending on the type of preservation; d: cross-field pitting in a one tracheid-thick late wood, locally limited to a single pit (arrow).

Fig. 1. *Agathoxylon desnoyersii* (Lemoigne) Philippe, Oxfordien moyen, Voray-sur-l'Ognon (Haute-Saône, France), échantillon MP1789 au Laboratoire de Paléobotanique de l'Université de Lyon (France). Microscopie électronique à balayage, vue radiale ; a : vue de la ponctuation radiale, ponctuations contiguës, soit unisériées (flèche blanche), soit bisériées alternes (flèche noire), rares paires opposées (flèche grise) ; b : vue de la ponctuation radiale à l'extrémité des trachéides ; noter l'extrémité spatulée avec une ponctuation trisériée alterne (flèche noire) et les zones étroites à ponctuations légèrement rondes et distantes (flèche blanche) ; c : champs de croisement, noter l'aspect variable selon le type de préservation ; d : ponctuation de champ au niveau d'un bois final limité à une assise, avec localement une ponctuation unique (flèche).

species) may correspond to Linnean (biological) taxa of different hierarchical order.

To sum up, a wood morphogenus groups fossil wood specimens fitting with a diagnosis, and morphospecies can be distinguished. These taxonomical units do not fit a priori with the genus and species level of neobotanical classification, morphogenus and morphospecies being hierarchically ordered but unranked taxa. Morphotaxa do not necessarily univocally fit with taxa designed for extant plants.

3. Is a subdivision of *Araucarioxylon* possible?

Fossils fitting with the *Araucarioxylon* wood-type, as described above, are encountered worldwide, from the Carboniferous (Devonian?) to the Present (Frentzen, 1931; Giraud, 1991). More than four hundred morphospecies have been described (partial reviews in Frentzen, 1931; Jeffrey, 1913; Schultze-Motel, 1962, 1964). Confronted to this unusually long time-span and numerous descriptions, several authors have tried to split or subdivide the morphogenus. Morgenroth (1883) and Felix (1886) proposed to limit the use of *Araucarioxylon* to the Mesozoic and Cainozoic material, and to group the Palaeozoic fossils within a taxon called *Dadoxylon*, an earlier nomenclatural synonym of *Araucarioxylon*. Caspary (1887) advocated the use of two names, *Araucarites* Göppert for those woods lacking axial parenchyma and *Araucariopsis* Caspary for the others. Knowlton (1890) choose to assign all the *Araucarioxylon*-species found once in connection with cordaites pith to the genus *Cordaites*. Considering that no clear line of demarcation could be drawn between them, Gothan (1905) recommended grouping all woods described as *Araucarioxylon* Kraus, *Araucarites* Göppert, *Cordaioxylon* Felix, *Cordaioxylon* Grand'Eury, *Cordaites* and *Dadoxylon* Unger under the later name. Zalesky (1911) thought that *Dadoxylon* should be used only for fossils with both primary and secondary xylem, while *Araucarioxylon* for tracheidoxyls, a choice which was later advocated by Prasad (1986). Seward (1919) introduced the use of trinomials, like *Dadoxylon* (*Araucarioxylon*) *novae zeelandiae*, for fossil woods of the *Araucarioxylon*-type which could “safely be assigned to the Araucariaceae”, and kept *Dadoxylon* binomials for wood of more uncertain affinities. Dealing with Palaeozoic taxa only, Frentzen (1931) distributed these woods within two groups according to if the radial pitting completely covered the tracheid or not. More recently, Lepekhina (1972) and Doubinger and Marguerier (1979) have proposed other taxonomical schemes.

Closely related genera were described as segregates from the main “*Araucarioxylon*” group, like *Dammaroxylon* Schultze-Motel and *Simplicioxylon* Andreanzenky. The former was distinguished (Schultze-Motel, 1966) on the basis of the occurrence of “*Randzellen*” (better translated as “marginal spaces” than as “marginal cells”), the latter as its ray cells are sometimes pointed (Philippe, 1993). The taxonomical relevance of these xylological features could be discussed, but might be of interest given the paucity of other characters. *Planoxylon* Stopes, basically woods of the *Araucarioxylon* type with *Abietineentüpfelung*, is definitely well enough circumscribed in both time (Mesozoic

and space (southern Gondwana) to be worth distinguishing (Philippe and Hayes, 2010). This is also recognised for *Australoxylon* Marguerier.

Because of sedimentological sorting, wood is rarely encountered in anatomical connection with other types of palaeobotanical remains. The *Araucarioxylon*-type of wood was observed connected or associated to Caytoniales, Glossopteridales, Cordaitales, Cycadales, Voltziales, Ullmanniales, Araucariaceae, Cheirolepidiaceae, etc., but such observations are rare and never evidenced a peculiar anatomical feature which could allow a subdivision of this set of woods.

At the morphospecies level several taxonomical reappraisals were attempted (Frentzen, 1931; Giraud, 1991; Lepekhina and Yatsenko-Khmelevsky, 1966), but such are getting more and more challenging given the multiplication of new names, regularly established with limited knowledge of relevant literature, based on poorly preserved specimens, or with poorly illustrated protologues. Often a new specimen is compared only with those species which have been described from the same geological stage. Various sets of fossil wood with an *Araucarioxylon*-type of anatomy were investigated with numerical taxonomy, including multivariate analyses, but described grouping or trends are mainly due to database incompleteness (Falcon-Lang and Cantrill, 2001; Giraud, 1991; Li, 1988). Booi (2010), applying several multivariate techniques to a large collection (ca 250 specimens) of araucarioid wood from the Palaeozoic of Sumatra, found a very varied but homogeneously coherent group. Even for the wood of modern Araucariaceae statistical approach has a low discriminative power (Ilic, 1995). Because they were closely similar to already described wood morphospecies, but slightly different, some fossils were used as type for “sister-species” and named accordingly, like *Dadoxylon parafuronii* Boureau & Koeniguer, *Dadoxylon subrhodeanum* Grand'Eury or *Dadoxylon pseudoparenchymatosum* Gothan. Such is common in neobotany, but less understandable for morphospecies, all the more since precaution is usually the main reason advocated for the founding of these “new species”.

The reasons which are most of the time put forward while a new *Araucarioxylon* morphospecies is described are, in increasing frequency order: geographical origin; age; and xylological singularity. In a wholly character-based approach, age and geographical origin of a fossil are irrelevant to its taxonomy (Bateman and Hilton, 2009; Frentzen, 1931). Singularity relatively to xylologically, most similar morphospecies is usually judged from what is known of anatomical diversity among modern Araucariaceae. Such is typical of confusion between morphospecies and species, is an induction on fossil taxonomy that cannot be justified by uniformitarianism, and underestimates the long-known intra-individual and intra-specific xylological variability documented by extant species (Patton, 1927; Pool, 1929; Welch, 1927). Particularly significant in this respect is the sentence by Evans (1934) “*a distinction between fossil Araucaria and fossil Agathis based solely upon the position of a few bordered pits in a fragmentary tracheid certainly appears quite valueless to any one with but a passing acquaintance of the many tricks which our Agathis*

australis plays with its pitting". This sentence was written well before the discovery of the Araucariaceae third extant genus, *Wollemia*, but the wood of the later does not differ significantly from the family pattern (Heady et al., 2002). It is a strong hypothesis to suppose that the systematical distribution of wood features, as well as the xylogenetic variability of taxa, remained unchanged through times, all the more since the number of extinct taxa is probably much higher than that of extant taxa.

Be the xylogenetic variability of modern Araucariaceae what it may, fossil taxa boundaries must be based on discrepancies within the morphological space described by the fossils. Could yet described fossil woods with an *Araucarioxylon*-type of anatomy be distributed within a morphological space, no clear boundaries would appear through what would be a continuous cloud as far as most if not all the xylogenetic variability of the fossil species can be observed within the extant *Araucaria araucana* (including rootwood and wood of traumatic area) (Gondran et al., 1997).

Focusing on one relatively short time interval and limited area, or dealing with a limited number of specimens, one might have the impression that fossil wood specimens with *Araucarioxylon*-type of anatomy can be distributed in discrete xylogenetic units. This is probably because taphonomical filter drastically sorts among the wood fragments getting into the sedimentary system. Only a low percentage of biological tree species and only some parts of their woody body are recorded in a geological stage fossil record. When only a few specimens are known, their xylogenetic disparity has a high probability to be discrete. With about 400 species yet described displaying the *Araucarioxylon*-type of anatomy and with an estimated number of three thousand published specimens at most for a 350 My time interval, the sampling is obviously meagre. Also induced by the taphonomical process is what could be named the pseudo-variability, i.e. the apparent variability which is due to poor preservation or erroneous interpretation. This is a common problem in palaeobotany, and does not spare *Araucarioxylon* (Savidge, 2007).

Whereas by other fossil wood morphogenera (e.g. *Xenoxylon* Gothan), clear xylogenetic discontinuities are observed, by what is usually called *Araucarioxylon* nothing similar is noted while applying a character-based and bottoms-up approach.

4. How to name *Araucarioxylon* taxa?

This point already inspired countless pages. For a long time, palaeobotanists have named their taxa on the basis of supposed relationships with extant taxa. If a fossil wood displayed araucarian radial tracheid pitting and araucarioid cross-fields, i.e. a wood anatomy similar to that of modern Araucariaceae, it had to be named *Araucar-ites* (Göppert, 1850; Tuzson, 1911) or *Araucario-xylon* (Kraus, 1870). As a matter of fact, such approach was still recently advocated (Yang et al., 2000). However, this way of naming fossils (identification *sensu* Bateman and Hilton, 2009) is clearly inspired by a fixist view of palaeontology, according which every fossil had to fit within a modern taxon, and is in complete contradiction with both the reality of

evolution and the ICBN. Practically, the name *Araucarioxylon* does not imply *per se* any systematic relationship with the Araucariaceae, nor a special type of anatomy. Etymology cannot compensate for a poor diagnosis or a poorly preserved type specimen.

Binomials have been used as a "short-hand" representation of a particular character suite (Bateman and Hilton, 2009). Therefore names like *Araucarioxylon biseriatum*, *A. parenchymatosum*, or *A. crasseradiatum* were given. Again these names are just labels on morphotaxa which are defined by a diagnosis and, if this is incomplete, by a type (provided it is well enough preserved, micron-scale details having to be observed).

Up to the 1980s, most authors used the taxonomical and nomenclatural framework proposed by traditional literature (see, for e.g., Kraus, 1870; Kräusel, 1949). Warnings about the invalidity or illegitimacy of the *Araucarioxylon* name were published (Gothan, 1904; Vogellehner, 1964), however, and the number of new *Araucarioxylon* binomials regularly decrease after 1920, becoming less frequent than the new *Dadoxylon* names (Fig. 2). Curiously, after the 1980s, the proportion of new *Araucarioxylon* binomials rose again (vs. *Dadoxylon*), and during the last decennia the former name completely dominated. Be that a matter of fashion, or a late consequence of Felix's proposal correlated to a decrease in the naming of Palaeozoic tracheidoxyls, anyhow *Dadoxylon* and *Araucarioxylon* are both invalid names. Now that it is clear that several extinct organisms have no extant equivalent, and that priority rules also the use of morphotaxa names, fossil wood nomenclature must be completely revisited (Philippe and Bamford, 2008).

At least 16 morphogenera were used for fossil wood having (or thought to have) an anatomy of the *Araucarioxylon* type, as defined above: *Agathoxylon* Hartig, *Araucariopsis* Caspary, *Araucarioxylon* Kraus in Schimper, *Araucarites* Endlicher *sensu* Göppert, *Araucaroxyylon* (as an orthographic variant, *vide* Fliche), *Baieroxyylon* Greguss, *Cedroxylon* Kraus in Schimper, *Cordaioxyylon*, *Cordaites*, *Cormarucarioxylon* Lignier, *Dadoxylon* Endlicher, *Dammarioxylon* Schultze-Motel, *Palaeoxyylon* Brongniart, *Peuce* Lindley & Hutton, *Pinites* Witham, *Platyspiroxylon* Greguss, *Pseudagathoxylon* Greguss, *Simplicioxyylon* Andreanzsky. In a previous nomenclatural study (Philippe, 1993), it was concluded that *Agathoxylon* Hartig is the earliest validly published name that can be used to name fossil woods with an *Araucarioxylon*-type anatomy. This proposition was either accepted, e.g. (Crisafulli et al., 2009; De Witt et al., 2009; Gnaedinger and Herbst, 2009; Ottone and Medina, 1995; Poole and Mirzaie Ataabadi, 2006; Salunkhe and Yagyani, 2006; Valenzuela et al., 1998; Zamuner and Falaschi, 2005), questioned (Falcon-Lang and Cantrill, 2001) or ignored, e.g. (Ash, 2003; Lucas et al., 2010; Morgans-Bell and McIlroy, 2005; Noll et al., 2005).

Of course, one may want to submit a proposal for the conservation of *Araucarioxylon*, but such would be difficult to defend given that *Dadoxylon* is used almost as frequently, that *Araucarioxylon* was neotypified by Andrews with a syntype (*A. carbonaceum* (Witham) Kraus) based on a poor sample (Witham of Lartington, 1833), and that even recently *Araucarioxylon* was used inconsistently (compare

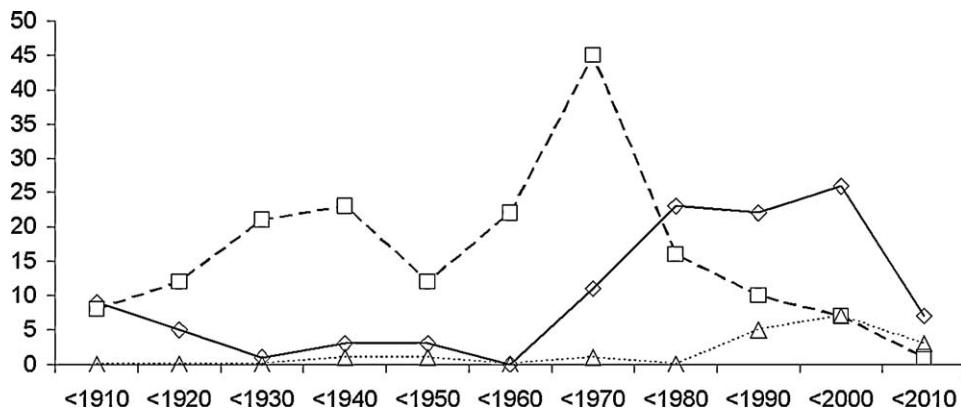


Fig. 2. Number of species described versus time for genera *Araucarioxylon* (diamond), *Dadoxylon* (square) and *Agathoxylon* (triangle). Note the sharp decline of total number after 2000.

Fig. 2. Nombre d'espèces décrites en fonction du temps pour le genre *Araucarioxylon* (losange), *Dadoxylon* (carré) et *Agathoxylon* (triangle). Noter le déclin brutal du nombre total après 2000.

e.g. Duan, 2000, and Wang et al., 2000). It is probably wiser to use *Agathoxylon*.

5. So, how many “*Araucarioxylon*” species?

It was exposed previously that the xylological variability of modern Araucariaceae is not relevant to the circumscription of fossil wood morphospecies. Palaeoxylological taxonomy must be based on character analysis and fossil wood disparity must be distributed among artificial taxa, ordered within a two-level only hierarchy.

The 428 species included in the database were taxonomically reappraised. For most of them (310) the protologue or a type could be accessed. Unfortunately, no decision could be made for 118 species, either as the original material was too poor or as we did not manage to get the original description. Among the 428 species of the database, 223 fit with the *Araucarioxylon*-type of wood as defined above. The distribution in time and space of this 223 species is very uneven: 12.3% were described from India, 10.5% from Germany and 9.1% from Russia, whereas three huge potential reservoirs of fossil wood diversity (Karoo formations, Madagascar and western USA) account as a whole for only 7% of the recorded species; 17% of the species are from the Permian, whereas only 7% from the Jurassic, which is however longer. The ratio of the number of species described vs. the duration is varying from stage to stage (Table 1), with clearly artificial peaks in the Permian and the Cretaceous. If, as supposed by Forey et al. (2004), about 50% of the existing fossil species are yet recorded, a conservative estimate of circa 800 species could be advanced.

Given the intrinsically small number of characters and of character states in the mature wood of the *Araucarioxylon*-type (Greguss, 1955; Jeffrey, 1913), and given the variability observed in fossil specimens, four hundred or more species is questioning. This forces to face a merger-splitter dilemma. A merger attitude would point out that, as no major xylological discontinuity can be observed among the fossil woods of the *Araucarioxylon*-type from at least the Early Permian (Wang et al., 2000) to the present, no morphospecies but one should be recognized. As the earliest wood described fitting with the *Araucarioxylon*-type, *Pinites brandlingii* Lindley & Hutton should probably be the basionym of that species (ICBN, art. 11.4). However, the corresponding new combination (*Agathoxylon brandlingii*) is not proposed here as the type material has not yet been reviewed.

Conversely, a splitter would argue that, as xylological variability can be distributed within several arbitrary classes, a large number of species can be recognized. For example, if four classes are made for radial pitting (mostly uniseriate, mostly biseriate, etc.), four classes for rings (lacking, weak, marked with gradual transition, marked with abrupt transition), four classes for rays (low, average, high, extra high), four classes for cross-fields (whatever the numerical values) and two classes for axial parenchyma (present vs. absent), then it is theoretically possible to recognize 512 species; and it would not be difficult to have much more.

The 1956 version of the code, by Lanjouw et al., 1956, used to define the form-species as entities “which for practical reasons need to be provided with binary names”. What should morphospecies be recognised for?

Table 1

Ratio of the number of recorded species with *Araucarioxylon* type of anatomy vs. duration of corresponding stage.

Tableau 1

Rapport du nombre d'espèces de type *Araucarioxylon* décrites, en fonction de la durée de la période correspondante.

Geological stage	Carboniferous	Permian	Triassic	Jurassic	Cretaceous	Tertiary
Duration (My)	60	48	51	54	81	65
Number of species recorded	9	39	25	17	66	13
Ratio	0.15	0.81	0.49	0.31	0.80	0.20

In the literature, wood morphospecies have been used for biostratigraphy, palaeobiogeography, palaeoecology, phylogeny, biodiversity analysis, etc. For all these applications, the wood species must have a limited extension in both time and space. Whatever the solution adopted to the merger/splitter dilemma, this condition of limited extension will not be fulfilled for woods of the *Araucarioxylon*-type.

Moreover, most anatomical features used up to now to distinguish species among this group are environmentally controlled. The seriation of radial pits and the number of cross-field pits are *pro parte* functions of tracheid width, itself a function of water availability. The ray height is, *pro parte* similarly, a function of the distance to the pith, and thus of trunk diameter. The wood of the Brazilian *Araucaria angustifolia* (Bertol.) Kuntze may have growth-rings or not depending of its provenance. These anatomical features are also genetically controlled, but this part of the determinism can only be deciphered with statistical analysis of numerous samples (Ilic, 1995). Such an approach is probably not realistically applicable to fossil wood.

6. Conclusion

Binomials, which are memory-friendly to most botanists, are conveniently used to handle fossil woods. In the first times of palaeoxylogy, when only a few specimens were studied, within what was then known as *Araucarioxylon*, anatomical variation was discrete. It was thus completely scientifically sound to establish morphospecies. Now that documented variability is more complete, there is apparently no reason anymore to distinguish species within this group of woods. As groundbreaking as it may appear, this conclusion is just the logical consequence of research progresses. There is a lot to learn about palaeobiogeography, palaeoecology or phylogeny using morphogenera only (Philippe et al., 2004, 2009). The latitudinal oscillation of the *Agathoxylon/Xenoxylon* Exclusion Line in Eurasia during the Mesozoic is potentially an interesting terrestrial climate proxy (Oh et al., *in press*). The conclusion that only one species should be recognized within *Agathoxylon* does not throw the interest of palaeoxylogy back into question, but rather urges the invention of postdescriptive palaeoxylogy.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.crpv.2010.10.010.

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