

A key to morphogenera used for Mesozoic conifer-like woods

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Abstract

There are many problems encountered in the literature in fossil wood taxonomy and nomenclature because the early descriptions and typifications do not match up to the rigors of modern methods and the much larger database that we now have. Redescriptions of specimens and misinterpretation of diagnoses have compounded the problems. In an attempt to correct these problems, we have reviewed the literature for the Mesozoic conifer woods, checked type material wherever possible and listed the most up to date and correct generic names (according to the IBCN). To make wood taxonomy easier to apply we have provided some clarity on terminology not covered by the IAWA Committee [IAWA Committee, 2004. IAWA list of microscopic features for softwood identification. IAWA J. 25, 1–70.] and produced a key for identification.

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1. Introduction

Since Darwin's times not only evolutionary studies, but also palaeoclimatology and palaeoecology, have mainly been based on marine organisms. The marine fossil record has the definitive advantage of being more ubiquitous and continuous when compared with the terrestrial fossil record which is often discontinuous both in time and space. Today, however, terrestrial ecosystems have awakened a renewed interest among palaeontologists. The recent burst of interest for past terrestrial climates has been catalysed by the threat of global warming and its dire consequences. Dinosaur-

omania has captured the attention of young and old with the marvellous multimedia animations available to everyone. Subsequently the understanding that evolution among terrestrial organisms could be quite peculiar, especially among higher plants, has also contributed to renewed interest for past terrestrial ecosystems.

Palaeobotanical contributions to these fields of research are significant, with wood being involved in modern approaches like organic geochemistry (Hesselbo et al., 2003; Hautevelle et al., 2006; Marynowski et al., 2007), and growth ring analysis (Creber and Francis, 1999; Falcon-Lang, 2000a,b, 2003). More traditional, taxonomy based approaches, such as NLR (Nearest Living Relative, Herendeen and Jacobs, 2000) and Coexistence Approach (Böhme et al., 2007) also gave good results, especially when integrating results into palaeobiogeographical syntheses (Philippe et al.,

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2003). Petrified wood, a common fossil and much better distributed than foliar or reproductive organ remains among sediments, less reworked than palynomorphs and representing on average 80% of any terrestrial ecosystem biomass, is a particularly suitable material for this kind of study (Martin-Closas and Gomez, 2004; Philippe et al., 2004).

Unfortunately fossil wood taxonomy and nomenclature, based mainly on pre-1930 literature, is a nightmare. As stated once by an anonymous reviewer “every example of bad practice one could possibly imagine can be found somewhere in the literature on fossil wood”. This prevents wood researchers from using a nomenclatural approach (Creber, 1972; Chapman and Smellie, 1992), or leads them to use review papers which have long been known to be out-dated, particularly that of Kräusel (1949). Several recent interesting studies pointed out the need for nomenclatural reappraisal (see e.g. Morgans, 1999; Harland et al., 2007). Erroneously sceptical statements such as, “It seems likely that wood anatomy nomenclature will always be a source of controversy,” (Jones et al., 2002) are mainly a result that very few authors really proceed to extensive literature survey before naming their specimens. Wood distortion and other tricks played by fossilisation processes are another frequent source of problems when turning to wood characterization (Gerards et al., 2007).

Over the past few years we have advocated that fossil wood taxonomy and nomenclature be reappraised (Philippe, 1995; Bamford and Philippe, 2001) and have undertaken partial revisions (Bamford et al., 2002; Philippe et al., 2002). Although we are of the opinion that we have achieved much towards sorting out the taxonomic problems, wood identification is still cumbersome. Here we set out a key to the genera of some Mesozoic conifer-like woods, more specifically Mesozoic pycnoxylic tracheidoxyls (Creber, 1972). These are fossil woods in which the woody cylinder is not dissected by thick parenchymatous wood-rays (so-called manoxylic woods, for example *Hermanophyton* Arnold or *Rhexoxylon* Bancroft), and composed mainly of axial tracheids and parenchymatous wood-rays, with a minor proportion of other cell types (axial parenchyma, axial and/or radial resin canals, ray-tracheids, etc.). These woods are homoxylic, i.e. earlywood cell axial diameter is uniform, with only a size-gradient between early- and latewood. On average pycnoxylic tracheidoxyls make up 99% of Mesozoic wood assemblages of pre-Cenomanian age, and commonly still dominate assemblages during the Late Cretaceous. Of course, while coping with millimetric specimens, a palaeoxylologist cannot be sure that it is not an isolated part of a

manoxylic plant. With modern wood, however, the manoxylic condition is usually unmistakable for pieces bigger than 0.5 cm³.

2. Methodology

2.1. Time interval considered

To the best of our knowledge we have considered all the genera that have been quoted for the Mesozoic. Since our focus has been on the Jurassic–Early Cretaceous period, we could be unaware of some publications about Triassic or Late Cretaceous woods, but we are certain that this is a small probability. Several generic names are considered here which have not yet been included in the Index Nominorum Genericorum (Farr and Zijlstra editors, electronic version at <http://ravenel.si.edu/botany/ing/>, accessed 3rd. March 2007), despite the fact they have been validly published.

2.2. Taxonomic principles

For any traditional palaeobotanical taxonomic study, the first step is to use the literature and decide to which taxon the new specimen belongs based on the protologues and the various subsequent emendations. Then the name that should be used for each recognized taxon is determined. Eventually, typification problems are dealt with, and synonymy lists set up. New taxa are described if required.

This kind of approach was regularly applied to Mesozoic tracheidoxyl xylogy, but in a way which rather increased confusion. There are several reasons for this. While trying to circumscribe what the taxa are, many authors have explicitly considered etymology as diagnostic, sometimes even against type and protologue indications.

In etymological wood anatomy, etymology is used at two levels, that of morphotaxa and that of descriptive terms. For example, the morphogenus *Cupressinoxylon*, is used for tracheidoxyls with an anatomy similar to that of recent *Cupressus* (or of recent *Cupressaceae*?, it is not always clear, see e.g. Vaudois and Privé, 1971). Moreover in the diagnoses terms like “cupressoid” or “abietinean” are used with reference to recent taxa and not given a clear definition. Considering etymology as diagnostic not only is against the ICBN (Preamble I reads: “the purpose of giving a name to a taxonomic group is not to indicate its characters or history ...”), but has also led to confused situations. For example, *Protopodocarpoxyton* Eckhold is a genus which was used by several authors to assign tracheidoxyls with mixed

type of radial pitting (araucarian and abietinean) and cross-field pits of the podocarpoid type. Since this last term “podocarpoid” is interpreted differently by the different authors, *Protopodocarpoxylo*n was used for very different woods. Moreover, one of its syntypes has araucarioid cross-fields (Lauverjat and Pons, 1978), which led to the inclusion in *Protopodocarpoxylo*n of even more different woods. Only a minority of palaeoxylological papers give a clear definition of or a reference to the terms they use, and even those authors mostly ignored other basic papers with well illustrated and defined terminology (such in e.g. Slyper, 1933; Greguss, 1955; Vogellehner, 1967a, 1968; Marguerier and Woltz, 1977; Chavchavadze, 1979; Garcia Esteban et al., 2002).

Tracheidoxyl taxonomy is a parataxonomy. This should not be based on hypothetical systematic relationships and descriptive terms defined only by their etymology. If woods of recent conifers were to be considered, a parataxonomy would not fit with normal taxonomy, even at generic level. For example, when considering cross-field pits some *Podocarpus* species would come closer to some Taxodiaceae than to other Podocarpaceae (Marguerier and Woltz, 1977). Moreover, we consider as unrealistic the assumption that the distribution of xylological variability among modern taxa reflects a situation which went unchanged all through the Mesozoic and Cenozoic. With no fossil record, botanists would have had to await the discovery of *Wollemia nobilis* in 1995 to learn that a member of the Araucariaceae could have leaves strongly reminiscent of *Cephalotaxus* (Cephalotaxaceae) or *Cunninghamia* (Taxodiaceae). For these reasons we think that tracheidoxyl parataxonomy should be autonomous, rest on clearly defined descriptive terms and avoid any etymology-based inference. This position is not new (see e.g. Nicol, 1834; Vogellehner, 1967a, 1968), nor extraordinary (see e.g. Mikhailov et al., 1996, about fossil eggshell parataxonomy, or Märss, 2006, about early vertebrates remains).

2.3. Procedure

Firstly we considered all genera to which Mesozoic tracheidoxyls have been assigned to date in the literature. We thus excluded genera where the diagnosis included features of secondary xylem and/or some other tissues (primary xylem, pith, phloem, bark, etc.) or morphological features (shoot size, branching, etc.). For example genera like *Woodworthia* Jeffrey, *Arboramosa* Savidge et Ash or *Svalbardoxylon* Vogellehner were not taken into account. The result of this review is a list of

111 generic names (Appendix A). This does not preclude that other genera already known in other stages will never be found in the Mesozoic.

The second step was to understand the descriptive terms used in original diagnoses. For this we checked

Table 1
Definitions for terms that are used here but are not in the IAWA's list of anatomical features of softwoods (2004)

Term	First quoted	Definition
Phyllocladoid	Kräusel (1917)	Fenestroid pit, usually single in a cross field, with pointed to sub-pointed tips, without areola
Podocarpoid	Gothan (1905)	An oculipore with a narrow slit-like sub-vertical aperture
Sanio rims or <i>Sanio's Querleisten</i>	Sanio (1873)	Band-like thickenings of the middle lamella, localised between two adjacent tracheid pits, also called crassulae
Araucarian radial pitting	Eckhold (1921)	State where more than 90% of pits on the radial wall of tracheids are contiguous with neighbouring pits; in this state pits are often somewhat flattened and when multiseriate are always alternately arranged; Sanio rims absent
Abietinean radial pitting	Eckhold (1921)	State where radial pits are separate, or at most 10% of radial pits are contiguous with one of the two adjacent pits or, if more crowded, are separated by Sanio rims; in this state pits are usually rounded. When biseriate or pluriseriate the pits are opposite. Sanio rims not always present
Mixed (or transitional) type of radial pitting, <i>Übergangsformen</i>	Eckhold (1921)	State where none of the above conditions are realized
Xenoxylean radial pitting	Müller-Stoll (1951)	State where radial pits are much flattened, more than twice as wide as high, contiguous with neighbouring pits, like in <i>Xenoxylon latiporosum</i> Gothan
<i>Abietineentüpfelung</i>	Gothan (1905)	Rounded pits, areolate or not, occurring on the transverse (tangential) wall of ray cells. Note: Kräusel's use of this term is not the same as Gothan's
<i>Juniperustüpfelung</i>	Gothan (1905)	Elongated pits, usually not areolate, occurring on the transverse wall of ray cells

the original material as much as possible, and if this was not available to us then the original illustration had to suffice. The use of terms proved to be inconsistent in the literature. One of the most inconsistently used terms is “podocarpoid”, which is applied to a type of cross-field pit. This term is not defined in IAWA compendium, albeit it was regularly used by palaeoxylogists since its first use by Gothan in 1905 (Marguerier and Woltz, 1977). The features originally used by Gothan to distinguish “podocarpoid” from “cupressoid” cross-field pits (i.e. narrow slit-like subvertical aperture) are considered in the IAWA compendium to fall with the variation range of the latter, making, “podocarpoid” a synonym of “cupressoid”. Not all modern *Podocarpus* species have all of the cross-field pits belonging to Gothan’s “podocarpoid” type (Marguerier and Woltz, 1977). This should not, however, limit the morphotaxon *Podocarpoxylon*, which is after all a concept created for fossil taxa, particularly since *Podocarpus* itself is a taxonomic choice (i.e. a genus that could be split or merged). Fossil wood anatomists are free to use or not to use *Podocarpoxylon* as diagnosed by Gothan. But they should be aware that the data they produce may not always be handled with a good knowledge of their inherent limits. We consider this case as quite typical of the dilemma into which a fossil wood anatomist is regularly plunged, as strictly applying nomenclatural rules sometimes leads to misunderstandings.

In creating the key for fossil genera we have had to use a unified terminology. For this we maintained the first definition given, to our knowledge, in literature. This largely fits with the well illustrated compendium set up by the IAWA committee (2004), to which the reader is referred. For the palaeoxylogy terms not in the compendium, the reader is referred to Table 1 and Figs. 1 and 2. Two of the best recent illustrated syntheses of softwood anatomical features are covered in Heinz (2004) and Garcia Esteban et al. (2002).

Palaeoxylogists have paid a lot of attention to the spacing of pits on tracheid radial walls, as well as to the pit outline (rounded vs. flattened). The IAWA compendium does not list those features. We have chosen to consider them because in several recent woods, e.g. among Podocarpaceae, pit spacing and disposition are very variable. Eckhold (1923) originally defined an “*araukarioide Typus*” and an “*Abietoide Typus*” to describe the type of pitting on the radial walls of tracheids. Those terms have been variously translated as “araucarian” and “abietinean” or “araucarious” and “abietineous”. As the Eckhold’s “-oid” suffix is mainly used now for types of cross-field pits, we preferred to use the most frequently used pair, i.e. “araucarian” and

“abietinean” for describing the pitting on tracheid radial walls. The intermediate type of radial pitting was originally named “*Übergangstypus*” by Eckhold (1923), which was latter translated as “transitional type”, “mixed type” and “generalized type”. Again we have adopted the most frequently encountered term in the literature, namely “mixed type”, for this character state.

The third step was to check whether the holotypes fit the original diagnosis. Indeed, in cases of any doubt, which is the case for most morphogenera described during the nineteenth Century as their original diagnosis is usually incomplete, the ICBN recommends turning to the type (ICBN, 2006, principle II and art. 7.9, but see also art. 7.2). If a type species was not designated we proceeded with typification (see *Ginkgoxylon* entry in Appendix A). If the type species was in contradiction with the diagnosis we considered corresponding names as “recommended not to be used”, although some of these genera are validly published (some similar cases are treated in Bamford et al., 2002; Philippe et al., 2002). Some taxonomic and nomenclatural notes are given in Appendix A.

Eventually we built a taxonomic key for the fifty-six morphogenera that had passed the third step. This key, therefore, is established on the basis of the features listed in original diagnoses and/or observed in the nomenclatural types of the genera only, irrespective of the fact that quite different woods may have been included afterwards into those genera, and that significant emendation might have been subsequently proposed (usually to fit the author’s taxonomical views rather than better circumscribe taxa). Again, etymology was not considered diagnostic, nor for the assignment of a sample to a taxon, nor for the definition of a technical term. This key is not free of any taxonomical judgement. We tried, however, to keep this to a minimum and have used it mainly to discard old and almost forgotten names (see Appendix A). Nevertheless, the fact that a genus is keyed here does not imply that we agree completely that it is wise to distinguish it. Since most of the protologues are not easy to obtain from all libraries, and not all anatomists are multilinguists, we have provided, in Appendix B, an English translation of the original diagnoses of the fifty-six genera.

Before using this key we would like to urge readers to pay special attention to fossilisation tricks. These are frequent and, albeit we cannot be exhaustive here, we would like to point out three main causes of error: a)-by fossil wood, areolate pits are quite often preserved as inner casts of pit chambers, this modifies greatly the aspect of radial pitting (on this important point see the

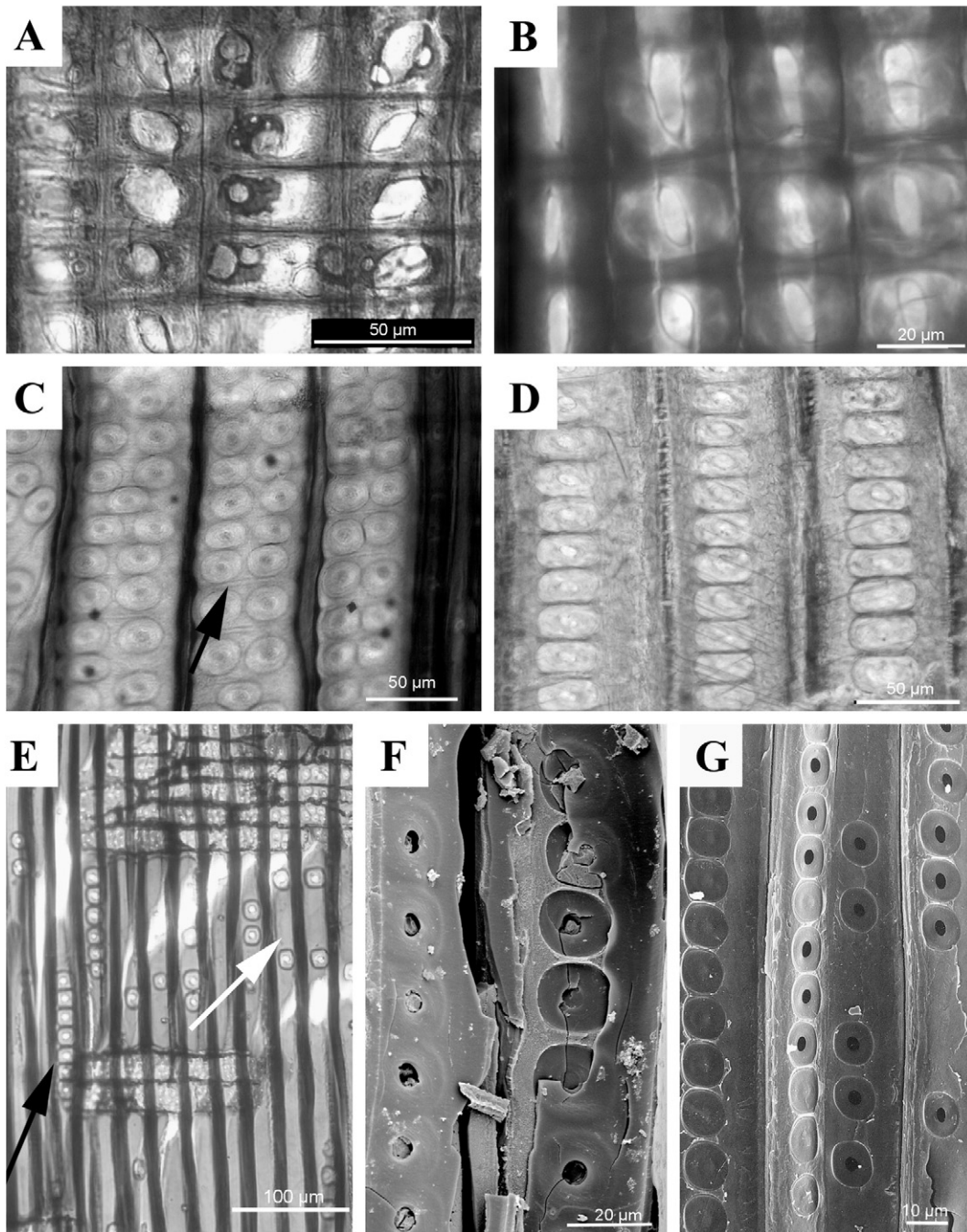


Fig. 1. A) *Xenoxylon phyllocladoides* Gothan, unknown age, König–Karl's Land, phyllocladoid oopores; B) *Xenoxylon phyllocladoides* Gothan, unknown age, König–Karl's Land, podocarpoid oopores; C) *Cedroxylon cedroides* Gothan, Early Cretaceous, Svalbard, Sanio rims (black arrow) and biseriata abietinean radial pitting; D) *Xenoxylon latiporosum* Gothan, unknown age, Svalbard, xenoxylean radial pitting; E) *Brachyoxylon notabile* Hollick *et* Jeffrey, Late Cretaceous of Kreischerville (New-York), mixed type of radial pitting with both araucarian (black arrow) and abietinean (white arrow) uniseriate radial pitting; F) *Agathoxylon* sp., Early Cretaceous of the Phu Phan Range (Thailand), two adjacent tracheids both with araucarian radial pitting but with different preservation (note how faintly the areola is marked in the tracheid on the left); G) *Brachyoxylon* sp., Early Jurassic of Mende (France), three tracheids, the one in the middle with two sub-radial faces (as it was alternate with adjacent tracheids), one with araucarian radial pitting, the other with abietinean radial pitting.

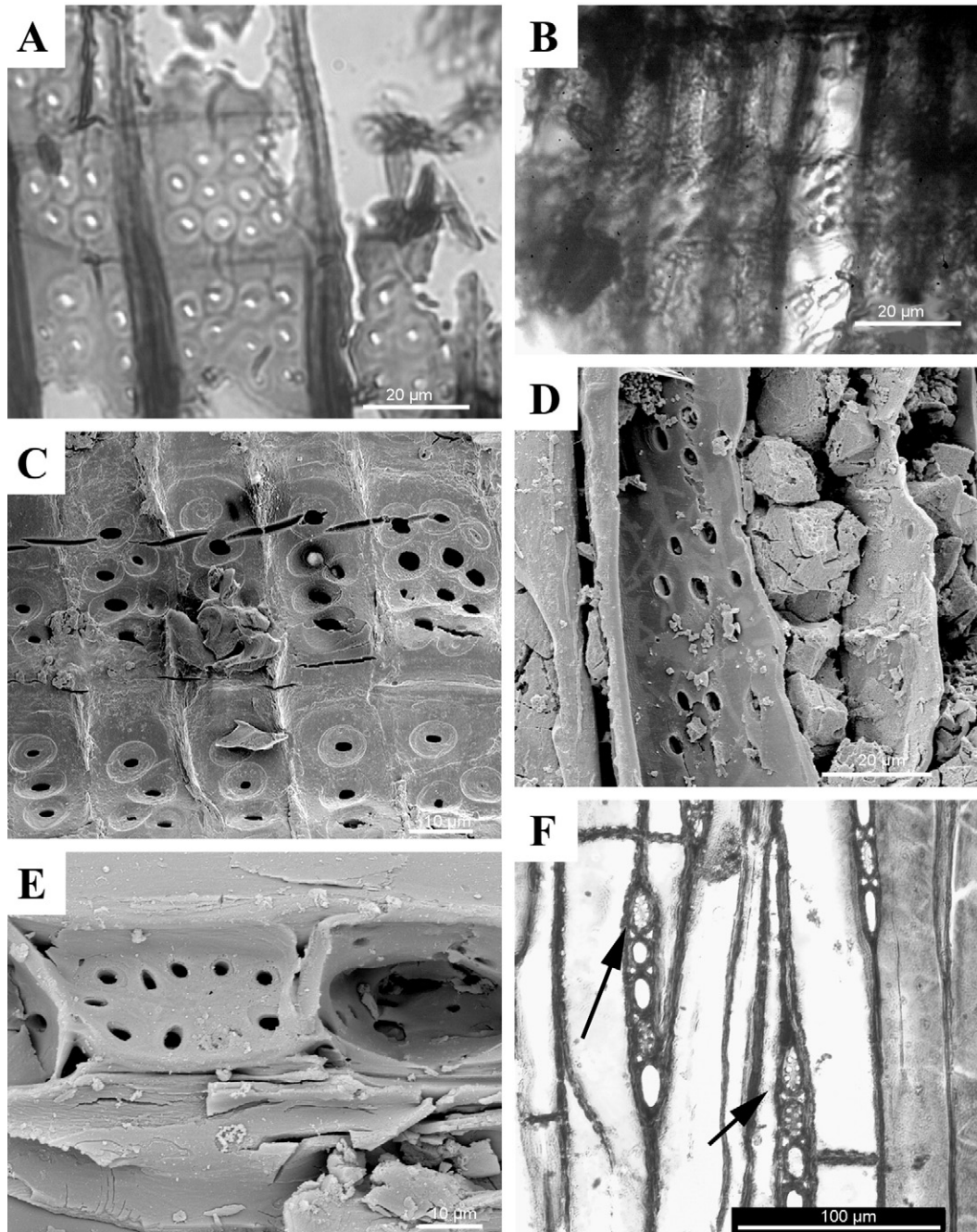


Fig. 2. A) *Brachyoxylon notabile*, Hollick *et* Jeffrey, Late Cretaceous of Kreiserville (New-York), well preserved araucarioid cross-fields in light microscopy; B) *Agathoxylon* sp., Middle Jurassic of Orme (France), poorly preserved araucarioid cross-fields in light microscopy; C) *Agathoxylon gardonense* (Crié) Philippe, Late Cretaceous of Charente (France), well preserved araucarioid cross-fields in SEM microscopy; D) *Agathoxylon* sp., Early Cretaceous of the Phu Phan Range (Thailand), poorly preserved araucarioid cross-fields in SEM microscopy; E) undetermined, Early Cretaceous of the Phu Phan Range (Thailand), *Abietineentüpfelung* in SEM microscopy; F) *Protopiceoxylon extinctum* Gothan, unknown age, Svalbard, *Abietineentüpfelung* (black arrows), note the septate tracheids.

still authoritative chapter by Gothan, 1905: 21, and his concept of *Steinkerne* preservation); b)- by charcoal and some types of lignite the pit aspect can be strongly

modified (see e.g. Gerards *et al.*, 2007), as pit apertures usually widen during the fossilisation process; c)- crystal fractures along cleavage planes, contact lines

between two adjacent crystals or grooves in tracheid tertiary walls are regularly misidentified as spiral thickenings. We also emphasize here that at least two dozen well-preserved cross-fields and tracheids, distributed all through the growth-ring, must be observed before making any assumption about generic attribution.

3. Key for Mesozoic homoxylous pycnoxylic woods

- 1 more than 30% of rays bi- or pluriseriate for most of their height ... 2, 2'
- 2 radial pits never scalariform ... *Yatsenkoxylon* Shilkina
- 2' radial pits at least locally scalariform ... 3, 3'
- 3 transverse walls of ray cells distinctly pitted (*Abietineentüpfelung*) ... *Sahnioxylon* Bose et Sah
- 3' transverse walls of ray cells thin and unpitted ... *Scalaroxylon* Vogellehner
- 1' all rays uniseriate, except for some local biseriation ... 4, 4'
- 4 radial pits at least locally scalariform ... 5, 5'
- 5 terminal walls of ray cells pitted (*Abietineentüpfelung*) or with thickenings and/or ray tracheids present ... 6, 6', 6''
- 6 biseriate rays numerous, radial pitting araucarian, concentric layers of axial parenchyma all through the growth-ring, early- and late-wood little differentiated ... *Lhassoxylon* Vozenin-Serra et Pons
- 6' biseriate rays numerous, rounded radial pits common, sharp limit and strong contrast between early- and latewood ... *Sahnioxylon* Bose et Sah
- 6'' rays all strictly uniseriate, rounded radial pits rare ... *Phoroxylon* Sze
- 5' all ray cell walls thin and smooth, unpitted, no ray tracheids ... *Paradoxoxylon* Kräusel
- 4' radial pits never scalariform ... 7, 7'
- 7 axial parenchyma present, clearly associated with the rays like in *Ginkgo biloba* ... 8, 8'
- 8 axial parenchyma not inflated, some tracheid tips bent radially along rays like golf clubs ... *Baieroxylon* Greguss
- 8' axial parenchyma inflated ... *Ginkgoxylon* Saporta
- 7' axial parenchyma present or absent, neither particularly associated with the rays nor inflated ... 9, 9'
- 9 terminal walls of ray cells pitted or with thickening and/or ray tracheids present ... Group A

9' all ray cell walls thin and smooth, unpitted ... 10, 10', 10''

10 araucarian pitting on radial wall of tracheids (i.e. with more than 90% of the pits contiguous, mostly deformed at contact, while biseriate or pluriseriate always clearly alternate, rarely subopposite; rare isolated pits are possible, especially in narrowest tracheids; Sanio rims absent; woods with radial pitting partially or completely xenoxylean are included here) ... Group B

10' abietinean pitting on radial wall of tracheids (i.e. with more than 90% of the pits separate, rounded, while biseriate or pluriseriate always clearly opposite; some contiguous pits are possible, and even locally short chains; rosette-like clusters of 3-4 pits sometimes encountered) ... Group C

10'' pitting on the tracheid radial wall not clearly belonging to one of the types above ... 11, 11'

11 various tertiary thickenings present on tracheids walls, no *Abietineentüpfelung* ... 12, 12'

12 callitroid thickenings abundant, Sanio rims absent ... *Protocallitrixylon* Yamazaki et Tsunada:

12' callitroid thickenings rare, Sanio rims present ... *Protelicoxylon* Philippe

11' no such thickenings ... Group D.

3.1. Group A (terminal wall of ray cells pitted to nodular)

- 1 araucarian, or araucarian and abietinean pitting on the radial walls of tracheids ... 2, 2', 2''
- 2 both vertical and horizontal non-traumatic resin-canals present ... *Palaeopiceoxylon* Kräusel
- 2' vertical resin canals only present in non-traumatic wood... 3, 3'
- 3 ray tracheids present, cross-fields with oculipores ... *Protopiceoxylon* Gothan; see also *Keleleerioxylon* Shilkina (the radial pitting of which is quite mixed).
- 3' ray tracheids absent, oopores at least in some cross-fields ... *Protopinuxylon* Eckhold
- 2'' resin canals absent, except occasionally for some traumatic canals ... 4, 4'
- 4 *Juniperustüpfelung* on ray cell transverse walls ... *Protojuniperoxylon* Eckhold
- 4' *Abietineentüpfelung* on ray cell transverse walls ... 5, 5'
- 5 radial pitting of mixed type, with frequent to dominant abietinean pitting *Araucariopitys*

Hollick *et* Jeffrey (Laurasian woods); *Thylloxyton* Gothan (a wood with traumatic resin pockets in rays).

5' radial pitting araucarian or slightly mixed type
... *Planoxyton* Stopes (Gondwanan woods)

1' pitting on the radial wall of tracheid definitely abietinean, with few exceptions ... 6, 6', 6''

6 resin canals absent, except occasionally for some rare traumatic canals, *Juniperustüpfelung* present ... *Juniperoxyton* Houlbert

6' only vertical resin canals regularly present, *Abietineentüpfelung* present *Keteleerioxylon* Shilkina (*Pinoxyton* Knowlton could key here, but the circumscription of this genus is dubious).

6'' both vertical and horizontal resin canals present, *Abietineentüpfelung* present ... 7, 7'

7 earlywood cross-field pits oopores, small or large, resin canal epithelial cells thin-walled or thick-walled ... *Pinuxylon* Gothan

7' cross-field pits never oopores, resin canal epithelial cells thick-walled ... 8, 8'

8 Ray tracheid tips elongated, crooked, overlapping one another ... *Laricioxyton* Greguss

8' Ray tracheid tips short, straight, not overlapping ... *Piceoxyton* Gothan

3.2. Group B (araucarian or xenoxylean radial pitting)

1 cross-fields of the araucarian type, i.e. with numerous contiguous unordered cupressoid to taxodioid oculipores ... 2, 2'

2 spiral thickening common throughout the wood ... *Prototaxyton* Kräusel *et* Dolianiti

2' spiral thickening absent ... 3, 3'

3 end wall of ray cells perpendicular or sub-perpendicular to the ray ... *Agathoxyton* Hartig; *Paratetraclinoxylon* Süß *et* Schultka (these two genera are very similar according to their original descriptions).

3' end wall of ray cells at least locally strongly oblique, 95% of radial pitting in long uniseriate chains of contiguous pits which do not extend across whole tracheid breadth ... *Simplicioxyton* Andreanszky

1' cross-fields different ... 4, 4'

4 all earlywood cross-fields occupied by one, very rarely two, large oopore 5, 5', 5''

5 oopore rectangular, occupying all or almost all the cross-field, even in the latewood, radial pitting xenoxylean ... *Xenoxylon* Gothan

5' oopore more phyllocladoid (i.e. pointed and oblique), usually somewhat bordered in the latewood ... *Protophyllocladoxylon* Kräusel

5'' oopore round and narrowly bordered all around ... *Circoporoxylon* Kräusel

4' not all earlywood cross-fields with a single large oopore ... 6, 6', 6''

6 all oculipores taxodioid, i.e. with an aperture exceeding the width of one border ... [*Metataxodioxylon*] Nadjafi (not a validly published name).

6' earlywood cross-fields with an oopore, or with one (two) oculipores, or with numerous intermediate forms. ... *Metapodocarpoxyton* Dupéron-Laudoueneix *et* Pons

6'' all oculipores cupressoid i.e. with a slit narrower than one margin ... 7, 7'

7 tertiary thickenings absent, cross-fields araucarioid ... *Agathoxyton* Hartig

7' tertiary thickenings present, cross-field not araucarioid ... *Protocallitrixylon* Yamazaki *et* Tsunada.

3.3. Group C (abietinean radial pitting)

1 in the earlywood oculipores always cupressoid, i.e. with a slit narrower than the margin, spaced, often ordered in rows and columns ... *Cupressinoxylon* Göppert (nom. cons. vide Bamford *et* al., 2002); *Tetraclinoxylon* Grambast; *Widdringtonoxyton* Penny; these three genera are separated only by quantitative features (Vaudois and Privé, 1971: 66) which by fossilisation process can be modified.

1' in the earlywood oopores to taxodioid oculipores (i.e. with the aperture wider than one margin), usually arranged irregularly ... 2, 2'

2 earlywood cross-fields in normal wood with unbordered oopores (a faint border exceptionally occurring), these usually less than four per field ... 3, 3'

3 thickenings abundant and various (spirals, trabeculae, callitroid thickenings) ... *Perisemoxylon* He *et* Zhang

3' tertiary thickenings absent ... 4, 4'

4 one (two) large elliptic oopore, usually oblique and pointed, per earlywood cross-field ... *Phyllocladoxylon* Gothan

4' one (two), rounded or at most ovoid oopore per earlywood cross-field, never with an oblique pore ... *Microcachryxyton* Torres *et* al., *Circoporoxylon* Kräusel (two genera with taxonomically very similar types and diagnoses)

- 2' earlywood cross-fields with oculipores ... 5, 5', 5''
- 5 spirals occurring regularly throughout the wood (beware that diagenesis artefacts are regularly being confused with true spirals) ... *Taxaceoxylon* Kräusel *et* Jain; *Oguraxylon* Nishida (the later with occasional traumatic resin canals)
- 5' spiral thickenings absent, radial resin canals present ... *Turkestanioxylon* Khudaiberdyev
- 5'' both resin canals and spiral thickenings absent (the following part of the key is only tentative) ... 6, 6'
- 6 cross-field pits numerous, often contiguous and alternate ... *Semicircoporoxylon* Süß *et* Schultka.
- 6' cross-field pits mostly less than four, spaced, sometimes ordered in rows ... 7, 7'
- 7 oculipores in earlywood cross-fields of the taxodioid type, i.e. with a tangential aperture, wider than one margin (but not bordered oopores or circopores), usually more or less horizontal ... *Sequoioxylon* Torrey; *Taxodioxylon* Hartig (two genera with very similar types and diagnoses).
- 7' oculipores not as above ... *Podocarpoxyton* Gothan; *Widdringtonoxylon* Penny (their protologues make these two genera very similar)

3.4. Group D (mixed type of radial pitting)

- 1 in the earlywood oculipores always cupressoid, i.e. with a aperture narrower than one margin ... 2, 2'
- 2' cross-fields of the araucarian type, i.e. with contiguous unordered and often alternate oculipores ... *Brachyoxyton* Hollick *et* Jeffrey
- 2' earlywood oculipores spaced in the cross-fields, most of the time regularly ordered, never clearly alternate ... 3, 3'
- 3 abietinean and araucarian pitting in different concentric zones *Zonaloxylon* Grauvogel-Stamm, Meyer-Berthaud *et* Vozenin-Serra
- 3' different types of radial pitting distributed through the wood ... here would key the concept usually called *Protocupressinoxylon* auct. (albeit almost all Mesozoic specimens assigned to this genus will key out as *Brachyoxyton*, see *Protocupressinoxylon* entry in Appendix A).
- 1' in the earlywood cross-field oopores to taxodioid oculipores (i.e. with an aperture wider than one margin) ... 4, 4'
- 4 earlywood cross-fields heterogeneous, with either a large oopore or a bordered oculipore with a

- narrow subvertical aperture ... *Metapodocarpoxyton* Dupéron-Laudoueneix *et* Pons
- 4' earlywood cross-field homogeneous ... 5, 5', 5''
- 5 only pointed oopores in the earlywood cross-fields ... *Protophyllocladoxylon* Kräusel; as the genus type displays some mixed radial pitting several authors include in *Protophyllocladoxylon* fossil woods with a *Phyllocladus*-like anatomy
- 5' at least some xenoxylean pitting on tracheid radial wall ... *Xenoxylon* Gothan
- 5'' Features in 5 and 5' absent ... 6, 6'
- 6 end walls of axial parenchyma nodular ... *Protoglyptostroboxylon* He Dechang
- 6' end walls of axial parenchyma smooth or axial parenchyma missing (the following part of the key is only tentative, as the meaning of terms is not consensual) ... 7, 7', 7''
- 7 pits in earlywood cross-fields of the taxodioid type, i.e. with a tangent aperture, wider than one margin (but not bordered oopores or circopores), usually more or less horizontal ... *Protaxodioxylon* Bamford *et* Philippe
- 7' pits in earlywood cross-fields at least locally oopores, with at most a faint border ... 8, 8'
- 8 large window-like pits in the earlywood cross-fields ... *Protosciadopityoxylon* Zhang, Zheng *et* Ding; *Protocircoporoxylon* Vogellehner [both with large subrectangular oopores in earlywood, probably taxonomical synonyms]
- 8' only small to medium sized oopores in earlywood cross-fields ... *Primopodocarpoxyton* Süß *et* Schultka
- 7'' pits in earlywoods not as in 7 or 7' ... *Protopodocarpoxyton* Eckhold (*nom. cons.*, vide Philippe *et al.* 2002); *Semipodocarpoxyton* Süß *et* Schultka (these genera are very probably taxonomical synonyms).

4. Conclusions

Although the formulation of this taxonomical key represents several years of work, and much commitment to advocate the application of ICBN (2006) to fossil wood, the key we have produced is not really revolutionary. Several parts of our key can be found in almost identical form in works like those of Slyper (1933) or Vogellehner (1967a, 1968). It is however completely different from Kräusel's key (1949) which does not respect the ICBN in countless cases, yet unfortunately served as a reference for so many later works. We include here several genera that had not

previously been considered in a general key. Furthermore, we have checked the nomenclatural validity of each genus included in our key. We are aware that, as in any taxonomical approach, our key is just a “state of the art”, and that some taxonomical points can still be discussed and revised. It is our sincere hope, however, that the key will help colleagues to name fossil woods in a more consistent manner, and that it will boost palaeoecological studies in the numerous fields for which palaeoecology is relevant, from gymnosperm phylogeny and palaeobiology to palaeobiogeography and palaeoecology.

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Appendix A. A list of generic names used for Mesozoic pycnoxylic tracheidoxyls, with some nomenclatural and taxonomical notes

Names given between square brackets are not validly published. Unless otherwise clearly specified, all names are considered as validly published, legitimate and accepted.

Format: genus name, author, (the first mention of a Mesozoic occurrence if different from the protologue) — notes

Agathites Tuzson — a junior taxonomic synonym of *Agathoxylon* Hartig.

Agathoxylon Hartig — albeit the type material might be lost (Philippe, 1993), we prefer not to propose a neotypification yet.

Anomaloxylon Gothan non Felix — a junior homonym of *Anomaloxylon* Felix and a taxonomic synonym of *Protocedroxylon* Gothan (Philippe and Cantrill, 2007).

Araucariocaulon Lignier — a junior taxonomic synonym of *Agathoxylon* Hartig.

Araucariopitys Hollick et Jeffrey (Hollick and Jeffrey, 1909: 54) — the original *descriptio generico-specifica* by Jeffrey (1907) included morphological and pit features, and expressed doubts about the relevance of the name for isolated secondary xylem. It was only in 1909 that this name was used for a “type of wood” (Hollick and Jeffrey, 1909: 54) together with *Brachyoxylon*.

[*Araucariorhyzoxylon*] Shilkina et Yatsenko-Khmelevskii — not a validly published name (*nom. nudum*).

Araucarioxylon Kraus — not a legitimate name (Philippe, 1993).

Araucarites Presl in Sternberg (Göppert, 1850: 158) — should not be used for tracheidoxyls, see Zijlstra and Van Konijnenburg-van Cittert (2000).

Araucarites Tuzson — a junior taxonomic synonym of *Agathoxylon* Hartig.

Arctoxylon Kräusel — replacement name proposed for *Anomaloxylon* Gothan; type seen, a taxonomical synonym of *Cedroxylon transiens* Gothan (Philippe and Cantrill, 2007) and thus *Arctoxylon* Kräusel is a taxonomical synonym of *Araucariopitys* Hollick et Jeffrey.

Baieroxylon Greguss (Greguss, 1961: 142).

Brachyoxylon Hollick et Jeffrey (Hollick and Jeffrey, 1909: 55).

Callitrixylon Greguss (Greguss, 1969: 102) — invalid name (Philippe et al., 1999a), used for an indeterminate Liassic wood specimen (Barbacka and Philippe, 1997); better not to be used.

Cedroxylon Kraus — better not use for Mesozoic woods (Bamford and Philippe, 2001).

Circoporoxylon Kräusel — in spite of the fact that several species were mentioned in the protologue without designation of a holotype this generic name was validly published by Kräusel in 1949 and is acceptable since this was prior to 1 January 1958 (ICBN art. 37.1). This name was quoted several times (e.g. Müller-Stoll, 1951; Boureau, 1956; Schultze-Motel, 1956) before it was typified by Kräusel and Jain (1964).

Colymboxylon Hartig — a taxonomical synonym of *Agathoxylon* Hartig.

Cupressinoxylon Göppert (Krendowskij, 1880: 269) — a *nomen conservandum* (Bamford et al., 2002). Originally this genus was provided with a diagnosis which includes bark and pith features. However it can also be used for isolated tracheidoxyls on the base of its protologue.

Cupressoxylon Kraus — an orthographic variant of *Cupressinoxylon* Göppert (Bamford et al., 2002).

Dadoxylon Endlicher — not a legitimate name (Vogellehner, 1964; Philippe, 1993).

Dammaroxylon Schultze-Motel — considered a taxonomic synonym of *Agathoxylon* as the intercellular spaces described as “*Randzellen*” are of unclear taxonomical value (Steinböck, 1926) and a possible fossilisation bias.

Elatoxylon Hartig — devoid of a clear diagnosis, based on contradictory syntypes, and almost forgotten, we do not recommend that this name be used.

[*Embergerixylon*] Lemoigne (Lemoigne, 1968: 155) — invalidly published name (Philippe, 1993).

Ginkgoxylon Saporta (Khudaiberdyev, 1962: 424) — this generic name was validly published independently several times (Andreánszky, 1952; Khudaiberdyev, 1962), but the first publication was in 1884 by Saporta (see Süß, 2003, for an outstanding review, unfortunately without type designation). As there is no material described in the protologue, we propose here *Ginkgoxylon gruetii* Pons et Vozenin-Serra (Cour. Forsch.-Inst. Senckenberg 147:204, pl. 2 Figs. 1–5, pl. 3 Figs. 1–12; 1992) as a neotype. This wood specimen fits well with Saporta’s diagnosis and is well illustrated (Pons and Vozenin-Serra, 1992; Kvaček et al., 2005). The use of *Physematopitys* Göppert, a possible taxonomic synonym not yet recorded in the Mesozoic, is to be avoided, *vide* Süß, 1988.

Glyptostroboxylon Conwentz (Natschokin, 1962: 290) — An intricate case, this genus has two syntypes (Conwentz, 1885). Andrews (1955) did the first lectotypification but at the same time elected the same species as lectotype for *Circoporoxylon* Kräusel (an error he repeated in 1970, deliberately ignoring the lectotypification of *Circoporoxylon* by Kräusel and Jain in 1964). Andrew’s choice, based on an automatic method (first species cited) may be superseded (ICBN, art. 8). The fact that Kräusel (1949) removed one of the syntypes from *Glyptostroboxylon* can no longer be considered an act of lectotypification (formerly so-called ‘residue lectotypification’, ICBN, Art. 7.11). Thus the *Glyptostroboxylon* type species was considered for long as *non-designatus* (ING), until Süß and Velitzelos in 1997 designated *G. tenerum* (Kraus) Conwentz. This generic name was used for the Mesozoic only by Natschokin (*G. senomanicum*, later transferred to *Protoglyptostroboxylon* by He Dechang in 1995), and woods from the Kimmeridgian of Tanzania (Kahlert et al., 1999; Süß and Schultka, 2001, 2006) with araucarian cross-fields (i.e. with numerous contiguous alternate oculipores). The presence of *Glyptostroboxylon* has not yet been demonstrated for the Mesozoic.

Homoxylon Hartig *non* Sahnii — although the type of the genus was assigned to the Abietineae (Bose and Sah, 1955), nothing in Hartig’s description nor in the poorly preserved type (Kräusel, 1919: 212) sustains this assignment. Diagnosis is vague, and this name should better not be used.

Homoxylon Sahnii *non* Hartig — a junior homonym of *Homoxylon* Hartig; the type was transferred to *Sahnioxylon* by Bose and Sah (1955).

Jeffersonioxylon Del Fuyeo et al. — type specimen being in contradiction with original diagnosis (authors illustrate cross-fields with three pits whereas both generic and specific diagnosis state “cross-field pits one or two”), and being poorly preserved (authors cannot decipher if cross-field pits are oopores or oculipores, Del Fuyeo et al., 1995: 114), we think this name should not be used before there has been a thorough review of this genus and the material assigned to it. It is probably a taxonomic synonym of *Agathoxylon* Hartig.

Juniperoxylon Houlbert (Kräusel, 1949: 177) — ill-defined in its protologue and typified by a species based on a poorly preserved specimen (Houlbert, 1910: 73), which we have not been able to locate to date. The two species assigned to this genus by Kräusel (1919, 1949) both have *Abietineentüpfelung* sensu Gothan (see Stopes, 1915: text-Fig. 42). Other mentions of this genus for the Mesozoic (Charrier, 1961; Lemoigne, 1967) are dubious.

Keteleerioxylon Shilkina.

Larioxylon Greguss (Harland et al., 2007: 175) — the material on which type species is based has never been reviewed and is apparently lost (Philippe et al., 1999a). We cannot thus recommend the use of this genus.

Lhassoxylon Vozenin-Serra et Pons.

Lithoxylon Scheuchzer — type from the Carnian of Stuttgart area (Csaki and Ulrichs, 1985), not reviewed; it is advisable not use this genus before reinvestigation.

Mesembrioxylon Seward — illegitimate name (Bamford and Philippe, 2001).

Metacedroxylon Holden — illegitimate junior nomenclatural synonym of *Protocedroxylon* Gothan 1910 (Philippe, 2002); lectotypified by Andrews (1955) who chose a species based on several samples, some from the Jurassic and some others from the Carboniferous (Philippe, 2002).

Metacupressinoxylon Torrey — albeit clearly given as a replacement name for *Paracupressinoxylon* Holden and based on the same type, this is not an illegitimate junior nomenclatural synonym as *Paracupressinoxylon* is not validly published in Holden (1913). It is, however,

a taxonomical synonym of *Brachyoxylon* Hollick *et* Jeffrey (Philippe, 2002).

Metapodocarpoxyton Dupéron-Laudoueneix *et* Pons.

[*Metataxodioxyton*] Nadjafi — given in a PhD thesis this is not a validly published name; we choose however to include it in the key as samples with this type of anatomy could possibly be discovered. However, as we cannot make reference to any published illustration and did not review the type material, we cannot yet validly publish this name.

Microcachryxyton Torres, Courtinat *et* Méon — although this name was given in the proceedings of a congress (Actas 7° congreso geológico Chileno, vol. 2), we consider it to be effectively published, because a corresponding volume was available for purchase by the general public. The name is also validly published despite that there is neither a Latin or English description nor diagnosis in the protologue, as slightly anterior to the 1 January 1996 (ICBN, art. 36.3).

Novoguineoxyton Boureau *et* Jongmans (attributed with some doubt to the Jurassic, this wood is very probably Permian in age, Bamford and Philippe, 2001) — not included in our key.

Oguraxyton Nishida.

Pagiophyllites Tuzson — a junior taxonomical synonym of *Agathoxyton* Hartig, as it is typified by *Pinites keuperianus* Unger, better known as *Dadoxylon keuperianus* (Unger) Endlicher, which has an *Agathoxyton*-type of anatomy (Vogellehner, 1965).

Palaeopiceoxyton Kräusel.

Palaeotaxodioxyton Frentzen — this generic name is typified by small isolated wood splinters, thus it is not certain if it originates from a pycnoxylic tracheidoxyl. Otherwise the type is amazingly similar to the very common and widespread *Taxodioxyton gypsaceum*. On the basis of its protologue *Palaeotaxodioxyton* Frentzen could be considered as a junior taxonomical synonym of *Taxodioxyton* Kraus; according to Kräusel (1921: 132–133), however, Frentzen's observations are erroneous.

Paracedroxyton Sinnott — a taxonomical junior synonym of *Brachyoxylon* Hollick *et* Jeffrey (Philippe, 2002).

Paracupressinoxyton Holden *ex* Torrey (Holden, 1913: 537) — a junior taxonomical synonym of *Brachyoxylon* Hollick *et* Jeffrey (Philippe, 2002). The name is not validly published by Holden (1913) as two species are included with neither a diagnosis nor a type designation. First valid publication is in Torrey (1923: 84). Thus *Paracupressinoxyton* cannot be considered as the correct name for *Protocupressinoxyton*, of which it is also a taxonomical synonym.

Paradoxoxyton Kräusel.

[*Paraphyllocladoxyton*] Holden — not a validly published name as two species are included in the protologue, with neither designation of a type nor a generic diagnosis. The lectotype is lost (Philippe, 2002) but its syntype makes *Paraphyllocladoxyton* a taxonomic synonym of *Protophyllocladoxyton* Kräusel. The latter is much used and well known whereas the former is almost forgotten.

Paratetraclinoxyton Süß *et* Schultka — four morphogenera have been described by Süß and Schultka on the basis of charcoalified wood from the Jurassic of Tanzania (*Paratetraclinoxyton*, *Primopodocarpoxyton*, *Semipodocarpoxyton*, *Semicircoporoxylon*; 2006). Their diagnoses are very similar, the main difference between them being the nature (i.e. cupressoid, podocarpoid or circoporoid) of the cross-field pits. The oculipore appearance in charcoal is, however, problematic. During cell wall vitrification there is indeed a phase during which the wall is somewhat ductile and tensions are released. Because of this temperature-dependant process, pores in charcoal have a tendency either to widen and to become more rounded, or to stretch and become more slit-like, depending on cell wall thickness and type of wood (i.e. compression wood or not), as recently demonstrated (Gerards *et al.*, 2007). If more emphasis is put on oculipore number and disposition than on their type, then all these four morphogenera are similar to *Brachyoxylon* Hollick *et* Jeffrey.

Perisemoxyton He Dechang *et* Zhang Xiuyi — besides one species (*P. bispirale*) another wood is described in the protologue as *P. sp.*, without designation of a type. Since the Sidney Congress in 1981, in cases such as this where a single binomial is validly published, the generic name to which it is attached is considered to be validly published (ICBN art. 42.2).

Peuce Lindley *et* Hutton (Witham, 1833: 71) — a poorly defined generic name, typified by Paleozoic material, should not to be used for the Mesozoic.

Phoroxylon Sze — see Philippe *et al.* (1999b) for the differences between *Sahnioxyton* and *Phoroxylon*.

Phyllocladoxyton Gothan.

Piceoxyton Gothan (Gothan, 1910: 20).

Pinites Lindley *et* Hutton (Göppert, 1850: 141, the attribution of *Pinites eggensis* Lindley *et* Hutton to the Jurassic is an error, vide Nicol, 1834). The lectotype (Andrews, 1955) is cordaitalean; recommended that it not to be used for Mesozoic tracheidoxyls.

Pinoxyton Knowlton — poorly defined in its original diagnosis, this generic name is based on a type species, *P. dacotense*. The type material was reviewed (Read, 1932; Medlyn and Tidwell, 1979), and is similar to *Protopiceoxyton* Gothan in having axial traumatic resin

canals only, ray tracheids and mixed type of radial pitting. The type material is in strong contradiction with the original diagnosis. As clearly explained by Medlyn and Tidwell (1979) *Pinoxylon* is the correct name for *Protopiceoxylon* Gothan. These authors wanted to propose conservation for the latter generic name, but never did so. This proposal is still badly wanted, all the more since several other authors (e.g. Süß and Velitzelos, 1993), following Kräusel (1949: 183), use the genus *Pinoxylon* for woods which are assigned by other authors to *Protopiceoxylon* (see e.g. Duan, 2000).

Pinuxylon Gothan (Kräusel, 1949: 163) — the assignment of Mesozoic tracheidoxyls to this genus was first proposed by Kräusel, who had a rather wide comprehension of this genus.

Pityoxylon Kraus — the lectotype (Andrews, 1955) is a species based on a piece of wood from the Triassic of Germany, described as having both axial and radial resin canals. This is surprising for such an old wood, as such condition is otherwise unknown before the latest Jurassic (Creber, 1972). The genus and lectotype both need revision. Furthermore, this genus is illegitimate since Kraus included in it one of the syntypes of *Pinites* Lindley et Hutton and several syntypes of *Peuce* Lindley et Hutton. It should not be used until revision. An orthographic variant, *Pitioxylon* Kraus, is used by Lemoigne and Rioult (1971).

Planoxylon Stopes — one of the two syntypes of this generic name is of dubious origin (see *Tiloxylon* entry). Fortunately that is not the one that was selected as lectotype.

Platyspiroxylon Greguss — the spirals mentioned in the diagnosis of this generic name are an alteration feature (Jefferson, 1987; Philippe et al., 1999a); genus should not be used.

Podocarpoxylon Gothan (Gothan, 1906: 456).

Primopodocarpoxylon Süß et Schultka — see *Paratetraclinoxylon*. The lattice-like structure mentioned in the diagnosis could be a mis-interpretation. Indeed cross-field pitting is observed with SEM from the ray side, whereas the ray cell wall is not preserved (i.e. external view of the tracheid wall). Araucarian pitting on radial walls of tracheids can be seen in the protologue (Pl. 2, Fig. 1).

Protaxodioxylon Bamford et Philippe.

Protelicoxylon Philippe.

Protobrachyoxyton Holden — type material lost; very probably a junior taxonomical synonym of *Brachyoxyton* Hollick et Jeffrey (Philippe, 2002); better not be used prior to revision.

Protocallitrixylon Yamazaki et Tsunada.

Procedroxylon Gothan — a junior taxonomical synonym of *Araucariopitys* Hollick et Jeffrey (Kräusel, 1919: 189).

Protochamaecyparixylon Giraud — a taxonomical synonym of *Agathoxylon* Hartig (judged from the protologue illustration).

Protocircoporoxylon Vogellehner — the type of this generic name, *Protocircoporoxylon capense* (Walton) Vogellehner, is based on material the age of which is unknown. The only source for silicified woods in the Algoa Basin is the Kirkwood Fm, of Berriasian age. We examined material from the Kirkwood Formation and found that their anatomy is similar to that described for the type species.

Protocupressinoxylon Eckhold (Eckhold, 1923: 491) — a nomenclatural synonym of *Protobrachyoxyton* Holden, 1913 (Philippe, 1993), but not of *Paracupressinoxylon* Holden ex Torrey (the mention of both syntypes of *Paracupressinoxylon* being included by Eckhold is an error of Vogellehner (1968: 152)). The name *Protocupressinoxylon* is illegitimate, and the circumscription of its legitimate nomenclatural synonym (*Protobrachyoxyton*) is doubtful (see this entry above). In xylogical literature *Protocupressinoxylon* is used by most authors as the name of a morphogenus including woods with mixed type of radial pitting and cupressoid oculipores. Most if not all the *Protocupressinoxyla* described to date clearly have cupressoid oculipores, but arranged in araucarioid cross-fields, which is not in contradiction with Eckhold's diagnosis but which puts them close to *Brachyoxyton* Hollick et Jeffrey (Philippe, 2002). In the literature there is a great amount of confusion because although some authors give a clear definition for "cupressoid oculipore", none to our knowledge have drawn a clear line between "cupressoid cross-fields" and "araucarioid cross-fields" (see however IAWA, 2004). In our opinion all the ambiguity about the use of *Protocupressinoxylon* originates here. In 1995 Philippe made two proposals, firstly to consider "araucarioid" a cross-field with numerous oculipores (either cupressoid or taxodioid) which alternate and which are contiguous (note that the areola of these semi-areolate pits is frequently faint or even not preserved in fossil wood); and secondly that "cupressoid cross-fields" be considered as a cross-field with few (usually no more than four) cupressoid oculipores, widely spaced and usually ordered in horizontal lines or columns. However, the earlywood of modern Araucariaceae very rarely has the cupressoid type of cross-field, whereas modern Cupressaceae s.l. very rarely have exclusively araucarioid cross-fields in the earlywood (but again this is not intrinsically relevant

to building a parataxonomy). Amongst Mesozoic wood species already described we cannot identify a clear and unambiguous candidate for a neotype for *Protocupressinoxylon*. Should such be identified, we think a proposal for the conservation of that genus ought to be put forward.

[*Protodacrydioxylo*] Philippe in Garcia et al. — not a validly published name, mentioned without xylological details in Garcia et al. (1998).

[*Protoginkgoxylo*] Khudaiberdyev (Khudaiberdyev in Sixel et al., 1971: 102) — this junior nomenclatural synonym of *Voltzioxylo* Torrey is not validly published (Philippe, 1993).

Protoglyptostroboxylo He Dechang (He Dechang, 1995: 10). The two morphospecies included in the generic protologue appear very similar (compare He Dechang, 1995, Pl. 6, Fig. 1 and Pl. 7, Fig. 2). The type *P. giganteum* He Dechang, is based on charcoalfied material, and thus the interpretation of the original illustration of cross-fields should be considered with great care (Gerards et al., 2007).

Protjuniperoxylo Eckhold (Eckhold, 1923: 491) — The lectotype chosen by Andrews (1955) for this generic name is based on a specimen whose transversal walls of ray cells are “not well enough preserved to show in radial section” (Stopes, 1915: 149). The other syntype has rays with *Abietineentüpfelung* and no ray-tracheids (Seward, 1919: Fig. 724 F), features that make the genus a taxonomic synonym of *Protopiceoxylo* Gothan. To be “saved”, i.e. used for woods with an anatomy fitting the original diagnosis, this genus has to be neotypified. The two syntypes aside, only one species was assigned to this genus, *P. arcticum* Selling, later recognized as the wood of a Cycadeoidea root (Selling, 1951).

Protophyllocladoxylo Kräusel — the type species (*P. leuchsii* Kräusel) is based on material said to be Danian (Late Cretaceous) in age (Kräusel, 1939), but with a wood anatomy which does not fit with this age; it could well be a reworked *Metapodocarpoxylo* sample (Kräusel, 1939: 18; Philippe et al., 2003) or even an older wood, because wood fitting Kräusel’s original diagnosis is encountered in the Gondwanan Paleozoic (Pujana, 2005). Type reappraisal is badly needed, and could lead to the reconsideration of *Paraphyllocladoxylo* Holden. It would probably be taxonomically wise to split *Protophyllocladoxylo*. Indeed assigned to this genus there is a group of Paleozoic species, with radial pitting exclusively araucarian, and a group of Mesozoic species, with radial pitting of the mixed type (sometimes strongly araucarian). There is, however, still too much taxonomical uncertainty about *Protophyllocladoxylo* type to start with a reappraisal of that genus.

Protopiceoxylo Gothan — see Philippe and Cantrill (2007) for lectotypification and lectotype illustration.

[*Protopinoxylon*] Nadjafi — given in a PhD thesis this is not a validly published name.

Protopinoxylon Eckhold (Eckhold, 1923: 491) — type seen in Copenhagen.

Protopitys (Kraus, 1882: 7) — the only mention of a Mesozoic species for this otherwise Paleozoic genus is *P. bucheana*, which was later assigned to *Paradoxoxylo* (Kräusel, 1955; Vogellehner, 1966; Süß, 1992; Süß and Steiner, 1992). We consider that this genus does not occur in the Mesozoic.

Protopodocarpoxylo Eckhold (Eckhold, 1923: 491) — *nomen conservandum*, Philippe et al. (2002).

Protopolyporoxylon Vogellehner — the type species of this generic name rests on a poorly preserved specimen, which is moreover lost (Philippe et al., 2006). We examined several topotypes which clearly fall within *Protopodocarpoxylo* (Philippe et al., 2006), and so we shall consider that this is a junior taxonomical synonym of *Protopodocarpoxylo*.

[*Protosciadopityoxylo*] Nadjafi — given in a PhD thesis this is not a validly published name.

Protosciadopityoxylo Zhang, Zheng et Ding — an independently and validly published name.

Prototaxodioxylo Vogellehner — a junior taxonomical synonym of *Brachyoxylon* (Bamford and Philippe, 2001).

Prototaxoxylo Kräusel et Dolianiti (Serra, 1969: 1) — This generic name rests on a type species, *P. africanum*, with *Spiroxylon africanum* Walton as a basionym, the age of which is unknown (Walton, 1925: 22). The genus original diagnosis clearly states that radial pits cannot be rounded and isolated. Thus only wood with strictly araucarian radial pitting should be assigned there. *Prototaxoxylo* Kräusel et Dolianiti is a junior nomenclatural synonym of *Spiroxylon* Walton *non* Hartig, as Walton clearly described *Spiroxylon* as a *nov. gen.* and was unaware of the existence of *Spiroxylon* Hartig. The type species of *Spiroxylon* Hartig is based on poorly preserved material (Kräusel and Dolianiti, 1958), but these authors should have made a neotypification rather than to propose a new name. The use of *Prototaxoxylo* is now well established, however, and this generic name should be proposed for conservation.

Pseudagathoxylo Greguss — a junior taxonomic synonym of *Simplicioxylo* Andreanszky (Philippe et al., 1999a).

Pteridospermaoxylo Greguss — a junior taxonomic synonym of *Agathoxylo*, as admitted by Greguss himself (Philippe et al., 1999a).

Sahnioxylon Bose *et* Sah — is validly published despite that no type is designated in protologue as this name was published before 1958 (ICBN, art. 37.1), as a matter of fact in 1955 (and not 1954 as usually indicated); a junior nomenclatural synonym and substitute to *Homoxylon* Sahnii, which is an junior homonym of *Homoxylon* Hartig.

Scalaroxylon Vogellehner.

Sciadopityoxylon Schmalhausen — fortunately enough for the stability of nomenclature, as it is probably a taxonomical synonym of *Xenoxylon* Gothan, the type of this name is apparently lost (we did not find it in St-Petersburg Komarov's institute where it is supposed to be housed).

Semicircoporoxylon Süß *et* Schultka — see *Paratetraclinoxylon*.

Semipodocarpoxylon Süß *et* Schultka — see *Paratetraclinoxylon*. Araucarian pitting on radial walls of tracheids can be seen in protologue (Pl. 5, Fig. 4), which does not fit well with diagnosis.

Sequoioxylon Torrey.

Simplicioxylon Andreanszky.

Suevioxylon Kräusel — the type and only species of this genus, supposed to be related to Angiosperms, is based on a specimen which is just a poorly preserved tracheidoxyl (Philippe and Gromiko, 2007).

Taxaceoxylon Kräusel *et* Jain — despite that no diagnosis is given in the protologue and that more than one species is included, we consider this generic name as validly published since a short sentence gives the essential wood features (Kräusel and Jain, 1964: 65).

Taxodioxylon Hartig (Bhardwaj, 1952: 31).

Taxoxylon Unger (Unger, 1859: 231) — In the protologue (1842) Unger used the spelling “*Taxoxylum*” which can be considered as an orthographic variant, even more so since in 1850 Unger switched to the modern spelling. According to Kräusel and Jain (1964) the specimen on which rests the type species of *Taxoxylon* Unger is a poorly preserved tracheidoxyl with resin canals. Unger's collection, in *Muséum National d'Histoire Naturelle* in Paris, has, under numbers 8765 and 8766 two slides labelled *T. goeppertii*, but without evidence that these are from type specimen. The wood on the slides is very poorly preserved, and we have not been able to observe any resin canals. Instead of using the neotypified *Taxoxylon* Unger, Kräusel and Jain preferred to introduce a new name, *Taxaceoxylon*. Since so many poorly preserved specimens of dubious affinities have been assigned to *Taxoxylon* (see e.g. Stopes, 1915: 204), their position is probably wiser. A validly published and sometimes quoted junior homonym, *Taxoxylon* Houlbert, is typified by a species *T.*

falunense Houlbert, which lacks tertiary spiral thickenings and has been transferred to *Taxodioxylon* (Vaudois-Miéja, 1971).

[*Telephragmoxylon*] Torrey — not validly published (ICBN 41.2 and 42.3).

Tetraclinoxylon Grambast (Desplats in Alvarez-Ramis *et al.*, 1981: 341).

Thuyoxylon Unger (Hartig, 1848: 138) — this generic name was first published as “*Thuyoxylum*” (same case as *Taxoxylon*). The only Mesozoic material assigned to this genus was originally described as *Pinites pertinax* by Göppert (1845: 148). It has typical araucarian radial pitting (op. cit. pl. II, Fig. 6) and comes from the Bajocian/Bathonian of Czestochowa area (Southern Poland), where *Agathoxylon* is known to occur (Gothan, 1906; Philippe *et al.*, 2006). We consider that the occurrence of this genus within the Mesozoic is not demonstrated.

Thylloxylon Gothan — type reviewed, taxonomically very close to *Protopiceoxylon* Gothan (Philippe and Cantrill, 2007).

Tiloxylon Hartig- the type species is *T. lindleyana*, with the basionym *Peuce lindleyana* Witham. This morphospecies, based on material said to originate from the Liassic of Whitby (UK), has a most intricate nomenclatural history (Vogellehner, 1968). It is based on a chimera (Nicol, 1834), which explains why Stopes observed in some slides xylological features which are otherwise unknown in Western Europe before the Late Kimmeridgian (Creber, 1972). We think this ill-defined generic name should better not be used.

Torreyoxylon Greguss — a taxonomic synonym of *Agathoxylon* Hartig (Philippe *et al.*, 1999a).

Trematoxylon Hartig — Mesozoic in age, and not Tertiary as stated in error by Andrews (1970), the type species has an anatomy strikingly similar to that of *Xenoxylon latiporosum* Gothan (Hartig, 1848; Kräusel, 1919). Hartig (1848: 188) states that the genus is frequent in Braunschweig and Hildesheim areas (Germany), a region where Toarcian *Posidonien-Schiffen* frequently yield *Xenoxylon sp.pl.* (Philippe, 1995). Thus *Trematoxylon* is very probably an earlier taxonomical synonym for *Xenoxylon* Gothan. Fortunately for the stability of nomenclature the type is lost. Better not to be used before type species revision.

Turkestanioxylon Khudaiberdyev (Khudaiberdyev *et al.*, 1971: 37).

Voltzioxylon Torrey — from protologue illustration a taxonomic synonym of *Agathoxylon* Hartig. The apparent spacing of pits on radial walls is an artefact (only pit chamber preserved, *Steinkerne* artefact, see Gothan, 1905).

Widdringtonioxylon Greguss (Desplats, 1978: 95) — a valid name (Philippe et al., 1999a), not to be confused with the following entry. Neither the material of the type species, nor that of the *W.* sp. described at the same time have preserved cross-field pits, and the original diagnosis gives no indication of these features. We think that the use of this generic name should be avoided.

Widdringtonoxylon Penny.

Xenoxylon Gothan.

Yatsenkoxylon Shilkina — the genus is validly published, with a diagnosis generico-specifica (ICBN, art. 42.1). To the best of our knowledge no generic diagnosis was subsequently proposed.

Zonaloxylon Grauvogel-Stamm, Meyer-Berthaud et Vozenin-Serra — close examination of type material figuration shows that in the tracheids with “spaced” radial pitting faint round rims occur around each “pit”. We suspect that the tracheids with “spaced” pits are tracheids where pits are preserved only as *Steinkernen*, and thus that the wood has araucarian radial pitting, which would make it very similar to *Agathoxylon* a very common wood type in the Triassic.

Appendix B. Original diagnoses of the genera included in the key. Those not originally in English have been translated. In order to limit as much as possible our interpretation while translating we tried to adhere as closely as possible to technical terms and wording used by the authors, and this is why the result sometimes reads oddly. In the cases where no diagnosis is clearly given (mostly in nineteenth century literature), a diagnosis has been compiled from the elements in the protologue

Agathoxylon Hartig: “Wood of conifer; rays uniseriate; no resin canals; axial parenchyma; cross-field pits contiguous” (translated from the protologue in German, Hartig, 1848: 189–190).

Araucariopitys Hollick et Jeffrey: “Wood tracheids with both araucarineous and abietineous pitting, the araucarineous pitting ordinarily confined to the ends of the tracheids. Traumatic resin canals resulting from injury often present. Medullary ray cells with abietineous pitting, *i.e.*, with pits on the horizontal and terminal walls of, as well as on those in contact with, the tracheids” (from the protologue, Hollick and Jeffrey, 1909: 75).

Baieroxylon Greguss: “Mesozoic gymnosperm wood with *Ginkgo*-like anatomy. Radial wall of some tracheids with helicoid thickenings. Radial pits 1–2 seriate, often with araucarioid flattening. Tracheid tips often club-shaped, bent along ray-cells. Rays 1–15 cells high, mostly uniseriate. Ray cell walls thin. In some oval

cross-fields 1–5 small araucarioid pits” (translated from the original diagnosis in German, Greguss, 1961: 142).

Brachyoxylon Hollick et Jeffrey: “Wood tracheids with both araucarineous and abietineous pitting, the araucarineous pitting ordinarily confined to the ends of the tracheids. Traumatic resin canals may be formed as the result of injury. Medullary ray cells with araucarineous pitting, *i.e.*, the walls smooth except those in contact with the tracheids” (from the protologue, Hollick and Jeffrey, 1909: 75).

Circoporoxylon Kräusel: “Gymnosperm wood built like *Phyllocladoxylon* or *Podocarpoxylo*n, the oopores of the cross-fields being however rounded or at most ovoid, but never oblique and elliptic” (translated from the protologue in German, Kräusel, 1949: 156).

Cupressinoxylon Göppert: “Log structure similar to that of living Cupressineae [...], wood composed of narrow and distinct growth-rings, latewood usually narrow with thick-walled flattened cells, earlywood much wider with thin-walled cells [...]. Tracheids intermingled with simple resiniferous cells. Pits round and uniseriate, in older logs also biseriate or tri- or quadriseriate, in the same horizontal plan, most of the time only on those tracheid walls that are opposite and parallel to medullary rays, but also sometimes on tangential walls and then smaller in every respect. Medullary rays homogenous, low and uniseriate composed of pitted parenchyma cells. Lower and upper walls of these with small pits, lateral ones with larger pits. Resiniferous canals most of the time formed of a simple row of elongated subquadrangular superposed cells, dispersed mainly among latewood cells” (translated from the original diagnosis in Latin, limited to secondary xylem features, Göppert, 1850:196).

Ginkgoxylon Saporta: “Gymnosperm wood. Areolated pits irregularly scattered and alternate, framed by sinuous furrows running between them or folded into areola around them. Ray cells narrow and elongated in radial section, broad in cross-section, forming a small number of superposed rows. Tracheids with convex walls and more or less sinuous, with ellipsoid cross-section” (translated from the French protologue, Saporta, 1884: 63).

Juniperoxylon Houlbert: Neither real diagnosis nor description is given in the protologue. The brief account given by Houlbert only gives some features of growth-ring pattern and the illustration is very poor. We use here the Kräusel protologue (1949) which reads “Conifer wood, cross-field pits in earlywood with oblique more or less narrow pores. Ray cell walls, at least the terminal ones, more or less strongly pitted (juniperoid pitting). Axial resiniferous parenchyma abundant, traumatic

wood never with resin pockets” (translated from the German, Kräusel, 1949: 174–177).

Keteleerioxylon Shilkina: “Wood with distinctly marked annual rings. Wood composed of tracheids, radial and axial parenchyma and epithelial cells of vertical resin canals. In transverse section the tracheids are rounded-polygonal, thin-walled in earlywood and with thickened walls in latewood. Tracheid pitting uniseriate. Biseriate pits opposite or sometimes subalternate. The pit apertures are rounded and included. Crassulae are present. Growth rings are distinct. The early-/latewood transition is gradual. Rays 1–24 cells high, uniseriate, sometimes locally biseriate. Pits taxodioid 1–3 (up to 4) per cross-field. Horizontal and tangential ray cell walls with abundant pitting (*Abietineentüpfelungen*). Vertical resin canals only, wall of epithelial cells weakly thickened. Horizontal resin canals and ray tracheids absent” (translated from the original diagnosis in Russian, Shilkina, 1960: 116).

Laricioxylon Greguss: “Resin ducts mostly in the latewood, the formers more or less parallel to the latter 170–180 µm in diameter lined with thick-walled epithelial cells. Medullary rays uniseriate, made of 1–20 cells in height, medullary rays containing resin ducts somewhat thicker and higher. Medullary ray cells 20–24 µm high, in the zones formed by medullary rays and tracheids 4–6 (8) simple piceoid pores, tip of transversal tracheids elongated, rostrum-like overlapping one another. Transverse tracheid walls smooth” (translated from the original diagnosis generico-specifica in Latin in the protologue, Greguss, 1967: 97).

Lhassoxylon Vozenin-Serra et Pons: “Pycnoxylic homoxylic wood; pith very reduced; secretory canals with constrictions; growth zones present, underlined by concentric parenchyma. Fibre-tracheids typically with rectangular lumen, their size and order irregular; radial pits areolate, with elongated lumen clearly of the araucarian type, 1–2 seriate, sometimes scalariform with intermediate types. Wood rays parenchymatous, slightly heterogenous, pitted on all their sides, 1–3 seriate, articulated and frequently confluent. Cross-fields with 1–2 oblique elliptical oopores. Vertical wood parenchyma abundant circum-medullary, in rows and diffuse” (translated from the original diagnosis in French, Vozenin-Serra and Pons, 1990: 116).

Metapodocarpoxyton Dupéron-Laudoueneix et Pons: “Homoxylic wood without secretory canals. Rays homogenous with smooth horizontal and terminal walls. Cross-fields with one, more rarely two pits, sometimes devoid of ornamentation. Cross-field pits of two types: oculipore or oopore with numerous transition forms. Radial pitting mostly of the araucarian type.

Axial parenchyma present. Thylosis septa in vertical fibre-tracheids” (translated from the original diagnosis in French, Dupéron-Laudoueneix and Pons, 1986: 160).

Microcachryxylon Torres, Courtinat et Meon: “Conifer secondary xylem, composed of tracheids with rectangular section and thin walls. Growth rings marked with one to four layers of flattened tracheids in the growth direction. Radial walls with pits uniseriate or biseriate opposite. Cross-fields with one or two large pits, irregular in shape, which occupy the whole field. Wood rays uniseriate and low; axial parenchyma present” (translated from the original diagnosis in Spanish, Torres et al., 1995: 1703).

Oguraxylon Nishida: “Coniferous wood belonging to Taxodiaceae; bordered pits on radial walls of tracheids are arranged separately and oppositely in one to two rows. Sanio rims clearly visible. Bordered pits on tangential walls are arranged separately in a single row, though sparsely. Rays all parenchymatous, always uniseriate, 2–30 cells high and are spaced between 1–7 rows of tracheids. Ray cells are pitted only on the radial walls: abietineous pitting not visible. Wood parenchyma is scattered throughout the wood, and more or less arranged in tangential rows. Traumatic resin canals sporadically present. Tertiary spiral thickenings are often seen on the walls of the tracheids.” (Original diagnosis by M. Nishida, 1974: 118.)

Palaeopiceoxylon Kräusel: “Radial pitting of the mixed type, otherwise like *Piceoxylon*” (translated from the protologue in German, Kräusel, 1949: 182). If completed with the elements given in the key in the same work, diagnosis will be: “Radial pitting of the mixed type, very dense; ray cell walls with *Abietineentüpfelungen*; with both horizontal and vertical resin canals”.

Paradoxoxylon Kräusel: “Secondary wood composed only of tracheids and medullary rays, similar to *Homoxylon* Sahni with regard to type and disposition of radial tracheids pits, the medullary rays however mostly uniseriate, horizontal and terminal ray cell walls thin, almost always unpitted” (translated from the original diagnosis in German, Kräusel, 1955: 25).

Paratetraclinoxylon Süß et Schultka: “Wood with structure of conifers, tracheids in cross-section round, in the transverse section irregularly arranged, intercellular spaces between tracheids present, bordered pits on radial walls araucarioid, axial parenchyma sparsely scattered, rays uniseriate, low, middle ray cells round, average height of cell less than 25 µm, horizontal walls smooth, cross-field pits podocarpoid to cupressoid” (original diagnosis by Süß and Schultka, 2006: 152).

Perisemoxylon He Dechang et Zhang Xiuyi: “Tracheids with bordered pits, spirals of thickenings in

internal walls of tracheids correspond to spiral of furrows in external ones. Ray cells with simple pits in radial walls” (English diagnosis in the protologue, He and Zhang Xiuyi, 1993: 264). The type illustration features abietinean radial pitting (op. cit. pl. 1 Fig. 1c) and cross-fields with 2–5 slightly bordered circopores (op. cit. pl. 1, Fig. 2d).

Phoroxylon Sze: “Coniferous(?) wood with abietinean pitting of medullary-ray cells. Growth-rings present, boundaries conspicuous. Spring wood comparatively narrow, strongly crushed, autumn wood dark brown, comparatively broad. Spring tracheids large, thick-walled, rectangular; autumn tracheids dense, small, thick-walled, squarish, somewhat rounded in diameter. Boundary pitting usually of scalariform, very rarely of reticulate, more or less araucarioid type. Resin canals absent, xylem-parenchyma indistinct. Medullary rays 2–25 cells high, generally 10–15 cells in height, all uniseriate. Ray cells all alike, parenchymatous, horizontal walls irregularly thickened, tangential walls with numerous small pits, lateral walls with 2–6 small, circular or oval, simple or half-bordered pits in the “field” (original *generico specifica* diagnosis for *P. scalariforme* in the protologue, Sze, 1951: 455).

Phyllocladoxylon Gothan: “Gymnosperm wood. Radial pits round, large, not contiguous; when multiseriate opposite. No tertiary helicoid thickenings. Ray cells without *Abietineentüpfelungen*; axial parenchyma regularly occurring. Cross-field pits mostly only 1–2 per field, typically large oopores” (translated from the protologue in German, Gothan, 1905: 102–103).

Piceoxylon Gothan: “Gymnosperm wood. Areolate pits rounded, large, not flattened, when pluriseriate mostly opposite. Spiral thickenings absent, or weak, in the latewood, rarely also in the earlywood. *Abietineentüpfelungen* well marked. Both axial and radial resin canals regularly present. Pits in tangential walls of tracheids numerous in latewood. Resin canal epithelial cells with thick walls; cross-field pits never oopores. Ray tracheids present, without indentations” (translated from the protologue in German, Gothan, 1905: 102–103).

Pinoxylon Knowlton: “Internal structure of the wood same as in *Pinus*, except in the absence of fusiform rays” (original diagnosis, Knowlton in Ward, 1900: 420).

Pinuxylon Gothan: “Gymnosperm wood. Areolate pits rounded, large, not flattened, when pluriseriate mostly opposite. No spiral thickenings. *Abietineentüpfelungen* or large window-like cross-field pits present; resiniferous parenchyma sometimes absent. Both axial and radial resin canals regularly present. Resin canal epithelial cells with thin walls, only rarely somewhat thick-walled; cross-field pits (earlywood!) always oopores. Ray tracheids with or

without indentations” (translated from the protologue in German, Gothan, 1905: 102–103).

Planoxylon Stopes: “Coniferous wood without, or with occasional resin canals. Regular growth rings. Tracheids with alternating, hexagonally bordered pits (2 or 3 rows) in spring wood; later-formed wood with single rows of adjacent or isolated pits. Pits present in tangential walls of late-formed wood. Rays almost entirely uniseriate, locally a few may be partly biseriate. Typical ‘Abietinean pitting’ of ray cells marked, apparent in transverse, radial, and tangential sections. Radial walls of ray cells pierced by a small number of pits per tracheid-field (1–3 vertical pairs according to position in growth ring), these pits sometimes clearly bordered. Wood parenchyma present between spring and last-formed wood of previous season” (original diagnosis by Stopes, 1916: 119).

Podocarpoxylon Gothan “Gymnosperm wood. Radial pits round, large, not contiguous; when multiseriate opposite. No tertiary spiral thickenings. Ray cell without *Abietineentüpfelungen*; axial parenchyma regularly occurring. Cross-field pits mostly only 1–2 per field, podocarpoid to partly unbordered” (translated from the protologue in German, Gothan, 1905: 102–103).

Primopodocarpoxylon Süß et Schultka: “wood with the structure of conifers, rows of tracheids of different diameter in the transverse section are adjacent to each other, bordered pits on radial tracheid walls abietoid, walls of ray cells thin and smooth, cross-field pits numerous, araucarioid, of lattice-like strut assemblies framing, pore of pits podocarpoid or circoporoid, axial parenchyma and resin channels absent” (original English diagnosis by Süß and Schultka, 2006: 137).

Protaxodioxylon Bamford et Philippe: “tracheidoxyls with radial tracheid pitting of the mixed type and taxodioid cross-fields, i.e. with usually 1–5 oculipores, in one or more horizontal rows, the diameter of aperture being greater than the width of the border (see Philippe, 1995), and the axis of this aperture being horizontal or slightly oblique” (original diagnosis, Bamford and Philippe, 2001: 293).

Protelicoxylon Philippe: “tracheidoxyls without secretory canals, with axial parenchyma; mixed type of radial pitting; some tracheids with various thickenings, spirals, Sanio rims, thin horizontal bars; growth rings faintly marked; rays uniseriate and homogenous, with unpitted cell walls; cross-fields with 1–5 cupressoid to dacrydioid oculipores” (translated from the original diagnosis in French, Philippe, 1995: 71).

Protocallitrixylon Yamazaki et Tsunada: “Coniferous wood, consisting of tracheids and ray parenchyma; lacking in resin canals in normal wood. Tracheids with tertiary callitroid-type and spiral thickenings. Bordered

pits on radial walls of tracheids araucarioid/protopinoid type. Cross-field pits half-bordered, with relatively narrow and inclined pit-aperture; 2–4 per field. Horizontal and tangential walls of ray parenchyma cells thin and smooth” (original diagnosis, Yamazaki and Tsunada, 1982: 75).

Protocircoporoxyylon Vogellehner: “Radial pits araucarioid or protopinoid. One cross-field pit, rarely two, broadly elliptic to rounded oopore with horizontal, rarely somewhat oblique long axis. Ray cell walls unpitted. Axial parenchyma absent” (translated from the original diagnosis in German, Vogellehner, 1967a: 40).

Protocupressinoxylon Eckhold: “Annual rings more or less marked, tracheids pits in various transitional arrangements, both *Abietineentüpfelung* and *Juniperustüpfelung* absent, no resin canals, cross-field pits cupressoid, axial parenchyma occasionally present” (translated from the original diagnosis in German, Eckhold, 1921: 4).

Protoglyptostroboxylon He Dechang: “In radial walls of tracheids pits araucarioid pitting or podocarpoid pitting, in cross field pits glyptostroboid pitting, all walls of ray cells unpitting. Plentiful longitudinal parenchyma cells, horizontal walls with pits. Resin ducts and ray tracheids absent” (original English diagnosis by He Dechang, 1995: 10).

Protojuniperoxyylon Eckhold: “Annual rings more or less marked, tracheid pits in various transitional arrangements, *Abietineentüpfelung* absent, but *Juniperustüpfelung* present, no resin canals, cross-field pits cupressoid, axial parenchyma occasionally present” (translated from the original diagnosis in German, Eckhold, 1921: 4).

Protophyllocladoxylon Kräusel: “Conifer wood without resin canals, radial pitting araucarioid, cross-field pitting phyllocladoid (oopores)” (translated from the protologue in German, Kräusel, 1939: 18).

Protopiceoxyylon Gothan: “Wood of Abietineae, normally only with vertical resin canals. These generally not very numerous (but in traumatic area very abundant, often associated in series); in traumatic area also here and there horizontal resin canals, within medullary rays, of uncommon size which indicates them as anomalies; otherwise without horizontal resin canals. Medullary rays uniseriate, cross-field pits small, rounded (which were certainly areolated); ca. 2–4 per cross-field. Axial parenchyma absent; the last cells of the annual ring with clear small tangential pits” (translated from the original diagnosis *generico-specifica* in German, Gothan, 1907: 32).

Protopinuxylon Eckhold: “Annual rings more or less marked, tracheid pits in various transitional arrangements, *Abietineentüpfelung* present, only normal vertical resin canals, horizontal (ones) only in traumatic areas, cross-field pits large oopores, no ray tracheids, no

axial parenchyma” (translated from the original diagnosis in German, Eckhold, 1921: 4).

Protopodocarpoxyylon Eckhold: “Annual rings more or less marked, tracheid pits in various transitional arrangements, both *Abietineentüpfelung* and *Juniperustüpfelung* absent, no resin canals, cross-field pits podocarpoid, axial parenchyma rare” (translated from the original diagnosis in German, Eckhold, 1921: 4).

Protosciadopityoxyylon Zhang, Zheng et Ding: “Growth rings present. The pitting on the radial walls of the tracheids are of transitional type between araucarioid and abietoid, namely protopinoid. Cross-field pits are sciadopityoid, or going by the name of fenestral form and sub-taxodioid mixed type. Xylem rays are composed of all parenchyma. Radially the ray cell on the horizontal and tangential walls are unpitted. Xylem parenchyma and resin canals are not present” (original English diagnosis by Zhang et al., 1999: 1313).

Prototaxoxyylon Kräusel et Dolianiti: “Secondary conifer wood, made of tracheids and medullary rays, the tracheids with spiral thickenings, their radial areolate pits in more or less araucarioid order, in any case never perfectly round and opposite, i.e. not as in Taxaceae” (translated from original diagnosis in German, Kräusel and Dolianiti, 1958: 126).

Sahnioxyylon Bose et Sah: “Wood compact, characterized by sharply marked growth-rings and composed of tracheids and rays. Spring and autumn zones sharply marked under the microscope, autumn wood more developed than spring wood. Medullary rays numerous, crowded, 1–4 seriate and 1–56 cells high. Pitting in the radial section most characteristic. Late wood possessing tracheids with multiseriate or biseriate, contiguous or separate bordered pits, earlywood tracheids showing a wide range of pitting varying from scalariform to multiseriate, pore of pits elliptical. Pits in the field 1–12, pores elliptical” (original diagnosis, Bose and Sah, 1955: 1).

Scalaroxyylon Vogellehner: “Secondary wood with preserved structure. Radial tracheid walls with scalariform pits only, with no tendency towards reticulation. Only radial ray cell walls pitted. Rays either multiseriate composed of both horizontal and vertical cells, or uniseriate composed mainly of vertical cells. Axial parenchyma and resin canals completely lacking” (translated from the original diagnosis in German, Vogellehner, 1967b: 216).

Semicircoporoxyylon Süß et Schultka: “Wood with the structure of conifers, in transverse section tracheids arranged irregularly and in short radial rows, bordered pits on radial walls abietoid, walls of ray cells thin and smooth, cells on average up to 20 µm high, cross-field

pits numerous, circoporoid, axial parenchyma and resin canals absent” (original English diagnosis by Süß and Schultka, 2006: 142).

Semipodocarpoxyton Süß et Schultka: “Wood with structure of conifers, in transverse section tracheids arranged irregularly and in radial rows, bordered pits on radial walls abietoid, walls of ray cells thin and smooth, cells on average about 30 µm high, cross-field pits podocarpoid, numerous, axial parenchyma and resin canals absent” (original English diagnosis by Süß and Schultka, 2006: 141).

Sequoioxylon Torrey: “Annual rings strongly developed; contrast between spring and summer wood very marked. Resin canals wholly traumatic and in one or both directions. Wood rays with a few oculipores or oopores on the lateral tracheid-field; other walls either smooth or sparingly pitted. Resinous wood parenchyma present, diffuse, sometimes confined to the summer wood. Tracheids with one to several rows of bordered pits separated by bars of Sanio, and when in more than one row, opposite” (original diagnosis, Torrey, 1923: 74).

Simplicioxylon Andreanszky: “Wood (secondary xylem) composed only of tracheids and medullary rays, tracheid tangential walls never with pits, in radial walls with areolated pits, always uniseriate, rounded, often somewhat flattened; medullary rays 2–17 cells high, cells two or three times higher than broad, smooth on radial walls with small pits, crack-like with ill-marked areola, in cross-fields by 3–10; concentric zones visible or faint” (translated from the original diagnosis *generico-specifica* in Latin, Andreanszky, 1949: 250).

Taxaceoxylon Kräusel et Jain: “The form genus *Taxaceoxylon* comprises fossil woods agreeing with the living Taxaceae in possessing simple rays, tracheids with spiral thickenings, their pits mostly round, uniseriate or biseriate opposite” (from the protologue, Kräusel and Jain, 1964: 65).

Taxodioxylon Hartig: “Wood of conifer; rays uniseriate; no resin canals; axial parenchyma; cross-field pits not contiguous; no tertiary thickenings; tracheids with 1–2 rows of radial pits, pits distant; ray cells parallel-sided, no more than 4–5 times longer than high; axial parenchyma cells parallel-sided, isolated or paired, 1–3 times higher than broad, as wide or wider than the tracheids when seen from the ray cell side” (translated from the protologue in German, Hartig, 1848: 189–190).

Tetraclinoxylon Grambast: “Wood with the organization of *Cupressinoxylon* (*sensu stricto*, Gothan, 1905). Cross-section of tracheids rounded. Cross-field pits with oblique slit-like pores. Neither Peirce’s

indentures nor thickenings of the tangential wall of ray-cells. No callitroid thickenings. Average height of ray cells less than 25 µm” (translated from the original diagnosis in French, Grambast, 1951: 283).

Thylloxyton Gothan: “Wood of Abietineae (with *Abietineentüpfelung* and) simple and reunified medullary rays; these, in tangential section (Pl. 6, Fig. 2) mimic resin canals, but do not host any characteristic resin canals, and instead a parenchymatous tissue with thylloses, which are often missing, completely because of bad preservation. Medullary rays otherwise uniseriate, some biseriate to triseriate, often without clear resin canals (Pl. 6, Fig. 2), complete transitional forms with resiniferous medullary rays. Pitting in earlywood araucarian, one-to biseriate, in latewood spaced, round (Pl. 6, Figs. 4 and 5). At the end of annual ring axial parenchyma frequent. Annual rings with well developed latewood zone. Ray pits mostly 2–3 per cross-field, small, rounded (unbordered?), in latewood apparently only one per cross-field (Pl. 6, Fig. 6)” (translated from the original diagnosis *generico-specifica* for *T. irregulare* in German, Gothan, 1910: 34).

Turkestaniioxylon Khudaiberdyev: “Annual rings well marked. Pits on radial walls of tracheids unibiseriate; in the latter case their disposition is opposite and they are separated by crassulae. Pits occurring on the tangential walls of some tracheids; they are small, close, and arranged without order. Wood parenchyma occurring; transverse wall smooth. Medullary rays uniseriate, low, rarely biseriate on 1–2 levels. Ray height reaching 2 to 23, most frequently 3 to 8 levels. Horizontal resin canals occurring, as usually set within the rays. Thick walled epithelial cells lining the canal. Ray cell walls always smooth. Cross-field pits taxodioid and glyptostroboid, 1–3 (4), arranged in horizontal rows” (translated from the original diagnosis *generico-specifica* for *T. metasequoianum* in Russian, Khudaiberdyev et al., 1971: 37–38).

Widdringtonoxylon Penny: “Growth rings clearly defined; moderately broad; tracheids of the early wood thin-walled and rounded; those of the late-wood thick-walled and rectangular. Resin parenchyma abundant and scattered. Resin canals wholly absent. Wood rays slightly resinous. Tracheal pitting uniseriate; pits circular and separate. Crassulae present. Transverse and tangential walls of ray cells entire; pitting of the radial walls consists of from one to four bordered pits per field; apertures usually lenticular and oblique. Rays one to sixteen cells high; individual cells broad and squarish. Tangential pitting common” (original diagnosis *generico-specifica* for *W. borealis*, Penny, 1947: 287). In a partial key Penny (op. cit.: 285) indicates that

Widdringtonoxylon is for wood of the *Cupressinoxylon* Göppert type with transverse walls of wood parenchyma cells uniform “falling within the range of structural variability of living *Widdringtonia*, *Callitris*, *Tetraclinis*, *Callitropsis*, and *Actinostrobus*”.

Xenoxylon Gothan: “wood distinguished by the large oopores of the medullary rays and the very large areolate pits, which are uniseriate and strongly flattened on both sides because of dense arrangement” (translated from the protologue in German, Gothan, 1905: 37).

*Yatsenkoxylo*n Shilkina: “Homoxylous wood with well-marked growth-rings, 1–3 mm wide, composed of tracheids, radial parenchyma, radial tracheids and epithelial cells lining resin canals. Tracheids are rather long, with rounded tips. Early wood tracheids 58–134 µm (tangential diameter) × 98–183 µm (radial diameter), in the latewood 38–79 µm × 29–93 µm. Pits on radial walls of tracheids only, uni-triseriate, mostly biseriate, seriation being a function of tracheid width and latewood being mostly with uniseriate pits. Pits are opposite, rounded, scattered, sometimes more close but never contiguous except for some rare star-shaped groups of three pits. Pits areolate, with a round pore and a torus. Crassulae are very abundant. Latest wood tracheids unpitted. No axial parenchyma. Growth-rings rather wide, with a gradual transition from early to latewood. Earlywood tracheids much larger than those of the latewood, tracheids’ cross-section quadrangular or polygonal/oval in the early wood, polygonal and isodiametric in the latewood, with sharp angles. Intercellular spaces absent. At growth-ring limit 2–3 rows of thick walled radially flattened tracheids. Earlywood about two thirds of growth ring width. Rays 1–57 cells in height, uni, bi or triseriate without resin canals, or fusiform with resin canal, mostly biseriate. Ray cells oval in cross-section, somewhat thick-walled, and separated by intercellular spaces. Ray tracheids present, the walls of which are sometimes undulated by uniseriate rays. Cross-field pits unfortunately unpreserved. Ray cell walls unpitted. Both axial and horizontal resin canals lined with thick-walled epithelium, axial ones isolated or in pairs in the latewood, horizontal ones rare, with few epithelial cells (about 6)” (translated from the original diagnosis *generico-specifica* in Russian for *Y. sibiricum*, Shilkina, 1963: 693–694).

Zonaloxylon Grauvogel-Stamm, Meyer-Berthaud *et* Vozenin-Serra: “Wood consisting of tracheids and rays. Vertical parenchyma and resin canals absent. Tracheid pitting occurring on radial walls only; pit apertures circular. Radial pitting of the mixed type, abietinean and araucarian pitting in distinct areas: abietinean pitting consisting of bordered pits circular, either spaced or contiguous, that do not occupy the entire width of the

radial walls; araucarian pitting consisting of contiguous and flattened bordered pits occupying the entire width of the radial walls. Rays uniseriate and short. Cross-field pits in vertical rows; pit aperture vertical to oblique, comprised within the boundary of the pit borders” (Original diagnosis in Grauvogel-Stamm *et al.*, 2003: 55).

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