Review of Palaeobotany and Palynology 234 (2016) 25–30

Contents lists available at ScienceDirect

Review of Palaeobotany and Palynology

journal homepage: www.elsevier.com/locate/revpalbo

Long overdue extinction of the Protopinaceae

Marion K. Bamford [a], Marc Philippe [b,*], Frédéric Thévenard [b]

[a] Evolutionary Studies Institute and School of Geosciences, University of the Witwatersrand, P Bag 3, WITS 2050 Johannesburg, South Africa
[b] Université Lyon 1 et UMR 5276 du CNRS, 7 rue Dubois, Campus de la Doua, F69622 Villeurbanne cedex, France

ARTICLE INFO

Available online 1 September 2016

Keywords:
Protopinaceae
Fossil wood
Gymnosperms
Mesozoic
Taxonomy

ABSTRACT

In 1917 the German fossil palaeobotanist Richard Kräusel proposed a new plant family, the Protopinaceae. This family was based on an anatomical feature (mixed type of radial pitting) observed in the secondary xylem of some Mesozoic gymnosperms. Kräusel's hypothesis was that the Protopinaceae had great phylogenetic significance, being an evolutionary link between Palaeozoic and modern conifers.
Since their inception the Protopinaceae have been a matter of several controversies. We examine here evidence accumulated in recent years and question the continued existence of this taxon. Not only is the taxonomic status dubious, but it is also no longer tenable that it represents a phylogenetically significant group. We recommend that the Protopinaceae, in name and concept, be put to rest before its 100th anniversary.

1. Introduction

Mesozoic wood anatomy is a small but crucial part of palaeobotany. Nonetheless, since the beginning of the twentieth century it has inspired passionate discussions (with contributions from Edward Jeffrey, Walter Gothan, Richard Kräusel, Irving Bailey, etc.), when our predecessors searched among the wood samples for evidence of the relative phylogenetic positions of the various conifer groups. At that time German postdoctoral student Kräusel (1917) proposed the Protopinaceae as a new fossil family, based only on one single anatomical feature: a mixed type of pitting on tracheid radial walls. Soon thereafter it was already suggested that this "family" had little phylogenetic relevance (Bailey, 1933).

Nevertheless, the name "Protopinaceae" is still often used, even in recent fossil wood anatomical (palaeoxylogical) papers. For example, Protopinaceae are referred to as a family in the systematic or discussion sections of papers like those of e.g., Youssef (2002); Morel et al. (2003); Lee and Yang (2006); Savidge (2007);Süß and Velitzelos (2010); Hickey et al. (2011); Kustatscher et al. (2013). One reason could be that authors are regularly asked to assign the wood fossils they describe to a family, while reviewers or editors regularly receive manuscripts assigning woods to the "Protopinaceae" without detailed justification. In almost every case, however, it is impossible to assign an isolated piece of fossil homoxylous wood to an extant or extinct botanical family.

This paper addresses the relevance of the Protopinaceae, a taxon at family-rank as suggested by the suffix.

2. Historical background

While studying Mesozoic fossil woods from Svalbard, Gothan (1910) noted that some had anatomical features similar to those which are characteristic of the Pinaceae among modern softwoods: heavily pitted ray cells and ray tracheids, pitted axial parenchyma, axial and/or radial resin canals. These woods also had, however, at least locally a pattern of radial pitting of tracheids similar to that of modern Araucariaceae, and of various archaic gymnosperms such as the Cordaitales or the Voltziales (Plate I, fig. 1). Gothan then proposed the hypothesis that these woods from Svalbard represented an extinct conifer group, which he informally called "*protoabietinean*". Kräusel later (1917) developed Gothan's idea, extending it by proposing the existence of a family of Mesozoic conifers, characterized by radial pitting of tracheids that is intermediate between that of modern Pinaceae and that of modern Araucariaceae (Plate I, Figs. 1–3). This pitting type is also called "mixed type of radial pitting", or "generalized type of pitting" or "transitional type of pitting" (Philippe and Bamford, 2008).

According to Kräusel, this family, which he named "*Protopinaceen*", was the phylogenetic stem of all modern conifer families, except the Araucariaceae which he considered as archaic (Kräusel, 1919). Soon afterwards, Kräusel's close friend Walter Eckhold developed the taxonomical consequences of this position in his thesis (Eckhold, 1921, 1923). This work was prepared in 16 months only, and presents neither new material, nor evidence that Eckhold re-examined any previously published material. It shows a good knowledge of the literature of that time, however, as it largely benefited from Kräusel's just published bibliographical synthesis (Kräusel, 1919). In his thesis Eckhold proposed not less than four new genera (*Protocupressinoxylon*, *Protojuniperoxylon*, *Protopinuxylon* and *Protopodocarpoxylon*). All are

* Corresponding author.
E-mail addresses: Marion.Bamford@wits.ac.za (M.K. Bamford), philippe@univ-lyon1.fr (M. Philippe), thevenar@univ-lyon1.fr (F. Thévenard).

http://dx.doi.org/10.1016/j.revpalbo.2016.06.006
0034-6667/

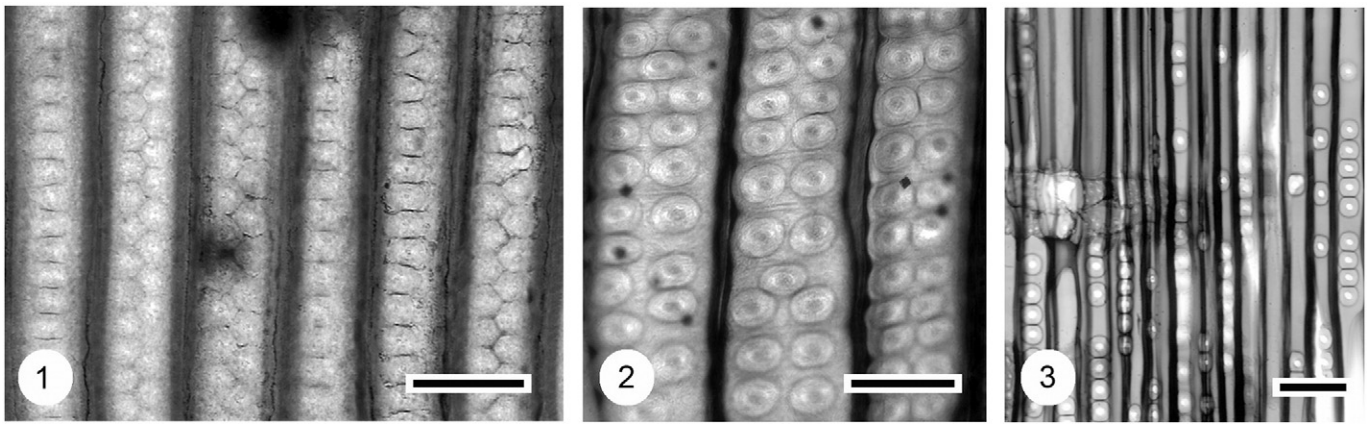

Plate I. Different types of radial pitting in homoxylous woods – 1 *Agathoxylon arizonicum* (Knowlton) nov. comb. (basionym *Araucarioxylon arizonicum* Knowlton, Proc. U.S. Nat. Mus. 11: 3, Pl. Figs. 1–5; 1889), sample 62069 in Shimakura's collection, Sendaï University, Japan ; typical uniseriate and biseriate araucarian pitting. – 2 *Protocedroxylon cedroides* (Holden) Eckhold, sample S1944 in Stockholm Natural History Museum; typical biseriate abietinean pitting. – 3 *Araucariopitys americana* Jeffrey, sample Oliver 88-2201 D in London Natural History Museum; mixed type of radial pitting.

based, at least partly, on heterogeneous syntypes and/or poorly preserved material (Bamford and Philippe, 2001; Philippe et al., 2002). Eckhold's thesis was merely a bibliographical review which, like many works of that time (see e.g. Holden, 1913), reasoned on induction from phylogenetical hypotheses, formalising them into nomenclatural proposals (cf. *Proto-podocarpoxylon* Eckhold, or *Meta-cedroxylon* Holden), and largely ignoring the contemporaneous efforts which were being made to stabilise botanical nomenclature (Briquet, 1906). Finally, Eckhold illustrated only two types of radial pitting (Fig. 1) and considered all the woods not fitting these types as "*Zwischenformen*" (intermediate forms).

In 1933 Bailey demonstrated that the so-called mixed type of radial pitting was a feature of little taxonomic relevance. Using modern *Cedrus* root wood Bailey evidenced the occurrence of the whole range of radial pitting types observed in the "Protopinaceae". Unfortunately, Bailey did not convincingly explain why this intermediate radial pitting is encountered in some Mesozoic fossil woods associated with other features, unknown in modern Pinaceae-like woods, for example, araucarioid cross-fields. Later Grambast (1952) stated that intermediate pitting is encountered in several woods from the Palaeozoic of the Southern Hemisphere, and in some Neogene woods as well, making it implausible, according to him, that this pitting could be characteristic of a particular group of Mesozoic conifers. Nevertheless, soon after (1967, 1968), Vogellehner published his *Prodromus zu einer Monographie der Protopinaceae* which vigorously reinforced the concept of a distinct family (Mussa, 1974; Tidwell and Thayn, 1985). In the 1980s several syntheses on secondary xylem evolution still referred to the Protopinaceae as a firmly established family (Vogellehner, 1983; Boureau and Marguerier, 1987; Müller-Stoll, 1987; Müller-Stoll and Schultze-Motel, 1989, 1990).

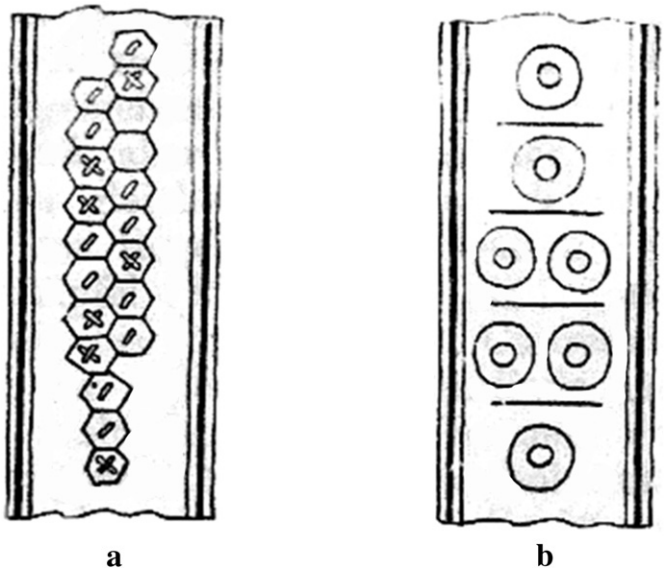

Fig. 1. Original Eckhold's illustration for the two types of pitting – a araucarian type – b abietinean type (Eckhold used respectively "*araukarioide typus*" and "*abietoide typus*".

3. The Protopinaceae, a "morpho-group" related to the Cheirolepidiaceae?

The taxonomy of isolated fossil organs has always been a difficult problem (e.g., Bateman and Hilton, 2009). For a long time the International Code of Botanical Nomenclature admitted the existence of form-taxa to cope with this type of material. The Code adopted in 1993 in Tokyo had an article (art. 3.3) acknowledging the existence of form-taxa at two levels, form-species and form-genus; form-genera "*not being assignable to a family*". No form-taxon at family rank was then possible, and the Protopinaceae were clearly an illegitimate taxon. Furthermore, in Saint-Louis (1999) and Vienna (2005) the manner in which the Nomenclatural Committee of the International botanical Congress treated taxa designed for fossils changed, and the broader concept of morpho-taxon was installed. It has however been removed from the Melbourne Code that was adopted in 2011, which prefers to use "fossil-taxa". Although it does not explicitely mention fossil-family as a possible taxon, the Melbourne Code does not forbid it (see McNeill et al., 2012, in particular art. 11.1).

Several extinct conifer families exist, usually established on reproductive structures, with a reasonable plausibility to fit within a phylogenetically circumscribed unit, for example the Miroviaceae or the Cheirolepidiaceae. This latter group of conifers flourished during the Mesozoic. Interestingly its time range (Middle Triassic - Late Cretaceous) coincides with the interval during which woods with intermediate radial pitting are most frequent (Eckhold, 1921; Müller-Stoll, 1987). This fact was used as the basis for the hypothesis that the "Protopinaceae" woods were, at least partly, members of the Cheirolepidiaceae (Alvin et al., 1981; Francis, 1983). The wood anatomy of the Cheirolepidiaceae is, however, poorly known, with few cases of in-situ wood (Zhou, 1983; Shilkina and Doludenko, 1985; Barale et al., 1991) and a few more cases of wood associated with leafy remains (e.g., Alvin et al., 1981; Francis, 1983; Zhou and Kirchner, 1992; Axsmith and Jacobs, 2005). Some observations of juvenile woods as