



BRILL

## ***Podocarpoxyton* Gothan reviewed in the light of a new species from the Eocene of Patagonia**

**Roberto R. Pujana\*** and **Daniela P. Ruiz**

Museo Argentino de Ciencias Naturales, Ciudad de Buenos Aires, Argentina

\*Corresponding author; e-mail: rpujana@macn.gov.ar

### ABSTRACT

A new species of *Podocarpoxyton* Gothan is described based on samples collected from sediments of the Río Turbio Formation. The fossil-bearing strata are lower Eocene (47–46 Mya) according to recent geochronological ages. The new species has indistinct growth ring boundaries, abundant and frequently tangentially zonate axial parenchyma, uniseriate pitting on radial walls, one half-bordered pit (= oculipore) with reduced borders and vertical aperture inclination per cross-field and medium height uniseriate rays. The new material is compared with all fossil-species of *Podocarpoxyton* and an inventory of all *Podocarpoxyton* species previously described is provided. Cross-field characters of the new species indicate affinity to the Podocarpaceae. The presence of Podocarpaceae wood augments other evidence of this family from the same stratigraphic unit.

**Keywords:** Fossil wood, wood anatomy, cross-field pits, conifers, Podocarpaceae.

### INTRODUCTION

The Podocarpaceae are distributed mostly across the southern hemisphere with about 156 species (Eckenwalder 2009). In the forests of Patagonia (subantarctic forests) the family is currently represented by four genera: *Saxegothaea* Lindley, *Podocarpus* Persoon, *Prumnopitys* Philippi and *Lepidothamnus* Philippi (Rancusi *et al.* 1987). Fossil woods with putative affinity to the Podocarpaceae have been described by many authors who have assigned numerous species to the genera *Podocarpoxyton* Gothan, *Protopodocarpoxyton* Eckhold, *Phyllocladoxylon* Gothan, *Mesembrioxylon* Seward, *Metapodocarpoxyton* Dupéron-Laudoueneix & Pons, *Protophyllocladoxylon* Kräusel, *Circoporoxylon* Kräusel and even *Cupressinoxylon* Göppert which could be related to the family. In Patagonia many *Podocarpoxyton* woods have been identified (Kräusel 1924; Del Fueyo 1998; Terada *et al.* 2006; Gnaedinger 2007; Raigemborn *et al.* 2009; Brea *et al.* 2011; Crisafulli & Herbst 2011). In this article a new species of *Podocarpoxyton* is described and compared with similar fossil-species from around the world, particularly from the southern continents and India.

Fossil floras from the Río Turbio Formation previously studied include woods (Ancíbor 1989, 1990; Brea 1993; Pujana 2008; Pujana *et al.* 2009), leaves (Berry 1937;

Hünicken 1955, 1967; Panti 2010, 2014; Fernández *et al.* 2012) and palynological remains (Romero 1973, 1977; Romero & Zamaloa 1985; Romero & Castro 1986; Guerstein *et al.* 2010; Fernández *et al.* 2012). According to these authors, the vegetation has been interpreted as being a forest dominated initially by Podocarpaceae (lower member) and later Nothofagaceae (upper member), with a diverse angiosperm component.

## MATERIALS AND METHODS

The fossils reported herein come from the lower member of the Eocene Río Turbio Formation that crops out in southwestern Santa Cruz Province, Argentina (Malumián & Panza 2000). The formation was assigned to the Eocene based on invertebrates and palynomorphs (Malumián & Panza 2000; Guerstein *et al.* 2010). Recently, detrital zircon U/Pb geochronology rendered an age of 47–46 Mya for the lower member of the Río Turbio Formation (Fosdick *et al.* 2015). Strata of the Río Turbio Formation were deposited in wave- and tide-dominated shallow, coastal marine, temperate environments (Malumián & Panza 2000; Pujana *et al.* 2009). The formation is approximately 600 m thick, divided into a lower and an upper member, and is separated from the underlying Cerro Dorotea Formation and overlying Río Guillermo Formation by erosional contacts (Azcuy & Amigo 1991; Furqué & Caballé 1993; Malumián & Panza 2000).

Two fossil wood samples were collected at the Santa Flavia Creek, near the city of Río Turbio, in southwestern Santa Cruz province, Argentina, at  $51^{\circ} 8' 34''$  S,  $72^{\circ} 8' 20''$  W (Fig. 1). The two specimens are silicified and well preserved, and found some meters from each other indicating that they could have originated from the same living tree. The fossil wood-bearing stratum is approximately 5 m above the “Complejo Carbonoso Inferior” stratigraphic unit (Pujana *et al.* 2009) described by Hünicken (1955). The stratigraphic level corresponds to the lower member of the Formation (Hünicken 1955; Malumián & Panza 2000). This locality also contains compressed dicotyledonous leaves of the Sapindaceae, Nothofagaceae, Lauraceae and Myricaceae (Panti 2010).

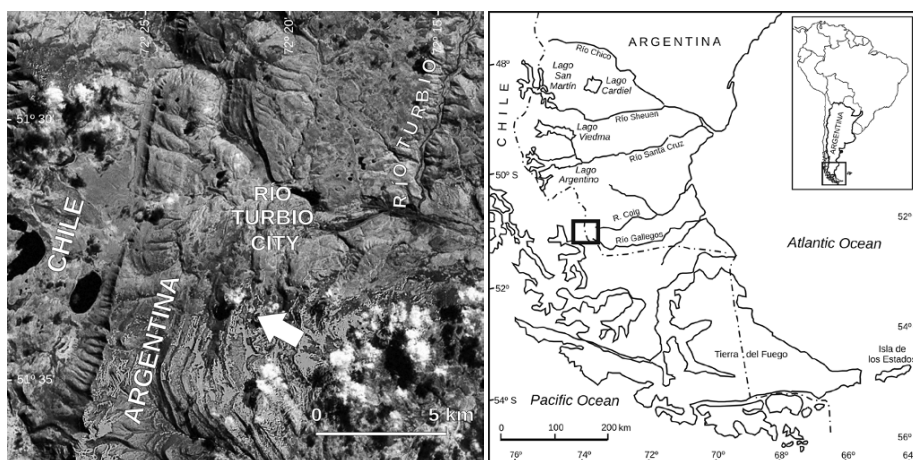


Figure 1. Map and satellite image showing sampling locality.

The specimens were thin sectioned in cross (transverse), tangential longitudinal and radial longitudinal sections following standard techniques for petrified woods and then studied using light microscopy. Acetate peels were also made following the recommendations of Galtier and Phillips (1999). Small fragments of the woods were observed under SEM (Philips XL 30). All measurements in the description are based exclusively on the holotype unless specified otherwise with at least 25 measurements or observations of each character made from each sample. The terminology follows that of the IAWA Committee (2004) for softwood identification wherever possible. However, since xylological variability among modern taxa reflects an end point of a dynamic situation during the geological past (Philippe & Bamford 2008), we have had to use terminology (*e.g.* abietinean radial pitting) discussed by Philippe and Bamford (2008) for Mesozoic fossil-genera delimitation as the features, and thus terminology, are not included in the list of the IAWA Committee (2004). The specimens are housed in the paleobotanical collection of the Museo Provincial Padre Molina, in Rio Gallegos, Argentina, under the numbers MPM PB 2249 and 2250. Slides bear the specimen number followed by an arbitrary lower case letter for identification purposes.

All extant wood examined for comparative purposes were those in the Herbarium of the Museo Argentino de Ciencias Naturales (BA) and from the Xylarium of the Facultad de Ciencias Agrarias y Forestales, UNLP (LP).

#### SYSTEMATIC PALEONTOLOGY

Genus: *PODOCARPOXYLON* Gothan

Type species: *Podocarpoxylon juniperoides* Gothan 1906 (in Gagel 1906)

*Podocarpoxylon multiparenchymatosum* Pujana, Ruiz, *spec. nov.* – Fig. 2–12

*Stratigraphic horizon*: Río Turbio Formation, lower member.

*Age*: Eocene.

*Type locality*: Arroyo Santa Flavia, Santa Cruz province, Argentina.

*Holotype*: MPM PB 2249.

*Paratype*: MPM PB 2250.

*Derivation of name*: after the abundance of axial parenchyma.

#### *Diagnosis*

Growth rings indistinct. Radial pitting bordered, uniseriate, mostly spaced (abietinean). Axial parenchyma abundant, diffuse and frequently tangentially zonate. End and horizontal walls of ray parenchyma cells smooth. Cross-field pits finely bordered, normally one half-bordered (= oculipore) pointed pit per cross-field with vertical to oblique included aperture. Rays exclusively uniseriate and medium in height.

#### *Description*

Growth rings indistinct, best observed macroscopically, weakly marked by the reduction of the radial diameter of the last 1–4 tracheids (Fig. 2) and with a width of c. 1.6–2.8 mm (c. 2.5–3.1 in the paratype). Transition from earlywood to latewood

gradual (Fig. 2). Tracheids more or less square in cross section, thin-walled; tangential diameter 21.8 (11.9–33.0)  $\mu\text{m}$ , radial diameter (earlywood) 26.7 (14.8–41.0)  $\mu\text{m}$ . Tracheid pitting exclusively uniseriate, mostly spaced (abietinean), bordered, circular, often (about 15–25% of the pits) contiguous but never flattened (Fig. 4–6) and 16.5 (11.9–21.4)  $\mu\text{m}$  in vertical diameter (Fig. 4–6). Axial parenchyma abundant, diffuse

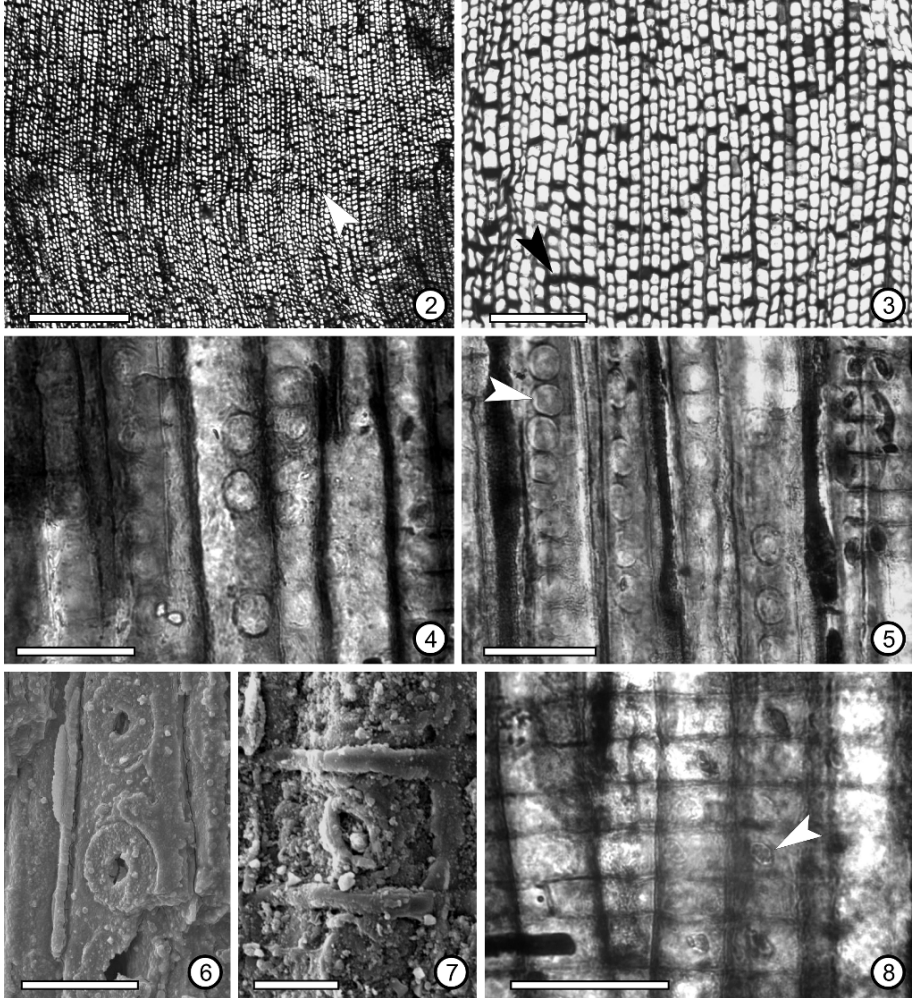


Figure 2–8. Wood anatomy of *Podocarpoxylon multiparenchymatosum*, MPM PB 2249. – 2: Transverse section (TS) showing indistinct growth ring boundaries (arrowhead). – 3: TS showing axial parenchyma (dark cells) frequently tangentially zonate (arrowhead). – 4: Radial longitudinal section (RLS) showing uniseriate bordered spaced pitting. – 5: RLS showing uniseriate bordered, spaced and contiguous (arrowhead) pitting. – 6: SEM image showing spaced radial pitting. – 7: SEM image showing a pointed cross-field half-bordered pit. – 8: RLS showing cross-field pits (arrowhead). — Scale bar for 7 = 10  $\mu\text{m}$ , for 6 = 20  $\mu\text{m}$ , for 4, 5, 8 = 50  $\mu\text{m}$ , for 3 = 200  $\mu\text{m}$ , for 2 = 500  $\mu\text{m}$ .



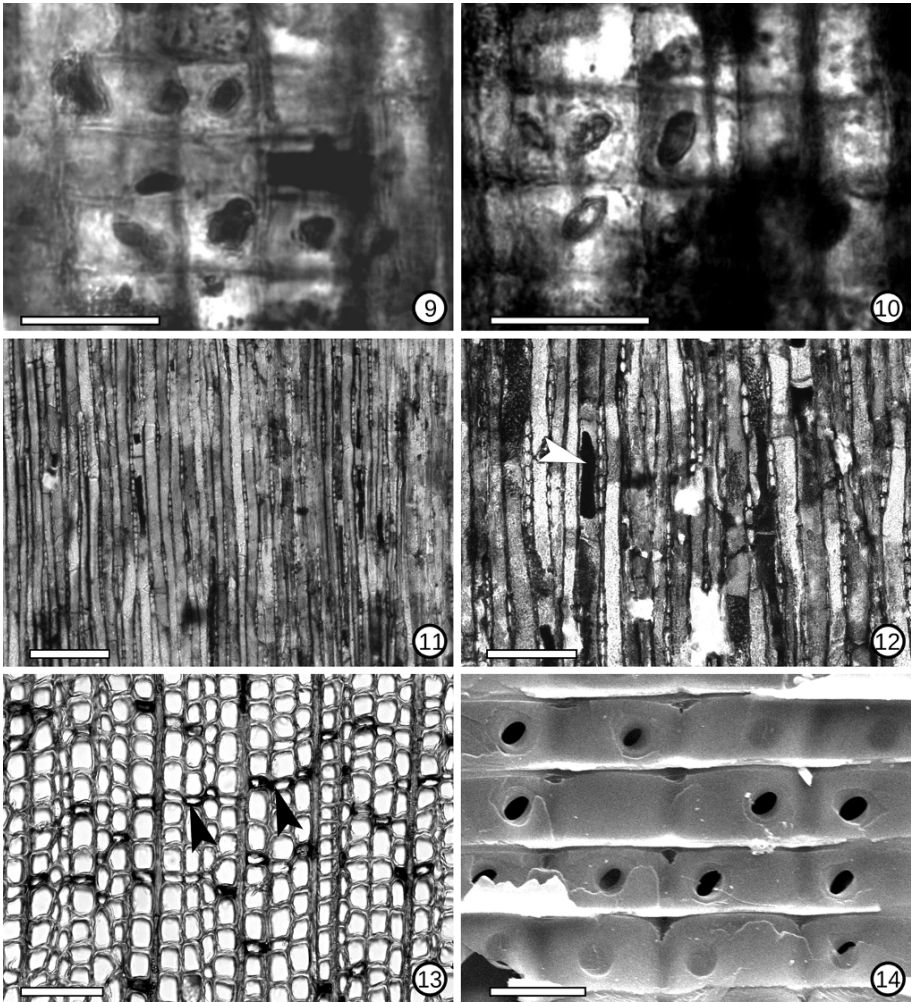


Figure 9–12. Wood anatomy of *Podocarpoxyton multiparenchymatosum*, MPM PB 2249. – 13 & 14. Extant wood of *Podocarpus parlatorei*. – 9: RLS showing cross-field pits. – 10: RLS showing cross-field pits. – 11: Tangential longitudinal section (TLS) showing uniseriate rays. – 12: TLS showing axial parenchyma (arrowhead). – 13: TS showing tangentially zonate axial parenchyma (arrowheads) similar to *Podocarpoxyton multiparenchymatosum*. LP-MP.IV.1. – 14: SEM image showing one pit per cross-field with vertical to oblique included aperture typical of many Podocarpaceae, including *P. multiparenchymatosum* fossil wood. BA FCEyN-A. — Scale bar for 9, 10, 14 = 20 µm, for 12, 13 = 100 µm, for 11 = 200 µm.

and frequently tangentially zonate (2–6 cell strands), composed of cells measuring 182 (126–257) µm in height with smooth transverse end walls (Fig. 3, 11, 12). Axial parenchyma cells filled with dark contents (Fig. 11, 12) and have a density of 127 (77–187) cells per mm<sup>2</sup> in cross section. End and horizontal walls of ray parenchyma cells smooth (Fig. 12). Earlywood taxodioid (*sensu* IAWA 2004) or podocarpoid (*sensu* Philippe &

Bamford 2008) cross-field pits rounded to pointed, half-bordered (= oculipore) with thin borders (or aperture wider than the border width) and 9.8 (6.7–12.7)  $\mu\text{m}$  in vertical diameter; with vertical to oblique (rarely horizontal) included apertures that sometimes reach the margin of the pit; one pit per cross-field, very rarely two pits or absent (Fig. 7–10). Rays exclusively uniseriate and 7.9 (2–24) cells in height (medium) (Fig. 11, 12). Ray cells 17.1 (13.5–22.3)  $\mu\text{m}$  in height. Ray frequency 5.7 (4–8) per mm.

IAWA Committee (2004) characters present: 41, 43, 44, 72, 73, 74, 76, 80, 85, 87, 94, 97, 103, 107.

### **Comparison with fossil woods**

The fossil specimens share the greatest anatomical similarity with the fossil-genus *Podocarpoxylon* and can be distinguished from other podocarpaceous genera: *Phyllocladoxylon* has simple large cross-field pits; *Circoporoxylon* has simple circular cross-field pits (Philippe & Bamford 2008); *Microcachryxylon* Torres, Cortinat, Méon has large simple pits (= oopores) in the cross-fields (Torres *et al.* 1994); *Cupressinoxylon* has cross-field half-bordered pits with wide borders (Philippe & Bamford 2008).

*Mesembrioxylon* is illegitimate and was created by Seward (1919) to include *Phyllocladoxylon* and *Podocarpoxylon* (Bamford & Philippe 2001). A number of *Mesembrioxylon* fossil-species have been transferred to other genera: *Mesembrioxylon fluviale* Sahni and *M. fusiforme* Sahni are now in *Phyllocladoxylon* (Sahni 1920; Kräusel 1949); *Mesembrioxylon sewardi* Sahni and *M. shanense* Sahni are in *Circoporoxylon* (Sahni 1920, 1938; Kräusel 1949); *Mesembrioxylon malerianum* Sahni is in *Protopodocarpoxylon* (Sahni 1931; Vogellehner 1967). *Mesembrioxylon libanoticum* Edwards is in *Metapodocarpoxylon* (Edwards 1929; Dupéron-Laudoueneix & Pons 1985).

More species of *Mesembrioxylon* have been described but differ from the fossils described here: *Mesembrioxylon carterii* Tidwell, Britt, Ash lacks axial parenchyma (Tidwell *et al.* 1998). *Mesembrioxylon chichibuense* Nishida & Nishida, *M. paliense* Mehta 1944 and *M. rhaeticum* McLean have simple pits in the cross-fields and are more similar to *Phyllocladoxylon* than to *Podocarpoxylon* (McLean 1926; Mehta 1944; Nishida & Nishida 1983). *Mesembrioxylon nihei-takagii* Nishida has similar tangentially zonate axial parenchyma, but usually more than one pit per cross-field although the author does not mention the cross-field aperture inclination or cross-field pit border width (Nishida 1966). *Mesembrioxylon pseudobedforense* Nishida and *M. obscurum* (Knowlton) Medlyn have contiguously arranged radial bordered pits (Nishida 1966; Medlyn 2002) and should probably be transferred to *Protopodocarpoxylon* or *Protophyllocladoxylon*. *Mesembrioxylon stokesii* Thayne, Tidwell from the Cretaceous of North America and Africa lacks axial parenchyma (Thayne & Tidwell 1984; Bamford & Corbett 1995) and was considered a *Podocarpoxylon* by Philippe *et al.* (2004).

According to the key of Philippe & Bamford (2008) *Podocarpoxylon* is a genus that groups fossil woods with the following characters: abietinean radial pitting (*sensu* Philippe & Bamford 2008), usually less than four half-bordered spaced pits in the cross-fields, with thin borders and apertures not horizontally inclined, and absence of resin canals and spiral thickenings. We therefore place our specimens in the fossil-genus *Podocarpoxylon* as erected by Gothan (1905), and accepted by Philippe

and Bamford (2008), namely “Gymnosperm wood. Radial pits round, large, not contiguous; when multiseriate opposite. No tertiary spiral thickenings. Ray cells 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)” (Philippe, Bamford 2008). Gothan’s original description describes the cross-fields of *Podocarpoxylon* as having mostly 1–2 podocarpoid (half-bordered pit with vertical to oblique aperture) to unbordered (simple or “eiporig”) pits per cross-field. Usually fossil woods with one or more podocarpoid cross-field pits would be included in *Podocarpoxylon* whereas, if only one large simple pit is present in each cross-field, the fossil wood would be assigned to *Phyllocladoxylon*. The term podocarpoid is, however, absent in the IAWA Committee (2004) code for softwood identification. According to this code the characteristics of the cross-fields of *P. multiparenchymatosum* would fit into the taxodioid type (“*sensu lato*”, including a tendency to horizontal or vertical aperture). In agreement with the IAWA Committee (2004) taxodioid cross-field pits have apertures exceeding the width of the border at its widest point, but refrains from mentioning the inclination of the aperture (whether they are nearly vertical or nearly horizontal). In tracheidoxyl taxonomy used to identify fossil wood, the inclination of the cross-field pit aperture is crucial for separating *Podocarpoxylon* (vertical inclination) from *Taxodioxyton* Hartig (horizontal inclination). Many authors include in their definition of podocarpoid cross-field pits an elliptic aperture that reaches the border of the pit at their longest axis (*e.g.* Marguerier & Woltz 1977). Although the cross-field pit apertures of *P. multiparenchymatosum* rarely reach the limit of the pit border, we include our material in *Podocarpoxylon* because of the overall suite of characters mentioned above.

Since the erection of *Podocarpoxylon* by Gothan (1905) at least 91 fossil-species have been named (Table 1; see pages 238–244). Some species exhibit different pitting arrangements or types of cross-field pits (*e.g.* mixed to araucarian radial pitting or apparently simple or cupressoid cross-field pits) and therefore the fossil-genus is in need of re-examination to ensure correct assignment of species to *Podocarpoxylon*. This is, however, beyond the scope of this paper.

The abundant, diffuse and frequently tangentially zonate axial parenchyma, uniseriate rays of medium height and usually one taxodioid/podocarpoid pit per cross-field with a vertical to oblique aperture of *Podocarpoxylon multiparenchymatosum* distinguishes our material from other species assigned to the fossil-genus and justifies the erection of a new fossil-species.

Numerous samples of *Podocarpoxylon* have been described from the southern hemisphere including several from Patagonia. However, *Podocarpoxylon* is present worldwide and includes many fossil-species from the northern hemisphere. Table 1 summarises the records of *Podocarpoxylon* along with their important diagnostic characters, age and location.

Many of the fossil-species described from the southern continents either lack axial parenchyma or are rare or scarce (Table 1). However, some fossil-species do exhibit common or abundant axial parenchyma and these have greater anatomical similarity to the fossils described herein: *Podocarpoxylon aegyptiacum* Kräusel, found in several

localities of Africa, differs mainly in having frequently more than two pits per cross-field and Philippe *et al.* (2004) consider this fossil-species to be a *Protopodocarpoxylon*; *Podocarpoxylon atuelensis* Gnaedinger from Patagonia has infrequent biseriate rays, up to four pits per cross-field and axial parenchyma in pairs (Gnaedinger *et al.* 2015); *P. austroamericanum* Gnaedinger from the Jurassic of Patagonia differs in having one to four cross-field pits and very low rays (Gnaedinger 2007); *Podocarpoxylon dunstani* (Sahni) Kräusel and *P. walkomi* (Sahni) Kräusel, both of which originally described as a *Cupressinoxylon* by Sahni (1920), differ in having more than one, usually two to six half-bordered, sometimes simple, pits per cross-field; *Podocarpoxylon mazzoni* (Petriella) Müller-Stoll & Schultze-Motel from the Paleocene-Eocene of Patagonia generally has biseriate radial pitting and frequent biseriate rays (Petriella 1972; Müller-Stoll & Schultze-Motel 1990). Two species have been described from the Eocene of Patagonia, namely *Podocarpoxylon palaeoandinum* Nishida (1984) with simple pits in the cross-fields (so its assignment to *Podocarpoxylon* is questionable) and *P. palaeosalignum* Nishida (1984) generally with two pits per cross-field and biseriate pitting. *Podocarpoxylon smythii* (Mueller) Kubart differs in having usually more than one pit per cross-field and frequent rays with biseriate portions (Kubart 1922). *Podocarpoxylon welkittii* Lemoigne & Beauchamp from the Cretaceous of Africa differs in its distinct growth rings and usually one to three pits per cross-field (Lemoigne & Beauchamp 1972). Finally, *Podocarpoxylon yallournensis* Patton from the Eocene–Oligocene of Australia differs in having more than one pit per cross-field and very low rays (Patton 1958).

Other samples from the southern continents and placed in *Podocarpoxylon* without any specific assignment have been described by Schultze-Motel (1966), Francis & Coffin (1992), Falcon-Lang & Cantrill (2000, 2001, 2002), Bamford & Stevenson (2002), Eklund *et al.* (2004) and Terada *et al.* (2006). Among these the closest anatomically to our samples are *Podocarpoxylon* sp. 2 described by Falcon-Lang and Cantrill (2000), but lacks the tangentially zonate axial parenchyma, and *Podocarpoxylon* form 1 described by Schultze-Motel (1966) with abundant axial parenchyma, uniseriate pitting, usually one pit per cross-field, etc., but the description is incomplete because of its poor preservation.

Although the Podocarpaceae today can be found predominantly in the southern hemisphere, many species of *Podocarpoxylon* have been described from northern latitudes. Of these fossil-species, those most similar to *P. multiparenchymatosum*, especially with respect to the axial parenchyma, from Europe (with at least 25 fossil-species of *Podocarpoxylon*) is *Podocarpoxylon bruxellense* Stockmans from Belgium, but usually has biseriate radial pitting and distinct growth ring boundaries (Stockmans 1936).

From North America at least six species of *Podocarpoxylon* have been described. The most similar is *Podocarpoxylon knowltoni* Kräusel but has very well marked growth rings and the radial pits are usually contiguous (Sinnott & Bartlett 1916; Torrey 1923; Kräusel 1949).

Numerous species of *Podocarpoxylon* have been recorded from across Asia, in particular India (Table 1). Several of them have axial parenchyma: *P. chandrapurensis* Rajanikanth & Sukh-Dev and *P. deccanensis* Trivedi & Srivastava usually have contigu-



ous radial pitting and are probably *Protopodocarpoxyton* (Rajanikanth & Sukh-Dev 1989; Trivedi & Srivastava 1989). *Podocarpoxyton kutchensis* Lakhanpal, Guleria, Awasthi has biseriate radial pitting and locally biseriate rays (Lakhanpal *et al.* 1975). *Podocarpoxyton muroshiense* Baranov & Nikolaeva is similar to *P. multiparenchymatosum*, but it has one or two simple to apparently cupressoid small pits per cross-field (Baranov & Nikolaeva 1956). *Podocarpoxyton tiruvakkaraianum* (Ramanujam) Trivedi, Srivastava has cross-fields with apparently large and simple pits (Ramanujam 1953; Trivedi & Srivastava 1989) and is probably a *Phyllocladoxyton*. From the Cenozoic of the Kuril Islands, *Podocarpoxyton kurilense* Blokhina has usually two pits per cross-field and sometimes biseriate portions in rays (Blokhina 1988).

A total of 91 *Podocarpoxyton* species have been named according to our survey (Table 1). One is illegitimate (*Podocarpoxyton dacrydioides* Cui; Cui 1995). Two fossil-species (*Podocarpoxyton itioportense* Desplats 1976 and *P. gangtaensis* Rai, Prasad, Prakash, Singh, Garg, Gupta, Pandey 2013) were not effectively published and have not been included in Table 1. “*Podocarpoxyton sequoianum* (Gothan) Torrey 1923” is probably a confusion by Kräusel (1949, p. 169) as Torrey (1923) did not make this combination and therefore is not included in Table 1. Eight have been formally combined and two have been synonymised with another *Podocarpoxyton* species. This leaves 77 *Podocarpoxyton* species although their correct systematic identity needs re-evaluation. Most of these *Podocarpoxyton* species in terms of numbers date from the Cenozoic (46%), followed by the Cretaceous (29%), then the Jurassic (15%), Triassic (8%) and Paleozoic (2%), which might suggest a progressively increasing diversity amongst this fossil-genus over time.

### **Similarities to extant woods**

The Podocarpaceae today show significant wood anatomical variability among its extant species (*e.g.* Greguss 1955; Patel 1967a,b; Marguerier & Woltz 1977; Rancusi *et al.* 1987; Woltz *et al.* 1998; Vásquez Correa *et al.* 2010). Following the IAWA Committee (2004) definitions, cross-field pits of the Podocarpaceae can be cupressoid (*e.g.* *Lepidothamnus fonkii* Philippi), taxodioid (*e.g.* *Podocarpus nubigenus* Lindler) or window-like (*e.g.* *Manoao colensoi* (Hooker) Molloy) (Patel 1967a; Rancusi *et al.* 1987; Woltz *et al.* 1998). Axial parenchyma is either present (*e.g.* *Podocarpus nubigenus*) or absent (*e.g.* *Prumnopitys taxifolia* (Solander *ex* Don) de Laubenfels) (Patel 1967b). Growth rings can be absent (*e.g.* *Podocarpus oleifolius* Don), indistinct or slightly marked (*e.g.* *Podocarpus guatemalensis* Standley) or well marked (*e.g.* *Podocarpus salignus* Don) (Rancusi *et al.* 1987; Vásquez Correa *et al.* 2010). Pitting may be almost exclusively uniseriate (*e.g.* *Prumnopitys andina* (Poeppig *ex* Endlicher) de Laubenfels) or frequently biseriate or more (*e.g.* *Retrophyllyllum minus* (Carrière) Page) (Greguss 1955; Rancusi *et al.* 1987). In some species radial tracheidal pitting is predominantly spaced (abietinoid) although other species exhibit contiguous alternate (araucaroid) pitting (*e.g.* *Podocarpus latifolius* Brown) (Greguss 1955). Many species usually have one pit per cross-field whilst others can have usually three or four pits per cross-field (*e.g.* *Dacrydium araucarioides* Brongniart & Gris) (Greguss 1955). Indentures are sometimes present in either the ray cells (*e.g.* *Saxegothaea conspicua*

Lindler) or in axial parenchyma (e.g. *Dacrycarpus dacrydioides* (Richard) de Laubenfels, *Podocarpus latifolius*) (Greguss 1955; Rancusi *et al.* 1987). Rays are commonly exclusively uniseriate yet some species show biseriate portions (e.g. *Podocarpus madagascariensis* Baker) (Marguerier & Woltz 1977).

This variability shown by extant members of the Podocarpaceae is not exclusively found among different genera, but can also be present within one species of the same genus.

*Podocarpoxyton multiparenchymatosum* shares characters with many extant species, and an affinity to a single species, or even a single genus, is difficult to assure. Several species of Podocarpaceae live today in Patagonia within the subantarctic forests: *Podocarpus nubigenus* differs from *P. multiparenchymatosum* in having usually biseriate radial pitting, locally biseriate rays and up to 3 pits per cross-field (Tortorelli 1956; Diaz-Vaz 1986; Rancusi *et al.* 1987); *Saxegothaea conspicua* has scarce axial parenchyma while *P. multiparenchymatosum* has abundant parenchyma (Greguss 1955; Rancusi *et al.* 1987; Gajardo *et al.* 1996); *Lepidothamnus fonkii* has up to four pits per cross-field; *Prumnopitys andina* has usually one large simple (“phyllocladoid”) pit (Woltz *et al.* 1998); *Podocarpus salignum* has probably the most similar wood anatomy to *P. multiparenchymatosum* but differs from our material by its frequent two pits per cross-field (Rancusi *et al.* 1987) and distinct growth rings. *Podocarpus parlatoarei* Pilger from northern Argentina, Bolivia and Peru is also similar to *P. multiparenchymatosum* with its tangentially zonate axial parenchyma and similar cross-field pitting (Fig. 13, 14), but differs in the presence of frequent crassulae and not infrequent biseriate pitting (Del Fueyo 1989).

## DISCUSSION

The presence of many supposed *Podocarpoxyton* in the northern hemisphere combined with the virtual absence of other podocarpaceous fossil remains (e.g. leaves, reproductive structures, pollen) substantiates the fact that the fossil-genus *Podocarpoxyton* may include wood from taxa other than those of Podocarpaceae. The high number of species assigned to *Podocarpoxyton* (at least 91) may have been the result of incomplete systematic descriptions, particularly concerning details of cross-field pits or by the different criteria used by researchers to delimit fossil-genera. According to recent revisions of Mesozoic conifer-like fossil-genera (Philippe & Bamford 2008) the number of species of *Podocarpoxyton* could be significantly reduced if a re-evaluation concentrated on the detailed description and illustration of well-preserved cross-field pits (such as width of the borders, size of the pit and aperture inclination).

Members of the extant Podocarpaceae are distributed mostly across the southern hemisphere and were once a common component of the southern floras of South America and Antarctica since at least the Triassic (Frenguelli 1944; Axsmith *et al.* 1998). During the Jurassic and Cretaceous they become particularly abundant (Archangelsky & Del Fueyo 2010; Peralta-Medina & Falcon-Lang 2012) with leaves frequently found since the Triassic (see references in Del Fueyo *et al.* 1990 and Cantrill & Poole 2012). Although species of Podocarpaceae fossil woods peak in the Cenozoic worldwide,

Podocarpaceae fossil woods were common in Patagonia during the Jurassic (Gnaedinger 2007) and Cretaceous (Del Fueyo 1998). Other megafloristic remains include female and male cones (Archangelsky & Del Fueyo 2010).

In the Eocene the Podocarpaceae was a common component of the floras of southern Patagonia (Romero 1977; Wilf 2012) and dominated the canopy of some Antarctic forests (Cantrill & Poole 2012; Pujana *et al.* 2014). In the Río Turbio Formation other evidence for the presence of Podocarpaceae include leaves of *Acropyle engelhardtii* (Berry) Florin found in sediments at a locality near to where our fossil woods were found (Hünicken 1955, 1967). Podocarpaceae pollen is also abundant in sediments of this formation, particularly in the older sections (lower member) where *Phyllocladites* Cookson is the most common pollen type (Romero 1977). The dominance of Podocarpaceae in southern Patagonia and Antarctic forests during the Eocene was to be replaced by the Nothofagaceae at the end of the Eocene and into the early Oligocene (Pross *et al.* 2012; Pujana *et al.* 2014) coinciding with a time of global cooling (Zachos *et al.* 2001).

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Table 1. Comparative table of all *Podocarpoxylon* species described. Data are extracted from the original species descriptions.

\*Original material revised. A = absent, D = distinct, I = indistinct, Is = uniseriate, 2s = biseriate, 3s = triseriate with the less frequently encountered characters in parentheses. Bold letters indicate characters shared with *Podocarpoxylon multiparenchymatosum*.  
 Note: *Podocarpoxylon itoportense* Desplats and *P. gangetensis* Rai, Prasad, Prakash, Singh, Garg, Gupta & Pandey are not included because they were not effectively published (Desplats 1976; Rai *et al.* 2013) according to art. 29 ICBN (McNeill *et al.* 2012, see text for details).

	References	Growth rings	Axial parenchyma	Cross-field pits	Radial pits	Rays [cells]	Observations / other references	Age and location
1) <i>P. aegyptiacum</i> Kräusel (= <i>Mesembrioxylon aegyptiacum</i> Bourreau)	Kräusel (1939), Bourreau (1948, 1950)	D	present	<b>1 (or more). Pits with vertical inclination</b>	1–2s	<b>Is. 1–10</b>	aff. <i>Protodocarpoxylon sensu</i> Philippe <i>et al.</i> (2004)	Cretaceous and Cenozoic, Africa
2) <i>P. ajkaense</i> Greguss	Greguss (1949), Ramanujam (1972)	D	scarce	<b>1 (2). Pits with vertical inclination</b>	<b>1 (2)s</b>	<b>1 (2)s. 5–15 (2–35)</b>		Cretaceous, Europe and North America
3) <i>P. angustiporosum</i> Schönfeld	Schönfeld (1955)	D	present	1–3 (4). Pits with diagonal aperture	1–2s	<b>Is. 6–8 (1–16)</b>	Crassulac	Cenozoic, Europe
4) <i>P. angustradiatum</i> Schultze–Motel	Schultze–Motel (1966)	A	absent	1–4 (5). Pits with reduced border and oblique aperture	2–3 (4)s	<b>Is. 1–20</b>		Cretaceous, Africa
5) <i>P. aparenchymatosum</i> Gothan	Gothan (1908), Pujana <i>et al.</i> (2014)	D	absent	2 (1–5). Pits with reduced borders and diagonal aperture, mostly near vertical	1–2 (3)s	<b>Is. 9 (1–17)</b>		Paleocene (?) – Eocene, Antarctica
6) <i>P. articulatum</i> Stüss & Velitzelos	Stüss & Velitzelos (2000)	D	rare	1–3. Pits “podocarpoid”	1–2s	<b>Is. mostly 1–20</b>		Cenozoic, Europe
7) <i>P. atuelensis</i> Gnaedinger	Gnaedinger <i>et al.</i> (2015)	D	present	1–2 (4). Pits “podocarpoid”	<b>1 (2)s</b>	<b>Is. 4 (2–10)</b>	Axial parenchyma in pairs	Jurassic, Patagonia
8) <i>P. australe</i> Kräusel (= <i>P. omphitii</i> (Mueller) Kubart)	Kubart (1922), Nobes (1922), Patton (1958)	I/A–D	present	1–2 (3–4)	<b>Is</b>	<b>1 (2)s. 4 (1–12)</b>	Striata, resiniferous ray cells, Kräusel (1949)	Eocene–Oligocene, Australia
9) <i>P. austroamericanum</i> Gnaedinger	Gnaedinger (2007)	D	present	1–4. Pits “podocarpoid” with reduced borders	<b>1 (2)s</b>	<b>Is. 3–4 (1–14)</b>		Jurassic, Patagonia
10) <i>P. bansuense</i> Prakash & Rajamkanth	Prakash & Rajamkanth (2004)	D	present	2–3. Pits “podocarpoid”	<b>1 (2)s</b>	<b>1 (2)s. 2–14</b>	Scarce axial resiniferous parenchyma	Cretaceous, India
11) <i>P. bedfordense</i> Stopes (= <i>Mesembrioxylon bedfordense</i> (Stopes) Seward, = <i>Protodocarpoxylon bedfordense</i> (Stopes) Kräusel)	Stopes (1915)	D	present	<b>1. Pits bordered with wide oblique aperture</b>	<b>Is</b>	<b>Is. 2–4 (1–10)</b>	Seward (1919) Kräusel (1949)	Cretaceous, Europe
12) <i>P. bruxellense</i> Stockmans	Stockmans (1936)	D	present	<b>1. Pits oblique to vertical</b>	1–2s	<b>1 (2)s. 7 (2–17)</b>		Cenozoic, Europe (continued)

(Table 1 continued)

	References	Growth rings	Axial parenchyma	Cross-field pits	Radial pits	Reys [cells]	Observations / other references	Age and location
13) <i>P. chapmanae</i> Poole & Cantrill *	Poole & Cantrill (2001)	D	rare	1–4. Pits with circular to obliquely elliptical aperture	1–2s	Is. 6 (1–42)		Cretaceous, Antarctica
14) <i>P. chandrapurensis</i> Rajanikanth & Sukh-Dev	Rajanikanth & Sukh-Dev (1989)	D	present	1–2. Pits apparently bordered	1 (2)s	Is. 1–18		Jurassic, India
15) <i>P. communis</i> Poole & Cantrill *	Poole & Cantrill (2001)	D	rare	1–3. Pits with circular to obliquely elliptical aperture	1 (2)s	Is. 5 (1–32)		Cretaceous, Antarctica
16) <i>P. dacrydioides</i> Zalewska	Zalewska (1953)	I	present	1–2 (3). Pits “podocarpoid” to “picoid”	1 (2–3)s	1 (2)s, 2–16 (1–31)	Zalewska (1955)	Cenozoic, Europe
17) <i>P. dacrydioides</i> Cui	Cui (1995)	D	absent	2 (1–3). Pits “podocarpoid”	1 (2)s	Is. 2–24	Illegitimate name, later homonym of <i>Podocarpoxylon dacrydioides</i> Zalewska	Cretaceous, Asia
18) <i>P. dakotense</i> Torrey	Torrey (1923)	D	absent	1. Pits “oopores” and bordered with slit-like apertures	1s	Is. 2–12		Cretaceous, North America
19) <i>P. decanensis</i> Trivedi & Srivastava	Trivedi & Srivastava (1989)	D	scarce	1. Pits large “taxodioid”	1s	1–2s, 2–17 (2–45)		Cenozoic, India
20) <i>P. donghuaiense</i> Li, Jin, Quan & Oskolski	Li <i>et al.</i> (2016)	D	absent	2 (1–4). Pits “cupressoid” or “taxodioid”	1 (2)s	1 (2)s, 5 (1–16)		Cenozoic, Asia
21) <i>P. danstani</i> (Sahni) Kräusel (= <i>Cupressinoxylon danstani</i> Sahni)	Sahni (1920)	D	present	3–6 or more. Pits simple	1 (2)s	Is. 5–10 (20)	Crassulac. Kräusel (1949)	Jurassic, Australia
22) <i>P. dusemii</i> Kräusel	Kräusel (1924)	D	absent	1 (2)	1s	1 (2)s, 1–20		Cenozoic (?), Patagonia
23) <i>P. feruglioi</i> Gnaedinger	Gnaedinger (2007)	D	absent	1–2. Pits “podocarpoid”	1 (2)s	Is. 1–10	Resin plugs	Jurassic, Patagonia
24) <i>P. fildesense</i> Zhang & Wang	Zhang & Wang (1994), Poole <i>et al.</i> (2001)	D	absent (?)	1–2 (4). Pits with narrow border and vertical aperture inclination	1s	Is. 2–8 (1–16)		Paleocene, Antarctica
25) <i>P. garciae</i> Del Fueyo *	Del Fueyo (1998)	I	scarce	1 (2). Pits circular, poor preservation	1 (2)s	Is. 2–3 (1–15)		Cretaceous, Patagonia
26) <i>P. godavarianum</i> (Sahni) Kräusel (= <i>Mesembrioxylon godavarianum</i> Sahni)	Sahni (1931)	A	present	2–6. Pits bordered with slit-like vertical aperture	1 (2)s	Is. 5 (2–15)	Kräusel (1949)	Triassic, Asia
27) <i>P. gothani</i> Stopes (= <i>Phyllocladoxylon gothani</i> (Stopes) Kräusel, = <i>Mesembrioxylon gothani</i> (Stopes) Seward)	Stopes (1915), Nishida (1966)	D	scarce	1. Pits large simple	1s	1s, 2–4 (1–10)	Seward (1919), Kräusel (1949)	Cretaceous, Europe, Asia (continued)



(Table 1 continued)		References	Growth rings	Axial parenchyma	Cross-field pits	Radial pits	Rays [cells]	Observations / other references	Age and location
28) <i>P. graciliradiatum</i>	Stüss & Veltzelos	Stüss & Veltzelos (2000)	D	<b>present</b>	1–3. Pits “podocarpoid”	1–2s	1s, mostly 1–30		Cenozoic, Europe
29) <i>P. helmstedtianum</i>	Gotwald	Gotwald (1966)	D	<b>present</b>	1–3 (4). Pits “cupressoid” to “taxodioid”	<b>1 (2)s</b>	<b>1s, 1–9</b>	Březinová <i>et al.</i> (1994), Sakala (2003, 2011)	Cenozoic, Europe
30) <i>P. indicum</i> (Bharadwaj) Bose & Maheshwari (= <i>Mesembryoxylon indicum</i> Bharadwaj)	Bose & Maheshwari	Crisafulli & Herbst (2008, 2011)	?	absent	2–3. Pits with narrow to wide oblique apertures	<b>1 (2)s</b>	1 (2)s, 8 (2–10)	Shearing-zones, Resin plugs. Bhardwaj (1953), Bose & Maheshwari (1974), Roberts <i>et al.</i> (1997)	Permian–Triassic, Northwest Argentina, Patagonia, Asia and Europe
1) <i>P. jago</i>	Bamford & Stevenson	Bamford & Stevenson (2002)	A	absent	<b>1. Pits with reduced borders with vertical to slightly oblique aperture</b>	<b>1s</b>	1 (2)s, 28 (6–42)	Ray cells tangentially wider than higher, Resin	Cretaceous, Africa
32) <i>P. juniperoides</i>	Gothan	Gothan in Gagel (1906)	D	rare	<b>1–2. Pits “podocarpoid”</b>	?	Not very tall	Ray cell thickenings	Cenozoic, Europe
33) <i>P. jurassicum</i>	Stüss & Schultka	Stüss & Schultka (2006)	D	absent	1–5. Pits “podocarpoid” with wide borders and vertical aperture	1s	<b>1s, 1–8</b>		Jurassic, Africa
34) <i>P. jurii</i>	Blokhina	Blokhina (1988)	D	<b>present</b>	<b>1–2. Pits with oblique to vertical aperture</b>	1s	1s, 1–17		Cenozoic, Asia
35) <i>P. knowltoni</i>	Kräusel (= <i>Podocarpoxylon mcgeei</i> (Knowlton) Sinnott & Bartlett described by Torrey 1923)	Torrey (1923), Schönfeld (1955)	D	<b>present</b>	1 (2–3). Pits “oo pores” and bordered with linear vertical apertures	<b>1 (2)s</b>	1 (2)s, Few–30 or more	Crassulac, Kräusel (1949)	Cretaceous, Europe and North America
36) <i>P. kraeusselii</i>	Rajanikanth & Sukh-Dev	Rajanikanth & Sukh-Dev (1989)	D	<b>present</b>	4–5. Pits elliptic and grouped	<b>1s</b>	<b>1s, 2–28</b>		Jurassic, India
37) <i>P. kubarrii</i>	Rössler	Rössler (1937)	D	scarce	<b>1 (2–4). Pits with wide aperture</b>	?	1 (2)s, up to 23	Crassulac and resin ducts	Cenozoic, Europe
38) <i>P. kulakubaitiamensis</i>	Agarwal & Rajanikanth	Agarwal & Rajanikanth (2004)	D	absent	<b>1–2. Pits “podocarpoid”</b>	1–2s	1 (2)s, 2–16		Cretaceous, India
39) <i>P. kurilense</i>	Blokhina	Blokhina (1988)	D	<b>present</b>	<b>1–2. Pits with vertical to oblique aperture</b>	<b>1s</b>	<b>1s, 1–17</b>		Cenozoic, Asia
40) <i>P. kutchensis</i>	Lakhanpal, Guleria & Awasthi	Lakhanpal, Guleria & Awasthi (1975)	<b>I</b>	<b>present</b>	<b>1–2. Pits simple or bordered, “podocarpoid” to “taxodioid”</b>	<b>1 (2)s</b>	1 (2)s, 1–41		Cenozoic, India
41) <i>P. latrobensis</i>	Greenwood	Greenwood (2005)	<b>I</b>	rare	1 (2). Pits with wide borders, aperture oblique to rarely vertical	1–2s	1s, 1–2		Miocene, Australia

(continued)

(Table 1 continued)	References	Growth rings	Axial parenchyma	Cross-field pits	Radial pits	Rays [cells]	Observations / other references	Age and location
42) <i>P. laurenzi</i> Kowalski	Kowalski in Laurens de la Barre & Kowalski (1920)	D	present	1–3. Pits sometimes bordered with vertical orientation	1–2s	1 (2)s. 6–8 (1–16)		Cenozoic. Europe
43) <i>P. filipipi</i> Kräusel	Kräusel (1949)	D	absent	1 (2). Pits bordered with vertical aperture	1s	1s (?)	Doliński <i>et al.</i> (1921), Rubczyńska & Zablocki (1924), Kräusel (1949)	Cenozoic. Europe
44) <i>P. mahabalei</i> (Agashe) Trivedi & Srivastava (= <i>Mesembrioxylon mahabalei</i> Agashe)	Agashe (1969), Trivedi & Srivastava (1989)	D	present	1. Pits "taxodioid"	1s	1 (2)s. 11 (1–30)		Miocene–Pliocene. India
45) <i>P. maderianum</i> (Sahni) Kräusel (= <i>Mesembrioxylon maderianum</i> Sahni, = <i>Protodocarpoxylon maderianum</i> (Sahni) Vogelheiner)	Sahni (1931)	D	absent	4–6 (3–10). Pits with narrow vertical aperture	1s	1s. 3 (1–8)	Kräusel (1949), Vogelheiner (1967), Bose & Maheshwari (1974)	Triassic. Asia
46) <i>P. mazzonii</i> (Petriella) Müller-Stoll & Schultze-Motel (= <i>Mesembrioxylon mazzonii</i> Petriella) *	Petriella (1972), Raigeborn <i>et al.</i> (2009), Brea <i>et al.</i> (2011)	I	rare	1–2. Pits with reduced borders or window-like	1–2s	1–2 (3)s. Up to 21	Crassulae, Müller-Stoll & Schultze-Motel (1990)	Paleocene–Eocene. Patagonia
47) <i>P. mcgeei</i> (Knowlton) Sinnott & Bartlett (= <i>Cupressinoxylon mcgeei</i> Knowlton)	Knowlton (1889)	D	absent	1–3. Pits simple (?) and oval	1–3s	1s. 2–49	Resin ducts, Sinnott & Bartlett (1916)	Cretaceous. North America
48) <i>P. microtracheidale</i> Süss & Schultka	Süss & Schultka (2006)	D	absent	2–6. Pits "podocarpoïd", vertical aperture	1s	1–2s. 1–5		Jurassic. Africa
49) <i>P. minor</i> Patton	Patton (1958)	I	scarce	1 (2–3). Pits with wide borders and vertical aperture	1s	1s. 2 (1–7)		Eocene–Oligocene. Australia
50) <i>P. multiparenchymatosum</i> Pujana & Ruiz *	This article	I	abundant	1 (2). Pits with reduced borders and oblique to vertical aperture	1s	1s. 8 (2–24)	Axial parenchyma tangentially zonate	Eocene. Patagonia
51) <i>P. muroschiense</i> Baranov & Nikolaeva	Baranov & Nikolaeva (1956)	?	present	1 (2). Pits simple or bordered	1s	1s. 1–10	Tracheid thickenings	Cretaceous. Asia
52) <i>P. palaeoandinum</i> Nishida	Nishida (1984)	I	present (?)	1. Pits simple, large and ovoid	1s	1s. 1–6 (13)		Eocene. Patagonia
53) <i>P. palaeosalignum</i> Nishida	Nishida (1984)	I	abundant	1–2. Elliptical or thick lenticular pit apertures	1–2s (?)	1s. 1–5 (10)		Eocene. Patagonia

(continued)

(Table 1 continued)	References	Growth rings	Axial parenchyma	Cross-field pits	Radial pits	Rays [cells]	Observations / other references	Age and location
54) <i>P. panthi</i> Bera & Sen	Bera & Sen (2004)	D	absent	1–2. Pits oval, simple or "podocarpoid", aperture oblique	1–2s	1s, 3–15 (1–42)	Some rays cells with resins	Cenozoic, India
55) <i>P. paratatifolium</i> Grant-Mackie	Vozenin-Serra & Grant-Mackie (1996), Crisafulli & Herbst (2009, 2011)	D	scarce	1–3. Pits with oblique aperture	1–2s	1s, 5 (3–15)		Permian–Triassic, Patagonia, Paraguay and New Zealand
56) <i>P. parthasarathyi</i> (= <i>Mesembryoxylon parthasarathyi</i> Sahni)	Sahni (1931), Bose & Maheshwari (1974)	I	absent	2–6. Pti. aperture narrow, obliquely vertical	1s	1s, 8 (1–18)	Kräusel (1949)	Triassic, India
57) <i>P. phyllocladoides</i> Müller-Stoll & Schultze-Motel	Müller-Stoll & Schultze-Motel (1990)	D	rare	1–2 (3–4). Pits with wide aperture	1 (2)s	1 (2)s, 1–14		Jurassic, Europe
58) <i>P. priscum</i> Prill (= <i>Circoporoxylon priscum</i> (Prill) Kräusel)	Prill (1913), Rössler (1937)	D	present	2–3 (4). Pits with oblique aperture	1 (2)s	1s, 1–20 (1–30)	Resin ducts	Cenozoic, Europe
59) <i>P. rajmahalense</i> (Jain) Bose & Maheshwari	Jain (1964)	D	absent	1–2. Pits "pinoid"	1 (2)s	1s, 4 (1–10)	Resin tracheids, Bose & Maheshwari (1974)	Jurassic, India
60) <i>P. sahni</i> (Ramanujam) Trivedi & Srivastava (= <i>Mesembryoxylon sahni</i> Ramanujam)	Ramanujam (1953), Trivedi & Srivastava (1989)	D	absent	1 (2). Pits simple	1 (2)s	1–2 (3)s, 8 (1–20)		Cenozoic, India
61) <i>P. sarmai</i> (Varma) Bose & Maheshwari	Varma (1954)	I	rarely	4 (2–3). Pits simple	1s	1s, 3–8 (18)	Bose & Maheshwari (1974)	Cretaceous, India
62) <i>P. schwendae</i> Kubart	Kubart (1911)	D	present	1–5. Pits bordered with vertical aperture	1–2s	1 (2)s, 1–13	Tracheid thickenings	Cenozoic, Europe
63) <i>P. schmidianum</i> (Schleiden) Kräusel (= <i>Pauce schmidiana</i> Schleiden, <i>Araucarioxylon schmidianum</i> (Schleiden) Felix, <i>Mesembryoxylon schmidianum</i> (Schleiden) Sahni)	Sahni (1931)	I	present	1–2. Pits with oblique to vertical aperture	1–2s	1 (2)s, 36 (1–100)	Resin parenchyma, Schmid & Schleiden (1855)	Cenozoic, India
64) <i>P. sciadopityoides</i> Shulkina	Shulkina (1967)	D	absent	1 (2). Pits large simple	1–2s	1s, 1–8	Crassulae	Cretaceous, Asia
65) <i>P. severzovii</i> (Mereklin) Jammolenko (= <i>Cupressinoxylon severzovi</i> Mereklin and <i>sensu</i> Kräusel (1949) is also synonym of <i>Cupressinoxylon sanguineum</i> Mereklin)	Mereklin (1855)	D	absent	1–4. Pits bordered	1s	1s, 1–6 (1–10)	Resin ducts, Jammolenko (1941)	Cenozoic, Asia
66) <i>P. solmsi</i> Stopes (= <i>Protocupressinoxylon solmsi</i> (Stopes) Kräusel)	Stopes (1915)	D	abundant	?	1 (2)s	1s, 2–5	With primary structures and traumatic resin ducts, Kräusel (1949)	Cretaceous, Europe (continued)

(Table 1 continued)

	References	Growth rings	Axial parenchyma	Cross-field pits	Radial pits	Rays [cells]	Observations / other references	Age and location
67) <i>P. speciosum</i> (Ramanujam) Trivedi & Srivastava	Ramanujam (1954)	D	abundant	2–4. Pits with oblique to vertical slit-like aperture	1–2s	1–2s, 6 (1–18)	Axial parenchyma with resins. Crassulae, Trivedi & Srivastava (1989), Süss & Velitzelos (2000)	Cenozoic, India
68) <i>P. spicatifoliformis</i> Naitschokin	Naitschokin (1962)	D	scarce	<b>1 (2). Pits bordered with narrow borders</b>	<b>1s</b>	<b>1s, 1–10 (1–25)</b>		Cretaceous, Asia
69) <i>P. sivanidzei</i> Barale, Jacobidze, Lebamidze & Philippe	Barale <i>et al.</i> (1991)	D	absent	1–3. Pits "podocarpoid"	<b>1 (2)s</b>	<b>1s, 9 (2–26)</b>		Jurassic, Europe
70) <i>P. taiynyrtense</i> Larischchev	Larischchev (1957)	D	present	<b>1 (2). Pits bordered with vertical aperture</b>	1 (2–3)s	1 (2)s, 2–16	Schultze-Moel (1966), Naitschokin (1968)	Cretaceous, Asia
71) <i>P. texense</i> Torrey (= <i>Taxodioxylon texense</i> (Torrey) Kräusel	Torrey (1923)	D	present	1–2. Pits half-bordered with lenticular aperture	1–2s	<b>1s, 2–10</b>	Crassulae, pitted ray cells, Kräusel (1949)	Cenozoic, North America
72) <i>P. titkense</i> Ram-Awatar & Rajanikanth	Ram-Awatar & Rajanikanth (2007), Crisafulli & Herbst (2010)	A	absent	6–8. Pits with ellipsoid aperture	1–2s	1–2s, 14–16		Triassic, Patagonia, and India
73) <i>P. tirumangalense</i> (Suryanarayana) Bose & Maheshwari (= <i>Mesembritylon tirumangalense</i> Suryanarayana)	Suryanarayana (1953)	?	absent	1–3 (4). Pits with wide borders, sometimes simple, slightly vertical aperture inclination	<b>1 (2)</b>	<b>1 (2)s, 1–15 (23)</b>	Bose & Maheshwari (1974)	Jurassic, India
74) <i>P. tiruvakkaranianum</i> (Ramanujam) Trivedi & Srivastava (= <i>Mesembritylon tiruvakkaranianum</i> Ramanujam)	Ramanujam (1953)	<b>1 ?</b>	present	1. Pit large rounded or oval pit simple	1–2s	1s, 18 (3–50)	Ray parenchyma with resins. Trivedi & Srivastava (1989)	Cenozoic, India
75) <i>P. totara</i> (Evans) Evans (= <i>Podocarpus totara</i> Evans)	Nobes (1922), Evans (1931, 1936, 1937)	<b>1 ?</b>	absent	<b>1</b>	<b>1 (2)s</b>	<b>1s</b>	Rays cells with resins. Kräusel (1949)	Cenozoic, New Zealand
76) <i>P. triassicum</i> Selmeier & Vogelhehner	Selmeier & Vogelhehner (1968)	D	present	1 (2–3). Pits simple and pointed	<b>1s</b>	1–3s, 1–12 (1–66)		Triassic, Europe
77) <i>P. trichinopolitense</i> (Varma) Bose & Maheshwari (= <i>Mesembritylon trichinopolitense</i> Varma)	Varma (1954)	D	rare	1–2. Pits simple, fusiform	<b>1s</b>	<b>1s, 2–6 (10)</b>	Bose & Maheshwari (1974), Süss & Velitzelos (2000)	Cretaceous, India
78) <i>P. tirotiense</i> Zalewska	Zalewska (1953)	D	scarce	1–2. Pits "cupressoid" to "picoid" vertical with arrangement	<b>1 (2)s</b>	1 (2)s, 1–45	Crassulae, Zalewska (1955)	Cenozoic, Europe
79) <i>P. ulugbegii</i> Junusov	Junusov in Gomolitzky <i>et al.</i> (1981)	D	abundant	<b>1–2. Pits "podocarpoid" or "diacrydoid"</b>	<b>1s</b>	<b>1s, 8–10</b>		Jurassic, Asia (continued)

(Table 1 continued)	References	Growth rings	Axial parenchyma	Cross-field pits	Radial pits	Rays [cells]	Observations / other references	Age and location
80) <i>P. umzambense</i> Schultz-Motel	Schultz-Motel (1966), Bamford & Stevenson (2002)	I	rare	1. Pits with oblique wide borders	1–2s	1 (2)s, 15 (1–19)		Cretaceous, Africa
81) <i>P. urutense</i> Khudalberdyev	Khudalberdyev (1958)	D	scarce	2–3 (4–5). Pits "taxoid" with narrow border and horizontal aperture	1s	1s, 1–12	Schultz-Motel (1966), Sliss & Veltzel (2000)	Cenozoic, Asia
82) <i>P. verticafis</i> Poole & Cantrill *	Poole & Cantrill (2001)	D	rare	1–5. Pits with steeply oblique apertures almost as large as the pit itself	1 (2)s	1s, 6 (1–36)		Cretaceous, Antarctica
83) <i>P. vikramii</i> Bande & Prakash	Bande & Prakash (1984)	I	scarce	1 (2). Pits circular to oval, wide, usually oblique (very rarely horizontal) apertures	1–2s	1s, 3–20 (1–42)	Crassulae	Cenozoic, India
84) <i>P. walkoni</i> (Sahni) Kräusel (= <i>Cupressinoxylon walkoni</i> Sahni)	Sahni (1920)	D	abundant	2–5 (6). Pits rounded or oval, simple	1 (2)s	1s, 5–12 (20)	Resin plugs, Kräusel (1949)	Jurassic, Australia
85) <i>P. washingtonense</i> Torrey (= <i>Taxodioxylon gypsaceum</i> (Torrey) Kräusel)	Torrey (1923)	D	present	2. Pits simple	1s	1s, few–25	Kräusel (1949)	Cenozoic, North America
86) <i>P. walkitii</i> Lemoigne & Beauchamp	Lemoigne & Beauchamp (1972)	D	present (?)	1–3	1s	1s, 1–18		Cenozoic, Africa
87) <i>P. woburnense</i> Stopes (= <i>Circopora xylon woburnense</i> (Stopes) Kräusel, = <i>Mesembrioxylon woburnense</i> (Stopes) Seward)	Stopes (1915), Nishida (1966), Khudalberdyev & Tashmukhamyedova (1981), Bamford & Corbett (1995)	D	present	1 (2). Pits large, roundish or slightly oval, narrow border or simple	1 (2)s	1s, low	Crassulae, Seward (1919), Kräusel (1949), Philippe <i>et al.</i> (2004)	Cretaceous, Africa, Asia and Europe
88) <i>P. yallourmensis</i> Patton	Patton (1958)	I	abundant	1–3 (4–5). Pit aperture broad or narrow	1 (2)s	1s, 2 (1–6)		Eocene–Oligocene, Australia