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A new species of *Protophyllocladoxylon* from the Upper Cretaceous (Cenomanian-Turonian) portion of the Winton Formation, central-western Queensland, Australia

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Abstract

Leaf floras in fluvial-lacustrine sediments of the Upper Cretaceous (Cenomanian-Turonian) portion of the Winton Formation suggest a community with co-dominance of angiosperms, conifers, ginkgo and other seed plants. To date wood floras associated with the Winton Formation have not been examined in detail. Winton Formation wood has been presumed to comprise araucarian, podocarp and taxodiaceous components, but this has been based largely on the identification of other plant macro and microfossils. Here we describe a new species of podocarp fossil wood from the genus *Protophyllocladoxylon* based on eleven specimens of silicified wood found as surface material at two broadly coeval sites in the Cenomanian-Turonian portion of the Winton Formation: QM L311 and Bladensburg National Park. The new species is characterised by the presence of araucaroid tracheid pitting and phyllocladoid oopores, the absence of oculipores, and the paired arrangement of the oopores within the crossfields. The recognition of *Protophyllocladoxylon* in the Winton Formation supports previous palynological frequency counts that suggest a dominance of podocarp conifers.

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Key Words: Cretaceous; fossil wood; Winton Formation

1. Introduction

Silicified wood is typically found on the surface at exposures in some parts of the Eromanga Basin of central-western Queensland, where terrestrial sediments of the late Albian–Turonian Winton Formation are exposed or partially overlain unconformably by Cenozoic alluvia. Because the rocks of the Winton Formation comprise the youngest Cretaceous strata of the Eromanga Basin (Gray et al., 2002; Tucker et al. 2013), and because the wood is more indurated compared with the surrounding sediment even where that sediment has been lithified (pers. obs.), this surface wood is considered to represent lag from upper portions of the Winton Formation that have previously eroded. Perhaps due to perceived uncertainty regarding its origin, and that it is not found in situ, this wood has received little attention in the published literature.

More broadly, the flora preserved in the Winton Formation provides an opportunity to understand Late Cretaceous floristic change from this part of the Southern Hemisphere (McLoughlin et al., 2010). Some of the earliest major works on the flora of the Winton Formation focused on the palynological record (Dettmann and Playford, 1969), which has been revisited and revised several times since (Peters, 1985; Dettmann and Clifford, 1992; Dettmann et al., 1992; Burger, 1993; Dettmann 1995; Martin, 1998). Recognized taxa include lycopsids, bryophytes, pteridophytes, gymnosperms and angiosperms. Angiosperms comprise both monocotyledons (Liliaceae) and dicotyledons, while gymnosperms comprise gnetophytes, podocarps, araucarians and taxodiod conifers. Despite this diversity, Dettmann et al. (2009) determined that 87% of the material at one of the better-sampled localities (QM L311) pertained to Podocarpaceae based on pollen counts. The first macrofossil assemblage (also from QM L311) from the Winton Formation was described by Peters (1985), and included wood, reproductive structures and isolated foliage. These fossils were permineralised and dating has been problematic. They comprise araucarian, podocarp and taxodiod material, with very little representation of angiosperms. Notably, although pollen frequency at this site suggests a dominant podocarp component, of the 15 kinds of cones Peters (1985) described, only five were assigned to Podocarpaceae.

More recently authors have described macrofossil floral assemblages from other sites in the Winton Formation. McLoughlin et al. (1995; 2010) recorded ferns (*Cladophlebis*, *Sphenopteris*, *Microphyllopteris* sp. cf. *gleichenioides*, *Phyllopteroides macclymontae*), sphenopsids (*Equisetites*), bennettitaleans (*Otozamites*, *Ptilophyllum*), conifers (podocarps and araucarians based on cone and leaf impressions), angiosperms (nine morphotypes) and other seed plants (*Gingko*, *Taeniopteris*). Similarly Pole (1999; 2000) and Pole and Douglas (1999) recorded cuticular specimens of bennettitaleans, conifers (Cheirolepidiaceae, araucarians, podocarps), monocotyledonous and dicotyledonous angiosperms, along with other seed plants (*Ginkgo*, a possible cycad).

In addition to the above, Bose (1955) described equisetalean rhizomes and nodal diaphragms; White (1966; 1974) and Chambers et al., (1998) have described araucarian leaf impressions; Peters and Christophel (1978) fern pinna aff. *Lygodium*, and Cupressaceae leaf scales; Dettmann and Clifford (2000) discoid liverwort gemmae; Clifford and Dettmann (2005) *Tempskya judithae* Clifford et Detmann, a permineralised false trunk of a treefern; and more recently Dettmann et al. (2009) described permineralised flowers.

Although much research has been conducted on the flora of the Winton Formation, most of this work has concentrated on pollen, leaf impressions and silicified material from QM L311, few studies have documented the silicified wood flora. Fossil wood is significant as it provides an insight into the canopy-forming vegetation and may give a different perspective from that seen in the leaf floras (Cantrill and Poole, 2005). Incorporating information on fossil wood would thus facilitate a more robust reconstruction of the Winton Formation's flora.

Only two unpublished studies have focused on the wood in any detail. Recently Dawson and Pole (unpublished) completed a preliminary study using two samples of fossil wood from the Winton Formation to determine climate. They identified one specimen as *Araucaria*-type wood and one specimen as a possible podocarp. From the figures provided, this second specimen appears similar to the material described herein. Peters (1985) described four *Araucarioxylon* – "parataxon" 1–4, and one

Coniferae-incertae sedis – “parataxon” 1, from QM L311. We consider these assignments in need of review as the described characters of some of the *Araucarioxylon* – “parataxa” suggest podocarpalean affinities.

We aim to describe the wood from the Queensland Museum and University of Queensland collections from the upper portion of the Winton Formation. The samples that have sufficient preservation to be identified are from a genus considered to be podocarp, but could not be assigned to currently described species. Thus, we describe a new species of *Protophyllocladoxylon* here.

1.1 Geological Setting

The Eromanga Basin is a major component of the larger Great Artesian Basin. The Great Artesian Basin covers 1.7 million square kilometres or approximately 1/5th of Australia’s landmass (Zhang et al., 2007). During the Early Cretaceous the Great Artesian Basin was inundated by an epeiric seaway (Draper, 2002), which may have extended across central Australia, linking the Great Artesian Basin and the Carnarvon Basin (Frakes et al., 1987). The timing of the cycles of inundation and regression is difficult to relate to global events, and may be related to regional tectonic events (Gallagher and Lambeck, 1989)

The Winton Formation represents a richly fossiliferous sediment infilling of the Eromanga Basin. The formation consists of complex and repetitive fluvial-lacustrine sediments, including fine- to medium-grained feldspatholithic or lithofeldspathic arenites, siltstones, mudstones and claystones (Fielding, 1992; Romilio and Salisbury, 2011; Romilio et al., 2013; Tucker et al., 2013) with very minor coal seams (Senior et al., 1978). These sediments have been interpreted as accumulating in a freshwater, broad fluvial–lacustrine environment, deposited on an extensive coastal plain as the epicontinental Eromanga Sea withdrew (Exon and Senior 1976; Tucker et al., 2013). At the time the upper portion of the Winton Formation was deposited, central-western Queensland would have been at approximately 50ºS (Li and Powell, 2001).

The Winton Formation crops out over an area from north-western New South Wales, to north-eastern South Australia and throughout central-western Queensland (Figure 1; Gray et al., 2002). It consists of Albian to Turonian strata (Tucker et al., 2013), representing the youngest part of the preserved basin fill. Exposures of this formation are scattered due to deep weathering and overlying alluvium. Until recently correlation between these scattered fossil-bearing surface exposures had been difficult. A recent study using U-Pb isotope dating of detrital zircons by laser ablation by Tucker et al. (2013) has been able to constrain the ages of many of the fossiliferous sediments of the upper-most exposed portions of the Winton Formation close to the Cenomanian-Turonian boundary. This includes QM L311 and Bladensburg National Park, from which the holotype and paratypes of this study were collected. Trenches excavated at fossiliferous sites suggest that the facies below the surface are similar to those at Lark Quarry and Bladensburg (Tucker et al., 2013).

2. Materials and Methods

The material prepared for this study was preserved as silicified surface material ranging from approximately half a metre in diameter to small, isolated pieces. All material collected from the field by the authors or available from the Queensland Museum was sectioned. It is important to note that approximately half of all wood samples prepared for this study could not be identified as they have poor cellular-scale preservation.

Preparation of the specimens was by conventional rock thin section, ground to varying thicknesses to account for the unique preservational characteristics of each specimen, averaging ~70 microns. The sections were oriented in transverse, radial longitudinal and tangential longitudinal planes. These sections were examined under a Nikon eclipse 50ipol and images captured using a Nikon DS – Fi1. Descriptions are primarily from the holotype, but where proportions were given, these have been sampled from both holotype and paratype specimens.

3. Systematic Palaeontology

Family Podocarpaceae

Protophyllocladoxylon Kräusel

Type species *Protophyllocladoxylon leuschii* Kräusel

Protophyllocladoxylon owensii sp. nov. Fletcher, Cantrill, Moss and Salisbury (Plate I, 1–10)

Holotype: QM F44339, one section in each of transverse, tangential longitudinal, and radial longitudinal planes (Plate I, 1–10).

Paratypes: QM F44330, QM F44331, QM F44332, QM F44333, QM F44334, QM F44335, QM F44336, QM F44337, QM F44338, and QM F1359.

Repository: Geoscience Collection, Queensland Museum, Queensland, Australia.

Type locality: QM L311, between Lovelle Downs Station and Elderslie Station, 38 km WNW of Winton and 8 km east of the Diamantina River (see Figure. 1), central western Queensland, Australia.

Other: Bladensburg National Park, central western Queensland, Australia.

Stratigraphic horizon: Late Cretaceous (Cenomanian-Turonian) portion of the Winton Formation of the Rolling Downs Group, central-western Queensland, Australia (see Figure 1).

Etymology: The specific epithet is named after the current Mayor of the Longreach Regional Council, and former Mayor of Isisford Shire Council Cr., R.L. (Joe) Owens, who has been a significant supporter of our team's research in the region since 2001.

Diagnosis: Growth ring boundaries are distinct. Tracheid radial pitting is predominantly alternate and contiguous (araucarian), uniserate in latewood, biseriate, rarely triseriate, in earlywood. Crossfield pits are typically phyllocladoid oopores or more rarely circopores; two per crossfield in earlywood, one in latewood. Rays are uniseriate, variable in height, and the walls are smooth. Axial parenchyma and resin canals are absent.

Description: In RLS, the tracheid pitting is predominantly alternate and contiguous. In the earlywood it is biseriate, rarely triseriate (Figure 2C), in the latewood, uniserate (Figure 2D). Some tracheid cells walls appear to be partially degraded (Plate I.2). The bordered tracheid pits are approximately 21 µm (horizontal) by 16 µm (vertical) and vary from elliptic to sub-hexagonal. Tangential tracheid walls are blank. Rays are abundant throughout. The crossfield pits are typically phyllocladoid oopores (Figure 2A) or more rarely circopores (Figure 2B), with grading between the two, but oculipores are absent. The phyllocladoid oopores are approximately 17 µm (longest axis, oblique) by 11 µm (shortest axis), whilst the circopores are 15 µm (longest axis, oblique) by 14 µm (shortest axis). The crossfields in this species have a high frequency of two oopores per crossfield pit in earlywood (0.93 as a proportion, as determined from this specimen and paratypes), and a high frequency of single pores in latewood (0.98 as a proportion, as determined from this specimen and paratypes). In TLS rays are uniseriate, and variable in height (2–18, in the holotype: Figure 2E). The ray cells are 17 µm (vertical) by 14 µm (horizontal). Ray walls are smooth (though see Pujana et al., 2014, notes on SEM and tangential pitting). Axial parenchyma are absent. No resin canals were observed. In TS and RLS the growth ring boundaries are distinct (Figure 2F). The tracheids are sub-rectangular to irregular polygonal and approximately 65 µm (length) by 33 µm (width) in the earlywood, 30 µm (length) by 38 µm (width) in the latewood. Tracheids are sometimes resin filled. In TS this seems to vary between specimens, with some have large sections of both early and latewood filled, some with only small irregular patches of resin filling, and others with an apparent bias to latewood cells being filled more than earlywood cells. In RLS, it appears to be biased to resin filling of only latewood. However, where earlywood is also in-filled with resin, the characteristics for identifying the wood are difficult if not impossible to see with transmitted light.

Comparison

According to Philippe and Bamford (2008), the araucaroid tracheid pitting, the presence of phyllocladoid oopores and lack of oculipores are features that distinguish *Protophyllocladoxylon* from other taxa of fossil wood. Based on these characteristics we have determined that the material can be assigned to *Protophyllocladoxylon*.

Of the 29 species of *Protophyllocladoxylon* thus far described (Zhang et al., 2010; Pujana et al., 2014) only four have the following characteristics in common with the specimens described here: marked growth rings, uniserate rays with heights including approximately 2–18 cells, uniserate and biserate (rarely triserate) tracheid pitting, alternate where biserate or triserate, oval and/or sub-hexagonal, and 1–2 simple circular to ovoid pits per crossfield and lack axial parenchyma. These species are *P. francisiae* Punjana, Santillana et Marenssi (Pujana et al., 2014), *P. indicum* Pant et Singh (Pant and Singh, 1987), *P. dolianitii* Mussa (Mussa, 1958) and *P. lechangense* Wang (Wang, 1993).

However, the following characters differentiate *P. owensii* from the previously described taxa. *Protophyllocladoxylon francisiae* (Pujana et al., 2014) is dissimilar from the specimens here in that the crossfield pits are elongated and contiguous where two are present, unlike those of *P. owensii*, and come from the Eocene of Antarctica.

Protophyllocladoxylon indicum (Pant and Singh, 1987) has irregular size and position of the crossfield pits within the crossfield, with pairs often conjoined, and some stacked vertically, whereas those of *P. owensii* are not conjoined, are not stacked vertically and are of a similar size throughout. *Protophyllocladoxylon indicum* comes from the Permian of India. *Protohyllocladoxylon dolianitii* (Mussa, 1958) differs in that is usually has only one elliptic oopore in the centre of the crossfield, not two in each crossfield in the earlywood and one in each crossfield in the latewood as is the case in *P. owensii*. *Protohyllocladoxylon dolianitii* is from the Late Carboniferous of Brazil. *Protophyllocladoxylon lechangense* Wang (Wang, 1993) appears to be different from the specimen described based on the description of Zhang et al. (2010), which states that the crossfield pits are both elliptic, like those described in *P. owensii*, but also rectangular with rounded corners (fenestral), which is not reported for the new morphospecies; however, the fenestral appearance may be a taphonomic feature. The images are of poorly preserved material, but they show that the crossfield pits were also horizontally aligned, and possibly continuous, compared to the oblique and spaced crossfield pits of *P. owensii*. *Protophyllocladoxylon lechangense* is from the Triassic of China.

The most similar taxon to *P. owensii* described by Peters (1985) is *Araucarioxylon* – “Parataxon 1”. Despite some similarities, there are differences such as the prevalence of uniserate tracheid pitting in Peters’ (1985) specimens, with only occasional biseration and the description of the crossfield pits as cupressoid rather than phyllocladoid, which is found in the new species. While these features may be correlated with age, we consider the specimens different enough that they should not be assigned to the new species.

4. Discussion

Protophyllocladoxylon contains 29 described species, in addition to the new species *P. owensii*, with a cosmopolitan distribution and temporal range that extends from the Carboniferous to the Eocene (Zhang et al., 2010; Pujana et al., 2014). *Protophyllocladoxylon* is generally considered to be allied to Podocarpacae, but some features, such as araucarian tracheid pitting, suggest affinities with Araucariaceae. The taxon also displays a high amount of morphological diversity (Pujana et al., 2014). Some species, including the type species, have only araucarian type tracheid pitting, while others have the mixed type (e.g. *P. cortaderitaense;* Menéndez, 1956; Wang, 1993; Phillipe and Bamford, 2008; Zhang et al., 2010), are predominantly multiserate (e.g. *P. subdiphterium*; Duperon-Laudouneneix, 1976), or predominantly or exclusively uniserate (e.g. *P. oolithicum*; Vogellehner, 1966). Pujana et al. (2014) state that pitting arrangement is a key feature for classifying at ranks such as family and genus, and thus this diversity of character states may be problematic in a taxonomic context. Alternatively, the differences may be correlated to developmental stage or age of the tree, or due to environmental impacts on growth. For example, the narrow tracheids in *P. owensii* produce single-file rows of tracheids, whereas the wider tracheids produce alternately arranged araucarian type pitting, and in rare, very wide tracheids, even three across. Wider tracheids are commonly found in juvenile wood and in wood growing in optimal conditions (Falcon-Lang, 2005), and thus identifications made on single pieces of fossil wood may not represent the true diversity of characters in the species in other age classes or growing conditions.

Wood assemblages give a unique insight into past communities and offer insight into canopy structure, in a way that coeval palynological or leaf assemblages do not (Cantrill and Poole, 2005). Integrating information from pollen, leaf and wood assemblages can be used to disentangle community structure, with the wood representing the canopy-forming element. The wood from the region directly around the town of Winton, at QM L311 and in Bladensburg National Park appears to be dominated by podocarps (as represented by material assigned to *P. owensii*). Wood assignable to araucarian taxa is rare but present, as is the false trunk of tree ferns (Clifford and Dettmann, 2005), but taxodiaceous conifers, angiosperms and gingko wood is thus far absent. The dominance of podocarp wood is supported by limited pollen count data that also documents abundant podocarp pollen, but leaf and permineralised assemblages indicate that other canopy forming trees such as Taxodiaceae were also likely to have been present. A re-evaluation of Peters' (1985) material, and further survey of the wood found throughout the Winton Formation is needed to determine community structure over its extensive geographic and temporal distribution.

Extant podocarps have a wide diversity of morphologies, but primarily inhabit rainforest or wet montane environments (Hill and Brodribb, 1999). *Protophyllocladoxylon* appears to have predominantly inhabited warm and wet areas throughout its long record (Zhang et al., 2010). This is in agreement with previous estimates of palaeoclimate for this portion of the Winton Formation that suggest mean annual temperatures of above 16 °C and mean annual precipitation between 1300 and 1600 mm (Fletcher et al., 2013; in press).

Araucarian trees are also present (Peters, 1985), mostly likely as infrequent canopy emergents; a role they play in many modern southern forest ecosystems (Hill and Brodribb, 1999). Interestingly, a mismatch between the composition and abundance of araucarian wood and leaf floras has been observed previously (Cantrill and Falcon-Lang 2001), and the same pattern is apparent in the Winton Formation. Whether this is due to taphonomic biases that preferentially preserve araucarian foliage over that from podocarps, or alternatively that araucarian wood is more readily degraded than podocarp wood and so biasing the assemblages remains to be determined. However, as noted above, approximately half of all wood samples prepared for this study were unable to be identified due to poor cellular-scale preservation. The potential for taphonomic bias to affect estimates of community structure should therefore not be dismissed.

4.1 Conclusion

The Winton Formation wood flora appears to be dominated by Podocarpaceae, including a new species described as *Protophyllocladoxylon owensii*. The composition of the leaf, cone and pollen flora on the other hand indicates the presence of araucarians, taxodiaceous conifers, ginkgos, cycads, ferns and angiosperms. This contrasts with the wood assemblage that is rich in one taxon, likely placed in Podocarpaceae. Thus, although previous studies found that the Winton Formation plant assemblages were broadly coeval and differ only slightly in taxonomic composition (McLoughlin et al., 1995), these results suggest there may be spatial heterogeneity across the landscape. Falcon-Lang et al. (2001) found that low density podocarp and taxodiod conifers dominated the mobile alluvial plains of Alexander Island, Antarctica, which were subjected to regular catastrophic flooding, while the more stable and protected sediments boasted a more diverse flora in a podocarp-araucarian rainforest. It may be that the discrepancy between the wood flora composition and other macro and microfloral evidence from the Winton Formation is representative of a bias towards the preservation of podocarp wood during flooding events because these trees were more dominant in flood prone areas. This possibility highlights the importance of interpreting individual aspects of the ecology of an environment, such as the taxonomic diversity of the wood, in the broader context of the palaeoenvironment. In this case it requires the interpretation of the wood taxa in the context of other plant macrofossils, spores and pollen, and sedimentological evidence to accurately reconstruct palaeo-landscapes.

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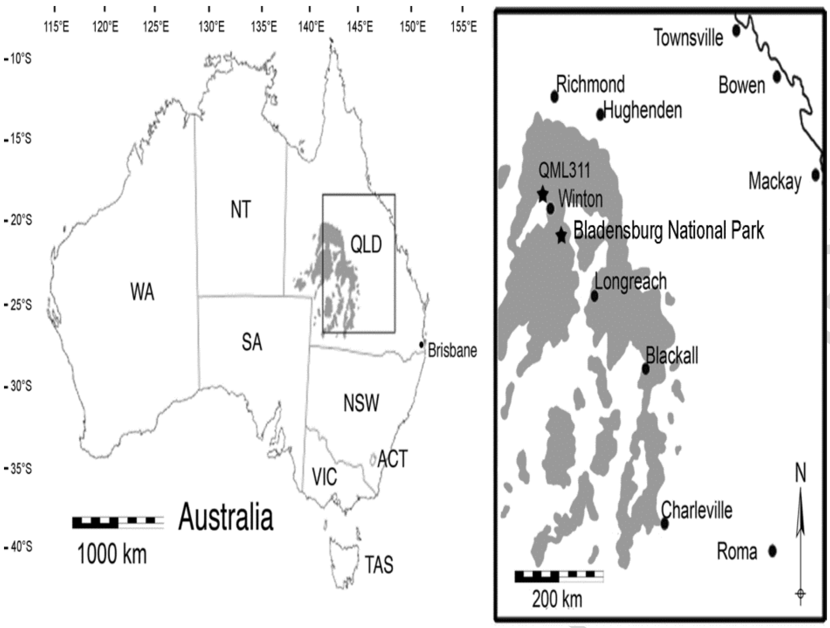
Figure Captions

Figure 1: A map of Australia showing the area where the Winton Formation crops out (in grey), which broadly corresponds to the Eromanga Basin. Also marked are the localities from which the holotype (QM L311) and paratype specimens (QM L311 and Bladensburg National Park) originate.

Figure 2: Schematics of the key features of the holotype, QM F44339, and paratypes; A – phyllocladoid oopores in radial crossfields; B – circopores in radial crossfields; C – earlywood trachied pitting in radial section; D – latewood

trachied pitting in radial section; E – rays in tangential longitudinal section; F – a growth ring boundary in transverse section.

Plate I: Photographs of the key features of the holotype, QM F44339, 1 – ray cells and tracheids, tangential section; 2 – taphonomic features, likely partial degradation of cell walls, radial longitudinal section; 3 – pairs of phylocladoid oopores in earlywood crossfields, radial logitudinal section; 4 – pairs of oopores, some circulopores, in earlywood crossfields, radial longitudinal section; 5 – uniserate and biserate tracheid pits, alternate where biserate, radial longitudinal section; 6 – ray cells, tangential section; 7 – a series of alternately arranged, biserate, sub-hexagonal, araucaroid-type tracheid pits, radial longitudinal section; 8 – overview of a portion of radial longitudinal section showing earlywood to latewood transition and latewood to earlywood boundaries; 9 – transverse longitudinal section showing earlywood to latewood transition and latewood to earlywood boundaries; 10 – overview of transverse longitudinal section showing earlywood to latewood transition and latewood to earlywood boundaries.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Townsville
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Figure1

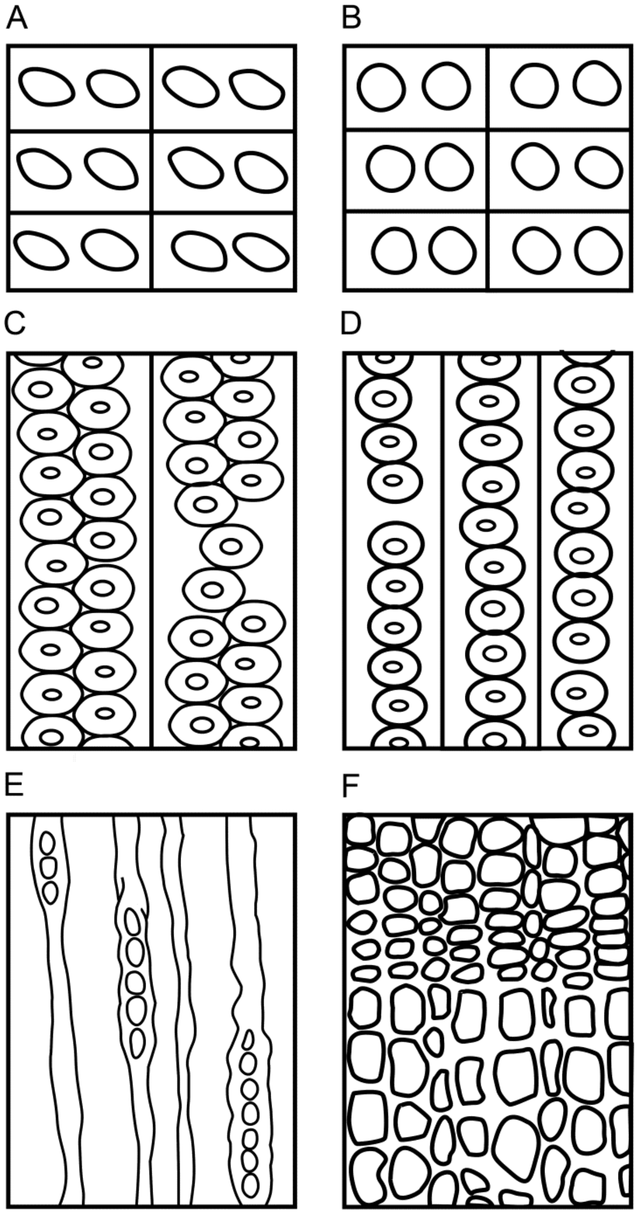

Figure2

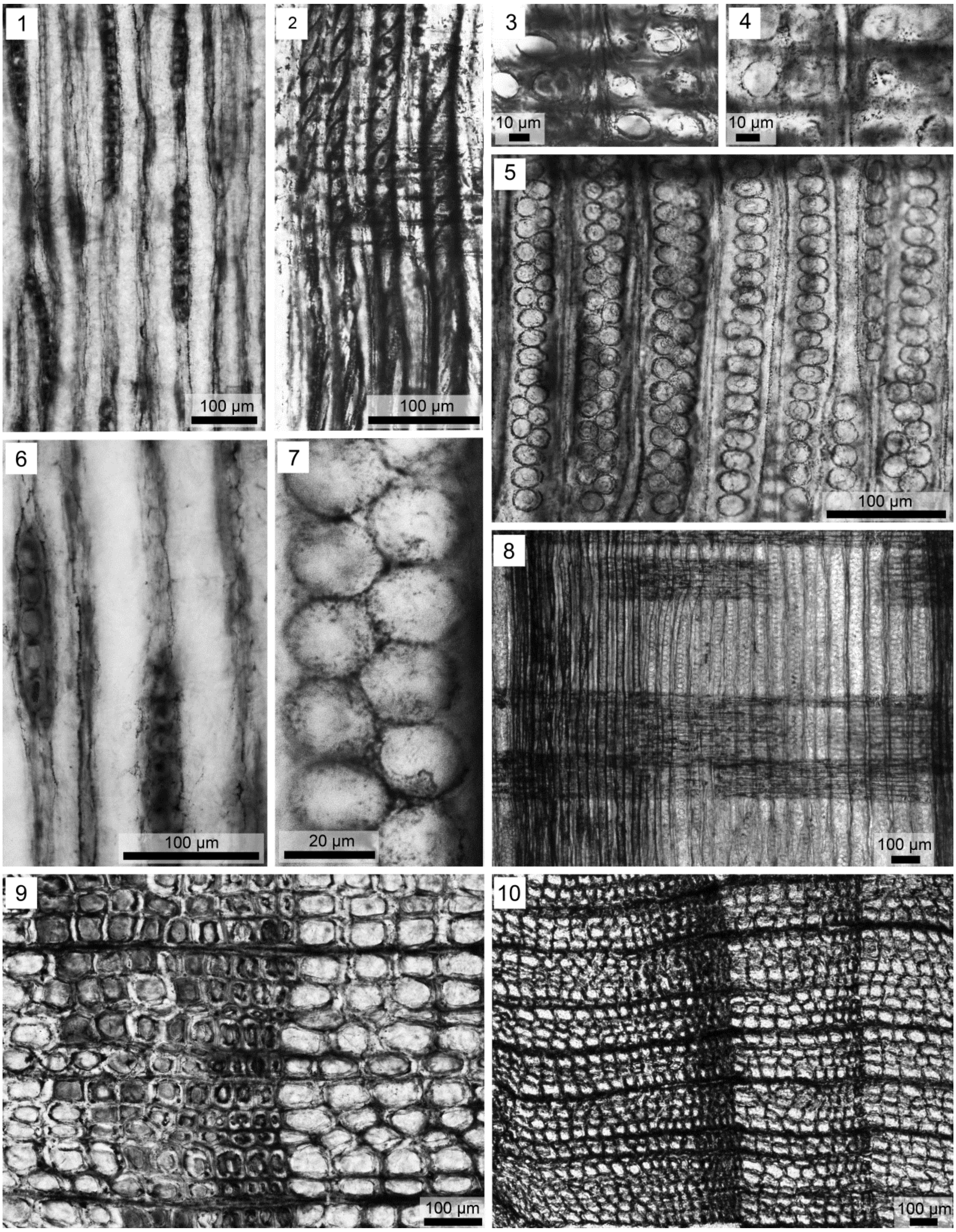
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Plate I

- Highlights
- A new species of *Protophyllocladoxylon* from the Late Cretaceous
- Paleoecological interpretation of a locality with conflicting macroflora evidence
- Possible evidence for flooding causing spatial heterogeneity in the flora