

additional water stress adaptations in grapevines, and may hopefully facilitate the development of cell wall constituents as indicators of water stress in real time in the vineyard.

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## ANATOMY OF LEAVES AND SEED CONES OF *DACRYCARPUS* (ENDLICHER) DE LAUBENFELS (PODOCARPACEAE) FROM THE MIOCENE OF SOUTHERN CHINA

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The genus *Dacrycarpus* (Endlicher) de Laubenfels (Podocarpaceae) with nine extant species is discontinuously distributed in tropical mountain rainfor-

ests of the southwestern Pacific region, ranging from New Zealand and Fiji to northern Myanmar and southernmost China, with the highest diversity in New Guinea (de Laubenfels, 1988; Eckenwalder, 2009; Farjon, 2010). However, fossil record indicates that *Dacrycarpus* was widely distributed in the Cenozoic floras of Australasia and Patagonia. The earliest *Dacrycarpus* megafossils so far found are from the Eocene of Chile, Argentina and Australia (Florin, 1940; Greenwood, 1987; Wells, Hill, 1989; Hill, Carpenter, 1991; Wilf, 2012). By the Oligocene, the distribution of *Dacrycarpus* was mainly limited to southeastern Australia and New Zealand (Cookson, Pike, 1953; Wells, Hill, 1989; Hill, Carpenter, 1991). The latest *Dacrycarpus* fossils are from the Miocene of Australia and New Zealand (Hill, Whang, 2000; Pole, 2007; Lewis, Drinnan, 2013). So far, however, no megafossil record has been reported from the Northern Hemisphere resulting in an incomplete understanding of the origin of the modern distribution pattern and phytogeographic history of *Dacrycarpus*.

The first Northern Hemisphere megafossils of *Dacrycarpus* represented by three-dimensionally preserved foliage, ovuliferous cones and pollen cones with *in-situ* pollen were obtained from the Miocene of the Guiping Basin, Guangxi Province, southern China. The typical features of these fossils are spirally inserted, decurrent on the axis, and dimorphic foliage leaves as well as the ovuliferous structures with a warty receptacle and a terminal seed cone containing one inverted ovule. An incompletely preserved pollen cone is subtended by a short stalk with a few bifacially flattened leaves. Microsporophylls are helically arranged, each bears two globular sporangia. Pollen grains have a prominent corpus and three sacci.

The new *Dacrycarpus* species possesses strongly dimorphic foliage leaves comprised of bifacially flattened ‘adult’ leaves on long shoots and bilaterally flattened ‘juvenile’ leaves on feather-like short shoots. The leaves on the short shoots generally show a complete transition from bifacial to bilateral, and the leaves on the fertile shoots often display intermediate stages of this transition. Bilaterally flattened leaves are distichous, falcate, straight to slightly apically incurved, and strongly keeled with a single prominently raised vein. The leaves are amphistomatic, with two longitudinal bands of stomata which run from the leaf base to the apex on each surface. Each band contains one to five rows of stomata (typically two or three). Stomatal axes are parallel to the midvein. Florin rings are prominent, sunken below the leaf surface. Stomatal complexes are paratetracytic, elliptical, with four to six subsidiary cells (mostly four). The leaf cross section is ellipsoidal to rhomboidal. The epidermis is covered by a cuticle. Hypodermis fibres are 3–5 µm in diameter. The vascular bundle is single, 30 µm wide. Tracheids of the vascular bundle possess scalariform and reticulate thickenings. A transfusion tissue is developed above the vascular bundle; it consists of reticulate transfusion tracheids up to 20 µm in diameter. A resin canal is up to 100 µm in diameter. Only a palisade mesophyll was occasionally observed in the bilateral leaves.

Bifacial leaves are small, scale-like, triangular to linear-lanceolate or sometimes slightly falcated, loosely to nearly appressed, strongly keeled, deployed on long shoots as well as at the base of short shoots and fertile structures. The leaf tip is incurved and the margin is entire. The leaves are amphistomatic; the stomata are confined to two more or less continuous bands on each surface, those of the adaxial surface are narrower and shorter than on the abaxial surface. The stomatal zone is one to four rows wide; the rows are parallel to the leaf longitudinal axis and separated typically by one to four epidermal cells. Florin rings are prominent. The stomata are paratracheal, elliptical, and with four to six subsidiary cells (mostly four). Epidermal cells are longitudinally oriented, with granular periclinal walls and smooth anticlinal walls. Leaf cross-section is triangular to rhomboidal. The epidermis is covered by a cuticle. The hypodermis consists of fibers 3–5  $\mu\text{m}$  in diameter. The vascular bundle is single, central, collateral, about 50–70  $\mu\text{m}$  wide. Tracheids of the vascular bundle are with scalariform and reticulate thickenings. Transfusion tissue is developed above the vascular bundle and gradually replaces the tracheids of the vascular bundle laterally. Transfusion tissue consists of reticulate transfusion tracheids up to 30  $\mu\text{m}$  in diameter. A large resin canal (60–90  $\mu\text{m}$  in the diameter) is present below the vascular bundle. Mesophyll is distinctly dimorphic only at the leaf base (an abaxial palisade mesophyll and adaxial spongy mesophyll are present). More distally, only the palisade mesophyll is developed. Abundant epiphytic and endophytic micromycetes were found on the leaves of the new *Dacrycarpus* species.

The leaf anatomical features of the new fossil *Dacrycarpus* are similar to those of extant species but there are some differences. The hypodermis in *D. imbricatus* (Blume) de Laubenfels is also developed in all leaf morphotypes but it possesses stronger fibres (up to 20  $\mu\text{m}$  in the diameter). Resin canals in *D. imbricatus* are smaller (up to 50  $\mu\text{m}$  in the diameter). In bifacial leaves, the palisade tissue is developed only on their adaxial side; the spongy tissue is abaxial, whereas the leaves in the fossil species possess adaxial spongy tissue and abaxial palisade tissue. In bilateral leaves of *D. imbricatus* only the palisade tissue is developed, as in the fossil species. The fossil species differs from the extant *D. dacrydioides* (A. Rich.) de Laubenfels by possessing fibres in all types of leaves, whereas in *D. dacrydioides* the fibers are present only in the leaves of long shoots. Moreover, the adaxial palisade tissue in *D. dacrydioides* is developed only in the leaves of the short shoots (Dörken, Parsons, 2016), but in the new fossil species it occurs in all types of leaves.

Ovuliferous shoots arise from the leafy long shoots and are composed of involucre leaves, a podocarpium and a seed cone. The involucre leaves are spreading or clasping the basal half of the podocarpium. Warty, bumpy podocarps are 2.3–4.1 mm long, composed of at least two expanded, fused leaves. The seed cones are terminal, oval-shaped, obovate and deployed singly or doubly on a podocarpium, consisting of an ovule, epimatium and fertile bract. The inverted ovule is surrounded

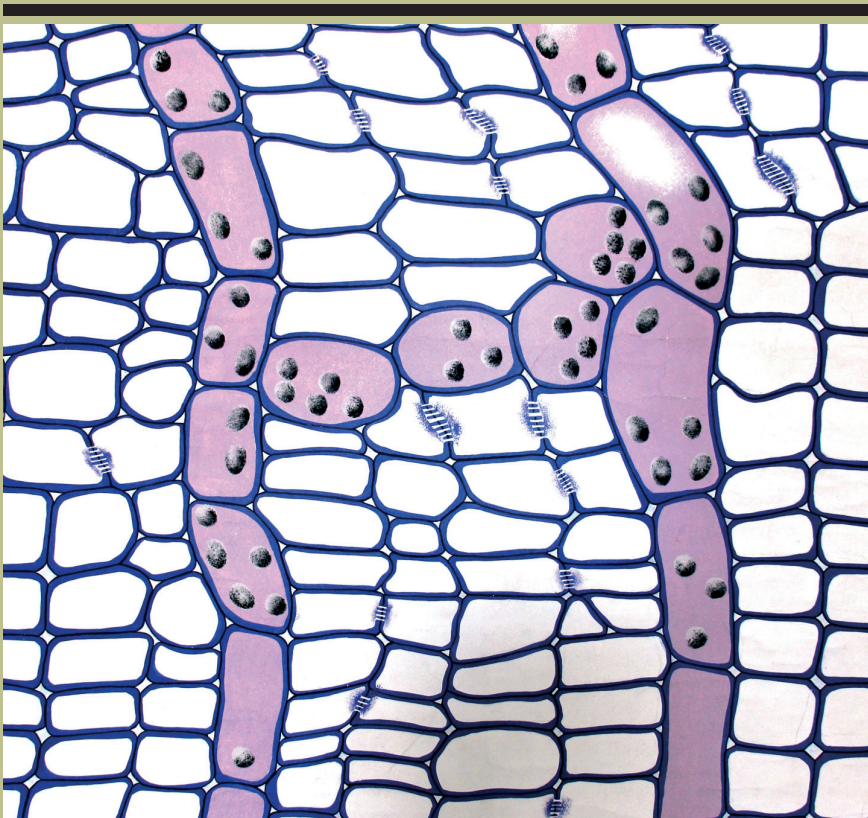
by the epimatium being partly fused with the fertile bract, forming a crest along one side of the epimatium that ends in a sideways beak. Computer tomography (CT) showed that the seed cone consists of nucellus remains and fertile bract fused to the epimatium, which in turn is fused to the seed coat (testa). The epimatium contains numerous resin canals filled by massive amber. The testa consists of a thick mesotesta layer and a thin endotesta layer. The exotesta is reduced, as previously shown for the *Dacrycarpus* seed cones by Melikian & Bobrov (2000).

Apparently, new fossil species represents the most complete and best-preserved megafossil remains of *Dacrycarpus* known to-date. Of all the extant species, this fossil species shows a close similarity in morphological and anatomical characters to *D. imbricatus*, the only species of *Dacrycarpus* presented today in China.

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ИМЕНИ М.В. ЛОМОНОСОВА  
БИОЛОГИЧЕСКИЙ ФАКУЛЬТЕТ

## PLANT ANATOMY: TRADITIONS AND PERSPECTIVES

АНАТОМИЯ РАСТЕНИЙ:  
ТРАДИЦИИ И ПЕРСПЕКТИВЫ

*Международный симпозиум,  
посвященный 90-летию профессора  
Людмилы Ивановны Лотовой*

**ЧАСТЬ 1**

# АНАТОМИЯ РАСТЕНИЙ: ТРАДИЦИИ И ПЕРСПЕКТИВЫ



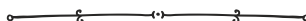
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*В двух частях*

## Часть 1

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Materials of the International Symposium  
dedicated to the 90th anniversary  
of Prof. **LUDMILA IVANOVNA LOTOVA**

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