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COMPARATIVE LEAF ANATOMY OF TRIGONOBALANUS FORMAN (FAGACEAE)

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SUMMARY

The leaf anatomy of the recently discovered Neotropical species *Trigonobalanus excelsa* is described and compared with that of the Old World species *T. doichangensis* and *T. verticillata*. *Trigonobalanus excelsa* appears to be very similar in its leaf anatomy to *T. verticillata* from Borneo and Sumatra.

INTRODUCTION

Recently Lozano et al. (1979) described a new Colombian species of the genus *Trigonobalanus* (*T. excelsa*, Fagaceae), before then only known from Malesia (Forman, 1964; Soepadmo, 1972). In a subsequent paper Hernandez-C. et al. (1980) provided more detailed morphological information and a discussion of the possible phytogeographical history of the species. Mennega (1980) described and discussed the wood anatomy. The leaf anatomy of *T. excelsa* was also described by Hernandez-C. et al. (1980); but its significance in discussing the infrageneric affinities of the three known species *T. excelsa*, *T. doichangensis*, and *T. verticillata* was not analysed. The latter two species were described anatomically by Cutler (1964). My own observations largely confirm those of these previous authors, but deviate in the interpretation of some characters (e.g. stomatal type), and add more detail and some corrections to the existing information. In this note the information on the indumentum is partly based on the analyses by Hernandez-C. et al. (1980) and Cutler (1964), because in some of the material at my disposal hairs had been shed or were caducous.

LEAF ANATOMICAL DESCRIPTION OF TRIGONOBALANUS EXCELSA G. LOZANO, J. HERNANDEZ & J. HENAO

This description is based on transverse and paradermal sections and cuticular macerations of the type material.

In surface view: *Hairs* thick-walled, solitary or in few-celled to almost stellate tufts, mainly confined to abaxial epidermis. In addition, basal parts of partly disintegrated or shed, thin-walled, probably glandular hairs (both cylindrical and capitate hairs recorded by Hernandez-Camacho et al., 1980) numerous on abaxial surface, infrequent on adaxial surface (fig. 1). *Cuticle* smooth. *Unspecialized epidermal cells* with straight to curved, usually sclerified walls (in adaxial epidermis sclerified cells confined to regions



Fig. 1. A. Thick-walled hairs, solitary and tufted. — B. Bases of thin-walled, caducous hairs (probably glandular), from adaxial epidermis (bottom) and abaxial epidermis (top).

overlying veins; in abaxial epidermis all cells sclerified except those over major veins and except subsidiary and guard cells of stomatal complex). Cell pattern over veins modified; cells here elongated parallel to venation. Stomata confined to abaxial epidermis, crowded in areoleae, cyclocytic with 5–6(–7) subsidiary cells; guard cell pairs (23–)24(–26) μ m long, (20–) 22 (–24) μ m wide.

In transverse section: Lamina dorsiventral c. 230 μ m thick. Cuticle 3 μ m thick. Adaxial epidermal cells taller than abaxial cells. Stomata in level with epidermis, with well-developed outer stomatal ledges. Adaxial hypodermis of weakly sclerified, translucent cells only locally developed near major veins and in basal part of lamina. Mesophyll composed of 2(-3) layers of tall palisade cells and abaxial spongy tissue. Midrib with convex adaxial and abaxial surface, supplied with a closed vascular system including 'medullary' vascular tissue (fig. 2). Entire system sheathed by sclerenchyma fibres. Ground tissue of midrib parenchymatous to collenchymatous, containing some weakly sclerified cells at periphery but wholly lignified in 'pith'. Vascular bundles of veins with sclerified bundle sheath extensions reaching upper and lower epidermis.

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Fig. 2. & 3.-2. Transverse section of midrib in middle of lamina. Sclerenchyma black. Xylem hatched. Phloem dotted. -3. Ibid. of basal part of lamina.

Petiole supplied by individual bundles at the base, becoming organized into a complex system in the distal end and basal part of lamina (fig. 3). Sclerenchymatous sheath of vascular system well-developed in distal end of petiole, absent from base but here ground tissue interspersed with brachysclereids. *Crystals* common as druses and clusters, infrequently also as solitary crystals in vicinity of vascular bundles.

COMPARISONS AND DISCUSSION

The leaf anatomy of Trigonobalanus excelsa is compared with the two Old World species T. verticillata Forman and T. doichangensis (Camus) Forman in table 1. The latter species have been described in detail by Cutler (1964), while Camus (1934) had also given a leaf anatomical account of T. doichangensis (under 'Quercus doichangensis'). Moreover additional herbarium material of T. verticillata (Malaya, KEP 110330) and T. doichangensis (Thailand, Van Beusekom & Geesink 4822) was sectioned to afford more detailed comparisons.

In table 1 both the shared and the distinguishing leaf anatomical characters of the three *Trigonobalanus* species are listed. Note that some of the characters listed for the Old World species differ slightly from those recorded by Camus (1934) and Cutler (1964) or were not considered by these authors. For instance, I deviate from Cutler by referring the stomatal complex of Trigonobalanus to the cyclocytic type instead of the anomocytic type: although of similar shape and size as the other epidermal cells, the cells surrounding the guard cells differ from these in either lacking sclerification or, in the case of T. doichangensis, in also lacking papillae. The guard cells are therefore surrounded by a ring

	T. excelsa	T. verticillata	T. doichangensis
Thick-walled, unicellular hairs partly tufted	+	+ .	-
Thin-walled, uniseriate cylindrical hairs	+	-	+
Thin-walled unicellular hairs	-	+	-
Stalked, multicellular 2-branched, stellate, or irregular hairs	-	-	+
Small capitate hairs	+	-	-
Unspecialized epidermal cells partly sclerified	+	+	+
Stomata cyclocytic with 56 subsidiary cells	+	+	+
Size of guard cell pairs (mean values)	au x 22 سبر 24 x 22	aau 33 x 33 aau	an 23 x 19 مسئر 23
Abaxial epidermis papillate	· _	-	+
Adaxial hypodermis locally differentiated	+	+	-
Midrib biconvex with vascular cylinder enclosing 'medullary' vascular tissue	+	+	+
Vascular bundles of veins with vertical bundle sheath extensions	+	+	+
Solitary crystals present in addition to clustered ones and druses	+	+	-
Brachysclereids in basal part of petiole	+	-	-

Table 1. Leaf anatomical characters of Trigonobalanus

of deviating cells, and the stomata should thus be classified as cyclocytic. Camus (1934) and Cutler (1964) did also not record the differentiation of the epidermal cells into sclerified and non-sclerified ones, but this character is common to all three *Trigonobalanus* species.

It is interesting to note that *T. excelsa* is leaf anatomically closer to *T. verticillata* (9 shared characters) than to *T. doichangensis* (7 shared characters). The mutual resemblance of the Neotropical *T. excelsa* with the easternmost Old World species *T. verticillata* gains in significance if one considers that the latter species shares only 6 characters with the other Old World species *T. doichangensis*. It should be stressed, however, that the diagnostic and taxonomic vallue of the characters listed in table 1 may vary and would require further testing. Moreover, quite a number of characters listed are of common occurrence throughout the Fagaceae (cf. Metcalfe & Chalk, 1950, and Camus, 1928–1954). Notably *Quercus, Lithocarpus, Castanopsis* and *Castanea* appear to share many leaf anatomical characters with *Trigonobalanus*. Unfortunately our knowledge of the leaf anatomical range in *Fagus* and *Nothofagus* is insufficient to allow further conclusions on the alliance of *Trigonobalanus* in Fagaceae. At present, leaf anatomy is certainly not in conflict with the generally accepted view (Forman, 1964; Cutler, 1964; and Soepadmo, 1962) that *Trigonobalanus* has close affinities with *Quercus*.

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