THE VEGETATIVE ANATOMY OF KOSTERMANSIA
MALAYANA SOEGENG

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SUMMARY

The anatomy of leaves, twigs, wood and seedling of Kostermansia Soegeng is described. A comparison with some species of Coelostegia and Durio indicates the close affinities between the three taxa, but also shows some differences in leaf anatomy, probably valuable for diagnostic purposes. The stomata in Kostermansia show a very remarkable arrangement in circles around the insertions of the scales.

INTRODUCTION

In 1959 Soegeng Reksodihardjo described the genus Kostermansia with one species, K. malayana from the Malay Peninsula. The new genus was said to be closely related to Durio and Coelostegia, and he listed macromorphological characters with the aid of which the three genera could be recognized, but which also indicated the strong affinities between the genera. An anatomical investigation of the genus has never been undertaken and was considered of some importance in order to fill one of the gaps in our knowledge of Bombacaceae anatomy and also to compare the results of macromorphology with those of vegetative anatomy concerning the affinities with Coelostegia and Durio. The choice of Kostermansia for a short study was all the more attractive since it would provide a most suitable subject to honour Dr. A. J. G. H. Kostermans, after whom the genus was named.

METHODS AND MATERIALS

The techniques employed in preparing anatomical slides and macerations and for making measurements are as previously described elsewhere (Baas, 1970).

Specimens used are listed below. Institutional wood collections are abbreviated according to Stern 1967. Specimens from Leyden (L) were used for leaf anatomy.
Coclostegia bornensis Becc, Malaya, FRI 3626 (L).
C. griffithii Benth., Malaya, FRI 90744 (L), slides FHOiv 716L, 7166 and 7167 (K-Jw).

Durio Ussocarpis Mast., Borneo, bb. 14394 (slide K-Jw); D. oxleyanus Griff., slides FHOU 7172 and 7173 (K-Jw); D. testidimarum Becc, Borneo, SAN 31421 (L); D. zibethimus Muir., Malaya, KEP 57405 (L), slide s.v. (K-Jw), India, Gamble 5074 (slide K-Jw). Durio spp. (aff. lowianus and malaccensis), slides FHOU 7169, 7170, 7171 and 7174 (K-Jw).

Kostermansia malayana Soegeng, Malaya, SFN $4673, SFN 37100 and Hassan (slide K-Jw). Durio spp. (aff. lowianus and malaccensis), slides FHOU 7169, 7170, 7171 WT 4400 and WT 5691 (KEPw) for wood anatomy.

ANATOMICAL DESCRIPTION OF KOSTERMANSIA MALAYANA

Leaf

In surface view: Cuticle smooth with internal coarse granules or holes (?) on adaxial surface, striated on abaxial surface. Adaxial surface mainly glabrous apart from area overlying midrib, where partly covered with scales. Epidermal cells with straight or slightly curved anticlinal walls. Mucilage cells with thicker walls and narrower lumina at high focus frequently present, surrounded by a circle of radially orientated unspecialized cells (fig. 1 and 2). Abaxial surface densely covered with sessile scales. Scales composed of numerous radial cells (fig. 3). Multicellular, 1 — 2 seriate, glandular hairs occasionally present underneath some of the scales. Unspecialized cells like those of adaxial surface. Stomata confined to abaxial surface, regularly arranged in complete or partial circles around the insertions of the scales and covered by the latter (fig. 4), anisocytic with bean shaped guard cells and subsidiary cells with more or less mucilaginous walls, swelling considerably in water. Diameter of guard cell pairs perpendicular to the pore 16 — 24 \( \mu \) (mean 20 \( \mu \)).

In transverse section: Cuticle 6 — 9 \( \mu \) thick. Adaxial epidermis composed of tall rectangular cells interspersed with mucilage cells with narrowly pointed apices and broadly globular bases, invading the palisade tissue below (fig. 2). Unspecialized cells of abaxial epidermis square; guard cells flattened. Bases of scales surrounded by thick cutinized walls (fig. 5). Mesophyll composed of 2 — 3 adaxial layers of palisade cells and very loose, spongy tissue. Midrib adaxially grooved and abaxially prominent with complex and variable arrangement of vascular bundles (e.g. fig. 6), the whole system sheathed with sclerenchyma fibres. Ground tissue of midrib collenchymatous to parenchymatous with occasionally some lignified cells in abaxial part and wholly lignified in
Kostermansia malayana Soegeng, leaf anatomy. 1. Adaxial epidermis in surface view; fig. 2. ibid. in transverse section; fig. 3. scale; fig. 4. abaxial epidermis in surface view; fig. 5. ibid. in transverse section; fig. 6. midrib; fig. 7. distal part of petiole; fig. 8. basal part of petiole.

Fig. 1-5 X 300; fig. 6 - 8, X 17. e = epidermis, g = glandular hairs, m.c. = mucilage cell, cavity or canal, p = palisade parenchyma, s = scale. Mucilaginous substance in fig. 2 dotted, surface of scale in fig. 4 grey, sclerenchyma in fig. 6-8 black, xylem shaded, phloem dotted.
central part included in vascular system. Vascular bundles of *veins* with tall vertical parenchymatous to sclerenchymatous bundle sheath extensions reaching upper and lower epidermis. *Petiole* densely covered with scales, supplied with complex vascular system consisting of a closed cylinder at the base and an almost closed horse-shoe-shaped arc at the distal end surrounding central vascular bundles in variable arrangement (fig. 7 and 8). The latter composed of peripheral xylem and central phloem with internal fibres, probably of pericyclic origin; the bundles representing folded or strongly incurved collateral bundles. The whole vascular system surrounded by a thin, sometimes incomplete, fibrous sheath. Ground tissue of petiole parenchymatous to collenchymatous. Parenchyma cells included within vascular system and some, cells of peripheral ground tissue with lignified walls. *Mucilage cells* present in adaxial epidermis (see above). *Mucilage canals and cavities* present in peripheral ground tissue of midrib in petiole, in some specimens also in central ground tissue of vascular system. *Crystals* of prismatic shapes, clusters and druses occurring with various frequencies and ratios in ground tissue of petiole and midrib and in parenchyma cells of bundle sheaths of veins. Phloem of midrib and petiole with infrequent prismatic crystals.

Axis (materials: one twig of 3 mm diam., and three twigs of 7 mm diam.).

*Epidermis* of young twigs with same indumentum as abaxial leaf surface. *Cork* arising in epidermis, composed of thin-walled cells which are flattened and rectangular in transverse and radial section and polygonal in tangential section. *Cortex* fairly broad, composed of peripheral small-celled, occasionally lignified, parenchyma and a fairly loose inner tissue of unliignified parenchyma cells interspersed with lignified ones.

*Perivascular fibre ring* almost closed in very young twigs, interrupted by broad phloem rays in older twigs. *Phloem* with sieve-tubes and companion cells in groups surrounded by parenchyma, fibres and rays. Fibres abundantly present in very irregular and frequently interrupted bands or diffuse groups. Phloem *rays* of two types: broad rays, strongly dilatated and triangular in transverse section and narrow rays without dilatation. Many of the axial phloem parenchyma cells and ray cells with lignified walls. *Secondary xylem* with conspicuous *growth rings* marked by thick-walled fibres of late wood and thin-walled fibres of early wood. *Vessels* diffuse, solitary and in radial multiples of 2 — 4 (—10), circular to oval or tangentially flattened if in multiples, perforations simple in oblique to horizontal end walls. Lateral wall pits abundant and in alternate arrangement, rounded polygonal, diam. 4 — 8 µ, inter-vessel pits bordered,
vessel-ray pits half bordered. Some vessels filled with dark brown solid amorphous contents. Fibres and parenchyma as in wood, apart from dimensions. Rays tending to be of two sizes: narrow 1- or 2-seriate rays and broad rays up to 4-seriate, heterogeneous, composed of upright to square cells; tile cells of the Durio type present abaxially from first growth period. Primary xylem in continuous closed cylinder. Node three-lacunar with three leaf traces, the central one moreover splitting into three just above the leaf gap. Pith composed of parenchyma cells with thin lignified walls, interspersed with two or three large mucilage canals. Mucilage cavities infrequently present in cortex but abundant in nodal region. Crystals present as cluster crystals and prisms in cortex and pith, as prisms in axial xylem and phloem parenchyma and in phloem rays.

Seedling

The following striking differences exist between the anatomy of the cotyledons and the hypocotyl and the anatomy of foliage leaves and twigs. Cotyledon: Cuticle and cell walls of the epidermis thinner. Mucilage cells more frequent. Indumentum consisting solely of infrequent multicellular glandular hairs occurring on both ad- and abaxial surface. Stomata, confined to the abaxial surface, randomly distributed, also anisocytic, but with a larger diameter perpendicular to the pore (26 — 30 µ). Fig. 9. Palisade tissue of the mesophyll less well developed. Vascular system of the midrib consisting of one large collateral bundle with an abaxial and adaxial fibre cap and a small phloem strand enclosed in the adaxial cap. Many of the vascular bundles of the veins embedded in the mesophyll and only about half of the bundles with vertical bundle sheath extensions. Petiole bearing stellate hairs rather than scales and supplied with a closed vascular cylinder in the distal end and an open arc at the base, without central bundles. Hypocotyl: Indumentum consisting of scales and of types intermediate between scales and stellate hairs. Cotyledonary node one-trace, one-lacunar.

Wood (materials: two samples of mature wood ex KEPw)


Microscopic features: Growth rings present, indistinctly demarcated by more thick-walled fibres of the late wood. Vessels diffuse, tending to form an oblique pattern, ca 3 — 4 mm², solitary and in radial
Kostermansia malayana Soegeng. Fig. 9. Abaxial epidermis of seedling in surface view, x 300, fig. 10. wood in transverse section; parenchyma distribution only indicated on the lefth, x 17.

Multiples of 2 — 3 (— 6), circular to oval (radially elongated) in transverse section, tangentially flattened if in multiples, tangential diameter 90 — 350 µ (mean 240 µ), radial diameter up to 450 µ walls 4 — 7 µ thick, vessel member length 360 — 1030 µ (mean 750 µ). Perforations simple in slightly oblique to horizontal end walls. Lateral wall pits alternate. Inter-vessel pits rounded polygonal, diam. 7 — 9 µ, with small oval or occasionally elongated and then coalescent apertures. Vessel-parenchyma and vessel-ray pits similar but sometimes unilaterally compound and less frequent with more wall surface between them. Some vessels in WT 5691 with brown to yellow solid amorphous contents. Tyloses not seen. Tracheids absent. Fibres arranged in radial rows, 15 — 30 µ in diam., walls 3 — 5 µ thick, 1050 — 2100 µ (mean 1670 µ) long, with minutely bordered pits with ± vertical slit-lite apertures, rather frequent and mainly confined to radial walls. Parenchyma paratracheal as one or two layers of flattened cells around the vessels and apotracheally diffuse and in irregular uniseriate lines, forming a network with the rays (fig. 10). Apotracheal parenchyma in long strands of 7 — 8 — 12 cells. Some cells of these strands are subdivided by thin walls, each daughter
cell containing a single rhomboidal crystal. Many of the non-crystalliferous parenchyma cells with brown contents. Rays ca 9/mm, 1—4-seriate, the number of uniseriates constituting about 1/3 of the total number of rays, multiseriates up to 1.2 mm high in WT 4400, up to 1.6 mm high in WT 5691, KIRIBS heterogeneous type IIB or virtually homogeneous, composed of erect or square and procumbent cells with brown contents and rows of empty tile cells of the Durio type. Rows of tile cells as seen in transverse and radial section, occasionally interspersed with square cells with brown contents, and with procumbent cells with brown contents where in contact with the vessels. Perenchyma and ray tissue non-storied. Silica bodies absent.

COMPARISON WITH SOME SPECIES OF COELOSTEGIA AND DURIO

Soegeng Reksodihardjo (1959: 1 and 1960: 271) stated that Kostermansia seems to be intermediate between Durio and Coelostegia. Although a thorough anatomical study of the last two genera is beyond the scope of this paper, some leaf sections of Coelostegia borneensis, C. griffithii, Durio zibethinus and D. testidunarum were prepared and investigated for comparison, and in addition all wood slides of Coelostegia griffithii, Durio lissocarpus, D. oxleyanus, D. zibethinus and several other, not confidently named Durio specimens from the Kew slide collection of the Jodrell Laboratory were studied. A further comparison with data from literature is also included below.

The leaves of the two Coelostegia species differ anatomically from Kostermansia in the presence of a multiple epidermis, the distribution of stomata, which is random or only very imperfectly arranged around the scale insertions, the shorter glandular hairs which are sunken in between the other epidermal cells, and the presence of crystalliferous cells with one-sided lignified wall thickenings in the peripheral cell layers of the petiole, the subepidermal layer on the abaxial side of the midrib and in the bundle sheath extension of the veins. Other characters such as mucilage cells in adaxial epidermis, vasculature of midrib and petiole are of the same structure as in Kostermansia (see also Dumont 1887: 177 and Havez 1950: 66). The wood of Coelostegia is identical to that of Kostermansia in all details.

The leaves of the two Durio species investigated differ from Kostermansia anatomically in the random distribution of stomata, the indumentum which consists of 6—10 armed stellate hairs and glandular hairs covered by large scales, and the absence of special mucilaginous cells in
the adaxial epidermis. The midrib and petiole structure is again fundamentally similar to that of *Kostermansia*. See also Dumont 1887: 176, Kuntze 1891: 197—202, 229—234 and 293—299, Solereder 1899, Gehrig 1938: 60 and Havez 1950: 62. Kuntze reported a three-layered epidermis for *Durio zibethinus*, but Gehrig stressed the variability of this character in the same species. Solereder mentioned the occurrence of mucilage cells in the adaxial epidermis of *Durio*, in contrast to my own observations. The wood of *Durio* is again identical with that of *Kostermansia* and *Coelostegia*. Characters variable within the genus or within the species such as ray width and height, degree of homo- or heterogeneity of the rays, vessel diameter and frequency of vessel multiples behave in such a way that both *Kostermansia malayana* and *Coelostegia griffithii* are within the limits of structural variation of *Durio*. For details about the wood anatomy of *Coelostegia* and *Durio* see Moll and Janssonius 1908: 404, Metcalfe and Chalk 1950: 237, Chattaway 1951, Desch 1954: 574 and 1957: 55 and Rao 1958: 186.

**DISCUSSION AND CONCLUSIONS**

Vegetative anatomy fully supports the suggestions by Soegeng Rekso-dihardjo (1959, 1960) about the close affinities of *Coelostegia*, *Durio* and *Kostermansia*. On the basis of leaf anatomy, *Kostermansia* seems to be closer to *Coelostegia* than to *Durio*, because of the absence of star-shaped hairs from the lower leaf surface in the first two genera. The presence of partly lignified crystalliferous cells in the leaf of *Coelostegia* and the conspicuous arrangement of the stomata in *Kostermansia* are the only two important characters from vegetative anatomy in which these two genera differ. *Durio* stands out from the other two genera by its complex indumentum. Kostermans (1958a: 2, and 1958b: 361) expressed as his view that differences between *Durio*, *Coelostegia* and *Neesia* may not be substantial enough to recognize them as distinct genera. It is interesting to note that the wood of *Neesia* is also very similar to that of *Coelostegia*, *Durio* and *Kostermansia* (Moll and Janssonius 1908: 378). The pollen grains of these four genera have also many features in common (see Fuchs 1965: 125 and literature cited by him). The question remains which taxonomic conclusions can be drawn from these similarities in anatomical structure. It is obvious that no objections from vegetative anatomy would exist against regarding *Coelostegia*, *Durio* and *Kostermansia* as belonging to one genus, since the anatomical differences could just as well exist between the species of one genus. It might well be,
however, that using anatomical characters only, the other two genera of Durionae, Neesia and Cullenia, could also be included in this taxon. The leaf and twig anatomy of the two latter genera is insufficiently known unfortunately. A very brief investigation of some species showed that the vascularization of the petiole in these genera is basically similar to that of the other Durionae (see also Havez 1950). More research is obviously needed, however, to use anatomical characters validly in delimiting genera within this group. The differences in leaf anatomy between Coelostegia, Durio and Kostermansia might be helpful in the identification of sterile material. The absolute diagnostic value of these characters remains to be assessed, however, because of the small number of specimens and species studied. The remarkable arrangement of stomata around the scale insertions in foliage leaves and the absence of such a pattern in the scale-less cotyledons tentatively suggest a morphogenetic interaction of scale initials and stoma mother cells during the ontogeny in Kostermansia. The result of this interaction is exactly opposite to the phenomena described by Binning 1948: 176 for Vriesia hieroglyphica, where the stomata are distributed at the greatest possible distance from the scales. Himantandra is, to my knowledge, the only other genus in which a distribution of stomata in close circles around the scale-bases has been recorded (Bailey, Nast and Smith 1943: 196). From the resemblance in wood structure one might expect Kostermansia to produce a timber of the same restricted applicability as Durio and Coelostegia (see Desch 1957: 58).

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