

VEGETATIVE ANATOMY AND TAXONOMY OF BERBERIDOPSIS AND STREPTOTHAMNUS (FLACOURTIACEAE)

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SUMMARY

The leaf and twig anatomy of *Berberidopsis* and *Streptothamnus* are described in detail. The two genera are very similar in most aspects of their vegetative anatomy and together take a very isolated position in the Flacourtiaceae on account of their xylem anatomy and stomatal type. Differences in indumentum, crystal complement and epidermal cell morphology (whether or not papillate) support the distinction of *Streptothamnus moorei* from *Berberidopsis* sensu Veldkamp, i.e., including *Berberidopsis corallina* and *B. beckleri* (formerly *Streptothamnus beckleri*).

INTRODUCTION

Literature on the vegetative anatomy of the Flacourtiaceae has been reviewed by Solereder (1899 & 1908) and Metcalfe & Chalk (1950). Leaf anatomical contributions after 1950 have been few and relate to a small number of taxa only: Golysheva (1975, *Idesia*); Merina & Medina (1967, *Casearia*); Nihoul-Ghenne (1956, *Aphloia*) and Pyykkö (1979, *Homalium*). *Berberidopsis corallina* was included in the treatment of Flacourtiaceae by Metcalfe & Chalk (1950) but their record of Rubiaceae (i.e., paracytic) stomata casts doubt on the identity of their material: as described below, *B. corallina* has cyclocytic stomata. Miller (1975) gave a comprehensive and detailed account of the wood anatomy of the family and included descriptions of *Berberidopsis corallina* and *Streptothamnus moorei*. He commented on the unusual combination of wood anatomical characters shared by these two genera, which put them in a isolated position in the family, and even suggested that a separate family status for the two genera could be supported. The scalariform perforations, exclusively solitary vessels and ground tissue tracheids would be indicative of an intermediate position between Dilleniaceae and Flacourtiaceae. Baas (1976) commented on the scalariform plates in *Berberidopsis* and *Streptothamnus*, emphasising their unusual occurrence in plants with a climbing habit.

In the present study the first leaf anatomical account, together with an anatomical description of twigs of both genera is given. The anatomical characters will be discussed with reference to Veldkamp's realignment (1984, this issue) of *Streptothamnus beckleri* in *Berberidopsis*, and to the systematic position of the two genera.

Microtechnical procedures and descriptions followed standard procedures given elsewhere (e.g. in Baas et al., 1982).

LEAF ANATOMICAL DESCRIPTIONS

***Berberidopsis beckleri* (F.v.M.) Veldk. – Fig. 1.**

Material studied: Australia, New South Wales, Constable 7070; Coveny et al. 6017; McGillivray & Coveny 423.

In surface view: Uniseriate, 2- or 3-cellular hairs present on lamina (50–100 μm long on lamina, up to 180 μm long on midrib). Abaxial epidermal cells bluntly papillate (except cells overlying midrib and major veins and cells of the stomatal complex). Anticlinal epidermal cell walls straight to curved. Stomata confined to abaxial surface, cyclocytic to bicyclic with one or two rings of 5–7 subsidiary cells; guard cell pairs (24–)27–29(–30) μm long, (24–)27–30(–33) μm wide.

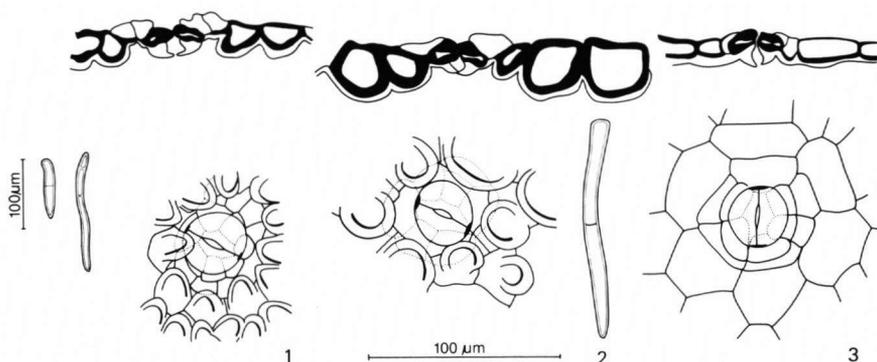
In transverse section: Lamina 160–180 μm thick. Adaxial cuticle 2–4 μm , abaxial cuticle 2–3 μm thick. Stomata with well developed outer cuticular ledges. Hypodermis of one cell layer only locally developed at the adaxial side of midrib and in leaf margin. Mesophyll dorsiventral with two palisade layers occupying about 2/5 to 3/5 of the lamina thickness and abaxial spongy tissue. Midrib flat to shallowly depressed adaxially, slightly raised abaxially, provided with a single, collateral, crescentiform vascular strand with thin adaxial and abaxial fibre caps or without supporting sclerenchyma fibres. Veins embedded in mesophyll, without sclerenchyma support, or major veins with small fibre caps; all veins with poorly differentiated parenchymatous bundle sheaths. Petiole at the base with a closed vascular cylinder opening up towards the distal end, supported by a sclerenchyma sheath at the base and with little or no sclerenchyma in the distal end; pith parenchyma at basal end lignified. Crystals present as druses in bundle sheaths, in the phloem of the midrib, petiole and major veins, and in the ground tissue of the petiole; solitary prismatic crystals observed in addition in bundle sheath cells of Coveny et al. 6017.

***Berberidopsis corallina* Hook. f. – Fig. 2.**

Material studied: Chile, Marticorena et al. 1089; Meyer 9766.

In surface view: Uniseriate, 2- or 3-seriate hairs (200–300 μm long) sparsely present on abaxial surface. Abaxial epidermal cells bluntly papillate (except cells overlying midrib and major veins and cells of the stomatal complex). Anticlinal epidermal cell walls straight to very slightly curved. Stomata confined to abaxial surface, cyclocytic with 5–6 subsidiary cells, sometimes with a bicyclic tendency; guard cell pairs (27–)29–31(–33) μm long, (24–)27–28(–32) μm wide.

In transverse section: Lamina 320–400 μm thick. Adaxial cuticle 5 μm , abaxial cuticle 2–3 μm thick. Stomata with well developed outer cuticular ledges.



Figs. 1–3. Camera lucida drawings of leaf epidermal features of *Berberidopsis* and *Streptothamnus*. Vertical scale line for hairs. Horizontal scale line for epidermis in transverse section (above) and in surface view (below). – 1: *Berberidopsis beckleri* (F.v.M.) Veldkamp. – 2: *B. corallina* Hook. f. – 3: *Streptothamnus moorei* F.v.M.

Hypodermis of one cell layer only locally developed at adaxial side of midrib and in leaf margin. Mesophyll dorsiventral with three layers of palisade cells occupying about $2/3$ of the lamina thickness and abaxial spongy tissue. Midrib shallowly depressed adaxially, slightly raised abaxially, provided with a single, collateral, crescentiform vascular strand supported by strong adaxial and abaxial fibre caps. Veins embedded in mesophyll, the major ones with strongly developed abaxial fibre caps and small adaxial caps; the minor ones with no or little supporting sclerenchyma; all veins with a poorly differentiated (outer) parenchymatous bundle sheath. Petiole with a nearly or completely closed vascular cylinder at the base, opening up towards the distal end, supported by little or no sclerenchyma; pith parenchyma lignified in Meyer 9766, unligified in the other specimen. Crystals present as druses in bundle sheath cells and ground tissue and phloem of the petiole; solitary prismatic crystals infrequently noted in *Marticoarena et al. 1089* only.

Streptothamnus moorei F.v.M. – Fig. 3.

Material studied: Australia, New South Wales, Tomlins s.n. (= NSW 59226).

In surface view: Hairs and papillae absent. Anticlinal epidermal cell walls straight to curved. Stomata confined to abaxial surface, bicyclic or cyclocytic with a (partly) double ring of 4–6 subsidiary cells; guard cell pairs (30–)31(–33) μm long, (29–)30(–32) μm wide.

In transverse section: Lamina 120 μm thick. Adaxial cuticle 4 μm , abaxial cuticle 2 μm thick. Stomata with well developed outer cuticular ledges. Hypodermis of one cell layer only locally developed at adaxial side of midrib and in leaf margin. Mesophyll dorsiventral with one layer of palisade cells occupying about $1/3$

of the lamina thickness and abaxial spongy tissue. Midrib flat adaxially and slightly raised abaxially, provided with a single, crescentiform, collateral vascular strand without supporting sclerenchyma, with poorly differentiated parenchymatous bundle sheaths. Petiole at the base with a closed vascular cylinder opening up towards the distal end, without supporting sclerenchyma; pith unligified. Crystals present as druses in bundle sheath cells and ground tissue of petiole.

Table 1. Differential anatomical characters of *Berberidopsis* and *Streptothamnus*.

	<i>Berberidopsis corallina</i>	<i>Berberidopsis beckleri</i>	<i>Streptothamnus moorei</i>
Twigs			
Distribution of druses	phloem, cortex	phloem, cortex	phloem, cortex, and pith
Distribution of solitary crystals	absent	cortex	phloem, cortex, and pith
Spiral thickenings in vessels	±	—	—
Leaves			
Druses in phloem	±	+	—
Solitary crystals	+ or —	+ or —	—
Epidermal papillae	+	+	—
Bicyclic stomata	±	+	++
Uniseriate hairs	+	+	—
Sclerenchyma support in midrib and major veins	+	+ or —	—
Pith in petiole lignified	+ or —	+	—

TWIG ANATOMY

In view of the great similarity in twig anatomy, a combined description of all three species is given below. Minor differential characters are included in table 1.

Material studied: Twigs c. 4 mm in diameter of *Berberidopsis beckleri* (Constable 7070), *B. corallina* (Marticorena et al. 1089), and *Streptothamnus moorei* (Tomlins s.n.).

Epidermal cells flattened. Cork not developed at this stem diameter. Cortex parenchymatous. Perivascular sclerenchyma composed of a solid ring of fibres and brachysclereids. Secondary phloem devoid of sclerenchyma. Secondary xylem traversed by narrow 1–3-seriate rays, mainly composed of upright cells. Vessel perforations scalariform with 15–30 bars. Faint spiral thickenings present in vessels of *Berberidopsis corallina* only. Fibres with distinctly bordered pits in radial and tangential walls (fibre-tracheids), non-septate. Axial xylem parenchyma very sparse as scattered apotracheal, very rarely also as paratracheal strands. Primary xylem poles accompanied by an internal ring of narrow, thick-walled pith cells. Central pith wide, heterogeneous, composed of large translucent cells intermingled with narrow cells with dark contents (probably tannin); all pith cells lignified. For crystals see table 1.

DISCUSSION

From the descriptions it becomes evident that all three species have many leaf and twig anatomical features in common. This can be taken as an indication of close mutual affinity, especially if the shared characters of *Berberidopsis* and *Streptothamnus* are contrasted with anatomical tendencies in the Flacourtiaceae.

Cyclocytic and bicyclic stomata (two closely related stomatal types) have not been recorded for the Flacourtiaceae. Paracytic or anisocytic stomata or their intermediate types are most common in the family, a minority (*Camptostylus* and *Scotellia* according to Solereder, 1908, and *Azara dentata* according to original observation) has anomocytic stomata. The latter type can intergrade with cyclocytic stomata in other families (cf. Baas et al., 1982) and may be considered related to the cyclocytic type. Non-septate fibres with conspicuous bordered pits in both radial and tangential walls (termed tracheids by Miller, 1975) and exclusively solitary vessels are other features not found elsewhere in the family. Other shared characters such as petiole and midrib vasculature, limited hypodermal development, composition of the pith and the perivascular sclerenchyma in the stem support the mutual affinity of *Berberidopsis* and *Streptothamnus*, but do not suggest a particularly isolated position in the Flacourtiaceae. A Dilleniaceous affinity as advocated by Miller (1975) on the basis of common wood anatomical characters (all of them primitive ones!) is not supported by the leaf anatomical evidence: hairs, stomatal types and crystals (raphides) of the Dilleniaceae are quite different from those of *Berberidopsis* and *Streptothamnus*. Based on overall vegetative anatomy it seems best to retain the two genera in a separate tribe or even subfamily in the Flacourtiaceae. The superficial resemblance between *Berberidopsis* and *Erythrospermum* commented on by earlier authors can be contrasted by differences in wood and leaf anatomy: *Erythrospermum* has laterocytic stomata (original observation; this type is termed intermediate between paracytic and anisocytic by Metcalfe & Chalk, 1950), crystalliferous epidermal cells, septate fibres and fairly common vessel multiples.

The differential characters in vegetative anatomy of *Berberidopsis* and *Streptothamnus* are summarised in table 1. Many of them, especially the crystal comple-

ment and lignification of the medullary ground tissue (pith) of the petiole are of very limited taxonomic value, and should be tested on their diagnostic worth in more samples. Character differences like cyclocytic versus predominantly bicyclic stomata and papillae present or absent can also be found within closely knit taxa (cf. Baas, 1970, 1975). All the same, the evidence from vegetative anatomy does lend support to Veldkamp's treatment of the genus *Berberidopsis* (1984, this issue) including two species: *B. beckleri* (formerly *Streptothamnus beckleri*) and *B. corallina*. They share epidermal papillae, uniseriate hairs and phloem crystals in the leaf. This combination of characters can be given more weight than the shared bicyclic stomata of *Berberidopsis beckleri* and *Streptothamnus moorei*, or the restriction of faint spiral vessel wall thickenings to *B. corallina*. One can also say that *Berberidopsis beckleri* from Australia is intermediate between *B. corallina* from Chile and *Streptothamnus moorei* (also from Australia) but closer to the former species in its leaf and twig anatomy.

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