Ledocarpaceae

Ledocarpaceae Meyen, Reise 1:308 (1834).
Vivianiaceae Klotzsch (1836).
Rhynchothecaceae Endl. (1841).

M. Weigend

Shrubs, rarely subshrubs or perennial or annual herbs, 0.3–1.5(–4) m tall, stems erect or ascending, strongly branched, often differentiated into sometimes spinescent brachyblasts and dolichoblasts, stems tough, initially with white or brownish pith, terete, with greyish brown bark, underground stems occasionally present. Indumentum of simple, unicellular trichomes and uniseriate trichomes with a single-celled gland-tip, usually very dense on leaves, stems, calyx and ovary. Leaves evergreen or semi-deciduous, opposite or subopposite, rarely in whorls of three, shortly petiolate to sessile, petiole with clasping base, estipulate, lamina entire or pinnatifid to pinnate to trifoliolate, margin entire or serrate; interpetiolar line often present. Inflorescences terminal cymoids or pleiothyrsoids, with monochasial to asymmetrically dichasial paraclades, often reduced to 2–3 flowers, or a terminal flower only, frondose-bracteose, individual flowers of *Balbisia* subtended by prophylls. Flowers perfect, actinomorphic, pentamerous; sepals free or united in proximal half, imbricate with valvate tips, persistent in fruit; petals 5(4 or 0), free, with contort aestivation; stamens (4, 5, 4 + 4)5 + 5, usually obdiplostemonous and heterantherous, typically 5 long and 5 short; filaments sometimes with pair of basal appendages; gynoecium of 3–5 carpels; style single, very short, with 3–5 long stigmatic branches; ovary 3–5-lobed, with 1–20, pendulous, campylotropous ovules in each locule; placentation axile. Fruits septicidal or septifragous capsules with five 1–many-seeded locules; embryo straight or cochlear with spirally folded cotyledons; endosperm present, exotesta poorly developed or absent, occasionally mucilaginous.

A family of four genera and about 18 species, mostly in Andean South America.

Vegetative Morphology. Ledocarpaceae are exclusively or predominantly shrubby. The shoots are strongly branched, and the shrubs regenerate with long and relatively thick and large-leafed dolichoblasts arising from the basal portion. In *Rhynchotheca* and some *Viviania*, some or most of the short lateral shoots turn into spines. In all shrubby species, the vegetative lateral axes have 1–several pairs of opposite, scale-like cataphylls, followed by progressively larger, regular foliage leaves. In *Balbisia*, most species have very short brachyblasts ($\ll$ 10 mm) with very densely crowded, often very short ($\ll$ 5 mm) leaves, which in some cases (*B. microphylla*) have the aspect of tiny hairy cones. Annual *Viviania tenuicaulis* lacks cataphylls, since it has no vegetative renewal shoots and its lateral axes develop in the distal portion of the shoot and immediately give rise to flowers. *Viviania elegans* has a slightly lignified, more or less plagiotropic axis with ascending flowering shoots. The herbaceous taxa in *Viviania* appear to be derived from a shrubby ancestor, which is supported by, for example, their highly derived inflorescence structure (see below). The root system of *Balbisia* (the only taxon in which I studied it) consists of a very extensive system of very finely branched roots.

The shape and size of the leaves are rather conserved in Ledocarpaceae. Leaves are always small with the lamina (2–)5–15(–25) mm long, usually opposite but occasionally in whorls of three on some or most nodes, and with always very short petioles ($<$ 5 mm). Leaf venation is weakly brochidodromous to craspedodromous, secondary veins directly entering the tips of leaf lobes or leaflets in *Balbisia* and *Rhynchotheca* but, in *Viviania*, the secondaries running towards the sinuses between the leaf lobes/serrations and branching there, so that one branch each of two neighbouring secondaries enters each leaf lobe. Leaf dissection is variable in all genera and even within individuals in *Rhynchotheca* (heterophyllous; the different leaf types have led to the description of three "varieties"; Knuth 1912). Some species of *Viviania* and *Balbisia* and flowering branches of *Rhynchotheca* have undivided leaves, whereas other species of these genera and the vegetative branches of *Rhyn-*

chotheca have pinnately lobed or – in the case of *Balbisia* – pinnate to trifoliolate leaves.

The indumentum consists mainly of simple, unicellular and usually acroscopic trichomes with an acute apex and relatively few uniseriate glandular trichomes with a single-celled glandular head. Branched, but unicellular "arbuscular" trichomes are found on the ovaries and abaxial leaf surfaces of *Viviania marifolia* and the leaves of *Balbisia peduncularis* and *B. microphylla*, giving these organs a densely tomentose appearance.

Vegetative Anatomy. Wood anatomy has been studied in detail in *Viviania* (Carlquist 1986), and is very similar in the other genera (pers. obs.). The shoots have a more or less extensive wood cylinder with a white or brown pith. The pith is parenchymatous with thin walls and extensive wall pitting in *Rhynchotheca* and *Viviania*, but sclerenchymatous with very thick, pitted walls in *Balbisia*. The wood of *Balbisia* and *Viviania* has distinct growth rings with wider vessels in early wood, but these are absent in *Rhynchotheca* (which is from permanently humid habitats). Axial parenchyma is absent in all three genera (contrary to Carlquist (1986), I was unable to confirm its presence in *Balbisia*). Rays are clearly absent from all three genera. Vessels are densely spaced in *Viviania* and more or less loosely spaced in the other two genera, where they tend to aggregate into radial rows of 3–4 (*Rhynchotheca*) or 6–10 (*Balbisia*). Vessels have simple perforation plates; lateral vessel pits are circular to elliptical, pit apertures are interconnected by grooves, and spherical tyloses are present in some vessels. Imperforate tracheary elements are present in the form of fibre tracheids, which have bordered (*Viviania*) or simple (*Balbisia*) pits and are occasionally septate. Sieve plastids are of the S-type (Behnke and Mabry 1977). The cortex is parenchymatous and lacks sclerenchymatous elements. The bark is well developed with regular, tanniniferous cork cells. Carlquist (1986) considers the wood anatomy of *Viviania* as strongly xeromorphic and indicative of secondary woodiness, i.e. indicating that the last common ancestor of Ledocarpaceae and Geraniaceae was herbaceous.

Leaf anatomy has been studied for *Balbisia* (Xifreda 1973), and I here supplement original observations in *Viviania marifolia* and *Rhynchotheca*. The lamina is flat, sometimes revolute in *Balbisia*, and variously lobed, serrate or entire. Both sides of the lamina are usually densely pubescent with simple or branched, unicellular trichomes, the abaxial side usually much more densely so, and often white from dense trichome cover, especially in *Viviania*. The epidermis is one-layered with distinctly papillose cells, especially on the abaxial side and above the leaf veins (e.g. *W. calycina*, *W. aphanifolia*, *R. spinosa*). Stomata are anomocytic. The lamina is bifacial, but the palisade parenchyma extends onto the abaxial surface along the lateral leaf margins in some species of *Balbisia* with very narrow leaf lobes (e.g. *B. verticillata*, *B. stitchkinii*). In both *Rhynchotheca* and *Viviania*, there is a more or less regular layer of cells closely resembling the palisade parenchyma above the abaxial epidermis, but with shorter cells. Otherwise, palisade parenchyma and spongiose parenchyma are approximately equal in thickness in all taxa, and the palisade parenchyma consists of 2–3 layers of relatively irregularly elongated cells. Crystal druses are frequent, especially in the spongiose parenchyma towards the abaxial surface in *Viviania* or in the palisade parenchyma towards the adaxial surface in *Balbisia*. The veins themselves have a distinct parenchymatous sheath in most species, and a sclerenchymatous sheath in *B. gracilis*. A pronounced collenchymatous tissue is found above the veins towards the abaxial surface in *Rhynchotheca*, towards the adaxial surface in *Balbisia integrifolia*, and towards both surfaces in *B. calycina* and *B. aphanifolia*.

Inflorescences. The inflorescences have not been subject to any detailed study so far, only those of *Viviania* have been illustrated (Lefor 1975), and an integrated interpretation is here offered for all three genera. The inflorescences are terminal and 1-flowered (often in *Balbisia*), (1)2–3-flowered (*Rhynchotheca*) or many-flowered (*Viviania*, most *Balbisia*). The many-flowered inflorescences are readily recognized as thyrsoids, with typically two very unequal pairs of paraclades; the distal pair is less developed whereas the proximal pair is more strongly developed and often overtops the distal dichasium. The paraclades are dichasial or show varying degrees of reduction towards a monochasial terminal portion, and are usually also frondose. Well-developed inflorescences of *Viviania marifolia* have two opposite pairs of more or less equally developed, dichasial paraclades; all internodes and the pedicels are well developed, and all bracts are developed like regular foliage leaves (frondose inflorescence). In some inflorescences, the distal paraclade pair is lost but its frondose bracts are still present; the lower paraclade pair is more or less reduced but both paraclades still