Buxaceae

Buxaceae Dumort., Comment. Bot.: 54 (1822), nom. cons.

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Evergreen shrubs or trees, rarely subshrubs or rhizomatous perennial herbs, glabrous, sometimes with uni- or multicellular hairs, monoecious, rarely dioecious. Leaves alternate or decussate, petiolate, rarely sessile, entire, rarely dentate, pinnately veined, less often tripliveined, estipulate. Flowers in axillary or terminal botryoids or spikes, the male above the female ones, or one female above the male, subtended by decurrent bracts, the female with prophylls. Flowers actinomorphic, hypogynous; male: tepals 4, decussate, rarely wanting; stamens free, 4, 6 or 8, antetepalous, or rarely up to 45 in a more complex arrangement, if 6, then two pairs opposite the inner tepals, often inserted around a pistillode; anthers dorsifixed, dithecal, tetrasporangiate, longitudinally dehiscent, borne on long filaments, rarely sessile; pistillode present or wanting; female: often larger than the male, fewer or solitary; tepals 4–6; ovary syncarpous with free stylodia, (2)3(4)-carpellate, sometimes with false septa; placentation axile; stylodia subulate, divergent, rarely connate at the base, stigmatic area decurrent along the ventral fold; ovules usually 2 per locule, anatropous. Fruit a dry capsule with persistent stylodia, loculicidally dehiscent into 2-horned valves, or indehiscent, subdrupaceous or berry-like. Seeds black or dark, frequently carunculate; endosperm copious, fleshy, oily; embryo straight, cotyledons flat.

A family comprising 5 genera with c. 100 species, distributed in the Northern Hemisphere of the Old and New World, extending to Andean South America and its Caribbean coast, to South Africa and Madagascar, and to peninsular Malaysia.

Vegetative Morphology. Most Buxaceae are evergreen shrubs or trees up to 15 m tall. Only *Pachysandra* comprises erect or prostrate subshrubs and perennial herbs. Its sympodial rhizomes have adventitious roots and develop simple or sympodially branched stems with alternate, apically clustered leaves. The leaves are alternate in *Styloceras*, *Sarcococca* and *Pachysandra*, decussate in *Buxus* and *Notobuxus*, where decurrent leaf bases form lateral internodal folds (Fig. 12A). In some Cuban *Buxus*, distichous leaves are interspersed with decussate pairs of very small ones inserted on short shoots. The leaves are usually entire but toothed in *Pachysandra*. Brochidodromous venation, occurring in *Sarcococca*, *Notobuxus* and *Buxus*, and variously modified in the latter, is regarded as basic. *Styloceras* and Asian *Buxus* species possess eucamptodromous venation. Cladodromous patterns are found in South African and Malagasy *Buxus*; *Pachysandra* has craspedodromous venation. Whereas the brochidodromous type prevails in the tropics, the derived patterns occur in subtropical and temperate regions of both hemispheres (Köhler 1993). Species of *Buxus* possess a grey, deeply fissured bark.

Vegetative Anatomy. Old World *Buxus* and *Notobuxus* species have a cortical vascular bundle in each angle of the branchlets, accompanied by fibre strands in the Eurasian taxa. Both are wanting in New World *Buxus* and the remaining genera (van Tieghem 1897; Mathou 1940). Elongated fibres and large stone cells are frequent in the primary cortex. Chains of small, irregularly thickened sclereids with oxalate crystals, surrounding a larger fibre ('Kristallkammerfasern'), occur in *Pachysandra*, *Sarcococca* and *Styloceras*. Secretory cells, often arranged in longitudinal rows, are frequent in *Buxus*, *Pachysandra* and *Sarcococca*, less prominent in *Styloceras* (Metcalfe and Chalk 1950). Vessels are mostly solitary and of small diameter, rather wide in *Styloceras*. They are of medium length in *Buxus* and *Notobuxus* but exceptionally long in *Sarcococca* and *Styloceras*, reflecting a continuous occupation of mesic sites (Carlquist 1982). They have scalariform perforations with a great range of numbers of bars (Köhler, unpubl. data). The fibrous elements are tracheids with bordered

pits similar to vessels. The axial parenchyma is diffuse apotracheal throughout the family. Uniseriate rays are as frequent as multiseriate ones. The heterogeneous rays of *Styloceras*, which are up to four cells wide, are most primitive. *Styloceras* is an unspecialized, highly mesic type, followed by *Sarcococca*, whereas *Notobuxus* and especially *Buxus* are more specialized in adaptation to xeric conditions.

The sieve element plastids represent a specific subtype, PVIc, with a globose protein crystal (Behnke 1982).

Leaf epidermis cells are thin to strongly cutinized in *Buxus*, and covered with epicuticular waxes. Their anticlinal walls are sometimes extremely thickened, confining lumina to a central canal or basal rests in Cuban *Buxus* (Köhler and Schirarend 1989). The indumentum comprises thick-walled hairs of one to several cells. Stomata are usually abaxial and are laterocytic, occasionally cyclocytic (Baranova 1980); they have prominent outer ledges which sometimes bear a peristomal rim. A hypodermis is present only in *Styloceras*. The mesophyll contains prominent secretory cells, which sometimes form a continuous hypodermal layer and may be interspersed with brachy- , osteo- or astrosclereids. Druses and solitary oxalate crystals are frequent; cells with coarse crystal sand are rarer. The vascular bundles are accompanied by arc-shaped or ring-like sclerenchymatous sheaths. The petiole is supplied by a median and two lateral bundles, the latter being replaced by fibre strands in Eurasian *Buxus*. The nodes are unilocular with one trace.

Inflorescence Structure. Inflorescences are axillary or terminal, rarely borne at the base of the stem (*Pachysandra procumbens*), and shortly pedunculate or sessile. In *Buxus*, *Notobuxus* and *Styloceras kunthianum*, they are usually botryoids with lateral male flowers and a terminal female flower. *Pachysandra* and some *Sarcococca* have open spikes with lateral male flowers in the upper part of the inflorescence and female flowers below. In the dioecious species of *Styloceras*, male flowers form long spikes sometimes terminated by a peloric flower; female flowers are solitary or in thyrses (von Balthazar and Endress 2002b).

Flower Structure. The bracts preceding the reproductive organs of male flowers are always arranged in a decussate pattern whereas the uppermost four, bract-like phyllomes are tepal-like and inconspicuous or whitish (*Sarcococca*) and creamy petaloid (*Buxus*). There are typically four stamens, in *Notobuxus* six or up to ten; in *Styloceras*, they are numerous. Filaments are long-exserted, stout, sometimes clavate. Anthers are introrse, dorsifixed with a protruding, ± coloured connective tip. The stamens are frequently inserted around a pistillode, which is quadrangular to 4-lobed, sometimes truncate in *Buxus* and *Pachysandra* or urceolate in *Sarcococca*, but very reduced in *Notobuxus* and absent in *Styloceras*. It possesses a nectariferous structure (Daumann 1974; Vogel 1998).

In the female flowers the carpels are usually preceded by a pair of prophylls and several spirally arranged bracts which are only weakly differentiated towards tepals (von Balthazar and Endress 2002b). The locules of the ovary contain two collateral ovules and are separated by spurious septa in *Pachysandra* and *Styloceras*. The stylodia are rather long, slender and recurved in *Styloceras*, erect-subulate in *Pachysandra*, more stout in *Sarcococca*, and short-divergent in *Notobuxus* and *Buxus*. Protuberances between the bases of the stylodia function as nectaries and are considered to be of androecial derivation (Daumann 1974).

Embryology. The anther wall has a 1-layered fibrous endothecium. The tapetum is secretory and its cells become binucleate. Pollen meiosis is simultaneous, resulting in tetrahedral or isobilateral tetrads. Pollen is 2-celled when shed (Davis 1966).

The ovules are anatropous, pendulous, with the micropyle towards the axis in *Buxus* and *Notobuxus* or averted in *Sarcococca*. They are bitegmic, crassinucellate with a pronounced nucellar cap; the micropyle is made up by the inner integument (Wunderlich 1967; Corner 1976). Protuberances of the placenta form an obturator in *Pachysandra*. A proliferation of the outer integument, forming a hood over the nucellus, develops a prominent caruncle in the latter (Channel and Wood 1987). The megaspores are arranged in linear (*Sarcococca*, *Pachysandra*) or T-shaped tetrads (*Buxus* and *Notobuxus*), the chalazal one developing into a Polygonum type embryo sac. The synergids have a filiform apparatus. The antipodes persist into postfertilization stages and a small degree of secondary multiplication has been reported. Endosperm formation is cellular, but nuclear in *Sarcococca* (Wiger 1935). Embryogeny follows the Onagrad type. Occasionally, parthenocarpy has been reported for *Buxus*, and some *Sarcococca* species seem to be obligate apomicts (Naumova 1980). Nucellar polyembryogeny is recorded for *S. humilis*.