

Pittosporaceae

Pittosporaceae R. Br. in Flinders, Voy. Terra Austr. 2: 542 (1814), nom. cons. (“Pittosporae”).

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Evergreen trees, shrubs, rhizomatous or not, sometimes procumbent or climbing or twining, occasionally epiphytic, often heteroblastic, glabrous or pilose, trichomes uniseriate, often with elongated or T-shaped terminal cell, with resin canals particularly in the bark, sometimes \pm aromatic; sometimes branches ending in thorns. Leaves simple, usually coriaceous and entire, rarely dentate (especially when juvenile), spirally arranged, sometimes pseudovercillate, without stipules. Inflorescences cymose or racemose, often panicles forming more or less dense corymbs, or single flowers. Pedicels usually bibracteolate; flowers actinomorphic, rarely zygomorphic, bisexual, sometimes unisexual (at least functionally), then plants monoecious, (sub)dioecious, gynodioecious or rarely polygamous; flowers 5-merous (except pistil); sepals imbricate or valvate, free or fused at the base, generally caducous; petals often clawed, completely free or fused at the very base, spreading from the base or coherent into a tube, imbricate, rarely valvate; stamens hypogynous, alternating with the petals; filaments hairy or glabrous, sometimes coherent to the petals when these are coherent, anthers sagittate or not, free or rarely apically coherent, dehiscing introrsely by longitudinal slits or (in *Cheiranthra* and a few *Billardiera* spp.) through apical pores or short slits, tetrasporangiate; ovary superior, sometimes stipitate, glabrous or pilose, 2(3–5)-carpellate, 1 or 2(–5)-locular, often incompletely so, with parietal, parietal-basal, or more rarely axile placentae; style simple, stigma inconspicuous, capitate or slightly lobed, nectary a sometimes strongly lobed ring at the base of the ovary, rarely vestigial or absent; ovules 1–many in each locule, anatropous, tenuinucellate, unitegmic. Fruit a loculicidal and sometimes also \pm septicidal capsule, or a fleshy or fibrous berry, rarely woody indehiscent. Seeds 1–several in each locule, sometimes brightly

coloured or blackish and coated with sticky material, rarely winged or arillate; embryo tiny, with 2, rarely 3, 4 or 5 cotyledons; endosperm well-developed, oily and/or proteinaceous. $x = 12$.

Nine genera and ca. 250 species. In temperate to tropical regions of Pacific Islands, New Zealand, Asia, Africa and particularly Australia.

VEGETATIVE MORPHOLOGY. Most species are small trees or shrubs, sometimes scandent or twining, but some *Pittosporum* species are up to 20 m high and a few species start as epiphytes. *Bentleya* and, to a lesser extent, *Pittosporum angustifolium* produce suckers from underground rhizomes. Cataphylls are usually present at the base of new shoots. Plants show considerable phenotypic plasticity, mostly due to different ecological conditions, but juvenile and adult leaves can also be rather different. Such heteroblasty has caused some taxonomic confusion, and different developmental stages were sometimes even considered different species (Chandler et al. 2007). Seedlings and intermediate leaves are reported to have sometimes a different form and a more or less deeply lobed, crenate or toothed margin, rarely (e.g. *Auranticarpa ilicifolia*) also with bristles, while the margin of mature leaves is mostly entire, very rarely undulate, toothed or crenate. In *Pittosporum* the branches (i) may be vegetative in the first year and produce a terminal inflorescence in the second year and have lateral vegetative branches, (ii) produce a pseudoterminal inflorescence from one of the terminal cluster of buds in the second year or (iii) are strictly sympodial (Gowda 1951).

VEGETATIVE ANATOMY. A review of most anatomical data can be found in Solereder (1898). Wood anatomy was studied in detail by Carlquist (1981), leaf anatomy by Wilkinson (1992). Four

types of trichome can be distinguished: (i) uniseriate with 1–3(–8) basal cells and an elongated, sometimes curling terminal cell, (ii) 2–6-celled basal stalk and 2-armed terminal cell, which might be curling or not, (iii) uniseriate without extended terminal cell, and (iv) uniseriate with 1–6 short or elongated terminal glandular cells. Crystals of calcium oxalate are common in the parenchyma, mostly as druses; in the phloem of *Pittosporum* and *Bentleya* small styloids and rhombohedra were found. The vessels of the wood are small compared to other families, perforations are generally simple, oblique. Paratracheal wood parenchyma is scanty, fibres usually are septate. *Pittosporum paniense* from New Caledonia has a primitive wood structure (Carlquist 1981). Schizogenous secretory canals are found in several parts of the plant, most notably in the bark and in the root, where they show a characteristic distribution similar to Apiaceae and Araliaceae, as already reported by van Tieghem (1884). He also noted the correlated typical duplication of the number of lateral roots localized on either side of the xylem poles, as the place at the apex of each xylem pole is occupied by a resin canal. Canals are found neither in the primary cortex nor in the pith. In the leaves they form a network and are located adjacent but not inside the phloem (Wilkinson 1992). Sticky resin with ethereal oils exudates when the canals are broken, and crushed leaves produce a characteristic resinous odour. Periderm origin was found to vary within the family, directly subepidermal (*Pittosporum*), in the third subepidermal layer (*Hymenosporum*), and on the border of primary to secondary cortex (*Billardiera*). Nodes are unilacunar or trilacunar with one trace per gap. Leaf venation is camptodromous or more rarely craspedodromous, veinlets are simple to 2- or 3-branched, stomata are paracytic. Epicuticular wax is mostly present as platelets of varying density and form, more rarely rodlets, the cuticle varies from smooth to striate. Epidermal anticlinal walls are usually straight, rarely undulate. A double leaf epidermis occurs in *Pittosporum* spp. Mesophyll is bifacial to less commonly isobilateral, veins imbedded or the larger ones frequently transcurrent in *Pittosporum*. Palisade cells are typically short and in several layers.

FLOWER STRUCTURE AND FLORAL BIOLOGY. Many species of *Pittosporum* have functionally unisexual flowers (see, for example, Gowda 1951; Cooper 1956; Haas 1977), with monoecy, dioecy (sometimes leaky), gynodioecy, rarely polygamy reported for various species of *Pittosporum* (e.g. Sakai et al. 1995; Cayzer et al. 2000; Clarkson et al. 2012; Schlessman et al. 2014). Anthesis of the species of other genera seems to be in general protandrous. Zhou et al. (2005) made a detailed comparison of functionally male and female flowers of *Pittosporum tobira*, which may occur in the same inflorescence. All floral organs are initiated in a strictly acropetal succession and the petal primordia join laterally at the time of initiation (early sympetaly; Erbar and Leins 1995, 2004). The flowers are usually actinomorphic, but more or less zygomorphic in *Marianthus*, and in *Cheiranthra* the anthers at anthesis are placed in a line on one side of the ovary by twisting of the filaments. The petals of flowers at anthesis are free or only very shortly connate at the base and are spreading from the base or coherent into a tube often longer than the ovary. Corolla aestivation is variable. Narayana and Radhakrishnaiah (1982) studied five species of *Pittosporum* and found contorted, quincuncial and cochlear ascending aestivation. Anthers are rarely apically coherent; their length seems to be more or less correlated with the length of the style, sometimes they cluster at three different heights (1 + 2 + 2 in *Hymenosporum* and *Marianthus*; Cayzer and Crisp 2004). The ovary can be distinctly stipitate; it can be 1-locular, or partly or completely septate, placentation is axile or parietal to parietal-basal. The sometimes deeply intruding parietal placentae are giving the appearance of axile placentation. The stigma is wet, capitate or lobed, rarely inconspicuous as in *Marianthus* (Cayzer et al. 2004). A more or less prominent nectary is present in most species, usually dark-green in fresh flowers. It does not develop as an outgrowth of the receptacle but at the dorsal base of the carpels, the nectar is exuded by nectary slits (Narayana and Radhakrishnaiah 1982; Erbar and Leins 1995). The nectary usually forms a more or less conspicuous ring, sometimes with conspicuous lobes alternating with the stamens, rarely restricted to the interstaminal areas (some

Billardiera spp.) or completely lacking in a few *Billardiera* spp. and in *Cheiranthera* (Cayzer et al. 1999, 2004). Many species have strongly scented flowers and a nectary indicating insect pollination, and some have brilliantly white flowers which may indicate moth pollination. For *Pittosporum dasyphyllum* with bisexual but self-incompatible flowers, bees and butterflies were reported as pollinators (Gopalakrishnan and Thomas 2014). In *Cheiranthera* the apical pores or short slits of the basifixed anthers and the absence of the nectary indicate “buzz-pollination”, and *Stenotritis* (Stenotritinae) bees were observed agitating flowers of a *Cheiranthera* species in Western Australia (Thorpe 2000).

POLLEN. The pollen grains of *Pittosporum* are tricolporate, 2–3-nucleate, exine more or less reticulate with little sculpturing (Gowda 1951; Haas 1977; Judd 1996).

KARYOLOGY. Several species of *Pittosporum* have been reported as having $2n = 24$, a number also found in *Billardiera* and *Auranticarpa* (cf. Cooper 1956; IPCN 2010).

EMBRYOLOGY. The ovule throughout the family is anatropous, unitegmic, tenuinucellar. The embryo-sac is of the Polygonum-type and the endosperm is nuclear at first (Mauritzon 1939; Narayana and Sundari 1981).

FRUIT, SEED AND DISPERSAL. The capsules open loculicidally, sometimes also septicidally, lacking a persistent central column. Indehiscent fruits are mostly fibrous or fleshy berries, the epicarp thin to leathery. The contrasting colours of the seeds coated with a sticky substance and surrounding capsule endocarp of *Pittosporum* species attract birds, often in large numbers (R.C. Carolin, personal observation; Judd 1996). The sticky, edible nature of the pulp is responsible for the birds dispersing the seeds internally or externally. The substance is produced by multicellular epidermal hairs in the septal region (Erbar and Leins 1995). It is often called resinous, while Erbar and Leins (1995) use the term ‘latex’, but the chemical composition seems to be unknown. The fruits of *Billardiera* are berries or berry-like with varying amounts of mucilaginous pulp which attracts birds and presumably assists in dispersal. *Rhyti-*

dosporum alpinum has flattened dry and indehiscent fruits. The exotestal seeds are more or less smooth, the tangentially elongated epidermis cells have thick outer walls, the parenchymatous endotesta contains tannins (Netolitzky 1926), the raphe is conspicuous. The seeds of *Hymenosporum* are winged and those of *Bursaria* spp. are flattened and are dispersed over short distances by wind. Two species of *Cheiranthera* have been reported to be arillate (Cayzer et al. 2007). The oily and starchless endosperm is usually hard, the embryo minute and located near the hilum. The seeds of *Pittosporum* occasionally have up to five cotyledons. The oily seeds of *Pittosporum hosmeri* are eaten (and dispersed?) by the Hawaiian Crow (Haas 1977).

PHYTOCHEMISTRY. Hegnauer (1969, 1990) gave a valuable overview. Many Pittosporaceae contain triterpenoid saponins which may be responsible for the medicinal and poisonous properties reported by some authors (Cooper 1956). The essential oils from roots and leaves contain monoterpenes, sesquiterpenes, diterpenes, alkanes and polyacetylenes, C_{15} -acetylene is common, falcari-none and falcarinol acetylene also present; flower and fruit oils may contain benzyl acetate, coumarins and furanocoumarins, monoterpenes and sesquiterpenes as major constituents. No iridoid compounds occur in the family, nor ellagic or gallic acids, proanthocyanidins seem to be absent or restricted to the seed coat (Jay 1969). Sesquiterpene lactones, acetate-derived anthraquinones, chlorogenic and quinic acids were found. Quercetin and kaempferol are flavonols observed in the family, in the seed oils C_{18} , C_{20} , and C_{22} fatty acids are common, but petroselinic acid is lacking (Stuhlfauth et al. 1985).

RELATIONSHIPS WITHIN THE FAMILY. Pritzel (1930) divided the family into tribe Pittosporaeae with a capsular fruit and tribe Billardiareae with a fleshy fruit. As Bennett (1972, 1978) pointed out, however, there is a morphological series from fleshy to dry fruits in *Billardiera*. Pritzel’s tribal distinction, therefore, is not satisfactory.

Cayzer et al. (2004), based on morphological characters, and Chandler et al. (2007), using DNA sequence data, recently studied infrafamiliar relationships and the monophyly of hitherto recognized genera. Based on these studies, *Citriobatus*

had to be included in *Pittosporum* and *Sollya* and *Pronaya* (morphological data only) in *Billardiera*. The monophyly of *Marianthus* was weakly supported by the morphological analysis, but not by the DNA sequence data (albeit based on insufficient sampling). The DNA sequence data suggest a sister group relationship of *Pittosporum* with a clade formed by *Aurantocarpa*, *Rhytidosporum* and *Bursaria*. This clade forms a trichotomy with a clade composed of *Billardiera*, *Cheir-anthera*, *Marianthus*, and *Bentleya* and the monotypic *Hymenosporum*.

AFFINITIES. The relationships of Pittosporaceae for some time were discussed controversially. Carlquist (1981) provided a useful summary of this. A rosoid affinity has been suggested, and Carlquist (1981) made the point that the trichomes support such a relationship. However, this would make Pittosporaceae the only family in that group with secretory canals and unitegmic ovules, and the absence of ellagic and gallic acids in Pittosporaceae also argues against this hypothesis. The aralioid group of families had also been suggested as possible relatives [see Takhtajan (1997) for a summary]. Van Tieghem (1884) already early proposed a close relationship to Apiaceae and Araliaceae after studying root anatomy and noticing the schizogenic secretory canals and their distribution and the similar development of lateral roots (one on either xylem pole) in the three families. The unitegmic ovules also supported such a relationship. Floral structure, especially the superior ovary, on the other hand, appeared rather different from other Apiales and prevented most taxonomists to follow van Tieghem's proposal (e.g. Pax 1891; Cronquist 1981). Erbar and Leins (1995, 2004) found early sympetaly in Pittosporaceae similar as in Araliaceae (*Hedera*, *Hydrocotyle*), however, and the gynoecial development as being only gradually different. Also, the position of the gynoecial nectary basically corresponds to that of other Apiales; it is always formed at the dorsal base of the carpels (Erbar and Leins 2004, 2010). The secretory canals are absent from the rays of Pittosporaceae whilst they are present in the aralioid group of families. Chemical characters, however, especially the lack of iridoids and the presence of falcarinone polyacetylenes, clearly support a relationship with Apiaceae and Araliaceae (cf. Judd

1996), although petroselinic acid, common in these families, was not found in the fatty acids of seed oils of Pittosporaceae. The sequence analysis of the chloroplast gene *rbcL* by Chase et al. (1993) and more recent DNA sequence data (e.g. Nicolas and Plunkett 2014) basically confirmed van Tieghem's (1884) old hypothesis. The data show that Pittosporaceae belong to a clade together with Apiaceae, Araliaceae and Myodocarpaceae, being sister to a clade formed by the other three families. Stevens (2001 onwards) lists several non-macromolecular and possibly synapomorphic characters supporting this clade, besides the typical development of lateral roots—e.g. absence of iridoids, presence of etheral oils and schizogenous secretory canals.

DISTRIBUTION AND ECOLOGY. The family is centred in the Australian region, where all genera occur, most of them are endemic there. However, most species occur outside that area, belonging to *Pittosporum*. As *Pittosporum* is not basal within the family, an Australian origin of the family is most plausible (Chandler et al. 2007). According to Nicolas and Plunkett (2014), Pittosporaceae diverged from the other Apiineae (suborder also including Araliaceae, Myodocarpaceae, Apiaceae) about 98 Ma ago. The minimum age of the Pittosporaceae crown group was estimated at about 19 Ma, clearly post-Gondwanan. *Pittosporum* is by far the most widely distributed genus. It occurs throughout the Indo-Pacific region, with species endemic to individual islands or groups of islands, into Africa and even to Madeira and Tenerife. This distribution may be the result of seed dispersal by birds. The Hawaiian species (11 spp.) form a monophyletic group, suggesting a single colonization event from South Pacific islands, while those of New Zealand (26 spp.) and New Caledonia (50 spp.) and many areas in the Pacific islands seem to belong to different unrelated lineages (Gemmill et al. 2002; Chandler et al. 2007). *Pittosporum* species of Hawaii show high levels of interspecific gene flow indicating lack of reproductive isolation (Bacon et al. 2011). *Hymenosporum* occurs also in New Guinea. Species of *Pittosporum* and *Hymenosporum* grow mainly in mesic habitats, although *Pittosporum* intrudes into moist sclerophyllous habitats of southern Australia when the nutrient status is raised. The other genera are usually found in

sclerophyllous communities. A few species of *Pittosporum* are considered weedy.

ECONOMIC IMPORTANCE. Species of various genera are used in floriculture and landscape gardening in tropical and Mediterranean climate regions. Some *Pittosporum* spp. in the Pacific region (Java, Fiji) are used as a fish poison. The fruits of some *Billardiera* species are edible (“apple berries”). *Pittosporum undulatum*, native to Australia, is sometimes considered a noxious weed elsewhere.

KEY TO THE GENERA

1. Anthers longer or as long as the filament or nearly so 2
 - Anthers clearly shorter than the filaments 3
2. Androecium zygomorphic; ovary stipitate; fruit a capsule 8. *Cheiranthera*
 - Androecium actinomorphic; ovary not stipitate; fruit indehiscent 6. *Billardiera*
3. Procumbent or prostrate shrublets; young stems with cobweb-like indumentum of uniseriate hairs with long curling end cell 3. *Rhytidosporum*
 - Trees or shrubs, not procumbent; indument absent or of different hair type 4
4. Plants spinescent 5
 - Plants not spinescent 7
5. Flowers appearing at base of the plant below the foliage; petals hairy outside; style twice the length of the ovary 9. *Bentleya*
 - Flower position different; petals mainly glabrous outside; style generally shorter than ovary 6
6. Petals spreading from the base, apically not strongly recurving; placentation axile; seeds dark red-brown, not immersed in glutinous material 2. *Bursaria*
 - Petals basally mostly cohering, apically often strongly recurved, placentation parietal with placentae sometimes protruding; seeds mostly orange to red, immersed in glutinous material 1. *Pittosporum*
7. Flowers zygomorphic; plants usually twining 7. *Marianthus*
 - Flowers actinomorphic; trees or shrubs, rarely twining 8
8. Petals 3–4 cm long; filaments hairy; seeds winged 5. *Hymenosporum*
 - Petals mostly shorter; filaments usually glabrous; seeds not winged 9
9. Hairs all or partly T-shaped; flowers functionally unisexual, plants monoecious or dioecious; seeds immersed in glutinous material 1. *Pittosporum*
 - Hairs all uniseriate; flowers bisexual; seeds not immersed in glutinous material 10
10. Small shrublets (5–20 cm high); flowers at base of plants; base of pedicels with several whorled bracts, bracteoles absent 9. *Bentleya*
 - Plants generally larger; flower position different; pedicel without bracts at the base, bracteoles present or absent 11
11. Hairs on vegetative parts without extended terminal cell; filaments widened at base or middle, not angular; ovary stipitate; capsule with seeds in 1 row per locule, seeds black and glossy 4. *Aurantiarpa*
 - Hairs on vegetative parts with extended terminal cell; filaments sometimes more widened at base, angular; ovary not stipitate; fruit indehiscent, seeds in 2 rows per locule, red-brown 6. *Billardiera*

GENERA OF PITTOSPORACEAE

1. *Pittosporum* Banks ex Gaertn. Fig. 82

Pittosporum Banks ex Gaertn., Fruct. Sem. Pl. 1: 286, t. 59, f. 7 (1788), nom. cons.; Cufodontis, Feddes Repert. 55: 27–113 (1952), rev. Afr. spp.; Zhang & Turland, Fl. China 9: 1–17 (2003), reg. rev.; Cayzer et al., Austr. Syst. Bot. 13: 845–903 (2000), reg. rev.
Citriobatus A. Cunn. ex Putt. (1839).

Shrubs or small trees, glabrous or with uniseriate or T-shaped hairs, sometimes spinescent. Leaves sometimes appearing opposite or whorled at the ends of branchlets, margin entire or subserrate, often undulate. Flowers in terminal or axillary panicles, rarely solitary, often functionally unisexual, the plants monoecious or dioecious. Sepals free or connate at base; petals free or shortly fused at base, connivent or coherent to about the middle or higher, glabrous or rarely hairy; anthers dorsifixed, dehiscing by longitudinal slits, shorter than the glabrous filaments, more or less strongly reduced in female flowers; ovary often stipitate, glabrous or pubescent, unilocular or imperfectly 2–5-locular, placentation parietal or parietal-basal; style short, stigma capitate or lobed, more or less reduced in male flowers; nectary at ovary base present, sometimes lobed. Fruit a thick-walled capsule or berry-like

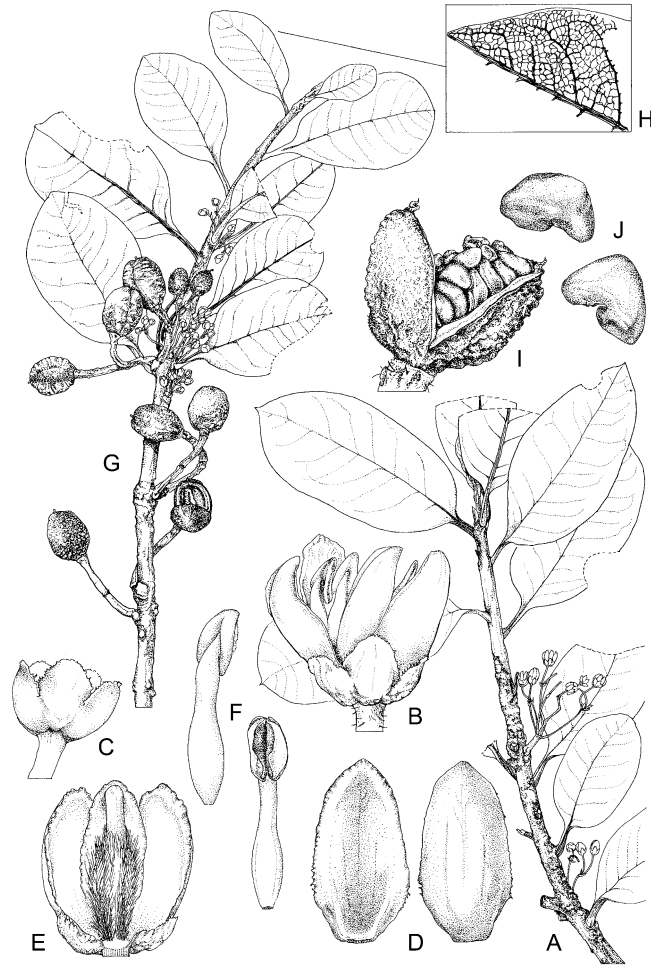


Fig. 82. Pittosporaceae. *Pittosporum spissescens*. A Flowering branch. B Flower. C Calyx. D Petals, adaxial and abaxial view. E Flower with sepals, petals and stamens removed. F Stamens, adaxial and abaxial view. G Fruiting

branch. H Abaxial surface of leaf, showing venation. I Fruit. J Seeds. (Utteridge 2000; drawn by Kathleen McKeehen; reproduced with permission from Kew Bulletin)

(pericarp hard or thin). Seeds mostly red, orange or blackish, usually surrounded by a sticky fluid, embryo sometimes with 3, 4 or 5 cotyledons. $2n = 24$.

Up to 200 species, mostly southern parts of Africa and the Indo-Pacific region, northwards to Japan. Mostly tropical and subtropical.

There have been several attempts to divide *Pittosporum* into subgeneric groups (see especially Schodde 1972) but they either appear to be quite unnatural or they only deal with parts of the overall distribution of the genus. Cayzer et al. (2000) found several well-supported infrageneric clades in Australian *Pittosporum*.

2. *Bursaria* Cav.

Bursaria Cav., *Icones* 4: 30 (1797); Cayzer et al., *Austr. Syst. Bot.* 12: 117–143 (1999), rev.

Much-branched shrubs or small trees often showing heteroblasty, lateral branches spinose at least when young, epidermis of young shoots with uniseriate hairs with elongated terminal cell or sometimes T-shaped hairs. Leaves alternate, sometimes clustered, entire or rarely toothed. Flowers very aromatic, bisexual or rarely unisexual, small, glabrous, usually in axillary or terminal racemes or panicles. Sepals free; petals free,

spreading from the base, white or cream; stamens free, anthers versatile, dehiscent by longitudinal slits, shorter than the filament; ovary 2(3 or more)-celled, glabrous or hairy, compressed, distinctly stipitate; style short, stigma slightly cleft, minute; nectary present, lobed. Fruit a thin-walled, strongly compressed loculicidal and partly septical capsule. Seeds often winged.

Eight species, eastern and south-western Australia, mostly temperate. *Bursaria spinosa* Cav. is a source of the medicinal drug aesculin and planted as a street tree.

3. *Rhytidosporum* F. Muell.

Rhytidosporum F. Muell., Plants Indigenous to the Colony of Victoria 1: 75 (1862); Cayzer et al., Austr. Syst. Bot. 12: 689–708 (1999), rev.

Erect to mostly prostrate undershrubs to 0.5 m high, often with underground shoots, young parts densely or sparsely covered with cobweb-like indumentum of uniseriate hairs with long curling terminal cells, rarely also with T-shaped hairs. Leaves entire or toothed at the apex. Flowers bisexual, solitary or several together in leaf axils or sometimes terminal. Sepals free; petals free, spreading from the base, glabrous, white, tinged pink; stamens free; anthers versatile, dehiscent by longitudinal slits, shorter than filaments; ovary glabrous, sometimes stipitate, 2–3-locular; style short, stigma usually minute; nectary at base of the ovary present. Fruit a loculicidal chartaceous capsule with fibrous compartments, or strongly flattened and indehiscent (*R. alpinum*). Seeds not winged, small.

Five species, temperate eastern and south-eastern Australia incl. Tasmania.

4. *Auranticarpa* L.W. Cayzer, Crisp & I. Telford

Auranticarpa L.W. Cayzer, Crisp & I. Telford, Austr. Syst. Bot. 13: 904 (2000); Cayzer et al., Austr. Syst. Bot. 13: 903–917 (2000), rev.

Small to medium-sized trees, indumentum exclusively of uniseriate hairs, terminal cell not elongated. Leaves alternate, sometimes appearing verticillate, margins entire and undulate, or slightly crenulate to toothed. Inflorescences multi-flowered, corymbose. Flowers bisexual, very fragrant. Sepals usually spreading from the

base, very rarely 6; petals free, spreading from the base, mostly glabrous, cream or white; ovary strongly stipitate, placentation axile, style stout, stigma minute; nectary small, at base of the stipe. Fresh capsule usually with red-orange pericarp, 2 (3)-locular. Seeds few, black, shiny, not immersed in sticky pulp. $2n = 24$.

Six species, mostly monsoonal northern Australia, one species southwards to New South Wales.

5. *Hymenosporum* F. Muell.

Hymenosporum F. Muell., Fragm. 2: 77 (1860).

Chelidospermum Zipp. ex Blume, Mus. bot. Lugd. batav. 1: 162 (1850), nom. inval.

Quinsonia Montrouzier (1860).

Shrub or small tree, hairs uniseriate without elongated terminal cell. Leaves alternate, often in pseudo-whorls towards the ends of the branches, entire, glabrous or slightly hairy on the lower surface. Flowers bisexual, fragrant, in loose terminal panicles. Sepals 5, free, hairy; petals 5, cohering into a tube to above the middle, hairy on the outside, colour changing during anthesis from white to yellowish; stamens free, filaments hairy; anthers clustering at three different heights at anthesis, dehiscent by longitudinal slits, shorter than the filaments. Ovary hairy, incompletely 2-locular, narrow; style long. Fruit a compressed, thick-walled loculicidal capsule. Seeds flat, winged.

One species, *H. flavum* (Hook.) F. Muell., eastern Australia and New Guinea, temperate to tropical, ornamental.

6. *Billardiera* Sm.

Billardiera Sm., Spec. Bot. New Holland 1, t. 1 (1793); Cayzer et al., Austr. Syst. Bot. 17: 83–125 (2004), phylog., rev.

Sollya Lindl. (1832) ("1831").

Pronaya Hügel (1837).

Scrambling or climbing rhizomatous shrubs; hairs uniseriate with 1–3 basal cells and an elongated terminal cell. Leaves sometimes clustering, entire. Flowers bisexual, solitary or in terminal cymes. Sepals free, usually unequal; petals clawed, briefly coherent into a tube to above the middle, or elliptic and spreading from the base, rarely hairy outside; stamens free; anthers

versatile, dehiscing by longitudinal or rarely apical slits, much shorter than the filaments or \pm equal to longer, sometimes recurving, rarely cohering apically; ovary sessile, 1- or 2-locular, hairy or not; style short; nectary conspicuous or vestigial to absent. Fruit a succulent or somewhat fibrous berry. Seeds not winged, embedded in a mucilaginous pulp or in fibrous tissue.

23 species, temperate eastern and southern Australia, some ornamental. The inclusion of *Sollya* as proposed by Cayzer et al. (2004) needs further study. The three species of *Sollya* are characterized by anthers which are apically coherent and equal to longer than the filaments.

7. *Marianthus* Hügel ex Endl.

Marianthus Hügel ex Endl. in Endl. et al., Enum. Pl. Hügel 8 (1837); Cayzer & Crisp, Austr. Syst. Bot. 17: 127–144 (2004), rev.

Twining woody perennials, hairs uniseriate with elongated terminal cell. Leaves alternate, shortly petiolate or sessile, stem-clasping and sometimes clustered into a funnel-shaped arrangement. Flowers solitary or in dense corymbose or umbellate axillary cymes, zygomorphic, bisexual. Sepals free, coloured similarly to petals; petals free to the base or coherent to above the ovary and becoming free with age, white, red, blue, cream-yellow, mostly glabrous; stamens free, at anthesis anthers clustering at 3 different heights (1 + 2 + 2), dehiscing by longitudinal slits, shorter than the flat slender filaments; ovary stipitate, glabrous or hairy, 2-locular; style slender. Fruit a loculicidal capsule with or without fibrous compartments. Seeds discoidal, reniform, rarely globose.

14 species, south-western Australia, one species into south-eastern Australia.

8. *Cheiranthra* A. Cunn. ex Lindl.

Cheiranthra A. Cunn. ex Lindl., Edwards' Bot. Reg. 20, sub. t. 1719 (1834); Cayzer et al., Austr. Syst. Bot. 20: 340–354 (2007), rev.

Shrubs with twining or flexuose stems, with erect, uniseriate trichomes without elongated terminal cell or glabrous. Leaves sometimes clustering, often narrow. Flowers bisexual, solitary or in lax corymbs. Sepals free, purple-green or blue; petals spreading from the base, mostly deep blue;

androecium zygomorphic at anthesis; anthers dehiscing by 2 apical pores or when cohering apically by slits, longer than filaments; ovary glabrous, 2-locular, stipitate, placentation axile; style subulate, curved; nectary absent. Fruit a capsule opening septicidally by 2 valves, sometimes additionally loculicidally. Seeds numerous, small, sometimes arillate.

10 species, temperate Australia, in eucalypt communities. As regards authorship of the name of the genus, see Cayzer et al. (2007).

9. *Bentleya* E.M. Bennett

Bentleya E.M. Bennett, Nuytsia 5: 401 (1986); Crisp & Taylor, Bot. J. Linn. Soc. 103: 109–115 (1990), rev.

Rhizomatous small shrubs 5–20 cm high, sometimes producing suckers, spinose or not, hairs uniseriate with elongated terminal cell. Leaves small, sometimes clustered or rosulate. Flowers bisexual, solitary, at the base of the plants below the foliage, with a whorl of bracts at the base of the pedicel. Sepals free, imbricate; petals hairy on both sides, greenish cream, cohering into a tube when young but separating at the base and remaining coherent in the middle or becoming completely free; stamens free, anthers dehiscing by longitudinal slits, shorter than filaments; nectary prominent, 5-lobed; ovary silky hairy, 2–3-locular, with numerous ovules on axile or parietal placentae; style hairy. Fruit a septicidal-loculicidal or loculicidal capsule. Seeds compressed.

Two species, south-western Australia.

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