Zygophyllaceae

Zygophyllaceae R. Br., Flind. Voy. Bot. app. 3:545 (1814).
Balanitaceae Endl. (1841).

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Trees, shrubs, subshrubs or annual or perennial herbs, often with jointed branches and swollen at the nodes; axillary or stipular thorns sometimes present. Leaves stipulate, opposite or less often alternate, bi- or trifoliolate or pinnately multifoliolate, rarely simple; usually petiolate, rarely with glandular dots, sometimes unequal; leaf(let) lamina entire, often asymmetric, flattened, fleshy or terete. Flowers solitary, paired or in few-flowered cymes, axillary or terminal, bisexual, actinomorphic or rarely slightly zygomorphic; sepals 4–6, ± free, rarely connate at base, usually imbricate, valvate in *Seetzenia*; petals free, often clawed, mostly as many as sepals, rarely 0; disc often present; stamens (5)8–12 as many as or twice the number of petals and then obdiplostemonous; filaments sometimes with basal scales or appendages; anthers introrse, dorsifixed, 4-sporangiate, with longitudinal dehiscence; ovary syncarpous, superior, sessile or shortly stipitate, angular, ribbed or winged, (2–)4–5(–12)-locular; style filiform or subulate; stigma capitate, clavate or slightly lobed or ridged; ovules 1 to many per locule, bitegmic, pendulous, usually with axile placentation. Fruit a loculicidal or septicidal capsule, or splitting into mericarps which may be winged, lobed or angled, spiny or tuberculate; rarely a 1-seeded drupe (*Balanites*). Seeds with or without endosperm; embryo straight or slightly curved.

Comprising 22 genera and 230–240 species in hot dry regions of Europe, Asia, Australia, Africa and the Americas.

Vegetative Morphology. Leaves are opposite in subfamilies Zygophylloideae, Larreoideae and Seetzenioideae, and alternate in Morkillioideae. In Tribuloideae, *Tribulopis*, *Neoluederitzia* and *Balanites* have alternate leaves; in *Tribulus* and *Kallstroemia*, they are opposite but unequal and are sometimes apparently alternate by abortion of the smaller leaf of a pair; in *Kelleronia* and *Sisyndite*, the lower leaves are predominantly alternate but the upper leaves may be opposite. In genera with opposite leaves, often only one branch develops at each node, so branching may appear alternate (e.g. in *Guaiacum*, *Porlieria*, *Zygophyllum*).

The leaves may be bi- or trifoliolate or pinnately compound, and are only rarely simple. Hunziker et al. (1977) regard multifoliolate as the more primitive condition, with the bifoliolate species representing a reductional trend in response to aridity. Other adaptations to the often extreme habitats where many members of the family are found include a similar pattern of reduction of leaf area. In some species such as *Zygophyllum dumosum* and *Sisyndite spartea*, the leaflets fall, leaving only the photosynthesing petiole or rachis. Simple leaves, as in *Zygophyllum simplex*, may have evolved as an extreme expression of this tendency.

As many species lose all their stems and branches under arid conditions, they are sometimes referred to as perennial herbs (e.g. by Borisova 1974). When a persistent woody base remains, however, it is more accurate to call the plants suffrutescent shrubs or, in Raunkiaer's classification, chamaephytes.

Nyctinasty is reported in some genera with pinnate leaves, notably *Porlieria*.

Vegetative Anatomy. The two main types of leaf anatomy represent different adaptations to often extreme habitats. Leaves may be succulent with a thin cuticle, shallow epidermis, slender veins, abundant water-storage and scanty mechanical tissue, as in many *Zygophyllum*, or have small leaves, small stomata and a high proportion of palisade tissue, as in *Larrea*.

The main types of mesophyll arrangement are dorsiventral, more or less isolateral, and centric (in cylindrical leaves, with central water-storage tissue). In leaves and leaflets with a flat lamina, venation is pinnate, reticulate, camptodromous-brochidodromous, with more or less straight primary veins, randomly ordered higher-order veins,

and incomplete or imperfect areoles (terminology from Hickey 1973); cylindrical leaves have one or two central veins with a peripheral network of smaller veins. There are sometimes abundant, dilated tracheoids associated with veinlet endings. Stomata are usually anomocytic, sometimes paracytic or weakly actinocytic. Trichomes are usually unicellular and either one- or two-armed; however, *Fagonia* has glandular trichomes with a unicellular head on a multicellular stalk (Fahn and Shimony 1996), and lobed, peltate trichomes were seen in two central Asian species, *Zygophyllum eurypterum* and *Z. darvasicum* (Sheahan and Cutler 1993).

In stems, there are commonly separate strands of thick-walled fibres and stone cells in the cortex. Phloem sieve elements are usually small (diam. 5–8 µm), with compound sieve plates. Sieve-element plastids are reported to be mainly S-type but P-type, with two different-sized protein crystals, have been seen in *Larrea divaricata* (Behnke 1988). There is much storeying of elements of the secondary xylem. The wood is characterised by short, frequently solitary xylem vessels with simple perforations, small alternate intervascular pitting and horizontal to oblique end walls. Other tracheary elements are narrow (< 25 µm) and short (80–160 µm); fibre-tracheids, libriform fibres and gradations between the two may be present; in several species there are also vasicentric tracheids. Rays are usually short and homocellular, mostly 1–2 (rarely 3–4) cells wide. Axial parenchyma is mainly apotracheal, occasionally paratracheal, diffuse or sometimes sub-reticulate; cells are fusiform, sometimes with cross-walls. *Balanites* is reportedly different from other members of the family in having taller, wider rays (up to 35 cells wide) and vestured intervascular pits, although vesturing has also been observed in several other members of the family (Parameswaran and Conrad 1982; Jansen et al. 2001).

Nodes are typically trilacunar; the three traces entering the base of the leaf are derived as a median and two 'split laterals' which depart at the lateral gaps and divide to girdle the stem towards each of the opposite leaves (Howard 1970).

Zygophyllaceae are one of about 18 families in which the C_4 photosynthetic pathway is found. All *Tribulus* so far examined have shown the C_4 pathway. However, *Kallstroemia* and *Zygophyllum* are among the few dicot genera reported to have both C_3 and C_4 species: all species of *Kallstroemia* except one, *K. perennans* (Smith and Robbins 1974), are C_4 plants but, in *Zygophyllum*, only *Z. simplex* has so far been categorised as C_4 (Welkie and Caldwell 1970; Sheahan and Cutler 1993). All C_4 species exhibit typical Kranz anatomy, except *Z. simplex* which has centric leaves, and the Kranz cells form an incomplete sheath around only the outer part of the vein.

Flower Structure. The flowers are insect-pollinated. They are most often axillary, sometimes terminal or leaf-opposed, and may be solitary or aggregated into few-flowered cymes. The calyx is uniseriate, sometimes unequal; where present, the petals are of the same number as the sepals and may be white, pink, purple, blue or yellowish (absent in *Seetzenia* and *Zygophyllum portulacoides*). A hypogynous disc is often present, although sometimes inconspicuous, and may be (4)5- or 10-angled or -lobed; nectariferous glands are also sometimes present (Fig. 173C). *Neoluederitzia* has a structure formed from scales enclosing the ovary which apparently arise from the disc, although according to Engler (1931), they are formed from the stamens. Stamens are usually twice the number of sepals, in two whorls; in *Tribulus*, *Tribulopis* and *Kallstroemia*, the antesepalous whorl may be sterile or absent. The anthers sometimes have winged filaments. Fringed or divided scale-like appendages occur in many taxa at the base of the filament; the presence or absence of these has sometimes been used to distinguish taxa but, in combined molecular and morphological analyses, this character appears to be useful only within individual genera. Carpels are usually of the same number as the sepals, but are double the number in *Augea* and *Kallstroemia*. The locules contain one to several ovules, although often only one matures.

Embryology. Information is summarised by Davis (1966) and Johri et al. (1992). Pollen tetrads are tetrahedral and decussate. Pollen grains are 2-celled when shed in *Zygophyllum* and *Seetzenia*, 3-celled in *Fagonia* and *Balanites*. Ovules are anatropous, bitegmic and crassinucellate; a single embryo sac develops, of the Polygonum type. Endosperm formation is nuclear, with wall formation beginning at the micropylar end. Embryogeny is mostly of the Solanad type, but *Tribulus terrestris* and *Zygophyllum fabago* are reported to be of the Caryophyllad type.

Pollen Morphology. Data on pollen morphology are mainly from Erdtman (1952); later studies include Mathur and Bhandari (1983), Lahham and