Staphyleaceae

Staphyleaceae Martynov, Teckno-Bot. Slovar: 598 (1820), nom. cons.

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Trees or shrubs, evergreen or deciduous. Leaves opposite, petiolate, pinnately compound, rarely unifoliolate, serrate, stipulate; stipels usually present but sometimes reduced to glands or absent. Inflorescences terminal or axillary in upper leaves, paniculate. Flowers perfect, hermaphroditic, actinomorphic; sepals 5, distinct or united, unequal, imbricate; petals 5, free, fused for part of their length or fused to form a short floral cup, unequal, imbricate in bud, often inserted on or below a crenate or lobed disk; stamens 5, arising outside of or between the lobes of the disk, alternate with the petals; filaments complanate; anthers 2-celled, dorsifixed, introrse, dehiscing longitudinally; ovary superior to partially inferior, 2–3(4)-carpellate, the carpels nearly free or united, sessile, the stylodia at least partially free but distally fused to form a capitate, wet stigma; placentation axile, ovules few–many in 2 series on ventral suture. Fruit a berry, a membranous inflated capsule, or a multifollicle; seeds with a straight, green embryo and copious or rarely scanty fleshy endosperm.

Two genera with 45–50 species, distributed widely in the Northern Hemisphere of both the Old World and the New, but extending beyond the equator in Ecuador, Peru, Bolivia, and Southeast Asia to Papua New Guinea.

Vegetative Morphology. All Staphyleaceae are woody, ranging from small stoloniferous shrubs (2 m) and small trees reaching 15 m (*Staphylea*) to upper canopy trees of 25–30 m (*Dalrympelea*). Stump sprouting of saplings and adult trees has been observed in tropical *Staphylea*. Buttressing is common in the larger tropical trees (*Dalrympelea*). Bark in *Staphylea* is gray to black and somewhat mottled, with or without lenticels. Bark in *Dalrympelea* ranges from creamy yellow and flaky ("*Dalrympelea*" [*Turpinia*] *calciphila*)[1] to smooth gray ("*D.*" [*Turpinia*] *grandis*). The branches of "*Staphylea*" [*Euscaphis*] *japonica* are glabrous.

Members of Staphyleaceae have opposite, decussate, and trifoliate or imparipinnately compound (rarely unifoliolate) leaves. The rachis is green, sometimes tinged with red ("*S.*" *japonica*), and glabrous to pubescent. Leaf margins are glandular and dentate, serrate, or crenate. Leaves are deciduous in temperate taxa, evergreen in tropical ones. Stipules are well developed and usually caducous. In most species of *Staphylea*, each leaf has a pair of free, multi-veined stipules. In *Dalrympelea*, the stipules of opposed leaves fuse, sometimes becoming bifid at the apex, often having colleters. Trichomes, when they occur, are of the simple, uniseriate and predominantly unicellular types.

Vegetative Anatomy. The wood anatomy of Staphyleaceae has been examined most recently by Carlquist and Hoekman (1985). Characters that unite the family are: vessels mostly solitary; vessel elements long with scalariform perforation plates; scalariform, alternate or opposite lateral wall pitting; and fiber tracheids with fully bordered pits. The woods of tropical members lack growth rings prominent in temperate taxa. Rhomboidal crystals, tyloses and dark-staining deposits are found in the wood of some, but not all, species.

The leaf cuticle is thin on both surfaces. Both the upper and lower epidermal layers are uniseriate; some species have a hypodermis on the adaxial surface. Stomata are confined to the abaxial surface, with both genera having anisocytic stomata (Metcalfe and Chalk 1950). Leaf venation with fibers is prevalent in most taxa, whereas fibers are notably absent in "*Staphylea*" [*Euscaphis*] *japonica*. Crystals are present in the leaves of both genera.

Inflorescence Structure. The many flowers are borne in terminal or axillary panicles or thyrses, held erect above the foliage, or drooping. Panicles range from 5 to 30 cm in length, can contain from

[1] Generic names for which the new combinations now becoming necessary (see section on Classification) do not yet exist are placed within quotation marks.

a few (< 20 in some *Staphylea*) to many (> 100 in some *Dalrympelea*) flowers, and can be either compact or lax.

Floral Structure and Anatomy. The descriptions of "*Dalrympelea*" [*Turpinia*] *formosana* and "*D.*" [*Turpinia*] *ternata* (Nakai 1924) specified dioecy, but later treatments described perfect flowers (Ka 1965; Li 1993). Floral morphology and anatomy of Staphyleaceae have been treated in detail by Dickison (1986). The calyx has (4)5 sepals, which are distinct or show various degrees of connation along their length, and are alternately positioned with an equal number of petals. Petals have a quincuncial aestivation, and are either essentially distinct or fused in a short floral tube, and are usually cream-white, or cream tinged with green, pink, or yellow. Stamens are borne opposite the sepals outside a lobed nectary disk; the filaments can arise either outside of, or between the lobes of the disk. The filaments are campanulate, and typically vary from pubescent to glabrous. Anthers are 2-lobed, 4-locular and dorsifixed, dehiscing with longitudinal slits.

The gynoecia are embedded in the nectary disk and consist of 2–3(4) carpels. The ovaries are more or less syncarpous, but in *S. japonica* the carpels are free from each other but adnate along their dorsal surface to the surrounding floral cup. The stylodia are largely free for most of their length, uniting distally to form a single blunt, often lobed, stigma. Each carpel has one locule containing 2–several ovules arranged in two rows, with axile placentation. Transmitting tissue leads from the stigma separately through the stylodia to the ovarian portions of the carpels. In most *Staphylea*, the ovules are covered with papillate transmitting tissue. Druses and frothy mucilage cells are widespread in *Dalrympelea* (Dickison 1986).

The sequence from apocarpous to more or less syncarpous ovaries was interpreted by Dickison (1986) as a progressive fusion. The peculiar fusion of the stigmas, and the occurrence of more or less free stylodia and carpels suggest, however, that apocarpy may be evolutionarily secondary. In such gynoecia, the stigma enhances selection of pollen tubes during their growth to the ovules (Ramp 1987). Thus, the gynoecium structure of *Dalrympelea* would appear pleisiomorphic, rather than derived. This may correlate with the fact that the vessels of *Dalrympelea* have the largest number of bars per perforation plate (Carlquist and Hoekman 1985).

Embryology. The embryology of "*Dalrympelea*" [*Turpinia*] *nepalensis* was studied by Narayana (1960). Meiosis in the pollen mother-cell is normal, and cytokinesis takes place by furrowing. Pollen tetrads are tetrahedral, and pollen grains are binucleate when shed. For Staphyleaceae in general, ovules are crassinucellate, bitegmic, and anatropous. The micropyle is formed by both integuments. Development of the embryo sac is of the Polygonum type (Johri et al. 1992).

Pollen Morphology. Pollen is tricolporate, circular to triangular in outline in polar view, and mostly spheroidal. Ectoapertures are long, recessed, and granular. The exine is stratified into tectum, columellae, foot layer, and endexine. The exine surface varies from foveolate to reticulate (Erdtman 1952; Lobreau 1969; Dickison 1987b).

Karyology. Chromosome counts have been reported for six species of *Staphylea* and three species of *Dalrympelea*. It has been proposed that the family has a base chromosome number of $x = 13$, with "*S.*" [*Turpinia*] *cochinchinensis*, $n = 13$; "*D.*" [*Turpinia*] *formosana*, $n = 11$; "*D.*" [*Turpinia*] *nepalensis*, $n = 13, 14$; "*D.*" [*Turpinia*] *pomifera*, $n = 13$; *S. bolanderi*, $n = 13$; *S. bumalda*, $2n = 26$ (Hsu 1968; Mehra and Khosla 1969; Mehra 1976; Gill et al. 1984). Putative polyploids include *S. colchica*, $2n = 52$; *S. pinnata*, $2n = 24, 26$; and *S. trifolia*, $2n = 78$ (Winge 1917; Foster 1933; Pogan et al. 1983). Foster (1933) observed secondary pairing in meiotic figures from pollen mother-cells of *S. trifolia*.

Pollination and Reproduction. *Staphylea* exhibit some vegetative reproduction via stolons, and often grow in groves of clones (Dore 1962; pers. obs.). Root suckering in *S. trifolia* is common (Garwood and Horvitz 1985). *Staphylea trifolia* is self-incompatible (Garwood and Horvitz 1985), and the remainder of the family is thought to be so, too. Flowers are protogynous, and bloom in the spring as the leaves are expanding in temperate *Staphylea*, and at the end of the tropical rainy season in tropical members. Twenty insect species have been reported to visit *Staphylea trifolia*, including species of short-tongued bees, long-tongued bees, and Diptera (Robertson 1889).

Fruit and Seed. The two genera of Staphyleaceae are most easily distinguished by fruit type. *Staphylea* fruits are either: inflated, membranous,