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## Stachyuraceae

Stachyuraceae J. Agardh, *Theoria Syst. Pl.*: 152 (1858), nom. cons.

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Small trees or shrubs, sometimes climbing, deciduous or evergreen, the branchlets with large pith, the winter buds small, with 2–4 outer scales. Leaves involute, alternate, simple, petiolate, membranaceous to coriaceous, glabrous or pubescent, serrate to serrulate; venation pinnate-reticulate; stipules small, caducous. Inflorescences axillary or terminal, racemes or spikes, erect or pendulous, few- to many-flowered, with each flower subtended by a bract; pedicel articulated or inconspicuous, apically with two basally united prophylls. Flowers bisexual or functionally unisexual and then plants dioecious, pedicellate or sessile; sepals 2 + 2, decussate, imbricate, the outer two smaller; petals 4, free, imbricate, yellow, greenish, pinkish or white; stamens 4 + 4, diplostemonous, distinct; anthers tetrasporangiate, deeply sagittate, opening by longitudinal slits, dorsifixed, introrse, versatile; nectary at base of gynoecium well developed on sepaline radii; carpels 4; ovary syncarpous, superior, incompletely 4-locular due to intrusion of parietal placentae, sometimes pubescent; style simple, short, apical, stigma wet, capitate; placentation parietal (in upper part of ovary) to axile (in basal part), ovules numerous, arranged in two alternating rows in each carpel, anatropous, crassinucellate, bitegmic. Fruit berry-like, with leathery pericarp and deciduous calyx; seeds numerous, small, with soft funicular aril and sclerotic testa; endosperm copious, fleshy, oily and albuminous, not starchy, perisperm 0; embryo straight, small, with short, fleshy funicle; cotyledons elliptic, flat, radicles short.  $n = 12$ .

A single genus with 16 species, temperate (to subtropical) eastern Asia from the Himalayas to Taiwan and Japan.

**VEGETATIVE MORPHOLOGY.** Stachyuraceae are shrubs or small trees generally not exceeding 5 m in height. Leaves are simple and serrate to inconspicuously serrulate. The leaf veins generally protrude into teeth. Leaf venation is pinnate-reticulate and

corresponds to the brochidodromous or eucamp-todromous type (Yu and Chen 1990; Klucking 1992). Stipules are present but early caducous. Epicuticular waxes of tubular or scaly shape, sometimes arranged as a rosette, were found on leaves or petioles (Ditsch and Barthlott 1994).

**VEGETATIVE ANATOMY.** The leaves are bifacial, the anomocytic stomata confined to the abaxial side. Nodes are trilacunar and the petioles have an arch-shaped strand accompanied by two smaller ones. Cluster crystals and tanniniferous cells are present in the parenchymatous tissue. Stem sections reveal that cork originates in the epidermis. The wood is diffuse-porous with distinct growth rings. Vessels are solitary or, less frequently, in radial multiples of 2–3 or in clusters. Vessel elements are 650–1,200  $\mu\text{m}$  long with oblique end walls. The perforation plates are scalariform with 30–50 bars. Intervessel pits are scanty and helical thickenings are indistinct. Fibre-tracheids are 8–35  $\mu\text{m}$  in diameter, the pits distinctly bordered, circular, 7–8  $\mu\text{m}$  in diameter, with oblique slit-like apertures. Wood parenchyma is fairly abundant, predominantly apotracheal, diffuse and diffuse-in-aggregates. Rays are uniseriate to multiseriate, the latter 2–6 cells wide and up to 2,700  $\mu\text{m}$  tall. Ray-vessel pits are usually opposite, circular or slightly elongated in horizontal direction, 4–6  $\mu\text{m}$  in horizontal diameter. Crystals are absent (van Tieghem 1900; Metcalfe and Chalk 1950; Suzuki et al. 1991).

**INFLORESCENCES.** The inflorescences are erect or pendulous racemes or spikes which usually appear on the branches of the preceding year (Li 1943). Each flower is subtended by a bract. The pedicels bear apically two prophylls which are united at the base. In distinctly pedicellate flowers, the pedicels are generally articulated.

**FLOWER STRUCTURE.** Most species (all?) of Stachyuraceae have bisexual flowers but are func-

tionally dioecious, with female flowers bearing staminodes and male flowers having a reduced pistil (Tang et al. 1983). The flowers are actinomorphic, tetramerous, and petal aestivation is irregularly imbricate. The androecium is diplostemonous and the anthers are tetrasporangiate, introrse, dorsifixed, opening by longitudinal slits. A connective protrusion is present but short. The superior, syncarpous, 4-carpellate ovary is elevated on a short stalk. The tips of the carpels are postgenitally united into a capitate stigma with a single surface. The ovary is incompletely 4-locular, since the carpel partitions are centrally not united in the middle and upper parts. A nectary is present at the base of the ovary (Matthews and Endress 2005). A detailed analysis of the floral morphology was given by Matthews and Endress (2005).

**EMBRYOLOGY.** The anthers consist of five to six cell layers: an epidermis, an endothecium, two to three middle layers and a tapetum. The formation of the wall corresponds to the Basic type. The tapetum is glandular and predominantly two-nucleate. Meiosis of the microspore mother cells results in tetrads of tetrahedral shape. Pollen grains are two-celled at the time of shedding (Kimoto and Tokuoka 1999).

Placentation is axile at the base of the ovary, parietal in the upper parts, due to the different degree of intrusion of the placentae. The ovules are anatropous, bitegmic, crassinucellate and syntropous. Meiosis of the megaspore mother cell results in a linear or T-shaped tetrad. The development of the embryo sac corresponds to the Polygonum type and embryogeny follows the Solanad type. Polyembryony is due to cleavage of the zygotic proembryo, or simultaneous development of zygotic and synergid embryos (Mathew and Chaphekar 1977). An obturator is not formed but a weakly differentiated hypostase can be observed in older ovules (Kimoto and Tokuoka 1999). The two integuments are not vascularized and both contribute to the micropylar canal. Fertilization is porogamous. Endosperm formation is of the Nuclear type (Mauritzon 1936; Satô 1976; Mathew and Chaphekar 1977; Kimoto and Tokuoka 1999).

**POLLEN MORPHOLOGY.** The pollen is tricolporate or tricolporoidate, subprolate to prolate. The sexine is slightly thicker than the nexine and  $\pm$  finely reticulate, with lalongate ora, about 24  $\mu$ m long (Erdtman 1952; Tang et al. 1983).

**KARYOLOGY.** Karyological analyses of five taxa showed a chromosome number of  $2n = 24$  (Kurosawa 1971; Tang et al. 1983).

**POLLINATION.** Reports of field observations are unknown but Stachyuraceae are most likely pollinated by insects.

**FRUIT AND SEED.** The fruits are berry-like and contain numerous seeds. The seeds are small, ellipsoidal, arillate and albuminous. The aril develops from the apical region of the funicle and grows towards the chalazal end of the ovule, eventually covering the entire seed from the micropyle to the chalaza. The testa comprises four to five cell layers and is completely sclerotic. The mechanically most specialized tissue of the mature seed are the cells of the exotesta, which consists of radially elongated cells of the outer epidermis, and thick-walled mesotesta and endotesta cells which are tangentially elongated. The inner integument disappears during seed ripening, except for the cells of the exotegmen which only lose their living content. According to Pritzel (1897), the endosperm is fleshy and oily but not starchy, and contains small proteinaceous particles. The embryo is straight, has flat cotyledons and a short radicle (Mathew and Chaphekar 1977; Kimoto and Tokuoka 1999).

**PHYTOCHEMISTRY.** Apart from trivial flavonols, proanthocyanidins and ellagitannins are known from *Stachyurus*. Particularly the latter group of compounds is strongly diversified, and more than ten different ellagitannins, based partly on different methylated derivatives of hexahydroxydiphenic acid, have been characterised. The cortex of *Stachyurus* is also known for one of the erratic occurrences of ecdysone in angiosperms (Hegnauer 1973, 1986, 1989, 1990 where references to original papers can be found; Han et al. 1995).

**AFFINITIES.** Originally, *Stachyurus* was included in Pittosporaceae but Gilg (1893) preferred to have it as a distinct family, which often was considered to be close to Flacourtiaceae or Ternstroemiaceae. Most more recent classifications (Dahlgren 1980; Thorne 1992; Takhtajan 1997) placed Stachyuraceae in Theales, except for Cronquist (1981) who included them in Violales. According to the APG II (2003), Stachyuraceae are assigned to Crossosomatales. Molecular studies based on *rbcL*