

Paeoniaceae

Paeoniaceae F. Rudolphi, Syst. Orb. Veg.: 61 (1830), nom. cons.

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Perennial herbs, halfshrubs or shrubs with herbaceous or woody stems, usually branched from cataphylls; rhizome and roots thickened, napiform or bulbous. Leaves large, deciduous, alternate, ternately or pinnately compound or dissected, petioles dilated at base, leaflets entire, 3–5-lobed to -parted, or dissected into linear segments, cuneate to rounded at base, with entire margin, with petiolules, often glaucous beneath; stipules 0. Flowers large, solitary, terminal on main axis or branches, actinomorphic, hermaphroditic, hypogynous, opening nearly flat, rarely connivent; receptacle more or less concave, preceded by 2–6 hypsophylls, the latter sometimes grading into sepals by shortening of internodes; sepals 3–5 or more, green, free, often reflexed, (herbaceous-) coriaceous, persistent; petals 5–10(–13), free, caducous, larger than or sometimes nearly as long as sepals, red, pink, white, sometimes yellow; stamens numerous; anthers dithecal, yellow, lateral, linear to elliptic-linear, opening lengthwise, connectives not projecting; filaments filiform; disk intrastaminal, membranaceous, coriaceous or fleshy, not nectariferous; carpels 2–8(–15), distinct, obliquely bottle-shaped, thick-walled; stylodia short, stigmas more or less circinate outside; ovules anatropous, with very thick integuments. Follicles thick-walled. Seeds purple-black to black, sometimes interspersed with sterile red “lure” seeds; endosperm copious. Flowering in spring to early summer, fruiting in summer to autumn.

One genus with c. 40 species, most in (warm-) temperate Eurasia, two in western North America.

VEGETATIVE MORPHOLOGY. Germination is hypogeous. The primary root is transformed into an perennating storage root, which is tuberous or napiform and then often branched, or a rhizome is formed, which bears variously thickened, distally fibrous roots (Fig. 95). The first flower is formed about 5 years from germination, after which the shoot starts branching (Ignat’eva 1995).

VEGETATIVE ANATOMY. The vascular bundles have tendencies to an amphicribal type (Worsdell 1908). The vessels are narrow and solitary, with scalariform, sometimes reticulate perforations. The fibres have distinctly bordered pits. In the phloem, little or no sclerenchyma is developed (Eames 1961). Secondary rays are formed from the very beginning of the formation of the secondary xylem, in contrast to the woody stems of *Clematis* and *Naravelia* in which secondary rays appear much later. This may suggest that *Paeonia* stems are primarily woody (Kumazawa 1935), in contrast to those of Ranunculaceae. Stomata are uniformly anomocytic and develop according to the aperigenous type (Hong 1989). Calcium oxalate is present as crystals.

FLORAL MORPHOLOGY AND ANATOMY. The phyllotactic spiral follows an angle of 137.5° and is continuous from the foliage leaves through the hyps-

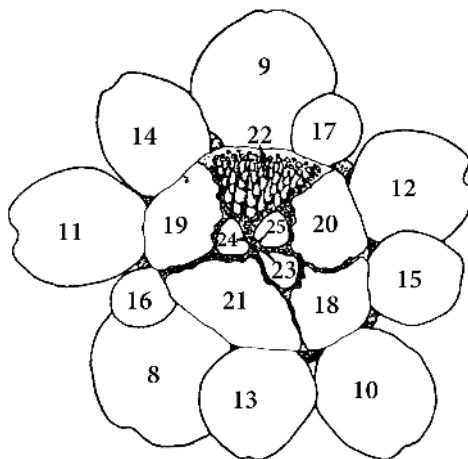


Fig. 92. Paeoniaceae. Floral bud of *Paeonia lactiflora*, seven perianth members removed, all other floral organs consecutively numbered, according to their sequence of inception; 18–22 are stamen groups originating on mounds (the stamen primordia drawn only on number 22), 23–25 are carpels. (Hiepkö 1965a)

ophylls, sepals, petals, and androecial mounds to the carpels, if the latter are not very few in number. There are transitional forms between hypsophylls and sepals, and between sepals and petals (Hiepko 1965b). The stamens develop in a centrifugal sequence on five mounds (Fig. 92; Schöffel 1932; Hiepko 1965a).

In the cross section of the pedicel, a central vascular ring and about five cortical strands are present. The cortical strands supply the sepals, petals and, to some extent, also the stamens and, from the central vascular cylinder, traces branch off to the petals, stamens and carpels (Sawada 1971). The disk (Fig. 93) is initiated after the stamens but receives also some vascular supply from the stamen trunks (Fig. 94; Hiepko 1966).

POLLEN MORPHOLOGY. Pollen is tricolporoidate and the sculpture of the exine in SEM is reticulate, foveolate or irregularly tuberculate-foveolate; thin sections in TEM show the exine composed of a perforate tectum to semitectum, columellae and a foot layer (Xi 1984). Kumazawa (1937) found that the exine is reticulate.

POLLINATION. Beetles seem to be the main pollinators. The disk does not produce nectar but pollen is produced in abundance. In the flowers of *P. delavayi*, *P. lutea* and *P. potanini*, Hiepko (1966) observed nectar secretion from vascular bundles which were initiated to supply stamens but the anthers of which were crushed by the expansion of the disk.

EMBRYOLOGY. The ovules are large and borne on placental projections. The inner integument is c. 4 cell layers thick, the outer one 14–20, exceeding the inner and forming the micropyle; these may be one of the thickest integuments of the angiosperms (Kumazawa 1938). The nucellus is crassinucellate but absorbed before anthesis. At anthesis, the embryo sac is directly surrounded by the inner integument (Kumazawa 1938). The aril is cushion-like, not enlarged, and slightly vascularized; a hypostase and a hypostase bundle are distinct. Abortion of ovules in a carpel is reported by Cave et al. (1961), Camp and Hubbard (1963), Shamrov (1997) and others, and may be common in the genus. The vascular supply of the ovules is complicated and extremely abundant, being far beyond present-day needs, which may indicate that formerly the ovules were much larger structures (Camp and Hubbard 1963). There seem to be several archesporial cells.

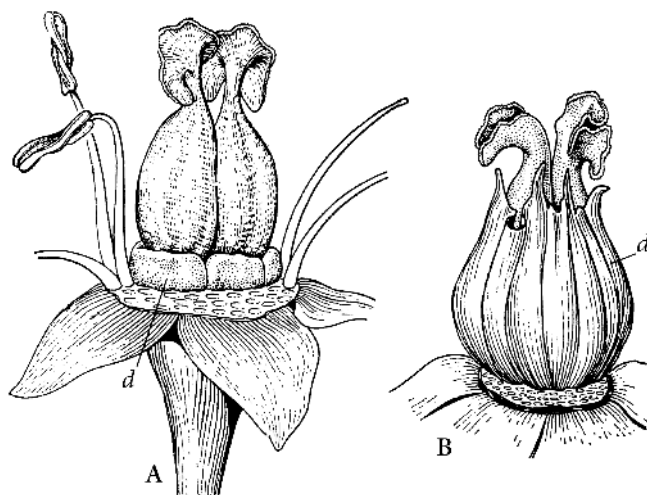


Fig. 93. Paeoniaceae. A *Paeonia anomala*, flower with petals and stamens removed (d = disk). B Same of *P. suffruticosa*. (Takhtajan 1981)

The embryo sac is monosporic and 8-nucleate; endosperm formation is of the Nuclear type. For further details, see Walters (1962) and Yakovlev and Yoffe (1961).

Embryogenesis is very particular. According to Yakovlev and Yoffe (1957), in *P. anomala*, *P. suffruticosa* and *P. wittmanniana* the first and several subsequent divisions of the zygote are not followed by wall formation. Thus, a coenocytic proembryo is formed in which free nuclei are distributed along the periphery of a central vacuole. This coenocytic condition is followed by cell wall formation. Among peripheral cells, several meristematic centres are formed which produce various protuberances. Of these, only one protuberance generally develops into an embryo. At the time of cell wall formation, 64, 128 and, rarely, 256 free nuclei have been counted (Carniel 1967). Murgai (1959) disagreed with the findings of Yakovlev and Yoffe (1957) whose observations, however, have been fully confirmed in many other species by several authors, including Cave et al. (1961), Yakovlev and Yoffe (1961), Walters (1962), Matthiessen (1962), Moskov (1964), Carniel (1967) and Mu and Wang (1985).

The embryogenesis of *Paeonia* is quite unique, and there is no intermediate condition between the coenocytic proembryo and the usual type of embryogenesis in angiosperms.

FRUIT AND SEED. The seed coat is juicy. The inside of the mature follicle is often red and, in some