
Leeaceae

Leeaceae Dumortier, Anal. Fam. Pl.: 27 (1829), nom. cons.

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Trees, shrubs, scramblers, or large perennial herbs; stems unarmed or with rows of prickles; tendrils 0. Leaves 1–4-pinnate to trifoliate or simple; stipules sheathing the petiole margins with conspicuous, persistent or caducous stipular wings; leaflets glabrous to pubescent with simple hairs, crenate to serrate to dentate at margin, teeth with small glandular apex, lower surface usually with specialized multicellular, stellate or globular caducous “pearl” glands. Inflorescence paniculate, often corymbiform, terminal or axillary, erect or pendulous. Flowers hermaphroditic, 5(4)-merous; calyx campanulate with triangular lobes and glandular tips; petals valvate, apically often cucullate, reflexed at anthesis, basally connate, adnate to staminal tissue and the lower portion of floral disc; floral disc tubular, intrastaminal; stamens 5 or 4, antepetalous, alternating with the lobes of floral disc, anthers tetrasporangiate and 2-locular, introrse and sometimes appearing extrorse; ovary superior but sometimes partly sunken in the disc, 2–3(–5)-carpellate but with a secondary septum in each carpel and 4–6(–10)-locular; ovule 1 per locule, anatropous, bitegmic and crassinucellate; style elongate; stigma discoid and capitate. Fruit a berry, rather dry, subglobose, purple, black or orange; seeds endotestal; endosperm ruminant with roughly 5 ingrowths; embryo linear. $2n = 24$ or 48 (rarely 20, 22, or 28).

A monogeneric family with 34 species in tropical and subtropical Asia, extending into the Himalayan region and Australia, and with two species in Africa and Madagascar.

VEGETATIVE MORPHOLOGY. Leeaceae are usually shrubs, herbs or small trees, sometimes with armed stems (*L. aculeata* and *L. angulata*). Unlike many Vitaceae, Leeaceae do not have tendrils. Stem growth is monopodial. Leaf form varies greatly, from simple to once to thrice pinnately compound (Fig. 77A–C). In most species, leaf morphology is highly variable and thus taxonomically unreliable

for species distinction (Ridsdale 1974). In the past, leaf morphology was considered to be taxonomically important, which led to a proliferation of species being recognized. Gerrath and Lacroix (1997) documented that seedlings of *Leea guineensis* exhibit a variable sequence of heteroblastic leaves, with simple leaves at the first four nodes, followed by compound trifoliate, pinnate and finally highly complex multipinnate leaves. In this species, at successive nodes the leaves become progressively more complex. There are no deeply lobed transitional forms as intermediates. Beyond the developmental variation associated with age and position, Ridsdale (1974) argued that leaves in *Leea* varied strongly according to habitat and ecological conditions. In some species, the leaf form is constant, such as in *Leea aculeata*, which has only once-pinnate leaves.

The petiole or base of the petiole expands to bear a stipular structure (Fig. 77D, E). Stipules are well developed in the family, enclosing the next youngest leaf and the rest of the shoot apex (Lacroix et al. 1990). They are caducous or persistent, and show a wide range of variation in shape from narrowly sheathing to short and obovate (Ridsdale 1974). Forest species mostly have elongated sheathing stipules, and those of secondary vegetation predominantly have short and obovate stipules. Stipules can also enclose the terminal inflorescence at its early developmental stage (Lacroix et al. 1990).

VEGETATIVE ANATOMY. There are usually globular or stellate “pearl” glands on the lower leaf surface. Stomata are cyclocytic, actinocytic, or rarely anomocytic (Ren et al. 2003). The mesophyll contains mucilage cells sometimes with raphides and usually with calcium oxalate crystals. Sieve-tube plastids are P-type I(b) (Behnke 1981).

The wood of *Leea* has numerous broad rays separating the narrow fibro-vascular bundles and vasicentric parenchyma. The vessels are small in

comparison with those in members of Vitaceae (Metcalf and Chalk 1950; Wheeler and LaPasha 1994; Poole and Wilkinson 2000), and are intercalated in the radial rows of woody elements. Between the bundles are linear uniseriate rays with small cells (Adkinson 1913). Most species have raphides present in the wood (Watari 1951; Prakash and Dayal 1963).

INFLORESCENCE AND FLORAL MORPHOLOGY. The inflorescences are usually terminal, and sometimes both terminal and axillary (Gerrath et al. 1990). They are basically strongly corymbiform-modified panicles in which repeatedly the basal internodia of the two lateral florescences elongate as strongly as the next internodium of the main axis. Sometimes the inflorescence is large and flat-topped, as in *L. indica* and *L. guineensis*. Reduction of the peduncles and/or lateral branches gives rise to condensed inflorescences, as in *L. congesta*.

The anthers are connivent laterally; at anthesis, they continue to reflex, separate from each other, and abscise at the base. Thus, depending on the developmental stage of flowering, the anther may appear introrse or extrorse. Many workers (e.g., Ridsdale 1974, 1976; Cronquist 1981; Li 1998) have stated that Leeaceae do not have a floral disc, and Ridsdale (1974) was of the opinion that there is a "staminodial tube" that he considered to be a whorl of modified stamens inserted in the corolla. Gerrath et al. (1990), however, demonstrated the presence of a floral disc, and found it inappropriate to designate the tube structure inside the stamen whorl as staminodial tube. They found that the floral disc is initiated from the base of the ovary in the regions between the stamens, and that its growth is also greatest between the stamens. The distinctive floral tube of Leeaceae is the result of intercalary growth of a meristem located below the points of insertion of the petals, stamens and the floral disc, uniting the lower portions of these organs (Gerrath et al. 1990).

EMBRYOLOGY. Pollen grains are trinucleate or rarely binucleate when shed. Embryo-sac development is of the *Polygonum* type. Endosperm formation is Nuclear, and embryogeny is Asterad.

POLLEN MORPHOLOGY. Pollen grains are tricolporate, angulaperturate, suboblate to subprolate, and have a mainly triangular amb; the tectum is reticulate and the colpi are generally 2/3 or 3/4 of the grain radius (Tarnavski and Petria 1968).

KARYOLOGY. The vast majority of chromosome counts in Leeaceae corresponds to $2n = 24$ (Ridsdale 1974; Sandhu and Mann 1989; Karkamkar and Patil 1992); some species are tetraploid with $2n = 48$. Karkamkar and Patil (1992) reported for *L. macrophylla* $2n = 24$, and for *L. robusta* $2n = 48$, whereas Ridsdale (1974) treated *L. robusta* as a synonym of *L. macrophylla*. *Leea indica* (including *L. sambucina*) was reported to have $n = 24$ (Gill et al. 1990; Karkamkar and Patil 1992), $n = 20$ (Nair and Namnisan 1957), or $n = 22$ (Vatsala 1960). Secondary constrictions, which are present in *L. aculeata*, may account for the aneuploid-like differences in *L. indica* (Ridsdale 1974).

REPRODUCTIVE BIOLOGY. The hermaphroditic flowers of *Leea* are markedly protandrous (Gerrath et al. 1990). Their pollination biology is unknown. The occurrence of "water calyces" in *Leea amabilis* is noteworthy: this Bornean plant has flower buds that are tightly closed by the valvately appressed calyx lobes, which are interdigitated with epidermal papillae. A liquid fills the space between the calyx and corolla; secretion of the liquid seems to take place from trichomes on the inner surface of the calyx lobes (Suessenguth 1953).

FRUIT AND SEED. Fruits in Leeaceae are subglobose, fleshy, 4–6-seeded berries. The seeds have a ruminated endosperm, which usually has roughly five ingrowths: one along the median plane, two from the raphe, and one at each lateral face (Fig. 76). The ingrowths may become more pronounced due to further branching as a result of localized meristematic activity. As in Vitaceae, the endosperm is

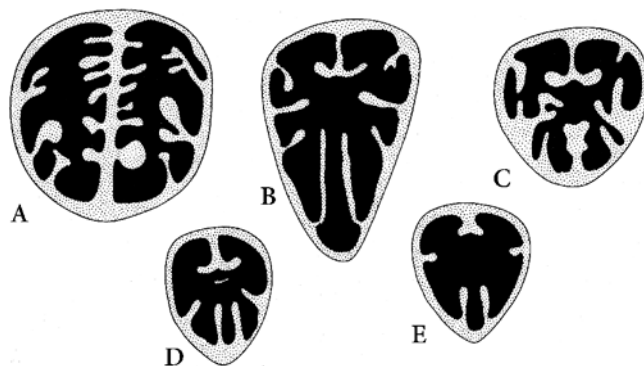


Fig. 76. Leeaceae. Median transverse section of seeds, showing variation of endosperm rumination. A *Leea acuminatissima*. B *L. coryphantha*. C *L. magnifolia*. D *L. compactiflora*. E *L. indica*. (Ridsdale 1974)