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## Gunneraceae

Gunneraceae Meissner, Pl. Vasc. Gen., tab. diagn.: 345, 346; Comm.: 257 (1842), nom. cons.

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Perennial herbs, either with ascending or creeping pachycaulous stems, covered with large leaf scars, apically with large to gigantic, long-petioled leaves reaching up to c. 5 m in height (*G. magnifica*), and between these often covered with conspicuous bracts protecting the inflorescence and vegetative buds, *or* stoloniferous and mat-forming, with short, upright stem portions bearing leaf-rosettes, reaching from 4 cm to about 1 m in height, *or* in one case (*G. herteri*), diminutive annuals. Leaves alternate, crowded at stem tips; petioles short to very long; lamina oblong to reniform or peltate, dentate, crenate or palmately lobed, the crenations and lobes with protruding hydathodes; venation in large-leaved species palinactinodromous with veins very prominent and projecting as ribs on abaxial surface, in smaller-leaved species actinodromous or pinnate and less prominent. Sometimes with more or less conspicuous, simple to much divided scales between the leaf-bases, stolons with paired, or single ochrea-like, bracts apically. Inflorescences axillary or pseudo-terminal, erect, simple or compound racemes, or spikes; lower flowers mostly pistillate, upper ones staminate, the middle ones sometimes perfect, or flowers all unisexual, in a few cases plants dioecious. Flowers small, bracteate or not, epigynous, sepals 2, anterior-posterior, valvate, sometimes obsolete, petals 2, transversal, mitre-shaped, slightly exceeding the sepals, caducous, in female flowers wanting; stamens 2(1), transversal, with short filaments; anthers dithecal and tetrasporangiate, opening by longitudinal slits; carpels 2, united to form an inferior, unilocular ovary; stylodia 2, transversal; stigmas dry, papillate; ovule solitary, pendulous from apex of locule. Fruit drupaceous, coriaceous to fleshy, oval to globose, green or bright red, rarely white or yellow. Seeds with a very small obcordate embryo embedded in copious, oily endosperm. Specialized organs containing endosymbiotic *Nostoc* cells are located in the stem between the leaf-bases of all species.

A monogeneric family with about 60 species, growing in cool and wet or damp habitats, from low altitudes to above 3,000 m, in South and Central America, Mexico, Hawaii, Africa, Madagascar, Tasmania, New Zealand, New Guinea and the Malayan archipelago

**VEGETATIVE MORPHOLOGY.** *Gunnera* comprises a wide spectrum of growth forms from giant to dwarf herbs, usually perennial, with erect or creeping stems, often forming mats or clumps by stolons originating from leaf axils on the stems and bearing leaf-rosettes apically, or more rarely by branching of the stems themselves (Figs. 59, 63). The main stem of the dwarf *G. herteri* is interpreted as a chain of sympodial units each consisting of a leaf and an extra-axillary inflorescence (Rutishauser et al. 2004), a structural pattern which may also be valid for other species of *Gunnera* (see Skottsberg 1928). Stolons occur in subg. *Pseudogunnera*, *Milligania* and *Misandra*. In *Pseudogunnera* and *Milligania*, two bud scales at the tip of the stolons precede the foliage leaves on the erect stem. These cataphylls are regarded by Wanntorp et al. (2003) to be homologous with a cap-like "ochrea", which in subg. *Misandra* occurs on the stolon as well as between the leaves of the upright stem. In subg. *Panke*, in which no stolons are formed, the stems are covered by numerous, large bract-like scales. Skottsberg (1928) and Wanntorp et al. (2003) consider also these scales to be cataphylls.

**VEGETATIVE ANATOMY.** (Information mostly from Wilkinson 1998, 2000). Nodes are multilacunar and multitrace. Leaves are bifacial, hypostomatous or amphistomatous; stomata are anomocytic. The lower leaf surface has always a smooth wax cover; the cuticle is smooth or (in some species of subg. *Milligania*) finely striate. Marginal leaf hydathodes with an epithem are found in all subgenera (Fig. 59D), while laminar hydathodes are restricted to subg. *Panke*. The leaf axils of *Gun-*

*nera herteri* contain 2–5 inconspicuous glandular colleters (Rutishauser et al. 2004). Unicellular hairs are widespread and lacking only in *G. herteri*; other hair types including uniseriate and multiseriate, stalked and globular hairs are found in subg. *Panke*. Domes of raised silicified cells (“warts”) on the upper leaf surface and spine-like emergences on petioles and the larger veins of the lower leaf surface are characteristic of subg. *Panke* (Fig. 59C, E).

The vascular systems of stems and petioles are typically polystelic. The bundles have the xylem surrounded by about six portions of phloem (amphicribal) and are sheathed by a well-defined endodermis with Casparian thickenings. In the stems of the pachycaulous, non-stoloniferous subg. *Panke*, the bundles may amount to several hundred per stem and in subg. *Gunnera* to about 60. Among the stoloniferous subgenera, the large-leaved subg. *Pseudogunnera* and the small-leaved subg. *Milligania* and *Misandra* have only few (3–5) larger and some smaller bundles, the latter to leaves and inflorescences. The vascular tissue of the stolons is not polystelic but siphonostelic (-modified); it consists of a single tube of xylem and phloem (*G. densiflora*), or of tubes of internal and external phloem separated by two tubes of xylem, and is surrounded by an endodermis. Vessel elements are usually very to moderately small; perforation plates in stolons and roots are mainly scalariform with few to many bars, and in the stems of large-leaved species simple perforation plates are more common.

Cluster crystals (druses) are widespread in various tissues.

Behnke (1986) found sieve element plastids containing protein crystals and starch grains (Pc type).

**FLOWER STRUCTURE.** The floral symmetry of *Gunnera* is most remarkable: the petals, stamens and carpels – at least the stylodia – are located in the transverse plane (Wanntorp and Ronse De Graene 2005), reminiscent of the position of these floral organs in Sabiaceae and, to some degree, in Proteaceae.

**EMBRYOLOGY.** In *Gunnera macrophylla* and *G. chilensis*, the pollen grains are two-celled at anthesis. The ovule is anatropous, bitegmic and crassinucellate, and the micropyle is formed by the inner integument alone. The embryo sac is tetrasporic and 16-nucleate (*Peperomia*-type) and, apart from the egg and the synergids, contains six antipodal cells and a group of cells fusing to form the secondary embryo sac nucleus. Endosperm development is cellular; the suspensor forms no haustorium (Modilewski 1908).

**POLLEN MORPHOLOGY.** Pollen of *Gunnera* is very distinctive, tricolpate, suboblate spheroidal (Fig. 60), and can be recognised by the fossaperitrate shape with bulging mesocolpia and the microreticulate exine, usually  $20\text{--}28 \times 25\text{--}37 \mu\text{m}$  (Erdtman 1952; Pragłowski 1970; Jarzen 1980; Wanntorp et al. 2004).

**KARYOLOGY.** Beuzenberg and Hair (1963) reported  $2n = 34$  for *Gunnera monoica*, *G. prorepens*, *G. densiflora*, *G. dentata* and *G. hamiltonii*, and several hybrids (all in subg. *Milligania*); the same number was counted for various South American species by Dawson (1983) and Pacheco et al. (1993).

**POLLINATION.** *Gunnera perpensa* shows all attributes of wind pollination (the general condition in the genus), such as high pollen/ovule ratio, strong protandry in the hermaphroditic flowers, and starch storage in pollen (Lowrey and Robinson 1988).

**FRUIT AND SEED.** The fruit is drupaceous, greenish-reddish, dry and relatively small (1–2 mm long) in subg. *Panke*, *Pseudogunnera* and *Gunnera*, in subg. *Misandra* and *Milligania* larger (up to 8 mm long), and often brightly coloured; *G. magellanica* is called “frutilla del diablo”, devil’s strawberry.

In the maturing seed, the integuments and nucellus disappear, with the exception of the outer epidermis of the outer integument which is made up of thin-walled cells filled with red sap; mechan-

**Fig. 59.** Gunneraceae. A–C *Gunnera manicata* growing in the Royal Horticultural Society’s garden at Wisley, Surrey, UK. A Whole plant. B One leaf measuring 94 in. (237.5 cm) in width and 77 in. (195.5 cm) in length. C An inflorescence (in spring) c. 2 ft. tall; note petiole with spine-like emergences to the right. D Marginal hydathodes

with terminal glandular tubes from a very young leaf of *G. chilensis*, scale bar = 1 mm. E “Warts” on the adaxial surface of a mature leaf of *G. chilensis*, scale bar = 0.25 mm. F *Nostoc* heterocysts in two large cells from a stem of *G. lobata*, scale bar = 50  $\mu\text{m}$ . G Heterocysts from F at arrows, scale bar = 10  $\mu\text{m}$ . (Orig. H. Wilkinson)