Hypericaceae

Hypericaceae Jussieu, Gen. Pl.: 254 (1789) ("Hyperica").

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Evergreen or sometimes deciduous herbs, shrubs or trees; glands or canals in most parts of the plant; xanthones widespread; hairs uni- or multicellular, eglandular, colleters common; terminal bud scaly or naked; leaves opposite, occasionally whorled or alternate, entire, estipulate; inflorescences terminal, more or less cymose, rarely axillary or flowers single, flowers polysymmetric, perfect, usually with prophylls; sepals free, (2–)4–5; petals (3)4–5, free; stamens (9–)∞, free or variously fasciculate or connate, anthers < 1(–1.2) mm long, dithecate, extrose, opening by slits, connective often with glands, staminodes alternipetalous or 0; nectary absent; ovary superior, 3–5-locular, placentation axile to parietal, ovules 1–∞/carpel, anatropous, bitegmic, tenuinucellate; stylodia free or basally more or less fused or style single, stigmas more or less expanded, smooth and sticky or ± punctate and papillate; fruit baccate or capsular, rarely a drupe; seeds small, winged or not, exotegmen lignified, with sinuous anticlinal walls; embryo straight or rarely curved; endosperm initially nuclear, often absent at maturity; germination epigeal, phanerocotylar.

A family with 9 genera and 540 species; ± worldwide.

Vegetative Morphology. Hypericaceae are mostly shrubs to trees, but there are some annual herbs (*Hypericum*). Taxa growing in drier regions (*Hypericum*, *Psorospermum* [= *Harungana*]) tend to develop a lignotuber, from which they sprout after fire or drought; root suckering occurs in *Hypericum* (Hagemann 1989 and references therein; Hagemann and Meusel 1984) and *Vismia*. Architectural models within *Vismia* vary (Vester 1999). Roots of some Hypericeae inhabiting swamps (e.g., *Triadenum*, *Hypericum*) are swollen and with air spaces. The terminal bud may lack scales, but in many species of *Harungana*, *Cratoxylum*, etc., it has two or more pairs of scales; in *Cratoxylum* it may abort. Leaves are opposite, rarely more or less irregularly spiral (e.g., *Harungana* [*Psorospermum alternifolium*]) or whorled. There are often colleters, but no stipules.

Multicellular stellate hairs characterize Vismieae; Hypericeae may be glabrous, but unicellular hairs are found in some *Hypericum*. Buds in taxa that lack scales are sometimes covered with dense indumentum, as in Vismieae; colleters then appear to be lacking.

The lamina is usually petiolate, although often sessile in *Hypericum*; the midrib is nearly always well-developed. Venation is commonly eucamptodromous or brochidodromous; it is close to parallelodromous or acrodromous in some species of *Hypericum*. The leaf margin is usually entire, but it may be crenate by glands (*Harungana*), or even lobate – and this can be true of the calyx as well – as in some species of *Hypericum*.

Vegetative Anatomy. Metcalfe and Chalk (1950) summarize early literature; more recent studies include those of Spirlet (1959), Baas (1970), and Gibson (1980). There is a complex system of spherical to more or less elongated schizogenous glands and canals associated with the vascular tissue, and also found in both the cortex and pith. In the appendicular organs of the plant, these may be more or less independent of the vascular tissue (e.g., Cicarelli et al. 2001a). There are also reddish to black glands (as in *Hypericum*) containing hypericin and related compounds (Robson 1977; Cicarelli et al. 2001b; Onelli et al. 2002); these are clusters of cells that initially have meristematic features but that eventually become filled with black material. Variation in such glands, schizogenous structures and epidermal features in the leaves is of taxonomic interest (Lü and Hu 2001; Lü et al. 2001). Cotyledons, filaments and petals commonly have canals.

The phellogen is always initiated in the deep-seated position in the pericycle (which may be lignified or not), both in stem and root. In

the stem, layers of cells, often with endodermal thickenings, are commonly interspersed with layers of unthickened cells in a polyderm (Mylius 1913); aerenchyma may develop (Schenck 1889). *Hypericum* has a clearly developed endodermis in the stem (cf. also some Bonnetiaceae).

Nodes are single trace from a single gap. The petiole bundle varies from simple, commonly being arcuate in *Hypericum*, to more complex, annular, with additional vascular tissue inside the annulus, as in *Vismia*. Similarly, the midrib bundle varies from arcuate to more or less annular, with phloem toward the outside. The vascular bundles of even the higher-order veinlets vary from being more or less transcurrent, joined to at least one surface of the lamina by echlorophyllous and often lignified tissue, to embedded; the latter condition is common. Anticlinal epidermal cell walls are straight to sinuous. Leaves are nearly always hypostomatic, but amphistomatic in some *Hypericum* (e.g., Lü et al. 2001); stomates are usually paracytic, but in Hypericeae they may be anomocytic or even cyclocytic (Vestal 1937). In *Harungana* [*Psorospermum membranaceum*], stomata occur in small groups.

Vessels are either single or in multiples, sometimes being in oblique lines. Perforation plates are usually simple, although they are sometimes scalariform. Pitting on tangential walls is generally alternate. Vasicentric tracheids have been recorded from a number of taxa. Wood parenchyma usually occurs, except perhaps in *Hypericum*. Septate fibers occur, either with or without nuclei, but their distribution is very sporadic.

Inflorescence Structure. The inflorescence in most species is modified cymose or thyrsiform, and a terminal flower is nearly always present. Flowers have both bracts and prophylls. In *Harungana*, bracts are recaulescent, being borne on the pedicel where the lateral flowers of the cymose inflorescence diverge (the prophylls are in turn borne along the pedicels of the flowers they subtend); *Vismia* tends to show this behavior. In some *Harungana* from mainland Africa, the vegetative and floral parts of the stem are not clearly separated, and the relationship of branches to subtending leaves is very complex.

Floral Structure. Sepals and petals are always present and free. Sepals are commonly five in number and quincuncial in aestivation, or four and decussate. When there are five petals, they are often contorted. Indumentum on the corolla in particular is uncommon, but all Vismieae have dense, unicellular hairs on the adaxial surface of the corolla. The androecium is fasciculate, often with five antepetalous fascicles (Fig. 68), but there may be only three or four (Fig. 69; see below). Staminodes, representing the alternipetalous whorl of the androecium, are common (rare in *Hypericum* itself), and are either three or five in number. Filaments are slender, the anthers are extrose, $< 1(-1.2)$ mm long, and often with simple anther glands at the apex between the thecae. There is no nectary at the base of the ovary, but the staminodes have been described as "nectariferous scales", and their vascular supply lacks xylem elements, as would be expected for nectaries (Ronse Decraene and Smets 1991).

There are usually three or five carpels; when there are as many carpels as perianth members, they are opposite the sepals. Placentation is basically axile, although the placentae may fail to meet in the middle, and it varies from axile to parietal within *Hypericum*. Stylodia are usually long and free (Figs. 68, 69), or are more or less fused to a single style (this varies infragenerically within *Hypericum*). The ovules are anatropous, tenuinucellate, and the micropyle is bitegmic; the inner integument may be up to seven cells thick, and there is an endothelium (Mourão and Beltrati 2001). In Hypericeae, the stigma is more or less punctate and the surface is papillate (Shivanna et al. 1989). In the rest of the family, the stigma is punctiform to more or less expanded, and the surface is more or less smooth.

Floral Anatomy and Development. Little is known about floral development and anatomy, the study by Payer (1857) still being useful; see also Sattler (1973). The androecium is basically diplostemonous. The stamen fascicles are antepetalous, and may originate with the corolla as complex primordia, or separately, or separately and subsequently forming complex primordia; the anther primordia may coalesce to form a ring primordium (see Ronse Decraene and Smets 1991 for a summary). Stamen development is centrifugal on the fascicles in those few taxa in which this feature has been observed (e.g., Leins 1964; Ronse Decraene and Smets 1991). The fascicles are supplied by a single vascular bundle. In taxa with three fascicles, vascular evidence (and gross morphology) shows that two of the fascicles, slightly larger than the others, are a fused pair of fascicles of a basically 5-fasciculate androecium (Baas 1970; Robson 1972, 1974, 1981). Staminodes