Krameriaceae

Krameriaceae Dumort., Anal. Fam. Pl.: 20, 23 (1829), nom. cons.

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Rhizomatous shrubs, subshrubs, or perennial herbs semiparasitic on the roots of a wide array of flowering plants. Leaves alternate, simple or trifoliolate, estipulate, entire, variously vestitured. Flowers axillary and single or in botryoid panicles, bisexual, zygomorphic, hypogynous with 5(4) purple, pink, or yellow showy, imbricate sepals and 5(4) petals, the 2 abaxial of which are reduced to glandular, lipid-secreting structures and the remaining 3(2) small and forming a flag inserted adaxially above the ovary. Stamens 4(3), 4-locular, curved, with stout filaments usually united basally, and anthers dehiscing by terminal pores; ovary superior, unilocular; carpels 2 but appearing singular due to the early abortion of one carpel; style stout, curved; stigma recessed; ovules 2, pendulous from the top of the ovary, anatropous, bitegmic. Fruits globose, nut-like, spiny capsules with the thin pericarp splitting irregularly, 1-seeded; seed large, lacking endosperm; cotyledons orbicular, ventrally flattened.

One genus with 18 species, primarily in warm arid and semiarid areas of North, Central, and South America, and sporadically in the West Indies.

Vegetative Morphology. *Krameria* species range from small trees (to 6 m) to sprawling herbaceous perennials. The root system consists of the remnants of the original tap root, and a series of lateral, adventitious roots (Musselman 1975) that branch sparingly. Individual roots are flexible, covered with a thick, soft bark. The shoots of some shrubby species are stiff, forming thorns at the branch tips. In a few woody species, the stems can be lax. The herbaceous species are invariably prostrate, dying back to a woody caudex during the winter or in dry periods. Leaves are alternate, usually simple, and entire. They can be sessile or petiolate, range in shape from linear to ovate, and vary between 3 and 35 mm in length. One species has trifoliolate, petiolate leaves. Leaf surfaces in all species are vestitured with trichomes ranging from sparsely strigose to densely tomentose. Vestiture is most pronounced on the young portions of the stems, with individual trichomes unicellular and thick-walled (Metcalfe and Chalk 1950). Some woody species loose their leaves during extremely dry periods.

Vegetative Anatomy. All *Krameria* species examined to date are obligate semiparasites. Young woody stems have an epidermis with highly cutinized cell walls. The cork arises deep in the stem, sometimes even within the pericycle (Metcalfe and Chalk 1950). The phloem appears to lack lignified elements. The xylem forms a continuous cylinder with faint rays. Both the diameter of xylem elements and the amount of pith vary between species (Metcalfe and Chalk 1950). The seedlings do not produce root hairs (Cannon 1910), and haustorial attachment must occur within a few months of germination, or seedlings die (Simpson 1989). Haustoria are formed only by young, adventitious roots. Penetration of the haustoria appears to be shallow (Cannon 1910), with connections to the xylem only (Kuijt 1969). The vasculature of the haustoria consists of elongate, storied vessel elements (Musselman 1975).

Stomates are present on both surfaces of the leaves. The outer epidermal walls and bases of the trichomes are cutinized. The leaves have three principal veins, each of which branches to form a network of veins supplying the entire leaf. The mesophyll includes scattered sclereids, and tanniferous material and crystals are common in unlignified cells. The xylem of the leaves lacks vessels and consists of tracheids overlain by a thin layer of poorly developed sieve tube elements (Sterling 1912; Metcalfe and Chalk 1950). Petiolar anatomy consists of a single, crescent-shaped (almost circular in some) vascular strand (Metcalfe and Chalk 1950).

Inflorescence Structure. The flowers are borne singly in the axils of leaves, or in terminal racemes or panicles. Individual flowering stalks

consist of a combined peduncle-pedicel with a pair of transversal prophylls where the two join. The flowering stalk contains a single undissected vascular cylinder (Musselman 1975). The pedicel and bracts persist if the flower is shed. The lengths of the peduncle and pedicels vary between species.

Flower Structure. Flowers are extremely modified, which led to almost 200 years of misunderstanding about the floral morphology and biology (Simpson 1982). It is now recognized that the flowers are not resupinate, and that the showy portions consist of the five (rarely four) free sepal lobes. The sepals have three principal veins, like the leaves. Only the upper surface, at least in *K. lanceolata*, bears stomata (Milby 1971). Two of the petals are modified into thick, orbicular to cuneate glands flanking, or slightly abaxial to, the ovary. Each of these small, fleshy structures is traversed by several veins (Milby 1971). The dorsal face of the glandular petals bears patches of secretory epidermal cells that secrete fatty oils under the cuticle. Once secreted, the oils are trapped until the cuticle is ruptured. The glandular cells can cover the dorsal petal surface or be restricted to the distal portion. The petaloid petals are small, strap-shaped or clawed, free or fused at the base, and form a flag inserted adaxially at the base the ovary. Each petal has a single vein (Milby 1971). All of the stamens are inserted on the base of the petaloid petals above the ovary. The veins of the sepals and petals are separated by a wide gap but, as suggested by the position of the stamens, those of the petals and stamens are close together (Milby 1971). In the common condition of four stamens, the stamens are didynamous, each supplied by a single vascular trace. The ovary is ovoid, densely vestitured and surmounted by a stout, glabrous style with a sunken stigma. The style and the stamens are curved and project outward from the plane of the flower. The flowers are nectar-less and fragrant. Fragrance appears to be concentrated in the glands, indicating that small amounts of volatile oils are dissolved in secreted lipids. The anthers have four locules that dehisce into a common, slightly conical terminal chamber through which the pollen is shed in a cylindrical mass. The ovary is bicarpellate, but early in ontogeny, the posterior carpel aborts. The abortive carpel has a vestigial locule, however, and a suture line demarks the boundary between the two, even in the mature ovary (Milby 1971). The fertile carpel bears two ovules, only one of which ever forms a seed. The ovules are crassinucellate and bitegmic, with the micropyle formed by the inner integument alone (Verkerke 1985).

Pollen Morphology. The pollen grains are shed as monads. Individual grains are isopolar, spheroidal, 26–38 µm in diameter, and striate with the striae perpendicular to the equatorial axis, tricolporate, triporate, or lalongate, or synorate (Fig. 72). The striae appear to be supported on stalks that penetrate a dense layer and then branch (Simpson and Skvarla 1981). The endexine is very thick.

Karyology. Chromosome counts have been made for eight of the 18 species. All species have a haploid number of $n = 6$ (Turner 1958; Simpson 1989). Individual chromosomes are metacentric (Teppner 1984) and large, with those of *K. secundiflora* recorded to be 24.6 µm long (Lewis et al. 1962) and those of *K. lappacea* to be 10–14 µm long in metaphase (Teppner 1984).

Pollination. All species of *Krameria* are pollinated by female solitary bees of the genus *Centris* (Apidae). These bees visit the flowers to collect oils secreted by the glandular petals. During oil collection, a female bee orients with the main axis of the flower, grasps the flag petals with her mandibles, straddles the stigma and anthers, and rubs her fore- and midlegs over the glandular patches, rupturing

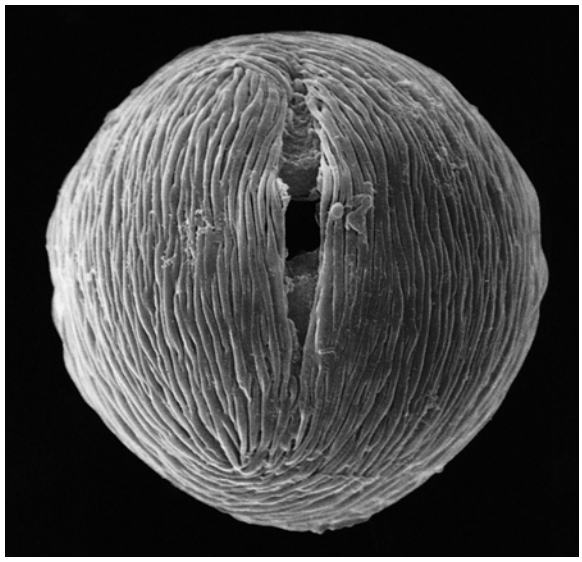

Fig. 72. Krameriaceae. *Krameria lappacea*, pollen grain, SEM ×2,400. (Photograph B.B. Simpson)