Haemodoraceae

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Haemodoraceae R. Br., Prodr. 1: 299 (1810), nom. cons.

Erect to decumbent *perennials* with a sympodial rhizome or a stolon, corm or bulb. Roots and subterranean stems often red or reddish. *Leaves* basal or cauline, distichous, generally ascending, straight, rarely bent or twisted; base sheathing and equitant, blades ensiform, unifacial, lanceolate, narrowly linear or acicular, hollow-tubular in *Tribonanthes*, entire, acuminate, mucronate, or aristate, glabrous or pubescent, flat, plicate in *Barberetta* and *Wachendorfia*. *Inflorescence* terminal on short to elongate aerial shoots, scapose to subscapose, bracteate, consisting of a simple raceme (*Barberetta*), a raceme or panicle of 1, 2, or 3–many flower clusters (*Haemodorum*), or a corymb, raceme, panicle or capitulum of simple, bifurcate, or trifurcate helicoid cymes. Inflorescence axes and bracts glabrous or canescent to tomentose. *Flowers* variously colored, pedicellate to subsessile, bisexual, ascending, divergent or pendulous, actinomorphic or zygomorphic, trimerous; perianth membranous to coriaceous, either composed of 3 outer and 3 inner imbricate, ascending to spreading, distinct or basally fused similar tepals (outer median tepal posteriorly positioned in zygomorphic taxa) or (in *Anigozanthos*, *Blancoa*, and *Conostylis*) perianth short to long tubular (tube rarely absent) with 6 monocyclic and valvate lobes, the tube splitting at anthesis along mid-anterior line in *Anigozanthos*; tepals or tepal lobes glabrous (*Haemodorum*, some *Phlebocarya* spp.) or canescent, hispidulous or tomentose externally. Trichomes tapering, pilate or branched. Stamens 6 or 3, then opposite inner tepals, distinct, inserted or exserted, free or adnate to perianth tube, equal or unequal in length and/or position; staminodia present in *Schiekia* and *Pyrrorhiza*; filaments terete to basally thickened or flattened; anthers oblong, straight or arcuate (apically mucronate, apiculate or laminar in some taxa), basifixed, subbasifixed or dorsifixed, 2-thecate, 4-sporangiate, longitudinally and introrsely dehiscent. Gynoecium of 3 fused carpels; ovary superior or inferior, glabrous or pubescent; ovary 3-locular or

(*Phlebocarya*) basally 3- and apically 1-locular or (*Barberetta*) 1-locular by abortion of lateroanterior carpels; placentation axile (basal in *Phlebocarya*); ovules 1–7 or numerous (ca. 20–50) per carpel, anatropous or atropous, hypotropous, pleurotropous or irregularly positioned; style terminal (subapical in *Barberetta*), terete or flattened on one side, straight (or curved), stigma oblong, ovoid or rudimentary, minutely papillate; septal nectaries present in most taxa. *Fruit* a 1–many-seeded, loculicidal to apically poricidal capsule, sometimes indehiscent (in *Anigozanthos fuliginosus* dehiscing along septae into 3 single-seeded mericarps). Seeds discoid, ellipsoid, ovoid or globose, smooth to longitudinally ridged, glabrous or hairy; endosperm starchy, embryo minute, positioned at micropylar end.

A tropical to temperate family of 13 genera and about 100 species distributed in eastern and southeastern N America, Cuba, southern Mexico, Mesoamerica, northern S America, S Africa, New Guinea and Australia.

VEGETATIVE MORPHOLOGY. The main subterranean stems bear distichous scalelike or photosynthetic leaves with axillary buds developing into lateral, propagative, or vegetative branches (Figs. 53, 54). They are rhizomatous (often with proliferative stolons), bulbous (in *Haemodorum*) or cormose (in *Pyrrorhiza* and *Tribonanthes*). The underground stems (and sometimes roots) of *Dilatris*, *Haemodorum*, *Lachnanthes*, *Pyrrorhiza*, *Schiekia*, *Wachendorfia* and *Xiphidium xanthorrhizon* have a red or orange-red to maroon color. Aerial stems are often cespitose and unbranched, terminating in a single scapose to subscapose inflorescence. In some species of *Conostylis* a rhizome gives rise to several sympodial above-ground stolons, each consisting of an elongate, virgate stem (an internode) terminating in a cluster of photosynthetic leaves.

Leaves arising from nodes of subterranean stems are bifacial, distichous, sheathing, scarious to fibrous and generally rudimentary. Aerial photosynthetic leaves are basal to sub-basal in all taxa (except the species of *Conostylis* with aerial branches). In all Haemodoraceae the photosynthetic leaves are distichous, unifacial, ascending, generally straight (distinctly cernuous and dorsiventral in *Xiphidium* and tortuous in *Conostylis* spp.). The leaf blades are flat, except in *Wachendorfia* and *Barberetta*, where they are plicate, and *Tribonanthes*, where the leaves are tubular. Some species of *Haemodorum* and *Conostylis* have subterete or acicular leaves. The margins are
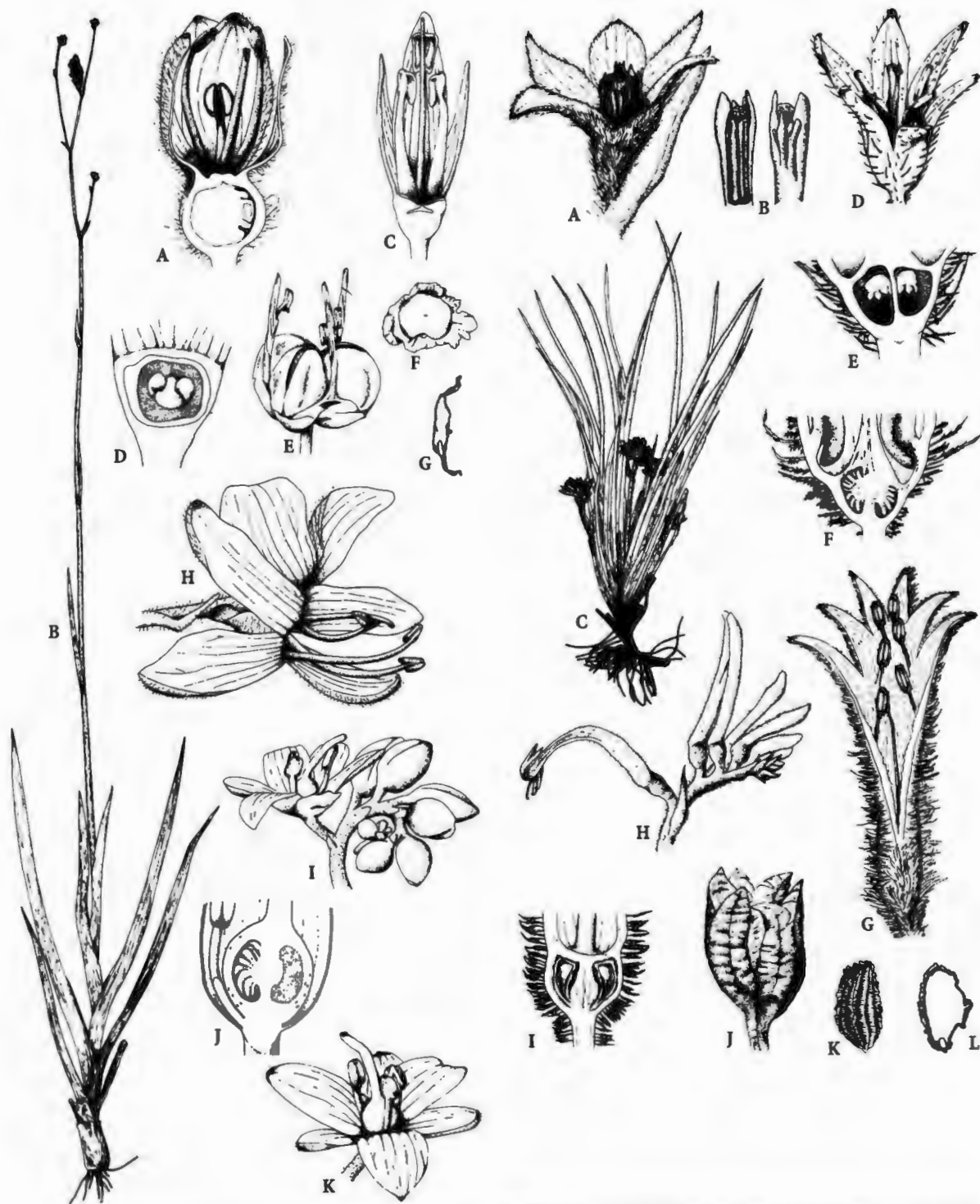
Fig. 53A–K. Haemodoraceae-Haemodoroideae. A *Dilatris pilansii*, flower in longitudinal section. B–G *Haemodorum spicatum*. B Habit. C Flower, three tepals removed. D Locule with ovary wall removed to show two ovules on placenta. E Mature capsule with the persistent tepals and stamens. F Seed, abaxial view. G Seed in cross-section with endosperm (*stippled*) and embryo (*white*). H *Wachendorfia thyrsiflora*, flower, showing one of the two basal pockets. I–K *Xiphidium caeruleum*. I Partial inflorescence. J Ovary in longitudinal section. K Flower. (Orig. M.G. Simpson)

Fig. 54A–L. Haemodoraceae-Conostylidoideae. A, B *Tribonanthes variabilis*. A Flower. B Stamen, abaxial (*left*) and adaxial view, showing lobed extension of connective. C–E *Conostylis aurea*. C Habit. D Flower. E Ovary, longitudinal section, showing pendulous ovules on apical placentae. F *C. aculeata*, ovary in longitudinal section. G *Anigozanthos humilis*, flower, abaxial view. H *A. manglesii*, partial inflorescence. I *A. fuliginosus*, longitudinal section of ovary. J–L *A. flavidus*. J Capsule. K Seed. L Same, longitudinal section, with endosperm (*stippled*) and embryo (*white*). (Orig. M.G. Simpson)

entire and ciliate or nonciliate, apices are acute to aristate, and vestiture ranges from glabrous to densely tomentose.

VEGETATIVE ANATOMY. (Based on Schulze 1893; Arber 1925; Stenar 1927, 1938; Green 1959; Cheadle 1968; Simpson and Dickison 1981; and Simpson 1990). The sieve-tube plastids contain cuneate protein bodies but lack starch and filamental protein. Oxalate raphides are common in all parts of the plant. Vessels are present in the roots but absent in the stems of all genera except *Lachnanthes*, which has stem vessels with scalariform perforation plates. The leaves lack vessels.

Mature roots consist of a uniseriate exodermis, a parenchymatous cortex, a sclerified endodermis, a 1-celled continuous pericycle, and a relatively small vascular cylinder. Root hairs arise only from short cells of the rhizodermis, which alternate with long cells. The vascular cylinder contains few (generally 4–5) xylem and phloem strands, the latter usually containing a single sieve-tube member. The root pith is sclerified. The vessels have simple perforation plates, except in *Dilatris* and *Tribonanthes*, which have scalariform plates.

The stem contains a 1-layered epidermis of longitudinally elongate cells, a parenchymatous outer region and a central parenchymatous ground tissue. The rhizomes and stolons – as well as the aerial stems – have a heavily sclerified cylindrical sheath (mechanical cylinder, Schulze 1893), within which is a cylinder of numerous vascular strands. Stem vascular bundles are collateral to amphivasal.

The leaf epidermis is composed of 1 layer of thin- to thick-walled, longitudinally elongate cells with straight to undulate anticlinal walls and a cuticle of variable thickness. Leaf trichomes occur on the margins and/or surfaces in some taxa and are mostly similar to floral trichomes (see Floral Anatomy, below). Stomata are paracytic.

In *Dilatris* there are spherical epithelial-lined mucilage chambers in the leaves and ovary. All (and only) members of Conostylidoideae have distinctive tannin cells scattered in various plant organs. These tannin cells are isodiametric to elongate with a thin tannin-impregnated wall and numerous, minute tanniniferous spherules just interior to the wall.

INFLORESCENCE STRUCTURE. The inflorescences mostly consist of 1 or more helicoid cymes arranged and aggregated in various patterns. They are bracteate, the bracts in cymose components generally appearing to be opposite or perpendicular to the pedicels. Within the subfamily Haemodoroideae the inflorescence may be a congested corymb of several bifurcate or trifurcate helicoid cymes (*Dilatris* and *Lachnanthes*); a corymb of simple helicoid cymes (*Pyrrorhizia*, *Schiekia* and *Wachendorfia*); or a thyrse with lateral helicoid cymes (*Xiphidium*). The inflorescence of *Haemodorum* consists of a panicle or simple to branched raceme of either 1, 2, or 3–many flower clusters, each flower being generally subtended by 2 bracteoles. The inflorescence of *Barberetta* is a "determinate raceme", which may have been derived by the reduction of a panicle with lateral helicoid cymes to single flowers.

In the subfamily Conostylidoideae *Conostylis* and *Tribonanthes* have a congested corymb or capitulum of a single bifurcate helicoid cyme; in *T. uniflora* the inflorescence consists of a single flower (apparently by reduction, as several vestigial bracts are present). *Phlebocarya* has a paniculate inflorescence consisting of a central main axis bearing short, lateral axes which terminate in an ascending bifurcate helicoid cyme pair. *Blancoa* has a thyrse with lateral bifurcate pairs of helicoid cymes having pendulous flowers. *Anigozanthos* has either a single terminal simple or bifurcate helicoid cyme or a panicle of bifurcate helicoid cymes.

FLOWER STRUCTURE. Flower color ranges from red, red-orange, yellow-orange, yellow, to green, white, or black. Flower size varies from 5 mm wide and long in *Barberetta* to over 9 cm long in *Anigozanthos*. The flowers are bisexual, short-pedicellate to subsessile and may be either actinomorphic and erect (pendulous in *Blancoa*) or zygomorphic and divergent. The external floral surface ranges from pubescent to tomentose (glabrous in *Haemodorum* and *Phlebocarya*) with dendritic, short to long tapering, and/or pilate trichomes. The perianth is trimerous and consists of 6 similar tepals, which are distinct to incompletely basally connate, or united into a tube with 6 distal lobes. With the exception of 3 genera (see below), the perianth is bicyclic and imbricate with 3 outer and 3 inner lobes. In species with zygomorphic flowers with this perianth type the outer posterior tepal is median in position. All but two members of subfamily Haemodoroideae have free tepals (Fig. 53). *Wachendorfia* and *Schiekia* are similar in that the outer posterior tepal is basally fused both to the outer latero-anterior tepals (forming distinctive pockets or pouches at their junction, Fig. 53H) and to the 2 inner latero-posterior tepals. In

subfamily Conostylidoideae, *Phlebocarya* and one species of *Conostylis* have free tepals, and all other genera possess a short to elongate tube (Fig. 54). *Anigozanthos*, *Blancoa*, and most *Conostylis* have a perianth consisting of 6 triangular monocyclic and valvate lobes both at maturity and during early development. The perianth lobes of *Tribonanthes* superficially appear valvate in open flowers but are clearly imbricate in bud. Stamen number in the Haemodoroideae is 3 (these opposite the inner tepals) or 1 in *Pyrrorhiza* (opposite the inner anterior tepal). All members of the Conostylidoideae have 6 stamens. The stamens are always distinct and either free or, in taxa with a perianth tube, adnate to the tepals. Narrowly lanceolate staminodes occur in both *Schiekia*, which has 2 staminodes opposite the outer latero-anterior tepals, and in *Pyrrorhiza*, which has 2 staminodes opposite the inner latero-posterior tepals. Anthers are equal or unequal in size and position, generally oblong, basifixed or dorsifixed, with 2 thecae, 2 locules, and dehisce introrsely by longitudinal slits. In some taxa of the Conostylidoideae, the anther is apically mucronate or laminar. *Tribonanthes* is distinctive in having a flattened, lobed flange extending from the stamen connective.

The gynoecium is syncarpous and the ovary is either superior, inferior or half-inferior. The ovary is usually 3-locular but 1-locular in *Barberetta* by abortion of the latero-anterior carpels or basally 3- and apically 1-locular in *Phlebocarya*. Placentation is axile, but basal in *Phlebocarya*. Placentae may be rudimentary or quite large and either basally surrounding the ovule or peltiform. The ovules range in number from 1 to many, are ellipsoid to ovoid, and in several taxa have a narrow micropylar extension. The style is terminal (subapical in *Barberetta*) and terete, with a minutely papillate rudimentary, ovoid, or globose stigma.

FLORAL ANATOMY. (Data from Simpson and Dickison 1981; Simpson 1990, 1993, 1998, unpubl.). Floral vasculature is basically similar in all investigated taxa. The pedicel contains numerous vascular strands arranged in a circle, with or without a central group of bundles. Three major strands arise from either the central or peripheral strands of the pedicel. Each bundle divides into 2 radially aligned strands, the inner becoming the dorsal carpellary bundle and the outer supplying the outer tepal and (in taxa with 6 stamens) a stamen. Slightly distal to the first 3 bundles, a second set of 3 major bundles branch off; each bundle divides radially, the outer entering an inner tepal, the inner a stamen. Mature tepals contain 3 main traces; stamens only a single, generally amphicribral trace. The remaining central vasculature enters the placentae, forming either a branched plexus or 3 pairs of placental bundles. Septal commissures commonly occur near the apex of the ovary. The style contains both a 3-lobed stylar canal (contiguous with the locules) and the dorsal carpellary bundles, which traverse the ovary apex to enter the style.

Septal nectaries, which occur in 11 of the 13 genera, consist of a flattened or convoluted canal, lined with a uniseriate endothelium. Septal nectaries of inferior ovaries open at the ovary apex; in superior ovaries, septal nectaries are either vestigial (*Pyrrorhiza*), open at the extreme ovary base (*Barberetta*), or open in the receptacular region within specialized basal pockets termed "perianth apertures" (*Wachendorfia* and Schiekia). *Xiphidium* and *Phlebocarya* lack septal nectaries; *Dilatris* has only vestigial, apical septal nectaries.

Cells containing oxalate raphide crystals are common throughout all flower parts. All members of the subfamily Conostylidoideae (but no members of the Haemodoroideae) have tanniniferous idioblasts, mainly in the placental tissues. The tannin cells are isodiametric to elongate with a thin, lignified wall and numerous lignified granular spherules located just interior to the cell wall. *Dilatris* is unique in the family in having spherical endothelial-lined mucilage chambers in the tepals and ovary wall.

EMBRYOLOGY. (Data from Stenar 1927, 1938; Dellert 1933; de Vos 1956; Simpson 1988; and Steinecke and Hamann 1989). Only a few genera – *Anigozanthos*, *Conostylis*, and *Tribonanthes* of the Conostylidoideae and *Dilatris*, *Haemodorum*, *Lachnanthes*, *Wachendorfia* and *Xiphidium* of the Haemodoroideae – have been investigated embryologically. Anther-wall development is of the monocotyledonous type. The tapetum is amoeboid. Radially oriented, lignified cell wall thickenings occur in the endothecial and middle layer cells. Microsporogenesis is successive, resulting in decussate to tetragonal tetrads. Pollen grains are binucleate at anthesis. Mature ovules are either anatropous or atropous and vary in position and shape. The ovules are bitegmic with integuments generally composed of 2 cell layers and crassinucellate. A parietal cell is present, with a nucellar cap developing in some taxa. Embryo-sac development follows the Polygonum type. The 3 antipodals are often large and either obpyriform or globose. Endosperm formation is Helobial,

with early cell formation in the chalazal chamber. The endosperm of ripe seeds has both starch and protein bodies. Embryo development is probably of the Asterad or Onagrad type, with the embryo small relative to the endosperm.

POLLEN MORPHOLOGY. (Data from Erdtman 1952, and Simpson 1983). All eight genera of subfamily Haemodoroideae have boat-shaped, sulcate, heteropolar pollen grains with a verrucose (in *Schiekia* foveolate) exine sculpturing. In contrast, the pollen grains in all six genera of Conostylidoideae have a characteristic rugulate sculpturing and circular apertures. They are either fusiform with 2 apertures (*Anigozanthos*, *Blancoa*, *Conostylis* spp., *Macropidia*), cylindric with 2 apertures (Phlebocarya), triangular with 3 apertures (*Conostylis* spp.), or globose with 7–8 apertures (*Tribonanthes*). Haemodoraceae all lack a typical tectate-columellate exine, a specialized feature for the family (Simpson 1983). A distinctive 2-layered exine, lacking a foot-layer, occurs in all Conostylidoideae and in four genera of the Haemodoroideae (*Barberetta*, *Dilatris*, *Wachendorfia*, and *Xiphidium*). *Lachnanthes* and *Haemodorum* possess a 1-layered exine; *Pyrrorhiza* has a 2-layered exine with a granular inner layer; and *Schiekia* has a 3-layered exine with a granular middle layer. An intergradation of exine-wall architectural types is evident in all family members (Simpson 1983). The apertural intine wall is generally 2-layered, with a thin inner cellulose layer and a thicker, largely pectic outer layer traversed by numerous radially aligned channels or vesicles. Pollen-wall development was studied for *Xiphidium* by Simpson (1989).

In *Lanaria*, *Lophiola*, and *Pauridia*, referred to Haemodoraceae in some recent treatments (Melchior 1964; Geerinck 1969; Hutchinson 1973), the pollen grains have a foveolate to reticulate wall sculpturing in a tectate-columellate exine. Thus, palynological evidence supports the placement of these three genera outside Haemodoraceae (Simpson 1983).

KARYOLOGY. To date, chromosome counts have been determined for 12 genera and ca. 33 species of the family. In subfamily Haemodoroideae, chromosome counts include: $n = 12$ in *Haemodorum*; $n = 15$ in *Barberetta* and *Wachendorfia*; $n = 19$ in *Xiphidium*; $n = 19$–21 in *Dilatris*; and $n = 24$ in *Lachnanthes* (monotypic). Chromosome numbers of *Pyrrorhiza* and *Schiekia* have not been determined. In the subfamily Conostylidoideae chromosome numbers include: $n = 6$ in *Anigo-*zanthos; $n = 11$ in *Tribonanthes* and $n = 7$ in *Phlebocarya*; $n = 8$ in *Blancoa*; and $n = 8$ (4, 5, 6, 7, 14, 16, 21, 28) in *Conostylis*.

POLLINATION. Species of the Australian *Anigozanthos*, *Blancoa*, and *Macropidia* are pollinated by honey-eater birds of the family Meliphagidae (Hopper and Burbidge 1978). *Conostylis*, also Australian, is pollinated indiscriminately by bees (*Halictus* sp. and *Apis mellifera* L.) and hybridization in sympatric populations is common.

A weak incompatibility system seems to occur in the S African *Wachendorfia paniculata*, which is apparently insect-pollinated (Ornduff and Dulberger 1978).

Buchmann (1980) observed that *Xiphidium caeruleum* in Panama is visitated by euglossine bees, which utilize a "buzz" vibrational mechanism to remove pollen.

Stylar enantiomorphy, in which the style is strongly oriented to the left or right, occurs in the S African *Barberetta*, *Dilatris*, and *Wachendorfia*, in the N American *Lachnanthes*, and in the S and Central American *Schiekia* and *Xiphidium* (Ornduff 1974; Ornduff and Dulberger 1978; Simpson 1990). Buchmann (1980) speculates that such floral enantiomorphy "may promote greater outcrossing between flowers (intermorphs) on different plants, due to increased pollinator movements."

FRUIT AND SEED. The fruit is usually a dry, loculicidal capsule or is indehiscent. It may be oblong, ellipsoid or ovoid in shape, often strongly 3-lobed and glabrous to pubescent. In *Anigozanthos* spp. the fruit splits partially along the septae into 3 mericarps with the incomplete loculicidal line of dehiscence resulting in apical pores. In *Anigozanthos fuliginosus* it dehisces along the septae into 3 mericarps (cocci) with a hard endocarp, each containing a single seed. In *Haemodorum* the apex of the inferior ovary swells during fruit development, resulting in what superficially appears to be a fruit derived from a superior ovary.

In *Dilatris*, *Haemodorum*, *Lachnanthes*, and *Schiekia* (Haemodoroideae) the seeds are glabrous, marginally winged and discoid, convex/concave with the hilum positioned centrally on the concave side. *Pyrrorhiza* has discoid seeds with a central, proximal hilum but with coarse, marginal trichomes. Seeds of *Wachendorfia* are globose and dark-tomentose, those of *Xiphidium* are globose and papillate and in *Barberetta* the seeds are ovoid, glabrous, and minutely papillate.

In the Conostylidoideae the seeds are small, ovoid, or globose and generally glabrous (longitudinally ridged in *Anigozanthos*). *Phlebocarya* has only a single, globose seed per fruit.

The seeds of all family members have a starchy endosperm and a minute, generally ovoid embryo positioned at the micropylar end. The seed coat is derived from both integuments, each of which contributes 2 cell layers (additional layers forming near the micropyle). In *Wachendorfia* the inner integument has a water-soluble violet-purple pigment as in *Tacca*.

DISPERSAL AND REPRODUCTIVE BIOLOGY. Fruit and seed dispersal are virtually unknown. The small, dry seeds suggest dispersal by wind and water. Seeds of several genera in the Haemodoroideae have a discoid, convex/concave shape and marginal wings, features which may promote dispersal by water. The fact that almost all genera of Haemodoroideae occur in wet or seasonally wet habitats may support this hypothesis.

PHYTOCHEMISTRY. The Haemodoraceae are chemically unique in being the only family of vascular plants to possess perinaphthenone pigments. These compounds are responsible for the red coloration which is prominent in the roots or rootstocks of some genera. The occurrence of perinaphthenone compounds was first reported in *Haemodorum corymbosum* by Cooke and Segal (1955), who named it haemocorin. Subsequently, eight genera and ten species in both subfamilies have been found to contain such pigments (Hegnauer 1986).

Chelidonic acid is reported in *Dilatris*, *Lachnanthes*, *Wachendorfia*, *Anigozanthos*, *Blancoa* and *Conostylis* (Ramstad 1953). Oxalate raphides occur in all Haemodoraceae.

Species of *Anigozanthos* and *Wachendorfia* were found to have cell wall-bound p-coumaric and diferulic acids, thus flourescent under UV light (Harris and Hartley 1980). The presence of these acids has been shown to be nearly consistent in taxa outside Liliiflorae proper. They are, for example, lacking in *Cyanella* and *Tecophilaea*, which argues against a close relationship between Tecophilaeaceae and Haemodoraceae but in favor of a close relationship between Haemodoraceae, Philydraceae and Pontederiaceae.

SUBDIVISION AND RELATIONSHIPS WITHIN THE FAMILY. As reviewed by Geerinck (1968), the classification of the Haemodoraceae has been variable and uncertain. Several authors have proposed different combinations of genera within tribes or subfamilies. In the present treatment, the Haemodoraceae are divided into two subfamilies: Conostylidoideae and Haemodoroideae.

The subfamily Conostylidoideae is distinguished by the occurrence of a rootstock and roots that lack a red pigmentation, 6 stamens, isopolar, rugulate pollen grains with 2–7 circular apertures, and distinctive tannin idioblasts (see Vegetative Anatomy and Floral Anatomy, above). In contrast, all genera of the Haemodoroideae (except for *Barberetta*) possess a rootstock and roots that have a red pigmentation, 3 stamens, unisulcate, heteropolar, and generally verrucate pollen grains, and lack tannin idioblasts.

Within Conostylidoideae, *Anigozanthos*, *Blancoa*, and *Conostylis* presumably make up a monophyletic group, which has been treated as a separate tribe, Conostylidoideae (Macfarlane et al. 1987). In this group *Anigozanthos* has a unique, apomorphic floral zygomorphy, caused by splitting of the perianth tube at anthesis. *Anigozanthos* probably arose from an ancestor of the large genus *Conostylis*, which would then be paraphyletic. Also *Blancoa* seems to have evolved from a paraphyletic *Conostylis*. Four species of *Conostylis* share with *Blancoa* a long, tubular perianth.

The relationships of the other two genera of the Conostylidoideae, *Phlebocarya*, and *Tribonanthes* are unclear. Each of these has been treated as separate tribes, Phlebocaryeae and Tribonantheae, respectively (Macfarlane et al. 1987).

The relationships within the Haemodoroideae are not entirely clear. Based on the most recent phylogenetic analysis (Simpson 1990), *Haemodorum* is the most basal genus, sharing some primitive features with members of the subfamily Conostylidoideae (e.g., in trichome anatomy, similar to that of *Phlebocarya ciliata*). The other genera of the Haemodoroideae appear to be united by derived floral trichomes, having a basal rosette of 3–4 epidermal cells (or evidence of such a rosette). *Dilatris*, *Wachendorfia*, *Barberetta*, *Schiekia*, *Pyrrorhiza*, and *Xiphidium* are united in having distinctive, derived pilate trichomes. Within this group, all but *Dilatris* are united in having a superior ovary and (with the exception of *Xiphidium*), infralocular septal nectaries (Simpson 1993). Within this superior-ovaried group, *Wachendorfia* and *Barberetta* are united in having a similar pollen ultrastructure (Simpson 1983, 1990) and *Schiekia* and *Pyrrorhiza* are united in having staminodes and similarities in ovule anatomy (M.G. Simpson, 1990, unpubl.). The exact relationship of *Xiphidium* to these genera is unclear.

The genera of *Hagenbachia*, *Lanaria*, *Lophiola*, and *Pauridia*, which were classified in the Haemodoraceae in some recent family treatments (see Melchior 1964; Geerinck 1969; Hutchinson 1973) are excluded from the family in the present treatment. *Hagenbachia* is a synonym of *Chlorophytum* (Anthericaceae) (Ravenna 1977). *Lanaria* differs from the Haemodoraceae in having tectate-columellate exine (Simpson 1983) and agrees better with Tecophilaeaceae in embryology (Steinecke and Hamann 1989) and seed morphology and chemistry (Huber 1969). *Lophiola* lacks perinaphthenones and has tectate-columellate exine (Simpson 1983). It is now shown to be a member of Melanthiaceae. Also *Pauridia* differs from the Haemodoraceae palynologically (Simpson 1983) and is retained in Hypoxidaceae (Geerinck 1968, 1969).

AFFINITIES. Recent evidence supports the very close relationship between Haemodoraceae, Philydraceae, Pontederiaceae, and possibly Commelinaceae. All investigated members of Philydraceae and the subfamily Conostylidoideae of Haemodoraceae and most members of Pontederiaceae have tannin idioblasts, a possible apomorphy uniting them (see Vegetative Anatomy and Floral Anatomy, above). Simpson (1983) demonstrated a striking similarity in pollen exine structure between members of the Haemodoraceae and Pontederiaceae, arguing for their close relationship. In addition to palynological similarities, these two families are similar (along with other monocotyledon families, particularly the Philydraceae) in other features. However, the Haemodoraceae and Philydraceae are similar in having derived, ensiform leaves, yet the Philydraceae and Pontederiaceae are similar in seedling morphology (Tillich 1995). Recent molecular studies (Chase et al. 1993; Duvall et al. 1993; Davis 1995) shows varying interrelationships of the Haemodoraceae, Philydraceae, Pontederiaceae, and Commelinaceae.

DISTRIBUTION AND HABITATS. *Lachnanthes* is found in N America, ranging from Nova Scotia in Canada, extending along the coastal plain of the southeastern USA to Cuba. *Xiphidium* occurs from S Mexico to northern S America, with one species in Cuba. *Schiekia* occurs in northern S America from Venezuela to Guiana. *Pyrrorhiza* is restricted to the isolated Mt. Neblina, Amazonas, Venezuela. *Barberetta* occurs in Transkei and Natal, S Africa, while *Dilatris* and *Wachendorfia* are endemic to the Cape, S Africa.

All Conostylidoideae are restricted to SW Australia. Finally, *Haemodorum* is widespread in Australia (incl. Tasmania) with its limit in New Guinea.

Xiphidium occurs in moist soils, often along watercourses. *Schiekia* is found in mountain savannas and woodlands, and *Pyrrorhiza* in cloud forests. *Dilatris* and *Wachendorfia* occur in sandy, sometimes wet habitats. Members of the Conostylidoideae and *Haemodorum* generally occur in open to closed, winter-wet, periodically burned sandy heath vegetation or woodlands.

ECONOMIC IMPORTANCE. Underground parts of several Australian species were roasted and eaten by aborigines (Millspaugh 1887). Narcotic effects have been attributed to the eastern N American *Lachnanthes caroliniana* (red root), from the roots of which an invigorating tonic was made by the Aborigines (Millspaugh 1887). The Australian *Haemodorum corymbosum* produces a red pigment (called hemocorin), which is said to have antitumor (Schwenk 1962) and antibacterial activity (Narasimhachari et al. 1968).

Several Australian species of Haemodoraceae, including species of *Blancoa*, *Conostylis*, *Haemodorum*, *Tribonanthes* and, especially, *Anigozanthos* are grown horticulturally. Finally, *Lachnanthes caroliniana* is listed as an aggressive weed in cranberry bogs (Robertson 1976).

KEY TO THE GENERA

1. Stamens 3 or 1 (Haemodoroideae)   2
 - Stamens 6 (Conostylidoideae)   9
2. Ovary superior   3
 - Ovary inferior   7
3. Stamen 1   5. *Pyrrorhiza*
 - Stamens 3   4
4. Corolla actinomorphic; inflorescence a simple raceme or a thyrse with lateral cymes   5
 - Corolla zygomorphic; inflorescence a congested corymb of helicoid cymes or sometimes (Wachendorfia) a thyrse with lateral cymes   6
5. Inflorescence a simple raceme; functional carpel 1; ovule 1; style subterminal   1. *Barberetta*
 - Inflorescence an elongate thyrse with lateral helicoid cymes; functional carpels 3; ovules 20–30 per carpel; style terminal   8. *Xiphidium*
6. Stamens unequal, the 2 latero-posterior anthers reduced; ovules 3–4 per carpel   6. *Schiekia*
 - Stamens equal; ovule 1 per carpel   7. *Wachendorfia*
7. Ovules 1 per carpel   2. *Dilatris*
 - Ovules 2 or more per carpel   8
8. Ovules 2 per carpel; flowers glabrous
                                                   3. *Haemodorum*
 - Ovules 5–7 per carpel; flowers tomentose
                                                   4. *Lachnanthes*

9. Perianth dicyclic; tepals imbricate (may superficially appear valvate in open flowers); flowers glabrous or white-lanate 10
− Perianth mostly monocyclic; tepals valvate; flowers tomentose with dendritic trichomes 11
10. Leaves tubular; inflorescence 1-flowered or a capitulum of a bifurcate helicoid cyme; flowers white-lanate
10. *Tribonanthes*
− Leaves flat to acicular; inflorescence an open, much-branched panicle of helicoid cymes; flowers essentially glabrous 9. *Phlebocarya*
11. Flowers actinomorphic; perianth tube, if present, not splitting along mid-anterior line 12
− Flowers zygomorphic; perianth tube splitting along mid-anterior line 13. *Anigozanthos*
12. Flowers pendulous; perianth pink-orange 12. *Blancoa*
− Flowers generally ascending; perianth mostly yellow or whitish, rarely orange to purplish 11. *Conostylis*

Subfamilies and Genera of the Haemodoraceae

I. Subfamily Haemodoroideae Dahlgren, Clifford & Yeo (1985).

Tribe Haemodoreae Benth. (1883), as Euhaemodoreae.

Rhizomatous, cormose, or bulbous herbs, mostly with red pigmentation in roots and rootstock; leaves flat to plicate; flowers actinomorphic or zygomorphic; stamens 3 or 1; staminodes present or absent; ovary inferior or superior; functional locules 3 or 1; ovule 1, 2, 5–7, or numerous per carpel; seeds glabrous, papillate, or hairy.

1. *Barberetta* Harv.

Barberetta Harv., Gen. South Afr. Pl., ed 2: 377 (1868).

Rhizomatous to cormose herbs, ca. 20 cm tall; cormels present in axils of scale leaves; leaves lanceolate, glabrous, plicate; inflorescence a simple raceme; axis and bracts pilate-hairy; flowers actinomorphic; tepals orange, distinct, imbricate, spreading, cuspidate; stamens 3, free; ovary superior functionally unilocular; posteriorly swollen, glabrous; ovule 1 per ovary, style anteriorly subapical; fruit an irregularly dehiscent, glabrous capsule; seed ovoid, glabrous, minutely papillate; $x =$ 15. Only one sp., *B. aurea* Harv., Transkei, Natal.

2. *Dilatris* Bergius Fig. 53A

Dilatris Bergius, Descr. Pl. Cap.: 9 (1767).

Rhizomatous herbs to 1 m tall; roots and rhizome red; leaves linear, glabrous; inflorescence a corymb of 3–5 bifurcate cymes; axes and bracts canescent; flower ± actinomorphic; tepals orange-yellow or mauve, distinct, imbricate, externally with minute, dark brown, circular papillae on apical parts; stamens 3, free, unequal, one anther large on short filament, 2 smaller on long filaments; ovary inferior, with long velutinous, and short, pilate hairs; style slightly curved; ovules 1 per carpel; seeds discoid, convex-concave, minutely papillose; $x =$ ca. 19–21. Four spp., Cape S Africa.

3. *Haemodorum* J.E. Smith Fig. 53B–G

Haemodorum J.E. Smith, Trans. Linn. Soc. (Lond.) 4: 213 (1798), Macfarlane, Fl. Australia 45: 134–148 (1987).

Bulbous (to cormose) herbs to 1 m tall; subterranean stems red; leaves narrowly lanceolate to acicular with sheath sometimes extending nearly to apex, glabrous; inflorescence a glabrous panicle or simple to branched raceme of 1, 2, or 3–many flowers; flower dark maroon, red to yellow, or greenish, actinomorphic, glabrous; tepals distinct, imbricate, ascending, ± coriaceous; stamens 3, free; ovary inferior; ovules 2 per carpel; fruit 3-lobed, glabrous, seeds discoid, glabrous, with a membranous, marginal wing; $x =$ 12. Twenty spp., Australia (including Tasmania) and New Guinea.

4. *Lachnanthes* S. Elliott

Lachnanthes S. Elliott, Sketch Bot. South Carol. Georgia 1: 47 (1816), nom. cons.; Robertson, J. Arnold Arbor. 57: 205–216 (1976).

Rhizomatous and stoloniferous herbs to 1 m tall; roots and rhizomes orange-red; leaves linear; inflorescence a pubescent corymb of trifurcate or bifurcate cymes; flowers yellow-green to yellow-white, actinomorphic, externally pubescent; outer tepals narrowly triangular, with a dark aristate tip, inner tepals oblong, involute; stamens 3; ovary inferior; ovules 5–7 per carpel, laterally exserted, enantiostylous; fruit globose, 3-lobed, pubescent to basally tomentose; seeds reddish, discoid, convex/concave, minutely scabrate; $x =$ 24. Only one sp., *L. caroliniana* (Lam.) Dandy, Cuba, southeastern USA and Nova Scotia.

5. *Pyrrorhiza* Maguire & Wurdack

Pyrrorhiza Maguire & Wurdack, Mem. N. Y. Bot. Gard. 9: 318 (1957); Maas & Maas-van de Kamer, Fl. Neotr. Monogr. 61 (1993).

Herbs to 1.5 m tall with orange-red corms aggregated in clusters; leaves narrowly oblanceolate, glabrous, coriaceous; inflorescence a corymb of 2–3 ascending helicoid cymes, axes and bracts tomentose; flowers zygomorphic; perianth basally orange-red, apically white; tepals distinct, the outer externally velutinous with pilate hairs; the inner glabrous; stamen 1, free, opposite inner anterior tepal; staminodes 2; ovary superior; ovules 2 per carpel; fruit ellipsoid, flattened on 3 sides, glabrous; seeds discoid, concave and glabrous on distal surface but with dense marginal hairs. Only one sp., *P. neblinae* Maguire & Wurdack, Mt. Neblina, Amazonas, Venezuela.

6. *Schiekia* Meisn.

Schiekia Meisn., Pl. Vasc. Gen. 1: 397, 2: 300 (1842); Maas & Maas-van de Kamer, Fl. Neotr. Monogr. 61 (1993).

Rhizomatous herbs to ca. 1 m tall; leaves linear to narrowly lanceolate, glabrous; inflorescence a corymb of simple helicoid cymes, axes and bracts canescent; flowers cream-white; zygomorphic; tepals imbricate; staminodia 2; stamens 3, free, the 2 latero-posterior stamens with short filaments and small anthers, anterior stamen relatively long with filament twisted and anther locules facing the curved stigma; ovary superior, glabrous; ovules 3–4 per carpel, anatropous; style flattened posteriorly, curved 90° (dextrorse in all material examined), with stigma laterally facing anterior anther; capsule widely obovoid, 3-lobed, glabrous; seeds dark brown, discoid-peltate. Only one sp., *S. orinocensis* (Kunth) Meisn., northern S America, Guyana Highland.

7. *Wachendorfia* Burm.   Fig. 53H

Wachendorfia Burm., L., Syst. Nat., ed 10, 2: 864 (1759); Helme & Linder, Bothalia 22: 59–75 (1992).

Rhizomatous herbs to 2.5 m tall, rhizomes red; leaves linear, entire, glabrous to hirsute, plicate; inflorescence a raceme of numerous, widely spaced 3–4-flowered helicoid cymes, axes and bracts canescent; flowers ca. 2 cm long, zygomorphic; tepals yellow to purplish, imbricate; stamens 3, free, anterior stamen curved to side opposite style; anthers sub-basifixed; ovary superior, densely pubescent; ovule 1 per carpel, anatropous, hypotropous; style posteriorly curved, enantiomorphic; fruit 3-lobed, ovoid, canescent; seeds ovoid, with a dark brown tomentum. $n = 15$. Four spp., sensu Helme, Linder (1992), endemic to the Cape region of S Africa.

8. *Xiphidium* Aubl.   Fig. 53I–L

Xiphidium Aubl., Hist. Pl. Guiane: 33 (1775); Maas & Maas-van de Kamer, Flora Neotr. Monogr. 61 (1993).

Rhizomatous and stoloniferous herbs to 0.5 m tall; leaves cernuous, lanceolate, with sheathing base, glabrous, margins minutely spinulose; inflorescence a raceme of helicoid cymes, axes and bracts pubescent with pilate trichomes; flowers ca. 10 mm wide, actinomorphic; tepals white, distinct, imbricate, membranous; outer tepals sparsely pubescent at apices and along lower midrib; stamens 3, free; anthers basifixed; ovary superior, very sparsely pubescent; ovules numerous (c. 30) per carpel, lanceoloid, atropous, generally hypotropous; style bent anteriorly near apex; capsule obloid-ovoid, orange, glabrous; seeds dark brown, globose or irregularly tetrahedric, papillate. $n = 19$. Two spp., Mexico, Meso-America, northern S America, and Cuba.

II. Subfamily Conostylidoideae (Lindley) MacFarlane & Hopper (1987).

Tribe Conostylideae Lindley (1847), as Conostyleae.

Rhizomatous to cormose herbs, without red pigmentation in roots and rootstock; leaves flat to tubular; flowers actinomorphic or zygomorphic; stamens 6; staminodes absent; ovary inferior or half-inferior; functional locules 3; ovules 1, 2, or numerous per carpel; seed glabrous, smooth or with longitudinal ridges.

9. *Phlebocarya* R. Br.

Phlebocarya R. Br., Prodr. 1: 301 (1810); Macfarlane et al., Fl. Australia 45: 55–148 (1987).

Rhizomatous cespitose herbs, ca. 0.5 m tall; leaves linear to acicular, straight to slightly flexuous, eciliate or ciliate, glabrous or pilose; inflorescence a panicle of bifurcate helicoid cymes; axes and bracts glabrescent or lanuginose, trichomes unicellular or dendritic; flower ca. 8–9 mm wide, actinomorphic; tepals white, distinct, imbricate, glabrous; stamens 6, free; anthers basifixed, apically mucronate to apiculate; ovary inferior, ovoid, glabrous; locules 3 below, 1 above by separation of septae; placentation basal; ovules 1 per carpel; capsule indehiscent, ellipsoid, glabrous, with a hard endocarp; seed 1 per fruit, globose, glabrous. $n = 7$. Three spp., endemic to SW Australia.

10. *Tribonanthes* Endl.   Fig. 54A,B

Tribonanthes Endl. in Endl. & Fenzl, Nov. Stirp. Dec.: 27 (1839); Macfarlane et al., Fl. Australia 45: 131–134 (1987).

Cormose herbs, to 40 cm tall; leaves narrowly linear, hollow-tubular, with long open sheath; inflorescence 1-flowered or a capitulum of a bifurcate pair of helicoid cymes, axes lanate, bracts glabrous; flowers actinomorphic; perianth short-tubular, white-lanate; perianth lobes imbricate, divergent, ovate; stamens 6, anthers dorsifixed, with apical laminar, cernuous appendage; connective extending as an erect, apically lobed flange; ovary inferior, globose; ovules numerous (ca. 50 per carpel), anatropous, heterotropous; stigma ovoid, basally pubescent, with 3 linear sclerous lobes; capsule indehiscent, widely ellipsoid, white-lanate; seeds globose-rectanguloid, glabrous. $n =$ 11. Five spp., endemic to SW Australia.

11. *Conostylis* R. Br.   Fig. 54C–F

Conostylis R. Br., Prodr. 1: 300 (1810); Macfarlane et al., Fl. Australia 45: 57–110 (1987).

Rhizomatous (some spp. stoloniferous) to erect, cespitose herbs; leaves basal or cauline, flat, or subterete, entire to bristly-ciliate; inflorescence a capitulum or corymb of bifurcate helicoid cymes; axes and bracts canescent to tomentose; flowers yellow, ca. 5–25 mm long, actinomorphic, generally tomentose with dendritic trichomes; perianth with a short to elongate tube (tube absent in *C. breviscapa*); tepals mostly valvate; stamens 6; anthers dorsifixed; ovary inferior; placentae occupying most of locule volume and covered by numerous ovules or restricted to apex of locule and bearing a few pendulous ovules; stigma 3-lobed; capsule generally ovoid. $n =$ 8 (4, 5, 6, 7, 14, 16, 21, 28). Approximately 45 spp., in six subgenera (sensu Macfarlane et al. 1987), endemic to SW Australia.

12. *Blancoa* Lindl.

Blancoa Lindl., in Edw. Bot. Reg., (1839); Macfarlane et al., Fl. Australia 45: 110–112 (1987).

Rhizomatous, cespitose herbs to ca. 25 cm tall; leaves narrowly linear to linear-falcate, ciliate, mucronate, canescent; inflorescence a raceme of bifurcate helicoid cymes, axes and bracts canescent; flowers pink-orange, 3.5–4 cm long, actinomorphic, tomentose with dendritic trichomes; perianth tube long, cylindrical; perianth lobes valvate; stamens 6; anthers dorsifixed; ovary half-inferior, ovoid; placentae rudimentary at apex of septae; ovules ca. 3 per carpel; stigma globose, slightly 3-lobed; capsule globose, tomentose. $n =$ 8. Only one sp., *B. canescens* Lindl., endemic to SW Australia.

13. *Anigozanthos* Labill.   Fig. 54G–M

Anigozanthos Labill., in Rel. Voy. Rech. La Pérouse 1: 409 (1800) [including *Macropidia fuliginosa* J. Drumm ex Harv.]; Macfarlane et al., Fl. Australia 45: 112–128 (1987); Anderberg & Eldenäs, Aust. Syst. Bot. 4: 655–664 (1991).

Rhizomatous, often cespitose herbs; leaves lanceolate to linear, mucronate, glabrous to canescent or glaucescent; inflorescence a terminal simple or bifurcate helicoid cyme or a loose panicle of generally bifurcate helicoid cymes, axes and bracts canescent to tomentose; flowers ca. 4–9 cm long, zygomorphic, outer surface with dendritic trichomes, inner surface glabrous; perianth tubular, longitudinally splitting along mid-anterior line during anthesis, cylindrical to funnelform or flattened by virtue of reflexed tepal lobes; perianth lobes valvate; stamens 6; ovary inferior, subglobose; placentae ellipsoid to rudimentary; ovules numerous or (in *A. rufus* and *A. pulcherrimus*) 2 per carpel or (in *A. fuliginosus*) 1 per carpel; stigma globose; capsule ellipsoid, with transverse wrinkles, splitting along septae and apically opposite locule; in *A. fuliginosus*, capsule dehiscing into 3 1-seeded mericarps surrounded by hard endocarp; seeds ovoid and glabrous or ellipsoid with longitudinal ridges. $n =$ 6. Twelve spp., endemic to SW Australia.

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