

Jean Gerrath · Usher Posluszny
Lewis Melville

Taming the Wild Grape

Botany and Horticulture in the Vitaceae

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Foreword

When we are asked what we do, at the first mention of the grape family (Vitaceae), people immediately focus on ‘grape’ and launch into their memories of family heirloom grapevines, questions about how to prune their grape arbours or queries about which wines to buy. Thus, over the years we have been forced to learn more about grape growing and winemaking than we had intended. However, ‘grapes’ are not especially typical of the Vitaceae, whose members demonstrate a wide range of forms and life histories. This book aims to place grapes (the genus *Vitis*) within their family and discusses the characteristics of the Vitaceae as a whole as well as how *Vitis* characteristics fit in with those of other family members. This book is a resource for those who want to learn more about grapes in general and provides a context for understanding the growth, development and life history of this poorly understood group of plants.

The book is divided into two sections. Section I consists of four chapters and focuses on the Vitaceae as a whole. Chapter 1 discusses the origin and general relationship of the family to other flowering plants its unique features, and describes the interrelationships and characteristics of its genera. Chapters 2 and 3 expand on some of the characteristics mentioned in the first chapter, with Chap. 2 emphasizing the vegetative characteristics (shoots, leaves and buds) and Chap. 3 the reproductive characteristics (flowers, fruits and seeds). These two chapters summarize much of our research work over the past 30 years. Chapter 4 is an identification guide to 19 species of North American Vitaceae, including 10 species of *Vitis*, and contains identification keys, descriptions and photographic illustrations for each species, again compiled by us and our students over the years.

Section II is divided into two chapters, and deals exclusively with *Vitis*. Chapter 5 summarizes the history of the human relationship with grapes and concludes with a section on the history of grape growing in Canada and the USA. Chapter 6 reviews the history and importance of grapevine identification (ampelography) in North America and concludes with descriptions and photographic illustrations of 30 of the most important cold climate cultivated varieties (cultivars) grown in Canada and the northern USA. It is an expansion of *A Midwesterner's Handbook to Grapevine Varieties* (Lehmann and Gerrath 2004). We have included three Appendices. The first two are illustrated, and explain the main characters used in *Vitis* identification (Appendix 1) and its complicated life history (Appendix 2). Appendix 3 is

a short glossary of common Vitaceae terms with references to helpful illustrations found throughout the book.

When we began this research over 30 years ago, the Vitaceae was an obscure family studied by very few botanists, and researchers focused almost exclusively on commercial grapes. Our developmental studies emphasized shoot growth and flowering patterns across the family, and often revealed patterns that did not fit easily into those found in other flowering plants. Recent molecular studies have shown that the family does not have any close relatives, and sits as a ‘sister’ to all of the other Rosids, one of the large subdivisions of angiosperms. The fact that we have emphasized how the growth and development of grapes is related to the other members of the Vitaceae gives our work a unique perspective, and brings together information that we hope will encourage botanists, horticulturists and people interested in learning more about grapes to expand their horizons to include these long-neglected, but important plants.

J.M.G.
L.M.
U.P.

Acknowledgements

This book is a compilation of the research done in our labs over the past 30 years. However, it owes much to others and we thank all of you for your contributions.

At the University of Northern Iowa, students Mike Maddox, Jim Uthe, Madhav Nepal, John Holding, Lee Trebbien, Erin Gitchell and Robin Flattery established and maintained the plants in the experimental vineyard and the UNI greenhouse under the supervision of staff members Ron Camarata, Billie Hemmer and Stephanie Witte. Lee Trebbien and Erin Gitchell also made careful observations and kept records of many of the greenhouse plants. Colleague Emily Lehman was instrumental in coordinating the production of *A Midwesterner's Handbook to Grapevine Varieties*. Paul Domoto and Gail Nonnecke at Iowa State University were very generous in providing information about commercial grape growing and growers, and allowed us access and fruits from the experimental vineyard at Nashua, IA. Likewise, Peter Hemstad at the University of Minnesota vineyard at Chanhassen, MN was always willing to answer questions and provide access. Martin Goffinet, Peter Cousins and Bruce Reisch hosted visits to the US Department of Agriculture (USDA) Germplasm Repository in Geneva Station, NY and graciously answered many questions about grape breeding. Paul Tabor at Tabor Home Winery in Baldwin, IA provided support and access in many ways for many years. Peter Cousins also provided plant material of many species from his USDA live plant collection at Geneva Station.

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Colleagues Jun Wen at the Smithsonian Institution, Stephen Manchester at the Florida Museum of Natural History and Stephanie Ickert-Bond at the University of Alaska, Fairbanks have all been generous with their insights into plant systematics and paleobotany in the Vitaceae.

The mistakes in the book, however, are ours, for which we take full responsibility.

J.M.G.
L.M.
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Chapter 1

Vitaceae Systematics (Origin, Characteristics and Relationships)

Introduction

The most common human interaction with the Vitaceae is through grapes and their most economically important crop, wine (Chap. 5). Most of us are less aware of the other Vitaceae in our midst, and even viticulturists, oenologists and plant biologists often fail to consider the biology of grape (*Vitis*) within the context of its family. At one time, this might not have mattered, but the age of genetic engineering and genomics requires consideration of grapes within a broader sphere in order to best make use of modern techniques of molecular genetics for crop production. This chapter is a brief summary of the geographic range and morphological characteristics of the genera and species in the family within the context of their phylogenetic relationships.

Most Vitaceae are climbing woody vines found growing up tree trunks, scrambling over brush, or climbing up rock faces. As is common in most woody vines, they use tendrils to attach to their substrate and support their biomass. However, Vitaceae tendrils are unique and morphologically distinct from those of all other flowering plant families because they are positioned opposite the leaves and are initiated independently at the shoot apex at the same time as the leaves (Chap. 2). This is the most obvious defining characteristic of the family. Although a small number of African succulent shrub species lack tendrils, these species have typical Vitaceae flowers, fruits and seeds.

Our understanding of the ecological importance of woody vines (lianas) in forests has lagged behind our general knowledge of forest ecology. This is partly because most of their mass is mixed with the tree canopy, making them hard to study and identify (Gentry 1991; Schnitzer and Bongers 2002). It is assumed that lianas act as mechanical parasites, using other plants or any other suitable support to climb to the top of the canopy where light levels are more suitable for photosynthesis (Gentry 1991). A study of vine photosynthesis and climbing mechanisms indicated that tendrill species, especially the Vitaceae, were the best adapted to low light (Carter and Teramura 1988). Lianas are usually more common in tropical forests, and this is true in the Vitaceae, despite the fact that grapes are important components

of temperate forests (Schnitzer and Bongers 2002). Tendril climbers such as grape are generally more abundant in young forests, perhaps because the host trees are smaller and more suitable for climbing using tendrils (DeWalt et al. 2000).

Non-Winemaking Uses of Vitaceae

A number of Vitaceae have been introduced into the landscape as ornamental vines. Probably the two most common species are Virginia creeper (*Parthenocissus quinquefolia* (L.) Planchon ex DC), a North American native which was introduced into Europe and is now naturalized there (Fig. 1.1c, d; Chap. 4), and Boston ivy (*P. tricuspidata* (Sieb. & Zucc.) Planch.), a species native to Japan and now found throughout Europe, Southern Canada and the USA, as well as China (Chap. 4, Chen et al. 2007). Both species are used extensively as building climbers, and named varieties have been selected (Dirr 1997). *Ampelopsis glandulosa* (Wallich) Momiy. var. *brevipedunculata* (Maxim.) Momiy. or porcelain vine, (formerly *A. brevipe-*

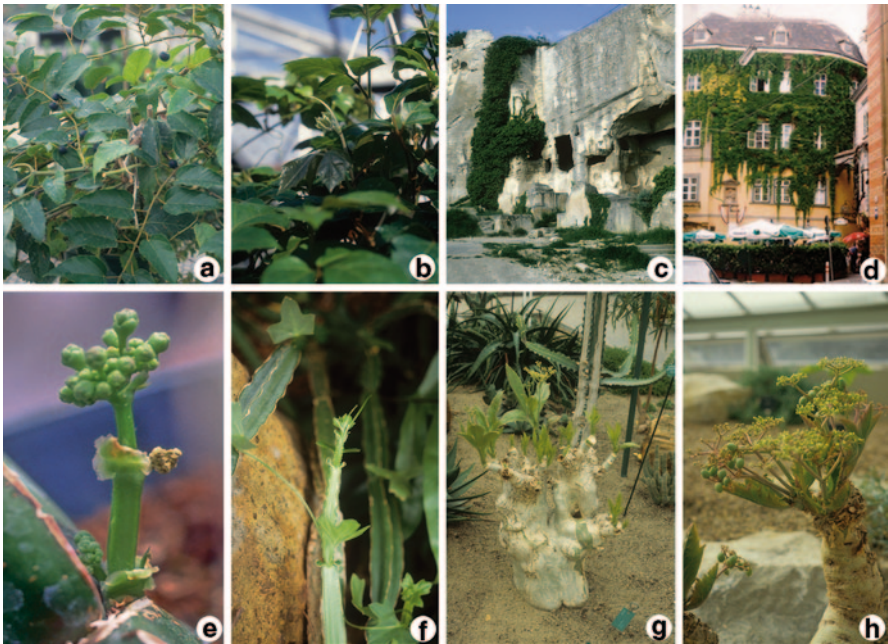


Fig. 1.1 Some ornamental species of the Vitaceae. **a** *Cissus rhombifolia*, University of Guelph. **b** *C. antarctica*, University of Guelph. **c, d** *Parthenocissus quinquefolia*. **c** Naturalized in Citadel des Baux, Provence, France. **d** Grown ornamentally in Vienna. **e, f** *C. quadrangularis* from Weimeia Falls, Hawaii. **e** Close view of a flowering shoot. **f** Tip of a vegetative shoot. **g, h** *Cyphostemma juttae*. **g** Plant in the Montreal Botanical Garden. **h** Flowering shoot with berries at the Princess of Wales Conservatory, Kew Gardens, UK

dunculata (Maxim.) Trautv.) is native to eastern Asia (Chap. 4). It was introduced into the USA as an ornamental climber as well, but has escaped, and is now considered to be an invasive weed in the USA, where it is sufficiently hardy to withstand winter temperatures to Zone 4 (USDA/NRCS 2008).

Other Vitaceae, such as *Cissus rhombifolia* Vahl (grape ivy, Fig. 1.1a) and *C. antarctica* Venten. (kangaroo vine, Fig. 1.1b) are commonly and easily grown in hanging baskets in indoor sites such as restaurants and shopping malls. There are also a number of species of *Cyphostemma* (eg. *C. juttai* (Dinter & Gilg.) Desc. Fig. 1.1g, h) and *C. bainesii* (Hook. f.) Desc.) and *Cissus* (eg. *C. tuberosa* DC. and *C. quadrangularis* L., Fig. 1.1e, f) that are prized in many succulent plant collections, both amateur and professional. Many of these succulents have interesting caudexes or swollen stems and are relatively easy to maintain (Fig. 1.2a, b, c, d, Fig. 1.3b, e). Because these species are not generally hardy and tend to be grown indoors in North America, they are not considered invasive.

Humans have also made use of the flexibility of the stems of the vine forms of the Vitaceae, which are sometimes used in binding and tying in tropical regions (Bodner and Gereau 1988). Stems of *Cissus quadrangularis* are also reported to be used locally as food (Mabberley 1995) and in some traditional indigenous medicines (Kannan and Jegadeesan 1998). However, by far the most well-known health-related claim for grapes (and red wine in particular) is related to the antioxidant property of the compound resveratrol. Resveratrol (3, 5, 4'-trihydroxystilbene) is a polyphenol which is induced by conidial germination of *Botrytis cinerea* (grey mould) and other fungi and it, in turn, inhibits further conidial spore germination (Bessis 2007). In humans it has been shown to act as an antioxidant (Yilmaz and Toledo 2004). It has also been shown to act at the cellular level to block mitosis and stimulate apoptosis (programmed cell death), and thus shows promise in reducing tumour growth (Bessis 2007 and articles therein). Thus, there may be some basis to the 'French Paradox', in which a diet which does not seem to be particularly 'heart healthy' appears to be counteracted by the ample consumption of red wine.

Morphological Characteristics of the Vitaceae

This section summarizes the major features of the Vitaceae but only in a general way. Chapters 2 (Vegetative Features) and 3 (Reproductive Features) contain the detailed descriptions, illustrations and explanations of their structure and development and Appendix 1 illustrates how to use these characters in identification.

Besides the above-mentioned leaf-opposed tendrils and inflorescences, the Vitaceae have only two other unique morphological features. First, the seeds have a distinctive pair of infolds on their ventral surface, and the chalaza position is uniquely on the dorsal surface of the seed (Chap. 3, Chen and Manchester 2011). This has made identification of fossil vitaceous seeds relatively straightforward (Chen and Manchester 2011). The other feature is the unique twinned microscopic structure

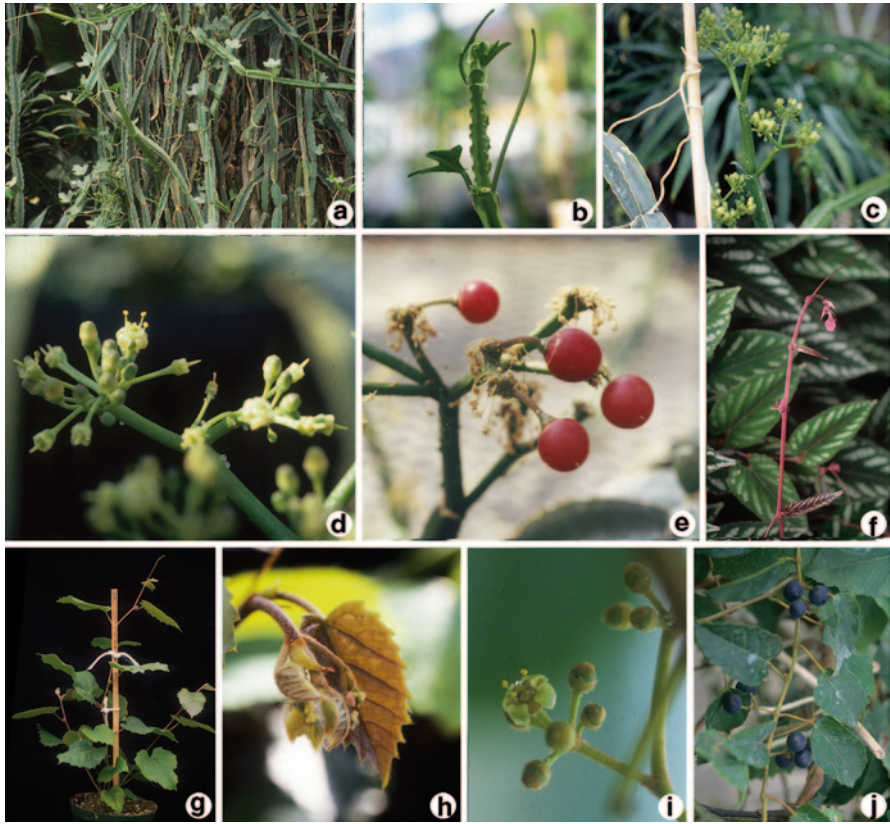


Fig. 1.2 Clade IV. **a–f** Subclade ‘Core *Cissus*’. **a–e** *Cissus quadrangularis*. **a** General view of plant, showing the distinctive 4-sided stems, tendrils opposite the relatively inconspicuous leaves. Waimaieia Falls, HI. **b–e** University of Guelph. **b** Shoot tip, showing the generally unbranched tendrils opposite the leaves. **c** Inflorescences along a reproductive shoot. **d** Close view of flowers at various stages on the same inflorescences. **e** Mature pink-red fruits. **f** *Cissus discolor*, Waimaieia Falls, HI. **g–j** Subclade ‘*Austrocissus*’. *C. antarctica*. University of Guelph. **g** Young plant, showing general form. The leaves are simple, with prominent teeth at the margins. **h** Shoot tip with young flower clusters forming opposite the leaves. Note the long, narrow stipules at the base of the leaves. **i** Flowers beginning to open in a cluster. This flower is at the ‘male’ stage, with the stamens and petals still present. **j** A shoot with clusters of round, black fruits opposite the leaves

of the calcium oxalate crystals which are distributed throughout the plant (Chap. 2, Cody and Horner 1983), clearly not a useful character for field identification.

Despite the small number of unique features, family members share a suite of characters that, in combination, make the Vitaceae a distinct, easy-to-recognize group. Among the vegetative features, leaf shape is probably the most widely used, especially in cultivar identification (Chap. 7, Galet 1979). Although the leaves of different species can be quite variable in form, with simple and variously compound blades (Chap. 2), leaf shape can vary on the same plant, with the result that leaf form has to be used with caution when identifying species (Fig. 1.4a). The Vitaceae have a pair of stipules at the base of the leaves that are usually quite prominent near the

shoot tip where the leaves are young (Figs. 1.2h, 1.3k, 1.4c). Often they cover the young shoot tip and fall off once the leaf matures. Microscopic studies indicate that they are variable enough that they may be used in identification (Chap. 2, Lacroix and Posluszny 1989). All of the Vitaceae that have been examined to date have small ‘pearl bodies’ that resemble insect eggs on their young stems, leaves and flowers. Microscopically, they consist of multicellular, stalked spheres, and they are often associated with stomata (Paiva et al. 2009). There are variations among species in their morphology, but it is not known if they could be used in identification (Chap. 2).

Differences in reproductive characters (Chap. 3) are quite subtle, and have not been exploited widely for identification below the genus level. The inflorescences, or flower clusters, are typically positioned opposite leaves (Fig. 1.2c) although there are a few species with terminal inflorescences (Figs. 1.3c, 1.4e) and others in which they appear to be axillary (Fig. 1.3f). The flowers themselves are small, and typically greenish and inconspicuous (Fig. 1.1h). The flower parts consist of a ring of small sepals that are fused with one another and may be pointed, variously lobed, or with indistinct tips. The petals cover the anthers and pistil, and form quite a distinctive ‘hood’ in some species (Fig. 1.3d, h). In *Vitis* (grape) the tips of the petals fuse to form a ‘calyptra’ or cap that falls off the flower at maturity (Chap. 3). The stamens are opposite the petals and equal in number (Fig. 1.5c), both features that are unusual in flowering plants. Typically the pistil consists of a disc-like stigma (although *Tetrastigma* has four distinct lobes), a short style, and a 2-chambered ovary with 2 ovules in each chamber. A floral disc usually develops from the base of the ovary, and secretes nectar in most genera. The variability in floral disc development and morphology is a useful identification feature. As might be expected, the nectar attracts insects, which are assumed to be the major pollinators of the flowers (Chap. 3).

Fruits in the Vitaceae are typically dark purple berries with 1–4 seeds (Figs. 1.4h, 1.5i), although some grape cultivars have green berries, and there are some species in the family with white, turquoise-blue, orange and red-magenta fruits (Figs. 1.2e, 1.3i). The most noticeable feature of a cut seed is its ruminant (folded) white endosperm, which takes up most of the seed volume. The actual embryo in the seed is very small and hard to find (Chap. 3). Taken together, this suite of characters defines a distinct plant family, and one that is not closely related to any other.

Relationships Within the Vitaceae—Systematics and Phylogeny

One of the main underlying principles of plant classification is that it should be ‘natural’, and reflect the phylogeny (genealogical relationships) of the groups in question. Before the advent of DNA sequencing and the accompanying modern molecular biological techniques, biologists had to rely on hypothesis of relatedness based mainly on shared morphological characteristics. Botanists produced phylogenies of many plant families using such techniques, but not for the Vitaceae.

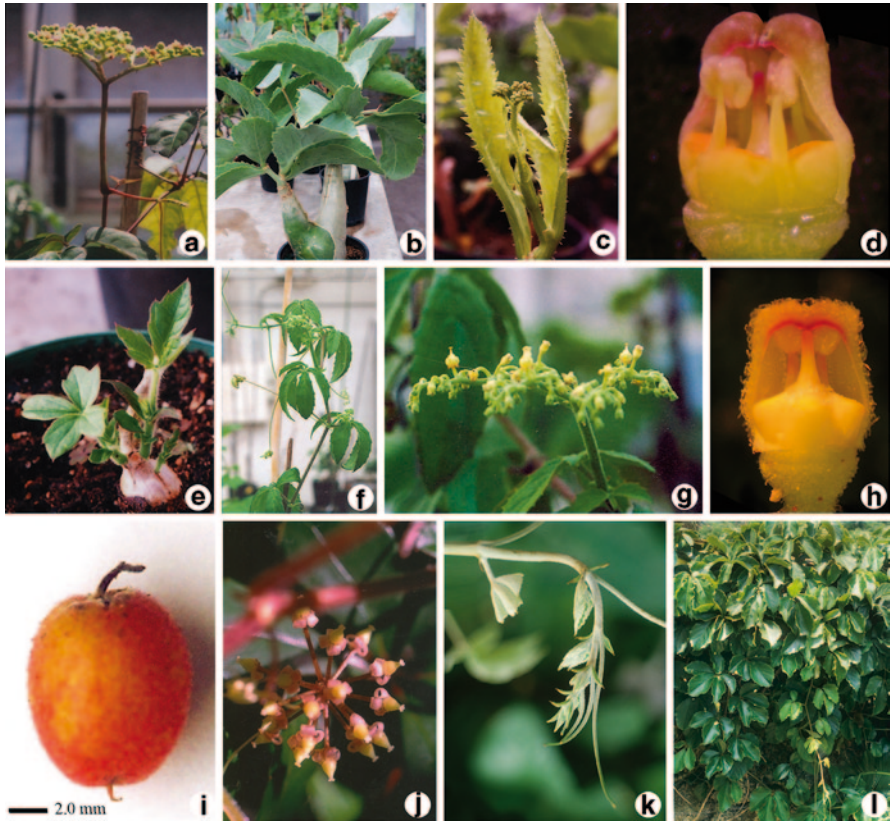


Fig. 1.3 Clade V. **a–i** University of Northern Iowa. **a** *Cayratia japonica*, general view of a plant in flower (see also Chap. 4). **b–d**, *Cyphostemma bainesii*. **b** General view of a potted specimen, about 3 years old, showing the large succulent leaves (some are simple and some are divided into leaflets). Note how the bark is shed as the succulent stem increases its girth. **c** Plant with a young terminal inflorescence. New growth is continued by buds lower down the stem. **d** Side view of a flower from which two petals have been removed to show the hooded petals, anthers releasing their pollen, and the four large, flat-topped floral nectary discs. **e–i**, *Cyphostemma sandersonii*. **e** Shoots sprouting from the swollen stem (caudex) after a dormant period. **f** Plant with tendrils opposite the leaves and inflorescences in the axils (*upper angles*) of the leaves. **g** Close view of an inflorescence. Flowers hang downwards until they open, after which they become upright. **h** Side view of a flower, showing the relative positions of the organs. Note the prominent hairs on the petals and the ovary. **i** Mature fruit, which is orange-red, oval, with hairs on the fruit wall. The style remains on the fruit in this genus. **j** *Tetrastigma* sp. Inflorescence of female flowers. Kew. **k, l** *Tetrastigma voinerianum*. **k** Shoot tip with tendrils at every node and white hairs on the young tissue. Golden Gate Park, San Francisco, CA. **l** General view of the plant and its palmately compound leaves. Fairchild Tropical Garden, Miami, FL

This may have been partly because, although the family is morphologically distinct, the morphological differences between the species are subtle, making it difficult to tease out relationships. The last complete treatment of the family was by Süssenguth in 1953, in German, which made it less accessible in North America. It was not

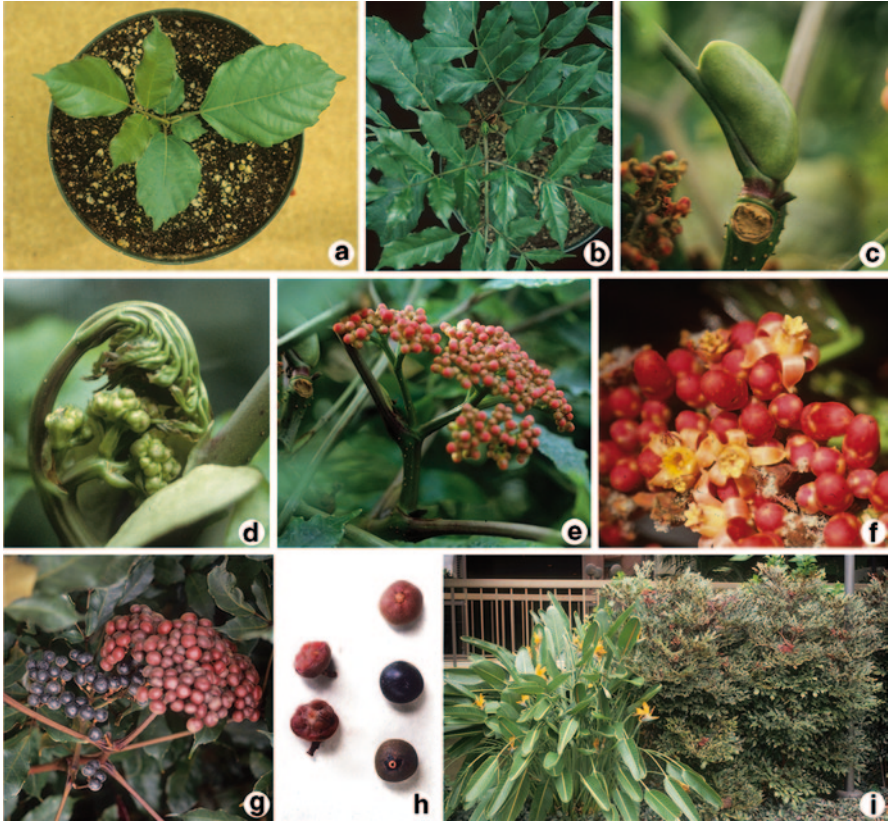


Fig. 1.4 *Leea guineensis* (*L. coccinea*) **a** Young seedling, showing the transition from simple to compound leaves. **b** Older potted plant, still in its juvenile, non-flowering phase. **c** Shoot tip completely enclosed by large stipules. **d** Stipules opening to reveal a young inflorescence. Note the two components; the terminal portion and a second, smaller portion in the leaf axil (*upper angle*). **e** Inflorescence at a later stage of development showing its terminal and axillary components. **f** Inflorescence showing the nonsynchronous development of the flowers. The flowers first go through a staminate (male) stage, in which the anthers open to reveal the pollen, followed by a pistillate (female) stage in which the anthers have been shed, the ‘staminodial tube’ is well developed, and the stigma is exposed. **g** Two mature fruit clusters, showing the range of colour, from red through mature black. **h** Mature fruits, which are not fleshy. The walls of some of the fruits have been peeled back to reveal the 6 seeds, each in its own chamber. **i** General view of a plant in fruit. Honolulu, HI

until 2002 that a phylogenetic analysis of the family was published (Ingrouille et al. 2002). Since then, as techniques and access to more species and DNA sequences have expanded and increased, the phylogeny of the Vitaceae has become much better understood and a reliable overall picture of the relationships among and within the genera has emerged (Liu et al. 2013; Lu et al. 2012, 2013; Nie et al. 2010, 2012; Ren et al. 2011; Rossetto et al. 2002, 2007; Soejima and Wen 2006; Trias-Blasi et al. 2012; Wen et al. 2007).

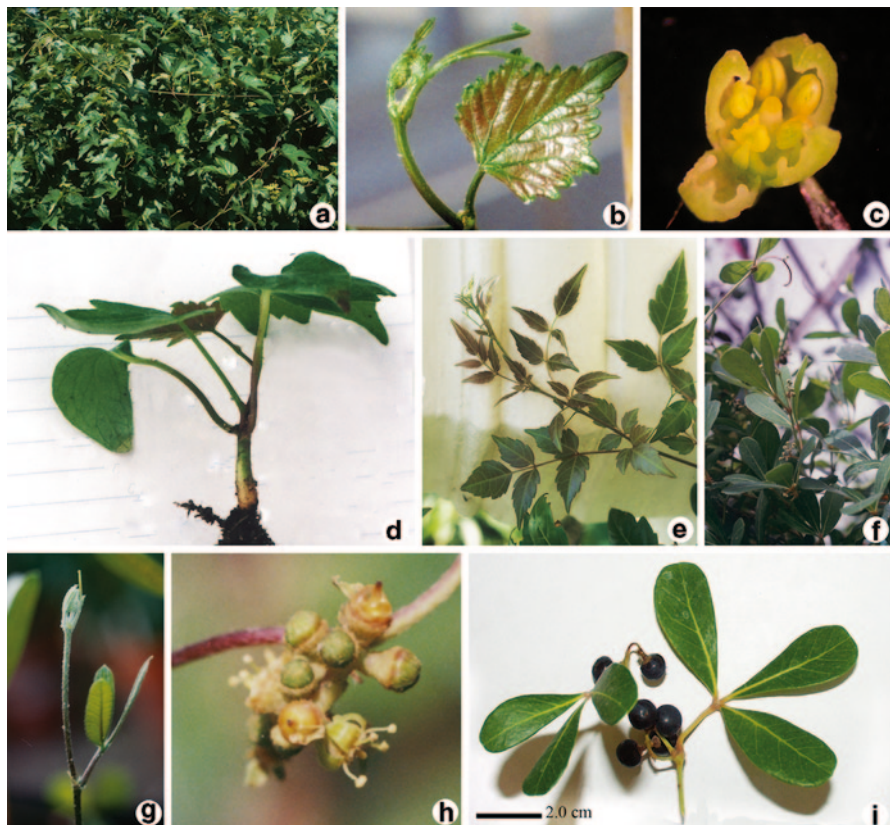


Fig. 1.5 Clade I. **a–d** *Ampelopsis humulifolia*. **a** General view of plant in bloom, showing the deeply lobed leaves, resembling hops leaves. **b** Shoot tip and tendrils opposite the leaves. **c** Flower just at the beginning of anthesis, with the anthers just beginning to open to reveal the pollen and the floral disc lobes between the filaments. **d** Seedling, showing the thickened hypocotyl at the base of the stem, below the seed leaves. **e** *A. cantonensis*. Vine with compound leaves. Kew. **f–i** *Rhoicissus digitata*. **f** General view of plant in bloom, with inflorescences opposite the leaves. **g** Shoot tip, showing tendrils (usually not branched) opposite the leaves. **h** Flower cluster, showing the general form of the flowers. **i** Cluster of black fruits at maturity

Order Vitales

The Vitaceae and their sister family, the Leeaceae, make up the order Vitales (Fig. 1.6). They are flowering plants grouped in the Eudicots, which typically have 2 seed leaves (cotyledons), flower parts in whorls, 5 petals, and pollen with 3 furrows, or colpae, as well as a number of more subtle features (Stevens 2001 onwards—APG website). For some time the position of the Vitales within the Eudicots was uncertain, but recent work has placed them in the largest subgroup, the Rosids, with about 70,000 species and 140 families (Wang et al. 2009). Rosids are the largest Eudicot group, and include such important families as the Fabaceae (bean),

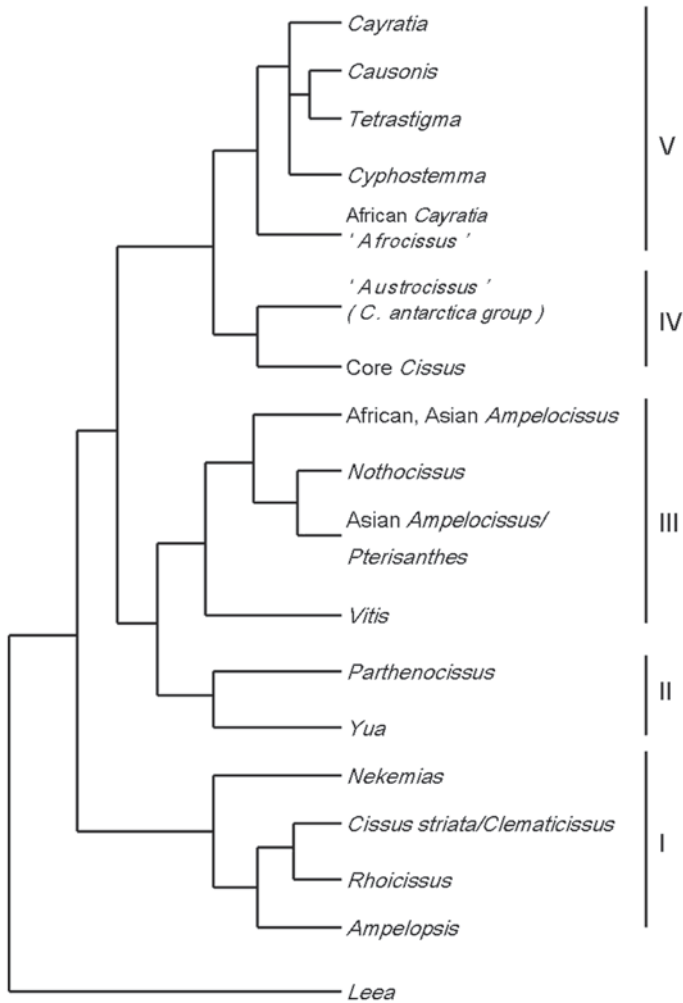


Fig. 1.6 Phylogenetic relationships in the Vitales. *Leea*, in the Leeaceae (see below) is sister to the Vitaceae, which is further subdivided into five groups or clades (numerals on the right) with a total of 16 subgroups that correspond to both formal and informal genera. (Adapted from Liu et al. 2013; Lu et al. 2013; Ren et al. 2011)

Rosaceae (tree fruits such as apple), Brassicaceae (soybean), Vitaceae (grape) and Cucurbitaceae (cucumber). They vary widely in form and biochemistry.

The Vitales form their own line, distant from and ‘sister’ to all the other Rosids. The Vitales-Rosid split is usually placed in the Cretaceous, about 100 million years ago (MYA). Members of the order share some characters, such as the presence of raphide (needle-like) calcium oxalate crystals in cells throughout the plant and ‘pearl bodies’ on the leaf, stem and floral surfaces (Chap. 2, Molina et al. 2013). They also share a similar leaf morphology (although this is variable—see Chap. 2), and an un-