

Chapter 2

Vegetative Features of the Vitaceae

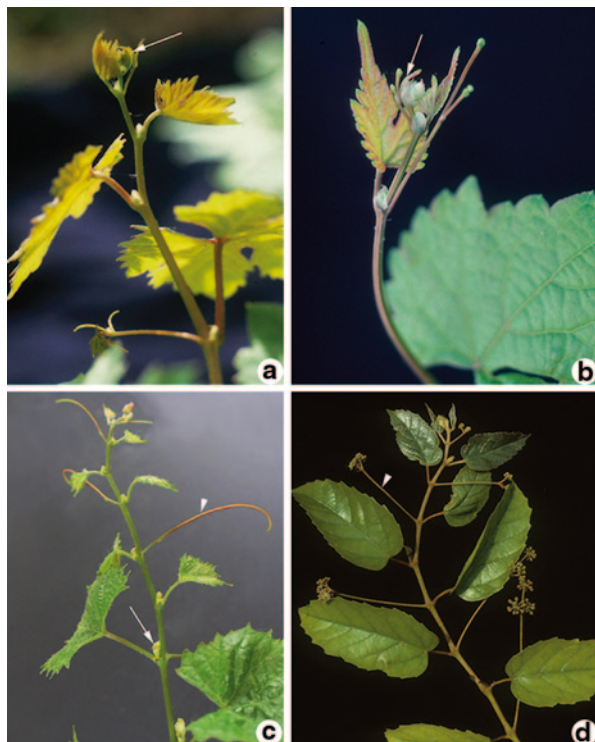
This chapter focuses on the morphology of the shoot and its components (leaves, buds and tendrils). The first section illustrates their overall arrangement on the mature shoot, which can be summarized by 5 shoot construction patterns found in the family. It is followed by more detailed treatments of each component and includes their initiation and early development, as well as their variability at maturity. The unique interrelationship between tendrils and inflorescences in the Vitaceae is also treated at length. We have devoted a section to illustrations of the main hair (trichome) types present because they can be useful in identification. Two anatomical features, pearl bodies and domatia, are of interest because they demonstrate the interdependence between plants and animals. The distinctive pearl bodies found on all shoot organs in the Vitaceae superficially resemble insect eggs and are thought to act as food bodies for insects. Domatia are present on the leaf undersurfaces of several species throughout the family and appear to harbor insects such as mites.

Shoot Patterns and Their Initiation

Because leaves form at the shoot tip (Fig. 2.1a, b arrows), their pattern of arrangement on the stem (phyllotaxis) is laid out from the beginning. There are many possible patterns of leaf initiation and development, and this contributes to the mature form of the plant (Fig. 2.1c, d, see ‘Leaf Development’ below). Lateral buds arise just below the shoot tip in the axil (upper angle) of the young leaf (Fig. 2.1c arrow), which means that their arrangement pattern is tied to the phyllotactic pattern for a particular species. Again, the timing and pattern of bud growth contribute to the overall morphology of the plant (Fig. 2.1a, c, see ‘Lateral Buds’ below). The Vitaceae are unique within the angiosperms in that another organ, the uncommitted primordium, is also initiated at the shoot tip (Gerrath and Posluszny 1988a, 1989a, b, 2007). It will mature into either a tendril or an inflorescence depending on a number of internal and environmental factors (see ‘Tendrils and Inflorescences’ below). It arises opposite the leaves, which is why the tendrils and inflorescences are opposite

Fig. 2.1 Young shoots.

a *Vitis riparia* shoot tip, showing the youngest leaves at the tip (arrow) alternating down the stem, with tendrils opposite the leaves and lateral buds at every node (Fig. 2.2 pattern 4). **b** *Ampelopsis glandulosa* with youngest leaves at shoot tip (arrow) and tendril/inflorescences opposite the leaves at every node (Fig. 2.2 pattern 5). **c** *Vitis rotundifolia* shoot, showing the pattern of alternating leaves with lateral buds in their upper angles (arrow) and tendrils (arrow-head) opposite every two of three leaves (Fig. 2.2 pattern 4). **d** *Cissus antarctica* shoot, showing inflorescences (arrowhead) opposite the leaves and lateral buds only at the tendrillless nodes (Fig. 2.2 pattern 2)



the leaves on mature shoots (Fig. 2.1c, d arrowheads). Thus, the mature morphology of a plant results from a combination of the patterns of organ initiation and their subsequent growth and development.

Leaves in most species of the Vitaceae are initiated alternately up the stem at an angle that approximates 180° from the previous leaf, which means that a two-dimensional drawing of a shoot pattern is relatively accurate. Figure 2.2 illustrates the five possible known patterns of arrangement of the leaves, lateral buds and tendrils in the family (Gerrath et al. 1998, 2001; Gerrath and Posluszny 2007). These shoot patterns are constant for a species and can be used in identification, although many patterns can be present within a genus. There are a few species of *Cyphostemma* (see Chap. 1; Fig. 1.1g, h) that exemplify Pattern 1 in Fig. 2.2, with buds in the axil of every leaf, terminal or axillary inflorescences and no tendrils (Gerrath and Posluszny 2007). In Patterns 2–5, tendrils (or inflorescences) occur opposite the leaves, with varying lateral bud patterns. Patterns 2, 3 and 4 have tendrils opposite every two of three nodes (Fig. 2.2b, d). This results in a tendrillless node (T_0), a lower tendril node (T_l) and an upper tendril node (T_u), labelled in Fig. 2.2d. Lateral buds are present only at the tendrillless node in pattern 2 (Figs. 2.1d, 2.2b). They are present at the tendrillless and upper tendril nodes in Pattern 3 and at every node in Pattern 4 (Figs. 2.1c, 2.2c, d). Both tendrils and lateral buds are present at every node in Pattern 5 (Figs. 2.1b, 2.2e). The fundamental 3-node rhythm of vitaceous

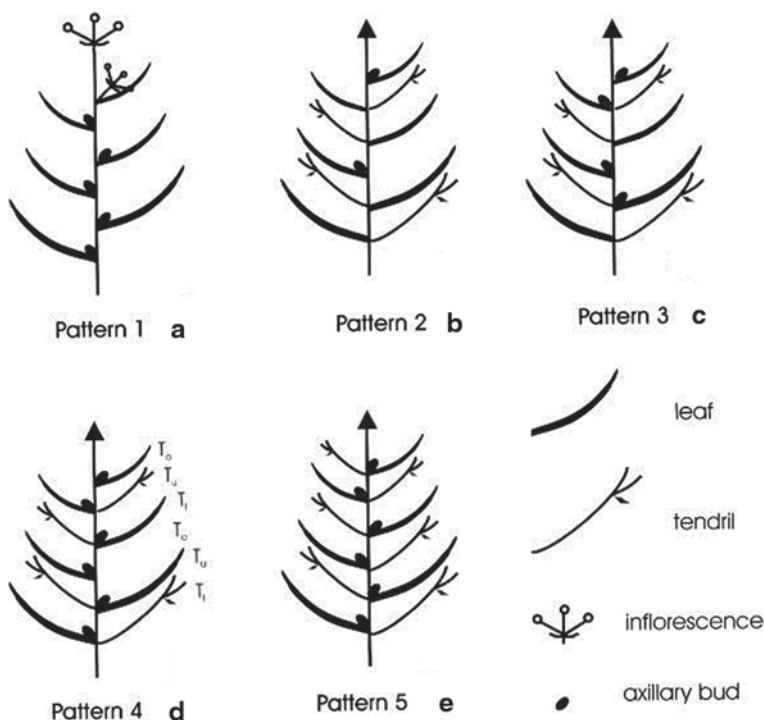


Fig. 2.2 Shoot patterns. **a** Species that exhibit Pattern 1 lack tendrils and have terminal or axillary inflorescences (see *Leea* or *Cyphostemma*, Chap. 1). **b** Pattern 2, in which tendrils are present opposite every two of three leaves, but lateral buds are found only at the tendrillless node. **c** Pattern 3 shows species with tendrils present at two of three nodes, but lateral buds are found only at the tendrillless and upper tendril nodes. **d** Pattern 4 plants again have tendrils opposite two of three leaves, but lateral buds are present at every node. **e** Pattern 5 shows plants with both tendrils and lateral buds at every node. (Reprinted from Gerrath et al. (2001); Fig. 1, with permission from University of Chicago Press)

shoots has been recognized for some time and has been correlated with the vascular pattern of the stem (Fournioux and Bessis 1973; Gerrath et al. 1998, 2001; Gerrath and Posluszny 2007 and references therein). Although there is no known biological significance to this rhythmic pattern, it can be important in physiological and anatomical shoot studies because the configuration of a node varies, depending on its position within the cycle (Gerrath 1988a, 1989a).

Interpreting the structures on a shoot tip takes some practice because they are small and tightly packed. We have found that the best approach is to work backwards, starting with a mature shoot. Once we have determined the mature pattern of leaves, lateral shoots and tendrils, we can find their primordia on a shoot tip at the microscopic level. Since each shoot apex is the meristematic region where cells divide to give rise to the other plant organs, it is called the shoot apical meristem (SAM; Fig. 2.3b6, 2.3d7). The leaves arise on the flank of the SAM and generally

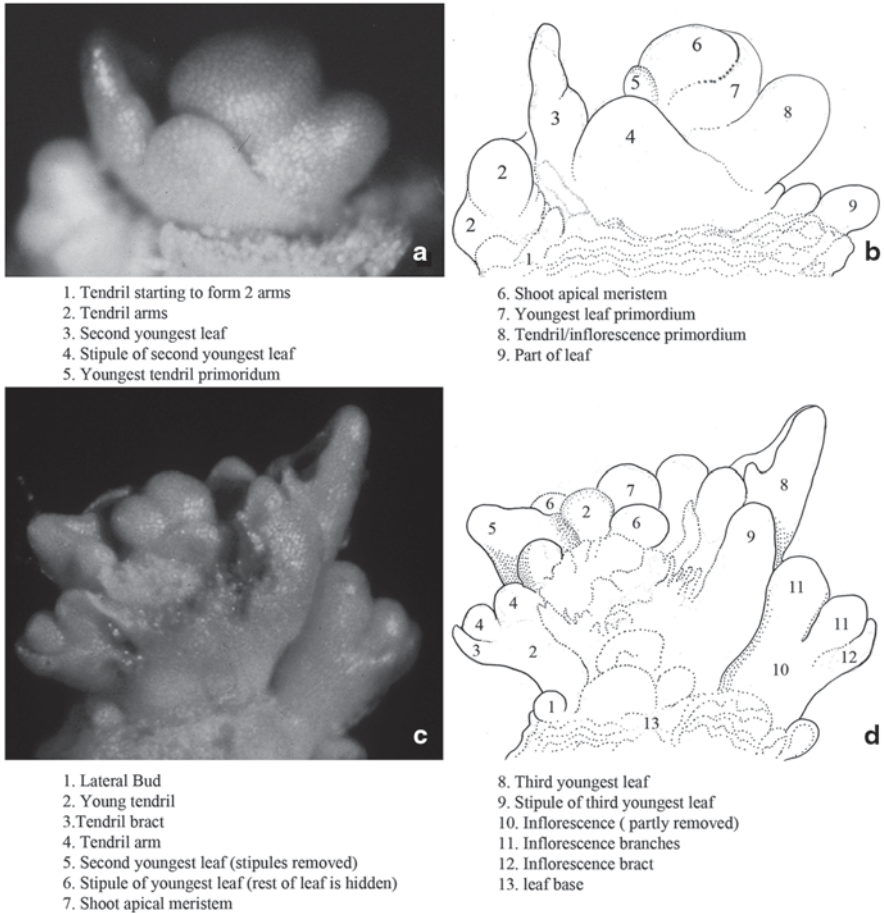


Fig. 2.3 Initiation of shoot organs at the tip. This is a pair of microscopic views of the shoot tip and an accompanying outline drawing with a numbered key to the various organs below each pair. Numbering is clockwise, beginning at the lower left. **a, b** *Ampelopsis glandulosa*. **c, d** *Vitis riparia*

appear flattened from inception. In the Vitaceae, these leaf primordia encircle at least half of the shoot tip (Fig. 2.3b7), and a pair of stipules forms at the ends of the horseshoe (Fig. 2.3b4, d6; see ‘Leaves’ below). A tendril/inflorescence primordium also forms on the flank of the SAM, opposite a leaf (Fig. 2.3b8, d2). It is knob-like and does not appear flattened. In order to see the lateral (axillary) buds as they form, the leaves and stipules have to be removed (Fig. 2.3d5, 13). The lateral buds form slightly later than the leaves and act as a sort of detached shoot apex with the capacity to increase the number of growing points on the plant (Fig. 2.3d1). They may remain dormant for some time or develop quite quickly into a visible shoot (see ‘Lateral Buds’ below).

The next three sections of this chapter discuss the origins, patterns and development of the leaves, lateral shoots and tendrils in more detail.

Leaves—Types, Initiation and Development

Variability in Leaf Form

The first leaves in a seedling are the embryonic seed leaves, the cotyledons (Fig. 2.4a). They vary subtly from species to species, but the general appearance of cotyledons in the Vitaceae is similar among all the species we have examined. The first ‘true’ leaf is more complex in form than the cotyledons (Fig. 2.4b arrow), although the plant may produce several leaves before the mature leaf morphology of that species is realized. Typically, in this family, the first 5–8 or more true leaves occur in a spiral pattern around the stem, and no tendrils are produced. Thus, these are referred to as the ‘juvenile’ leaves. Tendrils are a signal of reproductive maturity, and from that point the leaves are called ‘adult’ and are produced alternately on the stem, about 180° from one another (see ‘Shoot Patterns’ and Fig. 2.3).

Leaf blades in the Vitaceae demonstrate the full range of possibilities of form. They can be categorized as ‘simple’, with the blade consisting of an entire unit (Fig. 2.4c, f), or ‘compound’ (Fig. 2.4g, k), with the blade consisting of a number of leaflets. Compound leaves can be further subdivided into palmately compound, with all the leaflets originating from the same site (Fig. 2.4g, i), or pinnately compound, with several dozen to a few hundred leaflets per leaf arranged along a central leaf axis (Fig. 2.4j, k; Gerrath and Lacroix 1997; Jones et al. 2013).

Each leaf in the Vitaceae consists of the blade, the petiole (the stalk that connects the blade to the stem) and a pair of stipules, one on either side of the base of the petiole. In the Vitaceae, these stipules are usually quite prominent near the shoot tip (Fig. 2.4k, m, arrows). Often, they cover and protect the young shoot tip (Fig. 2.4k) and fall off once the leaf matures. Microscopic studies indicate that they are variable enough that they may be used in identification (Lacroix and Posluszny 1989).

Leaf Development

Leaves are initiated on the flanks of the SAM (Fig. 2.3a, b7), first as flattened structures that will become the leaf blade, accompanied by a pair of stipules at the base of the blade (Figs. 2.3a, b3, 2.4). As the blade continues to grow, it becomes folded in half along what will become its midrib, with each half developing as a mirror image of the other (Fig. 2.5a arrow). As the leaf matures, lobes develop along what will become the leaf margin, from the base to the tip of the leaf (Fig. 2.5a, b arrow, d). These lobes can themselves fold and form their own second-order lobes, resulting in a bipinnately compound leaf (Fig. 2.5e). Recently Jones et al. (2013) showed that up until this point, the pattern of leaf development in both simple and compound leaves in two North American species with widely differing mature leaf morphologies (*Ampelopsis cordata* with simple leaves and *Nekemias arborea* with

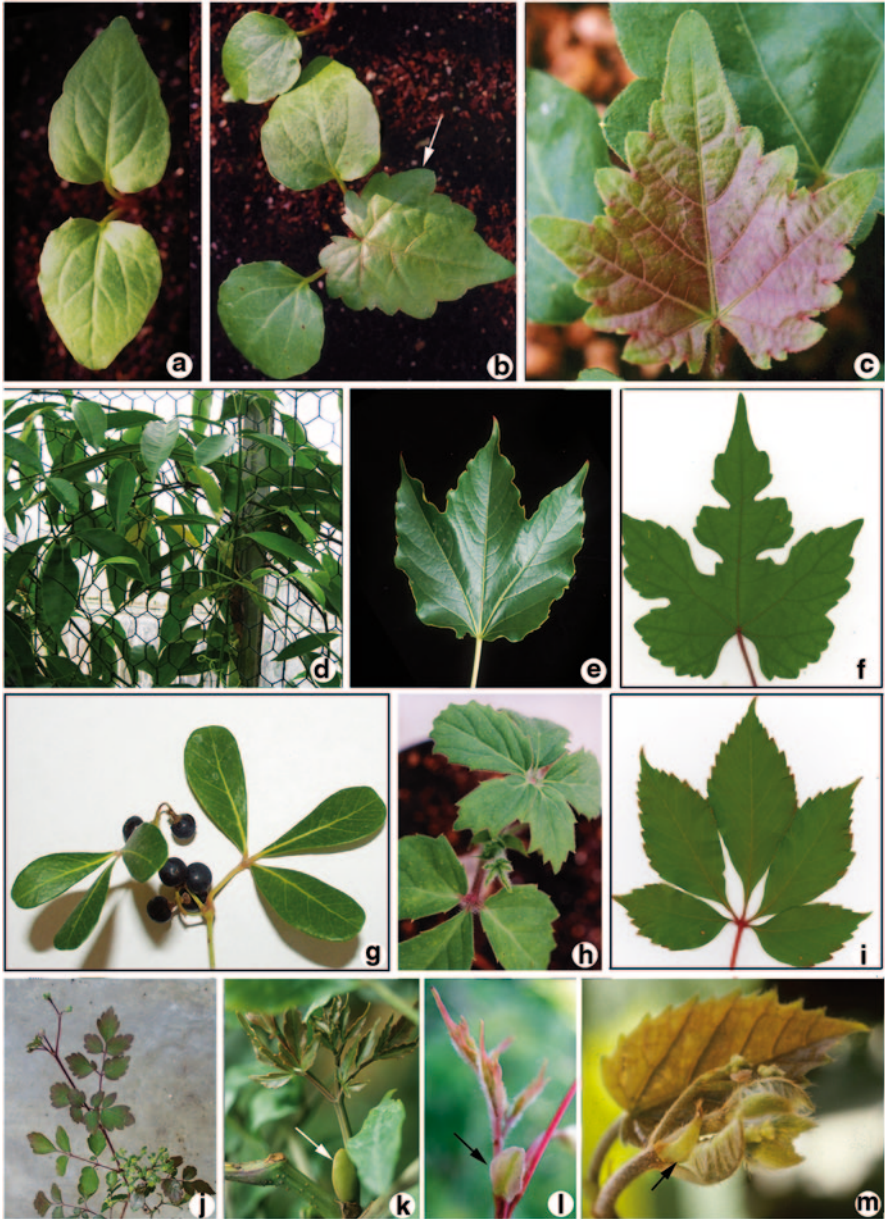


Fig. 2.4 Leaf morphology. **a–f** Simple leaves. **a–c** *Ampelopsis humulifolia*. **a** Seedling with two seed leaves (cotyledons). This shape is typical for the family. **b** Seedling at a later stage with its first true leaf (*arrow*). **c** An immature leaf. It is flat but has not reached its mature form, and what appear to be lobes will form the teeth along the leaf margins. **d** *Nothocissus spicifera* leaves with very few teeth. **e** *Parthenocissus tricuspidata* leaf with 3 lobes. **f** *Ampelopsis glandulosa* leaf with a complex lobed pattern but still a simple leaf because the lobes do not meet the midvein. **g–l** Compound leaves. **g** *Rhoicissus digitata* leaves with 3 leaflets (trifoliate). **h** *Cyphostemma sandersonii* showing a leaf with 3 leaflets followed by a leaf subdivided into 5 leaflets. **i** *Partheno-*

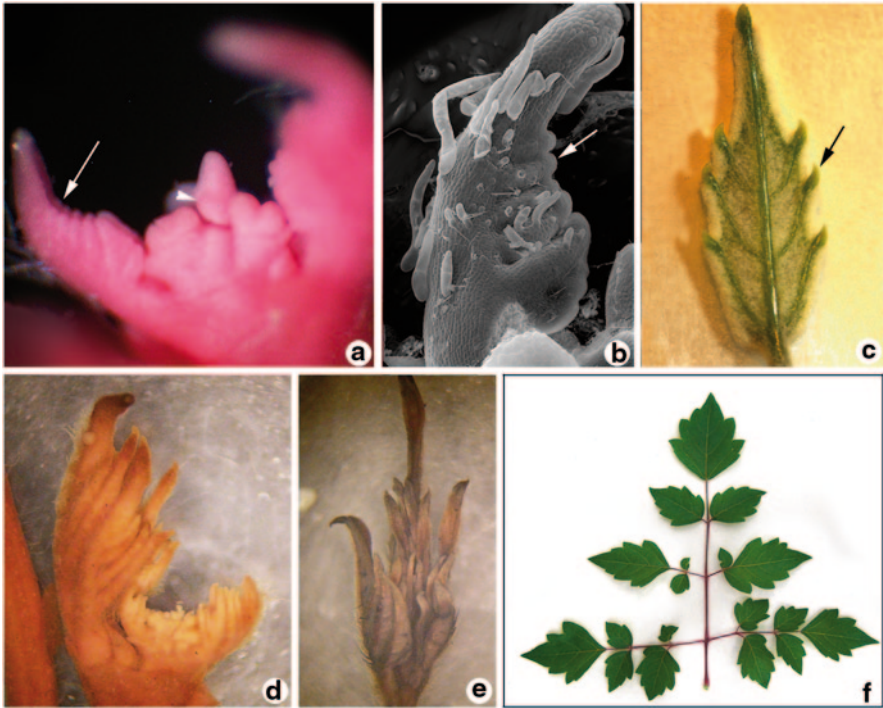


Fig. 2.5 Early development of simple and compound leaves. **a–c** Simple leaves. **a, b** *Ampelopsis cordata*. **a** Shoot tip, showing a young leaf (*arrowhead*) just beginning to form lobes. The next oldest leaf (*arrow*) has formed a number of marginal lobes. **b** View of one side of a leaf, showing the lobes (*arrow*) where the lateral veins will develop. They will become the teeth on the leaf margin. **c** *Pterisanthes polita* unfolded leaf, showing the developing teeth (*arrow*) along the leaf margins. **d–f** Compound leaves. **d–f** *Nekemias arborea*. **d** Shoot tip, showing the same basic pattern of development as in *A. cordata*, but in this case, the tissue between the lobes fails to continue development, leaving the possibility of leaflet formation. **e** Face view of a developing leaf in which the individual leaflets are becoming distinguishable. **f** Mature leaf, showing the bipinnately compound leaflet pattern. (Photo credits: **a, d–f** Ben Doughan; **b** Austin Jones; **c** Limin Lu)

compound leaves) appears identical. In a simple leaf (illustrated here by *Pterisanthes polita*), the tissue between the lobes continues to grow so that the lobes do not become separate but instead form the teeth along the margins of the leaf blade (Fig. 2.5c *arrow*). In contrast, in a compound leaf, the lobes continue to elongate faster than the intervening tissue, resulting in separation of the lobes to form individual leaflets (Fig. 2.5d–f). Thus, it is only later in development that the two types of leaf forms differ.

cissus quinquefolia leaf showing the 5 leaflets arising from a single point (palmately compound). **j** *Nekemias arborea* leaves, bipinnately compound, resulting in many leaflets. **k** *Leea guineensis* leaf, also bipinnately compound. The stipules of this leaf (*arrow*) cover the shoot tip that contains the primordia of younger leaves. **l** *N. arborea* leaf base, showing the typical ephemeral stipules (*arrow*) in the family. **m** *Cissus antarctica* shoot tip, showing hairy stipules (*arrow*)

An important class of transcription factors in plants, knotted-like homeobox (KNOX) genes, are important in shoot growth. Class 1 KNOX genes are normally expressed in the SAM of plants, where they maintain the indeterminate state of the cells. Typically they are not expressed in the leaf primordia of species with simple leaves. In contrast, in compound leaves, their expression can be detected early in formation of the lateral lobes. In the Vitaceae, KNOX is typically expressed in the lobes of both the simple and compound leaves (Bharathan et al. 2002). The most likely explanation for this observation is that the ancestral leaf state in the Vitaceae was compound and that simple leaves are a derived character in the family. This is consistent with the fact that leaves in *Leea*, sister to the Vitaceae, are compound (Chap. 1; Jones et al. 2013).

As the leaf matures, the developing veins follow the pattern of the leaf lobes (Jones et al. 2013). Structures known as hydathodes (common in many plants) form at the vein tips and form a conduit for liquid water (and salts) to leave the plant through the process of guttation. Guttation occurs under conditions of high humidity and damp soil, favouring uptake of water into the roots but preventing evaporation via the stomata in the leaves. Typically, a hydathode consists of a region of many xylem vessels that discharge the water via stomata-like water pores onto the leaf surface. The Vitaceae are unique in that guttation has also been documented in *Vitis* tendrils (Fig. 2.6d; Tucker and Hoefert 1968; Gerrath and Posluszny 1988a).

Lateral Buds: Pattern and Position

Lateral buds in the Vitaceae originate in the upper angle (axil) of the leaves and have the capacity to form new shoots that repeat the pattern of the main stem (Fig. 2.7a arrow). It is the lateral buds that form the reserve of growing tips that allow plants to survive drought, freezing, herbivory and pruning. The bud primordium has the capacity to remain dormant as a small mass of cells but typically develops further to form a lateral bud with at least a few leaves. In turn, lateral bud primordia and buds form in the upper angles of these leaves with the result that each visible lateral bud contains several smaller buds, each of which can grow out or remain dormant for many years, depending on environmental cues (Gerrath and Posluszny 1988a, 1989a, b, 2007). There are two fundamental patterns of lateral bud arrangement in the Vitaceae, the typical one found in *Vitis* and another, uncommon one, in which supernumerary buds also form.

Typical Bud Pattern

Figure 2.8 is a diagram of a cross section through a typical leaf axil (upper angle) in the Vitaceae. Beginning with the main stem, all of the lateral buds and shoots arising from this stem are 1° branches, the lateral buds in the leaf axils of these shoots

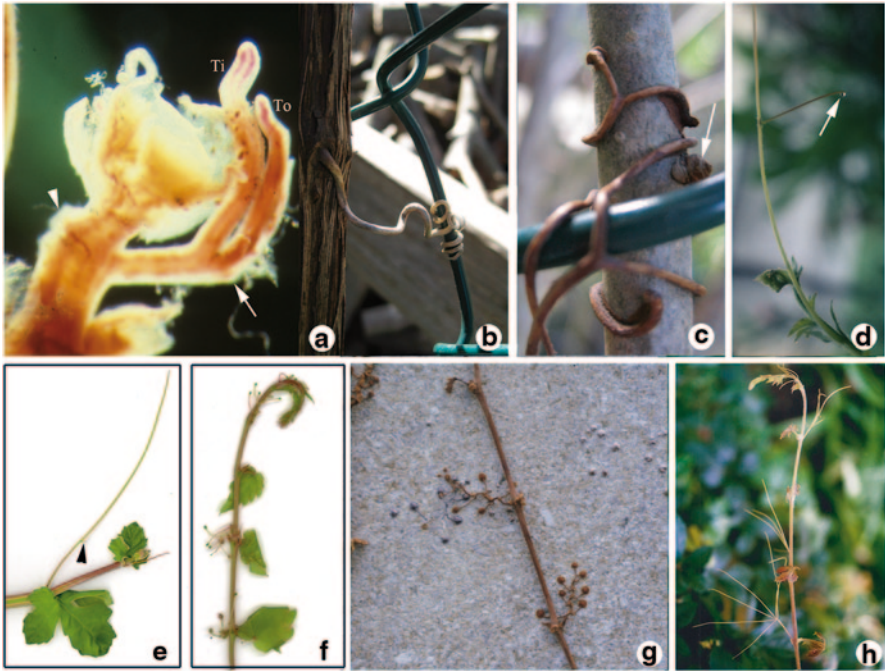


Fig. 2.6 Tendrils. **a, b** *Vitis riparia*. **a** Cleared shoot tip, showing a young tendril that has formed opposite a removed leaf (arrowhead), with its inner, main arm (T_i) and the outer arm (T_o) which forms in the upper angle of a bract (arrow). **b** Mature cane with a tendril, showing how its branches coil and provide support to the vine. **c** *Parthenocissus inserta* tendril tips (arrow) which have expanded and are adhering to a substrate. **d** *Cyphostemma simulans* tendril tip with a droplet of guttation fluid (arrow). **e** *Cissus aleyana* unbranched tendril with no branch arising from the bract (arrowhead). **f** *Parthenocissus tricuspidata* young tendril tips, showing the green pads developing prior to adhesion. **g** *P. tricuspidata* mature tendril tips adhering to a wall. **h** *Tetrastigma obtectum* tendrils in which the branches appear to arise from one point and are therefore digitate

are 2° branches and so on. In this way, the number of lateral buds in any bud that are capable of producing a leafy stem is very large and can appear very complex (Fig. 2.8). For this reason, this bud pattern is often called a ‘complex bud’ and is common in plants. The leaves of each order of shoots in *Vitis* are oriented at more or less 90° from the previous one so that the leaf at the bottom of the diagram is attached to the main stem, and the leaves attached to the 1° summer lateral are oriented 90° to the main stem leaf. This helps in the detection of the relationships of the bud orders to one another.

In *Vitis*, the summer lateral typically grows to form a small branch during the year in which the main shoot grows (Fig. 2.7a arrow, b star). Secondary lateral buds arise in the axils of the basal leaves of the summer lateral (Figs. 2.7b, 2.8) above the petiole of the leaf attached to the main stem (Fig. 2.7b arrow). In Fig. 2.8, the internodes between the leaves are compressed so they look directly opposite one another, but in reality they alternate. The outer leaves on the 2° laterals typically

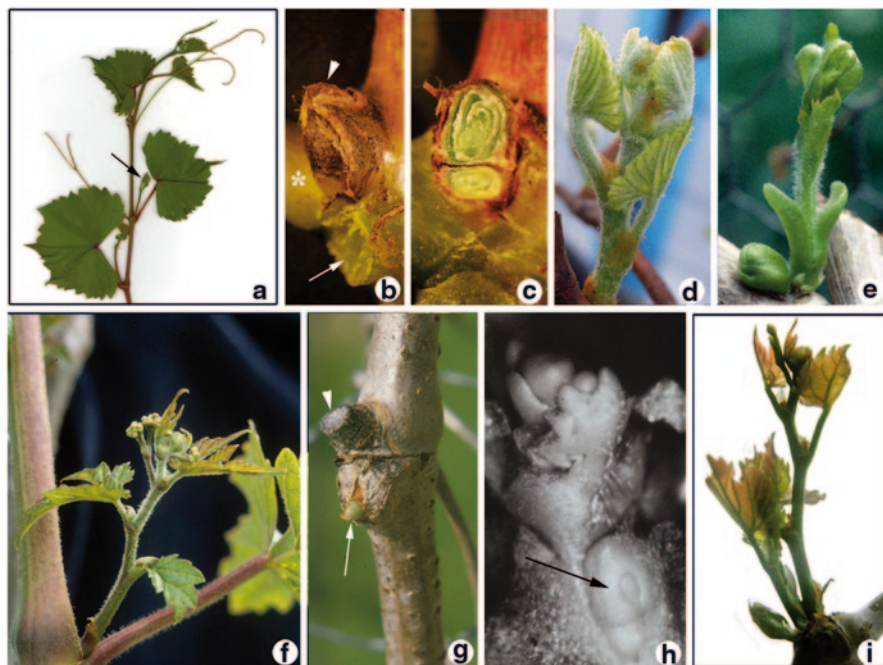


Fig. 2.7 Lateral buds. **a–e** ‘Complex’ bud pattern. **a** *Vitis rupestris* shoot with the typical pattern of alternating leaves with tendrils opposite them and lateral shoots (‘summer laterals’) arising in the leaf axils (arrow). **b–d** *Vitis riparia*. **b** A winter bud (arrowhead) covered by bud scales. The leaf below the bud (arrow) has fallen off, and the summer lateral (star) has been cut. **c** The same winter bud has been sliced across to show that it contains two buds, each with a central stem and surrounded by leaves. **d** Bud break in spring. **e** *Cyphostemma simulans* bud break, showing one bud extending from two green bud scales, and a smaller bud beside it. **f–i** Supernumerary buds. **f–h** *Ampelopsis glandulosa*. **f** Lateral ‘summer’ shoot which has the typical pattern with alternating leaves, inflorescences opposite them and lateral buds in the axil of each leaf. **g** A shoot from the following spring in which the ‘summer’ lateral has fallen off (arrowhead), and below it, a bud (arrow) is peaking through a pad of tissue formed from the base petiole. **h** A longitudinal view of a node, showing the well-developed first lateral and a vertical line of independent buds that will remain dormant over winter developing from oldest (arrow) to youngest. **i** A vertical series of *Ampelopsis humulifolia* buds in spring. (Figure 2.7h reprinted from NRC Research Press, Botany, Gerrath and Posluszny (1989b). Figure 55, with permission from NRC Research Press)

develop into overlapping bud scales that protect the buds which remain dormant and do not usually grow out until the following growing season (see Appendix 2). The leaves on these 2° buds are oriented in the same plane as those on the main shoot. Although the 2° buds remain dormant over winter, by autumn they have formed the leaves and clusters which will grow out the following growing season (Fig. 2.7c, 2.9). The bud that forms in the axil of the lowest (oldest) summer lateral leaf is called the primary bud by viticulturists, and the one that forms in the next oldest leaf axil is known as the secondary bud. Figure 2.7e shows both a primary

Taming the Wild Grape

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