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CHAPTER 1

Phenomenon of Guttation and Its Machinery

1.1 Introduction

Secretions in plants, animals, and humans constitute natural and fundamental metabolic processes vital for their life (Fahn 2000; Squires 2010; Vivanco and Baluska 2012; Wilson 2009). In plants, guttation is one of the conspicuous secretions, which has been known for about three-and-a-half centuries (precisely 348 years). Abraham Munting of Holland (now the Netherlands) was the first to discover this phenomenon way back in 1672, though the word 'guttation' was not in existence then. Moreover, the subject was not in the mainstream of research until about two to three decades ago, though the secretory tissues are present in most vascular plant species. The substances present in the secretions of hydathodes, secretory glands, and nectaries are mostly in unmodified or only slightly modified forms, and they are supplied directly or indirectly through vascular systems. Apart from these secreting organs, some other secreting tissues exist that secrete, for example, polysaccharides, proteins, and lipoids, and these substances are produced by them in their own cells. Secretory tissues usually contain numerous mitochondria; however, the distribution of other cell organelles varies in accordance with the materials they secrete. The side wall of the lowest stalk cell in the most glandular trichomes is completely cutinized, which prevents the flow of secreted materials back into the plant body. In this chapter, the occurrence and taxonomic distribution of guttation and morphological, anatomical, and ultrastructural aspects of hydathodes, that is, the mouths of guttation, have been described in some detail based on the current available information and discovery (Singh 2013, 2014a,b, 2016a,b).

1.2 Definition of guttation

The term 'guttation' (coined by Burgerstein in 1887) is derived from a Latin word *gutta*, which means 'drop'. It is also referred to as the secondary compound exudated from certain trees, that is, trans-1,4 polyisoprene, which has a lower molecular weight than that of natural rubber. The phenomenon of guttation and its process have been known for 350 years (Ivanoff 1963); however, its significance in plant physiology was not known (Stocking 1956a). It is basically a biophysical and physiological occurrence in which fluid is expelled out through the leaves. Guttation has many implications and applications in agriculture, in balancing the ecosystem, as well as in pharmaceutical and industrial products (Singh et al. 2008, 2009a; Singh and Singh 2013; Singh 2014a,b, 2016a,b).

Water loss in the form of liquid from the edges, surface, or tips of uninjured or undamaged leaves is called guttation. This is different from transpiration, in which water is lost in vapor form. Guttation occurs during minimal evaporation, with escalating water transport to the leaves. For example, guttation is observed in the early morning in case of grasses, where water droplets accumulate at the tip of the grass, which may be confused with dew. Exudation of water droplets or fluid occurs through specialized plant organs known as hydathodes (otherwise known as water stomata or water pores). These specialized structures are found at the tip of the leaf, its boundary or periphery, and on the leaf surface. Guttation assists the plant in getting rid of excess water along with certain dissolved materials, which is why it is also referred to as 'teardrops' of leaves. In case of land plants, the fluid is excreted intermingled xylem or phloem sap and is translucent. This is called 'terrestrial guttation' (Stocking 1956a). Guttation of submerged aquatic plants is called 'aquatic guttation' (Pedersen 1993, 1994, 1998). Moreover, space explorations have observed guttation in case of dwarf wheat plants, which is called 'aero-guttation' (Bugbee and Koerner 2002). The process is such that the more moisture the plant draws to itself, the more it throws off again (Kundt and Gruber 2006). Guttation builds up when the water transport exceeds the evaporation from leaves, which is usually the case during the night or early in the morning when the atmosphere is highly humid. In most environments, humidity is relatively low and usually the water of guttation evaporates as fast as it is exuded and therefore goes unnoticed. In other cases, guttation occurs on the leaf periphery (e.g. in case of lettuce) (Curtis 1943). This occurs because of the low surface tension of the guttate, which prevents water droplet formation. Before guttation, the formed water droplets gather in the leaves' convolutions. However, surface guttation should not be confused with either transpiration or condensation of dew on horizontal leaves.

1.3 Biographical sketch of Abraham Munting (1626–1683)—discoverer of guttation

Ivanoff (1963) wrote that Munting's name has not been mentioned in any of the history books of botany or plant physiology that he studied. This is adequate reason for developing a brief biographical sketch, from Munting's work 'Naauwkeuringe beschryving der aardgewassen', of a researcher who discovered the process of guttation. The English translation of the work states:

> The discoverer Abraham Munting, Hendrikszoon [son of Hendrik], Arts en Meester [Doctor and Master], was born on the '19th day of the summer month' [August?], 1626 in Groningen, Holland. Dr

Hendrik Munting was his father, who was a Professor at Groningen Academy. He excelled in the fields of Botany and Chemistry. One of his most popular works for which he is known is referred to as the 'Hörtus universae materiae medicae gazophylacium', published in the year 1646. The work listed out large varieties of gardening specific plants, such as medicinal, tulips, pinks, water hyacinths, and so on, which were cultivated by him. This printed publication work can be considered as the first ever catalogue for gardeners. Munting's maternal grandfather, Johan Reriaman, was treasurer of d'Ommelanden. His paternal grandfather, Joris Munting, was a gold and silver businessman.

At the age of 18 years, Munting started going to the college at Groningen. Later he lived in France for some time studying medicine and botany. He travelled extensively. Returning to Holland, he became a faculty member at the University of Groningen, where he worked for 24 years, earning eminence as a professor of botany and chemistry. With passing time, he advanced upon the work of his father. Between 1658 and 1683, he directed one of the best and most extensive botanical gardens of the time. Holland was already famous for its collection of plants. Building upon his father's gardens Munting cultivated a large collection of different species, which he named 'Paradise of Groningen'. He also grew many a rare species.

During a sojourn, in 1658, Munting was conferred the title of Doctor of Medicine, in France (Angers). In his professional career of 24 years, he worked on some brilliant pieces, some of which were published posthumously after his death, due to 'catarrhe suffoquant', on January 31, 1683. In 1680, he published works like 'Aleidarium' or 'History of the American Aloes'; in 1681, he published 'De vera antiquirum Herba britanica'. Munting's most famous work 'Naauwkeurige beschryving der aardgewassen' was published in 1696, 13 years after his death, which is an enlarged and revised version of his previous book 'Waare oeffening der planten', earlier published in 1672 and republished in 1682. The Latin editions of 'Naauwkeurige', which gathered much appreciation and recognition, were later republished in a series under the title 'Phytographia Curiosa', beginning in 1702. Plumier named a genus Muntingia in his honor. The genus consisted of a single variety of plant, which was then included under Rhamnus by Linnaeus and was named as *Rhamnus mican*, thus including Muntingia to the genus list of the Tiliaceae family.

Why was Munting's work not recognized by botanists? In this context, Ivanoff (1963) agrees with Michaud (1854) who stated that 'The Munting generation, though has [having] contributed to [the] cultivation of some rare as well as wide range of plants, however, made least contribution to the field of botany as a whole.' The process of guttation and its impact on a plant's water economy was not well understood or even recognized by botanists at that time.* Moreover, categories of injuries linked to guttation became topics for research much later, and they still require considerable attention from botanists.

* An explanatory note has been referenced over here that was presented by DeBary, the editor, who published it in Botanische Zeitung, which was followed by publication of a discussion on water pores. The discussion was held at Russian Botanical Society in Moscow, 1869. DeBary stated, 'Wenn Man bei einem zweige rifler geeigneten Pflanze, z.B. *Fuchsia globosa*, Wasser durch den massigefi Druck rifler Quecksilberaule in das Holz einpresst, so treten aisbald Wassertropfen aus den grossen Stomata hervor.' Here, no discoveries are mentioned; however, artificial guttation method was talked about, in which the cut part of stems or petioles of leaves showed artificial guttation under mercury pressure.

1.4 Phenomena resembling guttation

For the sake of clarity, it is pertinent to describe briefly a few other phenomena resembling guttation.

1.4.1 Dew

Dew is the condensation of atmospheric water vapor on the leaves of plants, especially when the atmospheric humidity is high and the nights are cool. It is different, however, from guttation where water generally comes out from within the leaves through hydathodes. Dew is relatively pure water, which does not contain anything except some gases of the atmosphere dissolved in it, whereas guttation fluid, which is actually xylem and phloem saps intermingled together, consists of both organic and inorganic substances.

1.4.2 Bleeding or oozing

In case of herbaceous/woody plants, sap exudation from a cut or injured stem is called bleeding or oozing. The bleeding rate can be either slow or fast depending on the root pressure in xylem (positive pressure), phloem pressure in sieve tubes, and the pressure around the injury. In a single day, 5–6 L of sap are exuded, and nearly 150 L of sap are exuded from the upper end of the trunk of a 30–40 feet high vigorous Indian date palm (*Phoenix sylvestris*), although the average yield is about 25–75 L of sap in a season (Bose 1923). The highest bleeding, about 50 L per day, is found in *Caryota urens*. The average sugar content of the sap is about 2–3 percent (Kramer 1949). The exudation of latex from rubber (*Ficus elastica*) is a relevant instance of bleeding. However, the mechanism behind bleeding is unclear. For exudation, many conditions are essential such as warm days and freezing nights during the winters and early springs when leaf expansions occur. During these freezing temperatures, the root systems are usually within the frozen soil (Johnson 1945). Hence, for the movement of sap, the plant roots must have moisture available, which favors bleeding. Exudation of water from detached pine needles was also considered to be due to processes distinct from those causing guttation (Kramer 1949).

1.4.3 Other plant secretions

Secretion assists the plant in conducting various functions such as attracting pollinators, disposing solutes, and taking up nutrients. Moreover, it helps the plant in maintaining the functionality of the secretory organs like that of the nectaries, salt glands, and trichomes, which are mainly found in vascular plants; however, both the secretory and retrieval mechanisms are not well understood (Pilot et al. 2004). Some of these secretory organs exudate unmodified or moderately modified materials that are directly/indirectly supplied from vascular tissues. Secretory tissues seem to have developed from secretory idioblasts scattered among the cells of ordinary tissues during the course of evolution. Subsequently, ducts and cavities seem to have developed and given rise to secretory trichomes (Fahn 1979, 1988, 2000). Certain substances, such as polysaccharides, lipophilic materials, and proteins, are secreted in the cells of certain types of secreting tissues. However, plasmodesmata present in the nectariferous tissue provide passage for the prenectar products to the secretory cells. The vesicles of dictyosomal origin generally tend to eliminate nectar, which is of phloem origin, from the secretory cells. The nectar secretion, which in some cases involves both these organelles, may be achieved eccrinally as well (Fahn 2000; Vivanco and Baluska 2012). Dictyosomes are known to synthesize carbohydrate, mucilages, and gums. Chloroplasts (or plastids) synthesize lipophilic substances, which are secreted by almost every cell compartment. In some cases, these substances move toward the plasma lemma. Resin or gum secretion from a plant part can occur as a natural process of exudation or because of certain external stimuli (e.g. microbes and growth substances) (Telewski 2006). Among the external stimuli, ethylene is considered as the most effective (Baluska and Mancuso 2009). The secretory tissues consist of numerous mitochondria; however, the concentration of other cell organelles depends on the nature of secreted substances. The secretory glands, which are modified cells (or hair), are usually not as tightly bound with the xylem tissues as in the case of hydathodes. Some glands secrete dilute substances consisting of sugar and salts, whereas some of them release enzymes, volatile oils, nectar, and resins. Thus, such exudation of sap is commonly referred to as secretion. It is apparently caused by forces that develop within the gland, but the mechanism of force development is unclear (Vivanco and Baluska 2012).

1.5 Taxonomic distribution of guttation

Guttation is observed in a wide range of angiosperms, gymnosperms, ferns, algae, and fungi. Early studies of hydathodes, the natural leaf pores through which guttation takes place, include those of Haberlandt (1914) and Lepeschkin (1923). Later studies reported this phenomenon and associated it to structures occurring in plants belonging to Crassulaceae, Moraceae, pteridophytes, and cereals (Maeda and Maeda 1987, 1988; Lersten and Peterson 1974; Rost 1969; Sperry 1983). A marked presence of hydathodes has been noted in many dicot families, which includes Salicaceae, Balsaminaceae, Rosaceae, Asteraceae, Begoniaceae, and Urticaceae (Brouillet et al. 1987; Chen and Chen 2005, 2006, 2007; Curtis and Lersten 1974; Elias and Gelband 1977; Lersten and Curtis 1982, 1985, 1991). Hydathodes are found on the entire leaf surface, tip, and edges (Singh et al. 2009a). Moreover, they exist on hypodermis of grape (*Vitis vinifera*) tendrils or submerged aquatic plants (Fahn 1979, 1988, 2000; Pedersen 1993, 1994, 1998; Pedersen et al. 1997; Tucker and Hoefert 1968).

1.5.1 Angiosperms and gymnosperms

Guttation has been noted across a wide range of plants in the plant kingdom, including lower as well as higher plants (Figure 1.1). However, it is not widely observed among the taxons. Burgerstein (1920) and Frey-Wyssling (1941) worked on a list of plant species showing guttation (around 333 genera and 115 families as listed by Bergerstein; 43 sub-alpine and alpine genus, that is, Equisetum to Salix as reported by Frey-Wyssling), which has now gained a status of a common phenomenon in case of plants. Burgerstein (1920) also suggested the process of guttation in case of woody and berbaceous plants. Twelve genera were left out by Burgerstein as reported by Klepper and Kaufmann (1966). As per the previous research, only three dicot families have laminar hydathodes (Lersten and Curtis 1991). In case of Urticaceae, a clear linkage was observed among the minor vein junctions in all five tribes. This was seen in 43 species belonging to 30 genera of which just one species did not have hydathodes. Adaxial hydathodes were observed in 28 genera. In case of *Elatostemeae* tribe, laminar hydathodes were observed in *Pilea* and *Pellionia* species, which are abaxial, adaxial, or present

(a) Horsetail (*Equisetum arvense*)

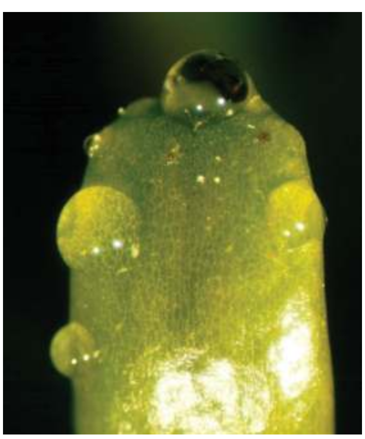
(b) Strawberry leaf (*Fragaria ananassa*)

(c) Wheat (*Triticum aestivum*)

(d) *Annual bluegrass (Poa annua)*

(e) Tomato leaf (*Solanum lycopersicum*)

(f) Garden *burnet* (*Sanguisorba minor)*



(g) *Water lobelia (Lobelia dortmanna)*

FIGURE 1.1 Guttation in the form of droplets in different plant species [*Source*: (*a*) https://commons.wikimedia.org/wiki/File:Dew_on_a_Equisetum_fluviatile_Luc_Viatour.jpg, (*b*) https://commons.wikimedia.org/wiki/File:Guttation_ne.jpg, (*c*) https://commons.wikimedia.org/wiki/File:Guttation_on_Christmas_Wheat.JPG, (*d*) https://commons.wikimedia.org/wiki/File:Leaves_with_drops.jpg, (*e*) https://botweb.uwsp.edu/Anatomy/images/hydathodes/pages/anat0976.htm, (*f*) https://commons.wikimedia.org/wiki/File:Sanguisorba_minor,_Botanischen_Garten_zu_Berlin.jpg].

on both sides of the leaf. As guttation was considered a widely occurring phenomenon by Frey-Wyssling (1941), he stated that the guttation process must be considered a crucial phenomenon in determining water and plant relationship. Pedersen (1993, 1994, 1998) has considered the guttation process as the sole method of transfer of water and nutrients throughout the plant, especially in case of aquatic and submerged plants, where transpiration is minimal.

In case of terrestrial plants, guttation is observed in herbaceous as well as woody plants, and it depends on environmental factors as well. Some of the examples are garden *Nasturtium*, lotus, *Colocasia*, strawberry, *Cucurbita*, *Abies balsamea*, and gramineous family. Broad-leaved trees show the phenomenon of guttation; however, it has also been readily observed in low-growing herbaceous plants. However, plants with reduced leaves, such as in the case of conifers, showed a lack of guttation or root pressure in a study (Kramer 1949). Conversely, Daniel (1949) noted the occurrence of root exudation in 8-month cultured plantlets of plant species like *Sequoia gigantea*, redwood trees, pine trees, Monterey pine, and Port Orford cedar.

Tall trees that grow in areas of high rainfall and humidity, such as tropical rainforest trees, show high guttation and low transpiration (Choat et al. 2012; McCulloh et al. 2011; Sperry 2011). It has been observed in trees like *Amborella* (a kind of shrub), *Trimenia papuana*, *T. weinmannifolia*, *Saruma henryi*, *S. glabra*, *S. chinensis*, *Kadsura longipedunculata*, *K. japonica*, and all Chloranthaceae genera; however, plant species having leaves with complete margins did not show guttation (*Austrobaileya*) (Feild et al. 2003; Feild and Arsens 2007). Furthermore, future studies are needed to determine the reasons for guttation in plants where root pressure is minimal or absent. The conditions favoring this process must be investigated. The effect of mycorrhizas on the guttation process is not well researched, neither has its role in water and nutrient uptake been stated variedly.

1.5.2 Pteridophytes

The fronds of many ferns in Polypodiaceae and Cyatheaceae possess swollen vein endings associated with specialized adaxial epidermal cells (Ogura 1972). Their structure is similar in all ferns (von Guttenberg 1934), including *Blechnum lehmannii* Hieron (Sperry 1983). The endings of developing fronds secrete water when transpiration reduces or stops. In some species, the secreted water contains salts, which form 'chalk scales' after the water evaporates. Guttation in gametophytes has been observed on illumination in certain fern species such as common horsetail (*Equisetum arvense*) and maidenhair spleenwort (*Asplenium trichomanes*). These are some of the classic examples or models for studying the mechanism of guttation in detail. On illumination, changes in the value of membrane potential have been recorded in the presence of an ion channel and proton pump inhibitors, in order to reveal the response nature and its connection to guttation. A potential role of potassium and chloride ion channels in light-induced guttation has been implicated (Szarek and Trebacz 1999).

1.5.3 Algae and fungi

The fungus *Pilobolus* has been studied as a model for guttation because of its fluid exudation capabilities (Tarakanova et al. 1985; Tarakanova and Zholkevich 1986) (Figure 1.2). Research was conducted on large *Pilobolus* cells that confirmed the link between a cell's electrical polarization and water flow occurring in a single direction. A positive correlation was observed in the fungus, taking into consideration the rate or intensity of guttation and membrane potential gradient value. Gareis and Gareis (2007) observed guttation in eight different kinds of ochratoxigenic isolates (from 11 known isolates) of *Penicillium nordicum* and *P. verrucosum*. The fluid exudates contained ocratoxin A and B in high amounts (these are mycotoxins) when the isolates were grown on high concentrations of mycotoxins from Czapek yeast extract agar for about 1 to 2 weeks (10–14 days) at 25°C. The production of exudates differs significantly depending on the growth media. For example, parallel culture of one strain each of *P. nordicum* and *P. verrucosum* on malt extract agar demonstrated the efficacy of this agar by yielding higher volumes of exudates. Similarly, a number of polypores, for example, *Polyporus squamosus*, exude droplets of water during their development. This fungus is parasitic and saprobic in nature, and it feeds on living or dead tree trunks/logs. This kind of guttation is similar to the 'dewatering' phenomenon that occurs in higher plants, thus presenting a good example of the guttation process (Emberger 2008). Moreover, algae (also genetically modified ones) have shown fluid secretions (Daniell et al. 2002).

FIGURE 1.2 A striking example of 'dewatering' process, i.e. guttation having a number of polypores exuding droplets of water during development of fungus *Polyporus squamosus* [*Source*: Emberger 2008].

1.6 Gateway of guttation: hydathodes as exit pores

1.6.1 Structural biology of hydathodes

In higher living organisms, both plants and animals, various physiological functions are based on the laws of division of labor because of the complexities of life activities. Individual functions are, therefore, performed by various separate sets of specialized tissues. Plants are known to possess specialized systems for various functions such as photosynthesis, transpiration, translocation of organic metabolites, solute and water absorption and transport, and the exit of guttation fluid from leaves. For example, transpiration, that is, the loss of water in the form of vapor, takes place through stomata, whereas guttation, again the loss of water but in the form of liquid, takes place through special structures called hydathodes. Thus, form and function are intimately linked to each other, they go hand in hand (Dodd and O'Sullivan 2012; Tyree and Zimmermann 2002). Below are, therefore, discussed the morphology, anatomy, and ultrastructures of hydathodes, that is, mouths without lips, for the exudation of liquid in guttation.

1.6.1.1 *Morphological and anatomical aspects*

During the 18th century, the guttation process was observed in case of barley, where water droplets were seen at its edges, especially during spring mornings. It was due to the positive root pressure. A similar phenomenon was observed in oat, wheat, and maize because of their large, conspicuous stomata at coleoptile apices that cause the water droplets to escape from these gaps when the atmosphere is moist. Currently, these pores are called water pores, and the discharge of water and solutes from the pores is termed guttation. As stated earlier, guttation is a widespread phenomenon, which is observable in many different families of plants. These plants are known to possess a specialized system for the exit of guttation fluid from leaves. Just as transpiration takes place through stomata, guttation occurs through special structures called hydathodes, which are also known as 'water stomata' or 'water pores'. Hydathodes are present at the tips, margins, and adaxial and abaxial surfaces of leaves (Chen and Chen 2005; Drennan et al. 2009; Lersten and Curtis 1991; Singh et al. 2009a).

The guttation fluid is usually exuded through these special structures known as hydathodes (Figure 1.3, a-h). In plants showing guttation and having these specialized structures, the hydathodes have less dense cytoplasm. Tracheids exist below the vascular bundles, which act as the passage for liquid flow with least resistance. In most of the angiosperms, the tracheids have been observed in association with parenchyma cells of the epithem, which has large intercellular spaces. The flow of water into the epidermis occurs through these intracellular spaces. Epidermal openings found above the epithem are usually incompletely differentiated stomata, which have lost the ability of opening or closing (Esau 2006). Some plant species lack epithem, whereas some plant species have a complicated association of the epithem with the secretory tissue (Aegthe 1951; Sperlich 1939). Sperlich (1939) presented a detailed study on hydathodes and water glands, and their structure and function, with respect to previous studies.

To understand the path of guttation, it is necessary to review briefly the present knowledge on the structure, function, and mode of action of the various guttation apparati. Hydathodes form the natural openings on the surface of leaves, which provide the least resistant pathway for fluid transmission that occurs through apoplastic or intercellular spaces found in epithem or mesophyll cells (Stocking 1956a). However, guttation can also occur through the cuticle (Lausberg 1935) or stomata (Bald 1952). Morphologically, the laminar hydathodes of *Ficus formosana* are complex epithem-type which consist of structures such as water pores, tracheid ends, epithem cells, and a bounding sheath layer. Each water pore is made of two guard cells, and these pores are permanently open. Thus, in reality, hydathodes are the apparatus of guttation, which are made of stomata-like pores in the epidermis and epithem, having a large chamber composed of masses of thin-walled parenchyma cells and a sheath layer that surrounds its tissue (Dieffenbach et al. 1980a).

Each hydathode is formed of colorless epidermal cells. Parenchymatous and loose tissue lies beneath the hydathodes, which are known as 'epithem'. It is also known as 'transfer tissue'. The cells of epithem are soft and made of loosely arranged thin-walled parenchyma cells and without chloroplast and are involved in absorption and secretion. Surrounding the epithem is a mass of chlorenchymatous tissue. In the anterior part of epithem, a cavity is present which is called 'water cavity'. Each hydathode opens to the exterior by means of a pore in the leaf epidermis. Hydathodes always remain open but exert flow-controlling effect on the exudation. In fact, hydathodes are the structures that mediate guttation. Among dicots, they have been reported to occur in many families

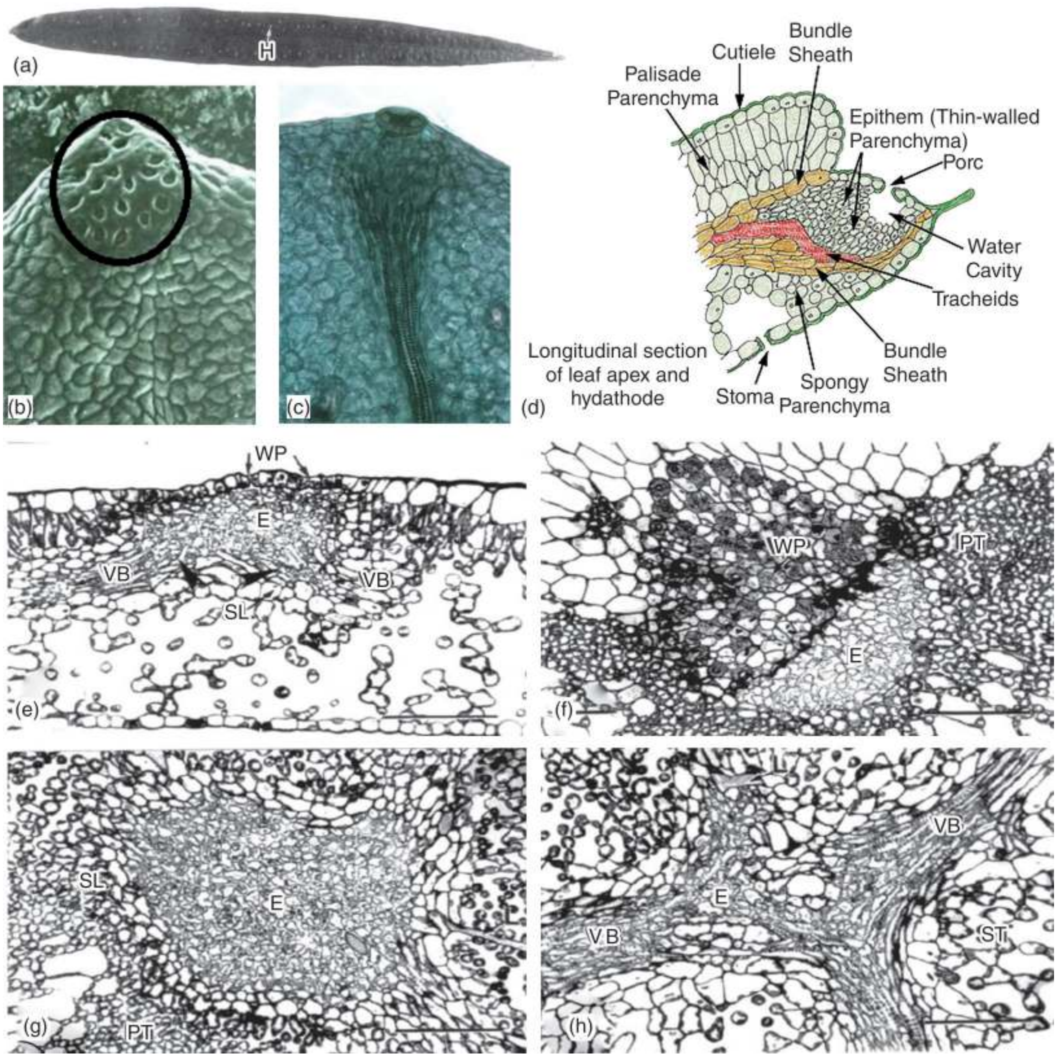


FIGURE 1.3 External and internal features of the laminar hydathodes in *Ficus formosana* Maxim (*a*, *e*–*h*) [*Source*: Chen and Chen 2005] and (*b*, *c*) *Physocarpus opulifolius* (L.) Maxim [*Source*: Lersten and Curtis 1982]. (*a*) Hydathodes on the adaxial surface of the leaf and scattered in a linear arrangement between the midrib and leaf margin. White points indicate hydathodes. (*b*) Magnification of hydathodes (circled). (*c*) Light micrographs of the longitudinal section of the leaf, showing a laminar hydathode. (*d*) Drawing of a longitudinal section of the hydathode [*Source*: http://www.plantscience4u.com]. (*e*) Resin-embedded cross-section of a hydathode. Outer surface consisting of epidermis and water pores; inside region included with the epithem consisting of a group of small lobed cells; two vascular bundles extending upward (arrowheads). (*f*) Oblique paradermal section of the hydathode through the epidermis level, showing the vicinity of a hydathode consisting of water pores and epidermis cells. (*g*) Paradermal section of a hydathode through the middle level of epithem, showing the epithem consisting of a group of small lobed parenchyma cells and surrounded by a sheath layer. (*h*) Paradermal section of a hydathode through the vascular bundle level, showing four vascular bundles and their tracheid element junction under the epithem. Scale bars = 50 mm. E, epithem cell; H, hydathode; PT, palisade tissue; ST, spongy tissue; VB, vascular bundle; and WP, water pore.