Secretory Structures

Introduction

A secretory structure is essentially any structure, simple or complex, that produces a secretion within, on, or from a plant. We witness secretion in plants daily from watching butterflies or other animals search for nectar rewards in flowers and experience the scent of the plant or as we encounter the sting of nettle plants during a walk in the woods. Secretory systems may be classified by their location in the plant, but they may also be named according to the product or products that are exuded including ones termed nectaries, hydathodes, glandular hairs/trichomes, salt glands, colleters, crystal-containing idioblasts, tannin cells, internal oil glands and cells, resin ducts, as well as protein and gum-secreting systems. Secretory products may be released externally onto the surface of an organ (as in the case of nectaries, hydathodes, and salt glands), internally from a cell into canals (as in resin ducts), or into subcuticular cavities (as in **glandular trichomes**).

While secretory activities are found in virtually all plant cells at some time during their life, there are isolated individual cells (idioblasts) and cell complexes (glands) whose primary function is to perform secretion on a regular basis. Single-cell secretory structures are called granular cells, in contrast to multicellular structures that are referred to as glands. Secretory structures are important to plants because they reward pollinators by providing nectar, attract prey, excrete dissolved substances, or help in defense of herbivory. They may also accumulate in a vacuole of a cell in the form of crystals (as in crystal-containing idioblasts) or amorphous inclusions (as in tannin and oil cells). Plant secretory products have played important and interesting roles in human history (Stewart 2009).

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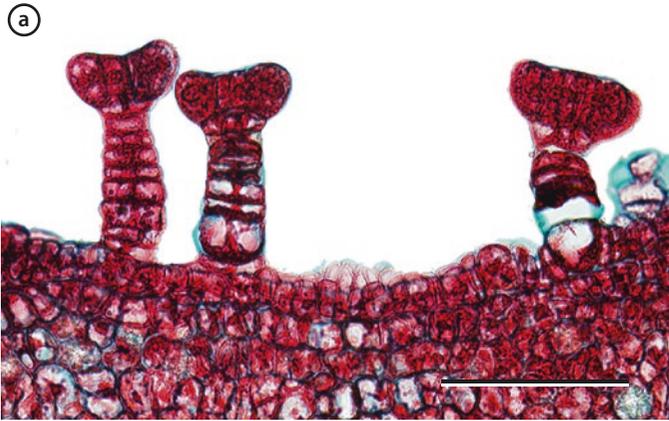## 13.1 External Secretion Involves Moving Substances to the Surface of the Plant

External secretory systems include those systems that are located on, within, or just below the epidermal layer. These systems include glandular trichomes that include, but are not limited to, colleters and stinging trichomes. Other secretory structures include nectaries, hydathodes, and salt glands.

13.1.1 Glandular Trichomes

Glandular trichomes (glandular hairs) of various morphologies are formed on the surface of the aboveground parts of plants, such as stems, leaves, bud scales, and reproductive organs (◘ Fig. 13.1a). These structures are of epidermal origin and secrete substances external to the plant. Given the epidermal location of many glandular trichomes, detailed information on the anatomy of basic trichome structures can be found in ► Chap. 9. However, glandular trichomes are also associated with more specialized structures such as colleters and stinging trichomes, as well as specific types of secretions including essential oils.

Fig. 13.1 **a** Three stalked, glandular trichomes on the surface (pericarp) of a black walnut (*Juglans nigra*) fruit. Scale bar = 50 μm. (RR Wise)
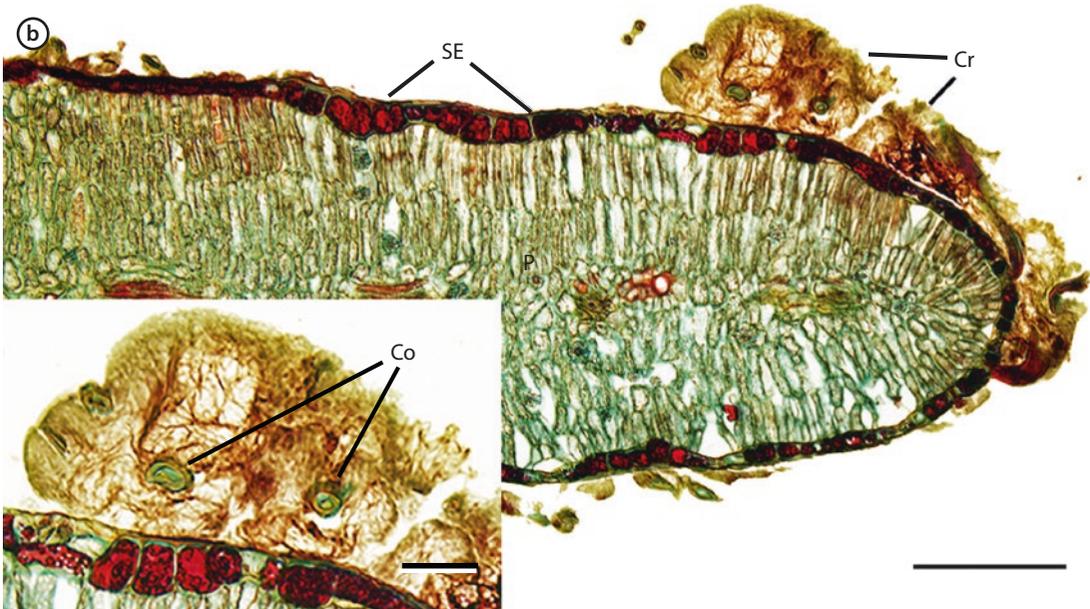
Fig. 13.1 **b** Colleters are glandular trichomes producing a sticky hydrophobic secretion known as creosote. Shown here are colleters on the leaf of the creosote bush (*Larrea tridentata*). The leaves have an outer layer of secretory epidermis (SE, stained dark brown or red) covering a parenchymatous mesophyll (P, lightly stained due to vacuolation). Two colleters (Co) are seen in cross-section in the insert. Secreted creosote (Cr) is external to the leaf and appears light brown to reddish due in part to an accumulation of carotenoids. Scale bars = 100 μm for main image and 50 μm for insert. (RR Wise)

13.1.2 Colleters

Colleters are multicellular glandular trichomes of a leaf or bud scale that generate a resinous, hydrophobic secretion (Esau 1953). Colleters often produce **terpenes**, which are lipophilic substances that provide defense against insects and fungi. While colleters in some plants are quite large with several layers of cells, such as on leaves of the creosote bush, they appear as thin trichomes embedded in a large accumulation of secretion (■ Fig. 13.1b). The creosote

bush inhabits the deserts of western North America. Their leaf secretions reduce transpiration and help the plants survive the very arid conditions. The stomata typically only open during the morning when humidity is high, but close down by midday to prevent water loss. Thus, photosynthesis only occurs in the morning.

Box 13.1   Diversity of Colleter Anatomy and Function in the Rubiaceae

Colleters are plant secretory structures that produce a sticky exudate. The secretions primarily serve to protect leaves from desiccation or a meristem from desiccation, insect attack, or pathogen attack. But not all colleters are the same. Judkevich et al. (2017) recently conducted a thorough study of colleters on both vegetative and reproductive organs in the Spermacoceae, a tribe within the Rubiaceae family known to have a diversity of colleter types. The "standard" colleter type is defined as a multicellular trichome with a central axis made of parenchyma tissue with a secretory palisade layer. The standard type of colleter was found on the stipules, calyx, and bracteoles and on buds found on the underground rhizomes of a few species. Other nonstandard colleters were green, due to the presence of an active chlorenchyma. The fate of the photosynthate produced by that tissue is unknown. It may contribute to the production of the secretion or to the overall photosynthesis of the plant. The colleters of two species had a vascular connection to the vasculature of the stipule or calyx to which they were attached. This study revealed the diversity of colleter types within a single plant taxon and indicates that colleters may serve multiple functions within the angiosperms.
Reference: Judkevich et al. (2017).

13.1.3   Stinging Hairs

Stinging hairs, which produce toxic substances stored in the cell vacuole, are a special type of glandular trichome. Plants associated with stinging hairs are often found in the Urticaceae and Euphorbiaceae, but also can be found in other families. These structures are used to defend plants from herbivores. In the case of the stinging nettles, *Dendrocnide* and *Urtica*, the stinging hair consists of an elongated tapering, needlelike stinging cell structure up to 1.5 mm long, whose basal part is covered by smaller supporting cells which in combination form a pedestal (◼ Fig. 13.1c). The stinging cell terminates by a small head and neck (◼ Fig. 13.1d) whose thin wall is very fragile due to its impregnation by silica (◼ Fig. 13.1e, f). The wall be easily broken during contact with skin and may then release a complex mixture of stinging and irritating chemicals into the skin in a manner somewhat similar to a hypodermic needle, thus being an effective retardant to animals that otherwise may have foraged on the plant.
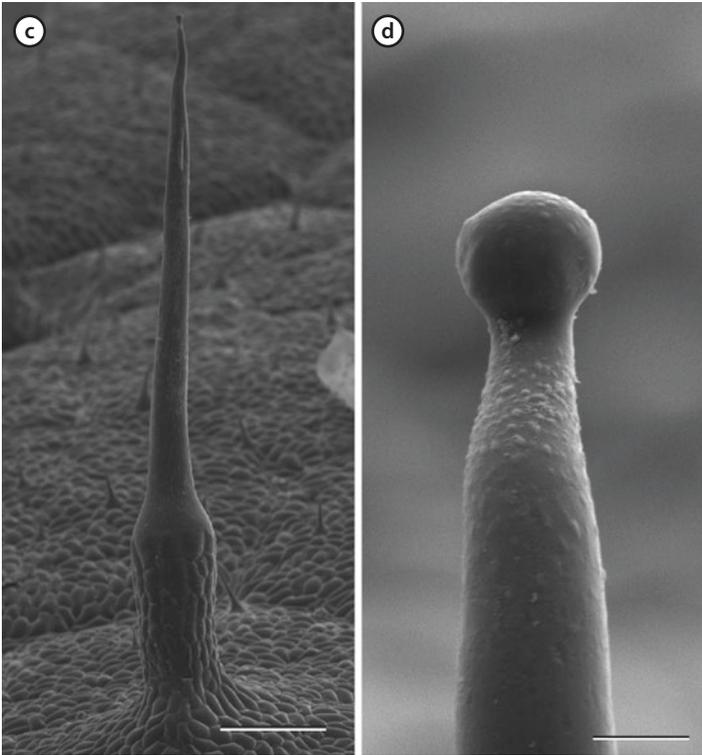
🔲 **Fig. 13.1** **c, d** Views of a stinging hair of the stinging brush (*Dendrocnide moroides*) as visualized with scanning electron microscopy. Scale bars = 250 μm in **c** and 10 μm in **d**. (**c, d** RR Wise)

The scanning electron microscope generates highly detailed electron micrographs by capturing and imaging the electrons emanating from a specimen's surface upon bombardment with source electrons (🔲 Fig. 13.1e). In addition, X-ray photons are also emitted as a result of the electron bombardment, and the energies of those X-rays are specific for the element from which they were emitted. In short, an X-ray microanalyzer attached to a scanning electron microscope allows one to "take pictures" of specific elemental sites. Typically, this technique is called "X-ray elemental microanalysis" (XRMA). The walls of the stinging nettle hair as well as other smaller trichomes are clearly visible as containing silicon in 🔲 Fig. 13.1f.

13.1.4 Nectaries

Nectaries secrete a sugar solution called nectar. The sugars may be complex but most often are comprised of a mixture of sucrose, glucose, and fructose. Nectaries are most often associated with flowers (**floral nectaries**), but may also develop on leaves and stems (**extrafloral nectaries**). Floral nectaries may be located in many floral parts such as stamens (intrastaminal nectaries) or at the base or on top of the ovary (septal nectaries; refer to 🔲 Fig. 18.2g, h). While conspicuous flowers attract floral visitors, nectar typically
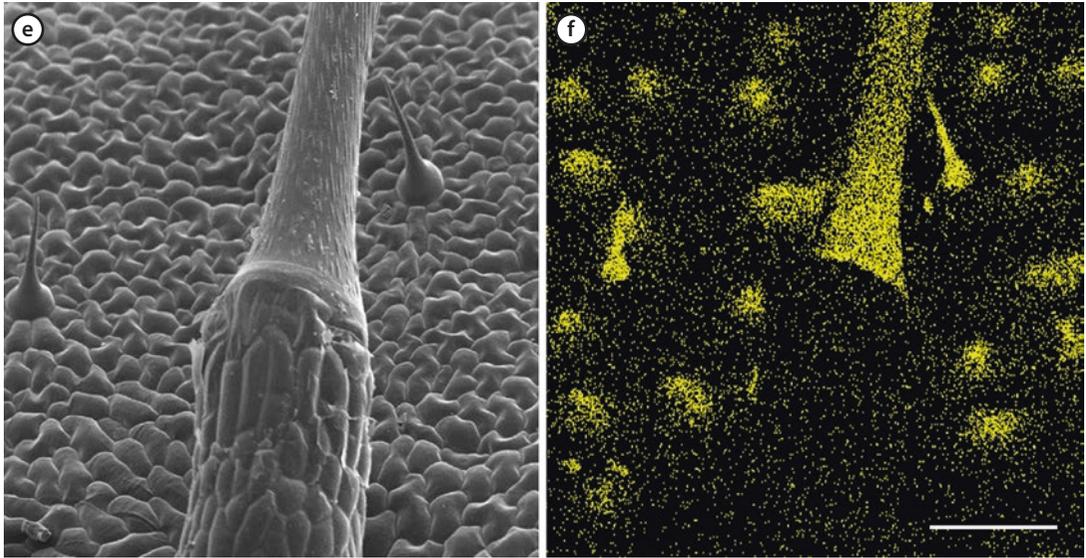
☐ **Fig. 13.1   e**, **f** Base of a common nettle (*Urtica dioica*) stinging hair as visualized with **c** scanning electron microscopy SEM and **d** an X-ray elemental map **d**. The location of silicon is indicated as yellow pixels in **d**. Scale bar = 100 μm for both panels. (**e**, **f** RR Wise)

acts as a reward to pollinators. Extrafloral nectar may also attract animals, such as ants, that defend the plant from other herbivorous insects. Nectaries vary greatly in morphology and anatomy, which is not surprising given the diversity of structures where they may be located.

There are a variety of structural patterns for nectaries (☐ Fig. 13.1g), but they are mostly represented by small protuberances where nectar collects in a reservoir (☐ Fig. 13.1h). The nectary comprises a single-layered epidermis and three or four layers of small subepidermal cells (☐ Fig. 13.1i). Beneath these are found several layers of larger parenchyma cells. Epidermal cells have a thin, permeable, reticulate cuticle with associated swellings that coincide with the middle lamella between adjoining epidermal cells.

Nectar is thought to pass both along the apoplast and symplast and then eventually through the stretched and distended or broken cuticle. The secretory cells are collenchymatous and nucleated and have numerous pits with plasmodesmata, mitochondria, rough endoplasmic reticulum, and plastids with many plastoglobuli but few lamellae. Sub-secretory cells contain fewer plastids than secretory cells. Vasculature supplies the gland with water and carbohydrates for sugar synthesis. The process of nectar secretion may cause the separation of the cuticle from the outer periclinal walls of the palisade-like cells forming the secretory epidermis. In fact, it may be necessary for the cuticle to rupture before insects can access the nectar.

Nectaries outside of floral structure are referred to as extrafloral nectaries and may be located on leaf blades or petioles of the leaf (☐ Fig. 13.1j, k). They typically produce sugar complexes along with smaller amounts of amino acids and organic acids. Cells of the nectaries have extensive plasmodesmata that may aid in the transport of sugars to the nectary surface, just below the cuticle, which
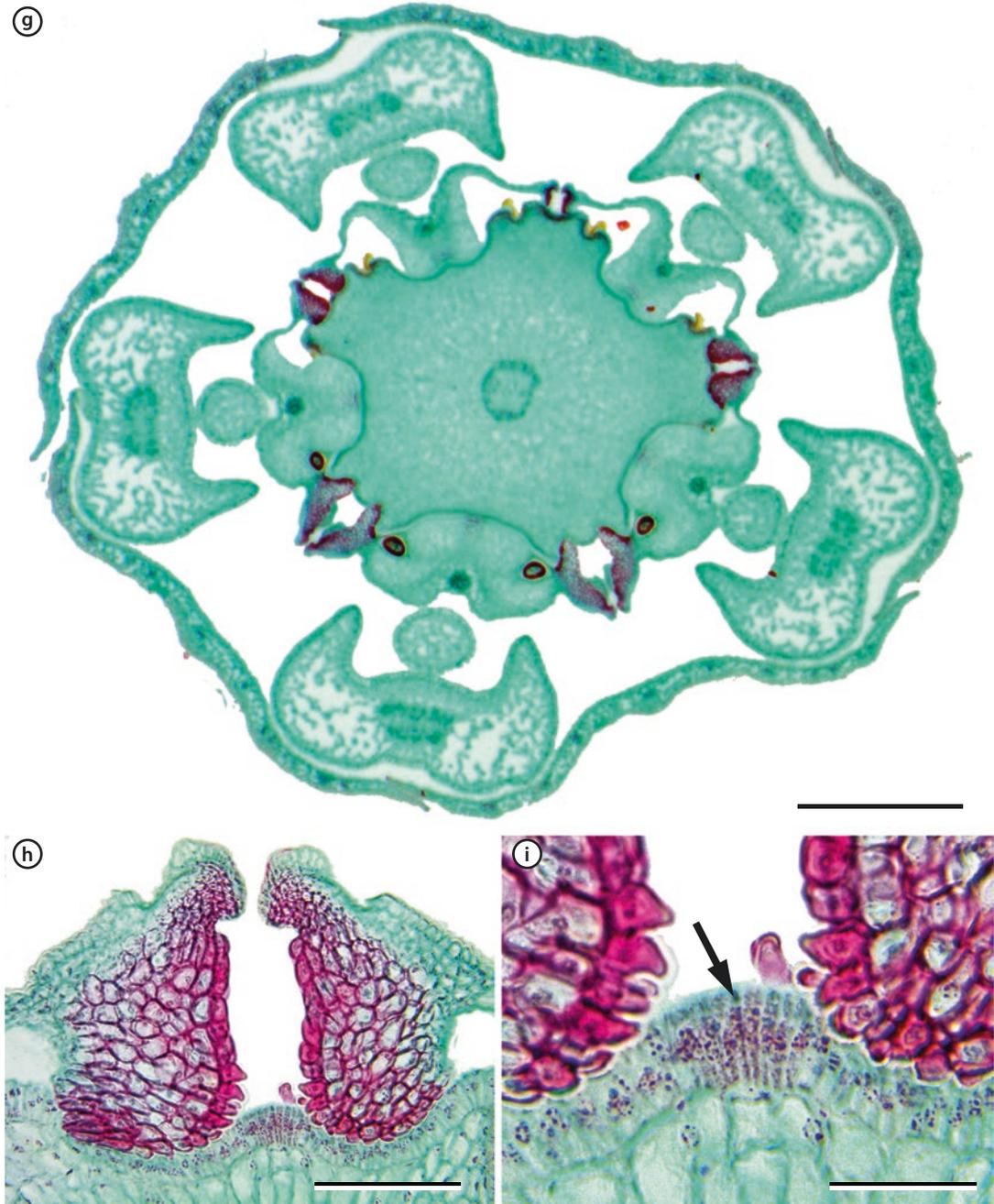
◧ **Fig. 13.1   g–h** Floral nectaries of milkweed (*Asclepias* sp.). **g** Cross-section of a milkweed flower showing an arrangement of five floral parts and five nectaries. Lignified cells at the margins of the nectary stain red. The lignified hoods covering the nectariferous tissue require some effort on the part of pollinators (bees, wasps, and butterflies) to access the nectar. This insures the pollinator will occupy to flower long enough to pick up a pollen sac for transfer to the next flower. **h** Higher magnification of a single nectary. **i** Detail of the nectariferous tissue, indicated by the arrow. Scale bars = 1 μm in **g**, 25 μm in **h**, and 10 μm in **i**. (**g–i** RR Wise)
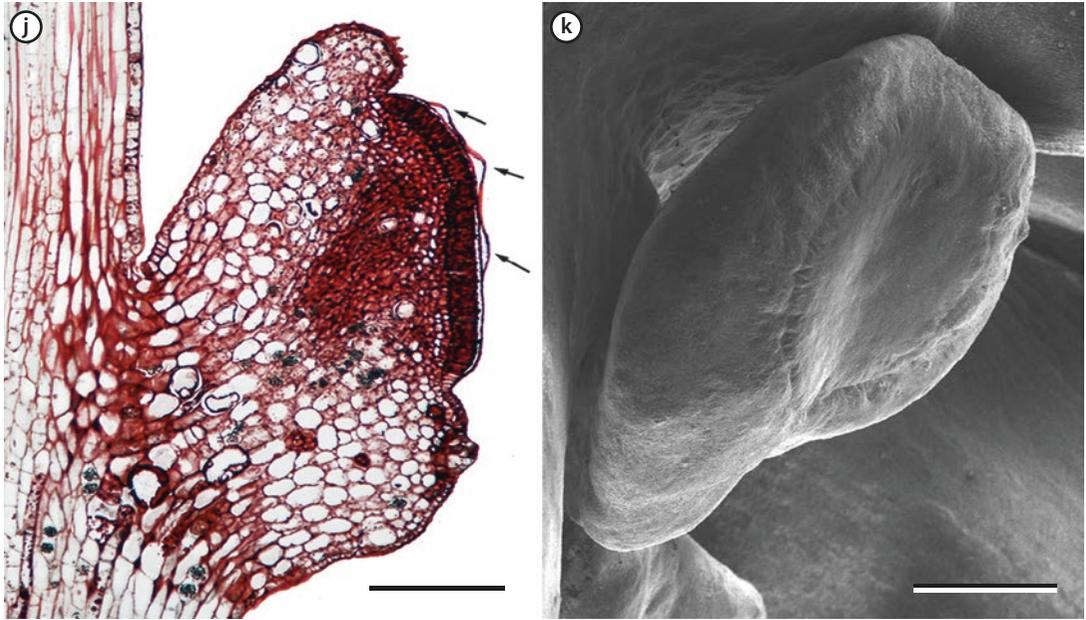
Fig. 13.1   j, k Light micrograph **j** and scanning electron micrograph **k** of extrafloral nectaries from the leaf petiole of castor bean (*Ricinus communis*). Note the separation of the cuticle from the gland surface in **j** (*arrows*). Scale bars = 250 μm in **j** and 500 μm in **k**. (**j, k** RR Wise)

will eventually rupture and release the sugars. Extrafloral nectaries primarily attract ants, which in turn provide significant protection for the plant by attacking and warding off herbivores. About 100 plant genera have evolved this complicated mutualistic relationship; they are aptly named "myrmecophytes" ("ant plants") (Del Val and Dirzo 2004).

13.1.5   Hydathodes

Hydathodes are external secretory structures that exude water with dissolved substances such as amino acids and/or low concentrations of salts. The water excreted by hydathodes appears as droplets on the surface of the organ, in a process called guttation. The process is usually noticed in early morning when there is high humidity. Two types of hydathodes are recognized: (1) *active*, the form of glandular trichomes in which water is actively exuded by secretory cells that are not connected to water-conducting tracheary elements, and (2) *passive*, usually located at leaf margins or tips of leaves (■ Fig. 13.1l, m). In passive hydathodes, water is supplied by vascular bundles (■ Fig. 13.1n) and then passes through intercellular spaces of a tissue called the **epithem** composed of mesophyll cells that represent modified vascular bundle ends. Eventually, water is exuded onto the leaf surface through modified stomata, which are permanently open.
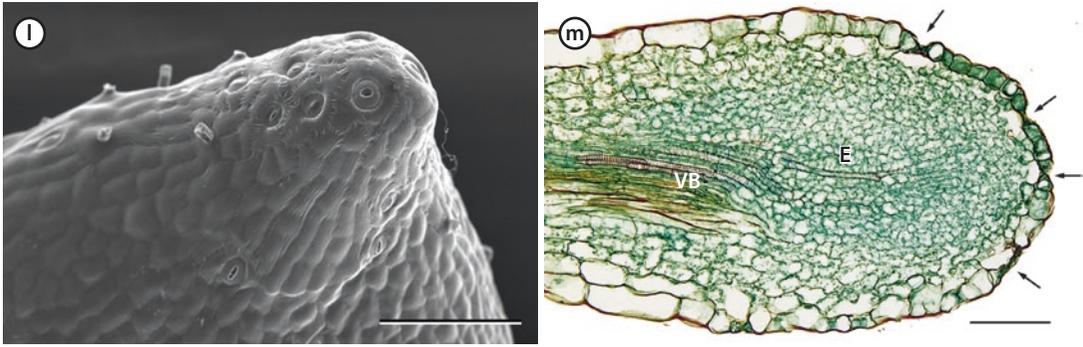
◐ Fig. 13.1 **l** SEM of a chrysanthemum (*Chrysanthemum* sp.) passive hydathode at a leaf tip showing multiple stomata that are open. **m** Terminal leaf margin of cabbage (*Brassica oleracea*) revealing a passive type of hydathode with a large epithem (E), which fills almost the entire mesophyll and permanent stomatal openings (*arrows*). Water is supplied by the vascular bundles (VB). Scale bars = 200 μm in **l** and 250 μm in **m**. (**l**, **m** RR Wise)
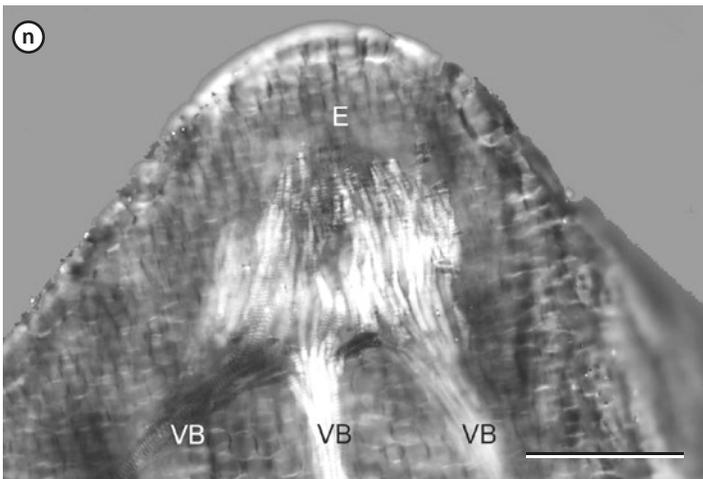
◐ Fig. 13.1 **n** A single hydathode in the leaf of the lyre-leaved sand cress (*Arabidopsis lyrata*). The image was taken with differential interference contrast (DIC) illumination, which highlights the lignified cell walls of the tracheary elements in the vascular bundles (VB). The epithem (E) is between the vascular bundles and the hydathode tip. Scale bar = 200 μm. (RR Wise)

13.1.6 Salt Glands

Halophytes are plants that grow in salt water or on saline soils. However, salts (sodium chloride being the main, but not only form) are toxic to most plant physiological processes. Halophytes therefore have evolved two different salt management strategies. The first is to retard salt uptake at the root cells to prevent it from entering the water of the transpiration stream. Red mangrove (*Rhizophora mangle*) is a salt excluder, and its roots are effective barriers to salt uptake. Black mangrove (*Avicennia germinans*) uses a second strategy, salt excretion. These plants take up salts, but then excrete the
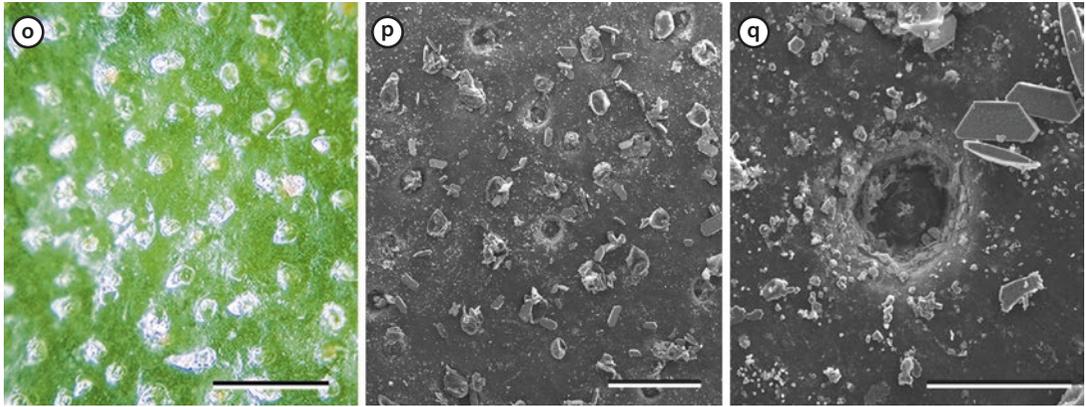
◘ Fig. 13.1   o Salt crystals on surface of a black mangrove (*Avicennia germinans*) leaf. **p** Surface detail showing numerous salt glands and crystals on leaf. **q** A single salt gland showing dried crystals of salt. Scale bars = 400 μm in **o**, 200 μm in **p**, and 50 μm in **q**. (**o–q** RR Wise)

salt at the terminus of the transpiration stream (i.e., the leaf), using specialized external secretory structures called **salt glands** on the leaf surface (◘ Fig. 13.1o–q).

13.2   Carnivorous Plants Have Evolved External Secretory Structures as a Mechanism for Nutrient Acquisition

Plants species evolve structures that have many different secretory functions. In this section, the focus will introduce some of the ecological anatomy of external secretory structures of carnivorous plants.

Certain plants are capable of growing in nutrient-depleted environments despite also having photosynthetic activity. Among these is a group that derives their essential elements from animal sources and may thereby be called "carnivorous plants" (although Darwin 1875 officially used the term "insectivorous plants"). Almost 600 species and subspecies of carnivorous plants have been identified (Barthlott et al. 2007). Many carnivorous plants have reduced root systems relative to their noncarnivorous plants and are adapted to trapping and digesting insects, arachnids, slugs, worms, caterpillars, and, upon occasion, small animals, such as frogs or mice.

Bog plants, such as those shown in ◘ Fig. 13.2a, b, grow in waters with an acidic *p*H, often from 4.0 to 6.0. Under such conditions, elements such as nitrogen, phosphorus, and calcium precipitate out and are not available for uptake. Nitrogen in particular may often be scarce in the environment, but for green plants it is an essential nutrient for proteins and nucleic acids. Thus, without specialized adaptations, plants cannot survive because the building blocks for compounds needed for growth are missing.

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◘ Fig. 13.2 **a, b** Typical scenes from a bog in northern Wisconsin in which various types of carnivorous plants may be found among the grasses and sphagnum moss. Pitcher plants (*Sarracenia purpurea*) are seen in **a** and sundew (*Drosera intermedia*) in **b**. Scale bar = 5 cm for both panels. (**a, b** RR Wise)

Carnivorous plants, such as the Venus flytrap (*Dionaea muscipula*), have developed a unique means of survival in that ecological niche due to extracting key elements from various animal forms of life that can provide a good source of elements and energy-laden compounds which are missing from the soil and water solutes. For such carnivorous plants, this is accomplished by relatively simple means of physical and chemical activities by actively trapping prey with a modified, hinged leaf.

Let us consider the Venus flytrap that has modified leaves with secretory hairs which attract many animal species by exuding mucopolysaccharides and other sugars from glands at the base of rim-mounted hairs (often referred to as cilia). The modified leaves also have terminal lobes that are hinged along the midrib and can snap closed when trigger hairs (modified trichomes) are contacted (◘ Fig. 13.2c). In most cases there are three or four such trigger hairs located on each lobe. When an object contacts two of the three hairs within about 20 s (or even contact with one such hair twice in that period of time), a small electrical signal is activated through the phloem that opens pores in the inside cells of the lobes that are filled with water, and, once opened, the water flows to the outside of the lobes causing the two lobes to collapse and close on the object that caused contact with the trigger hair.

The rims of the lobes have a large number of spikelike trichomes (or cilia), which, like bars in a cell, entrap the organism inside. However, there remains space between the bars large enough for very small organisms to make their way out thus relieving the flytrap plant from wasting a good deal of effort for too small of a reward. In addition to food from animal digestion, flytraps also carry out photosynthesis, in fact direct sunlight is favored, and those flytraps in
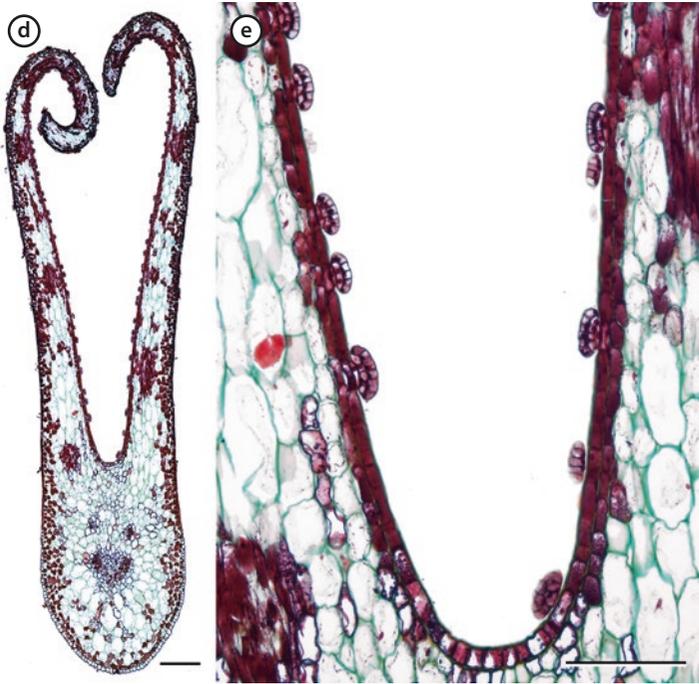
■ **Fig. 13.2   c** A Venus flytrap (*Dionaea muscipula*) showing the trigger hairs (H), which initiate the closure of the trap, and the marginal modified trichomes (or cilia, C). Scale bar = 1 cm. (RR Wise)

high light levels usually have traps with red anthocyanin pigments, whereas those in lower light levels are more green or yellow-green. The Venus flytrap is native to bogs and swamps of North Carolina, in the southeastern USA.

In review, physical contact creates a small ion flow (modified electrical current), which activates the release of water pressure in parenchymatous cells that cause the leaf lobes to collapse within about one-tenth of a second. Normally, the leaf trap stays closed for 1–5 days before reopening.

This sets the stage for the next event, the release of secreted proteolytic enzymes from glandular trichomes within the trap that envelop the prey and digest it (■ Fig. 13.2d, e). These also include strong acids like phosphoric, nitric, or hydrochloric acids that kill and degrade the body of the prey. The digestive glands will absorb the released nutrients, which are carried in the phloem, and to some extent through the apoplastic components of the plant cellular structures.

Some carnivorous plants, termed "pitcher plants" (■ Fig. 13.2a), employ a more passive means of entrapment by virtue of its funnel-like modified leaf that contains trichomes that exude secretory attractants, as well as ones that are angled in a downward direction. When the "pitcher" is dry, insects such as ants may largely keep their grip in moving about the interior of the funnel (actually the adaxial leaf surface). However, when the pitcher is wet due to rain or heavy dew, the trichomes as well as wax crystals over the inner funnel surface become very slick, and the invasive organisms lose hold and slide to the bottom of the funnel where secreted digestive

◘ **Fig. 13.2**   **d**, **e** A closed Venus flytrap (*Dionaea muscipula*) in cross-section. Entire leaf showing that the entire adaxis (inner surface) is lined by numerous peltate digestive glands. **e** Higher magnification view of the trap and glands. Upon closure of the trap, the glands begin secreting digestive fluid, which fills the enclosed space around the prey. The same glands are involved in the absorption of digestive products from the trap interior. Digestive glands consist of a layer of secretory cells, two layers of filling cells, and a basal cell. The dark-stained cells in the mesophyll of the trap wall are tannin-containing cells. Scale bars = 250 μm in **d** and 50 μm in **e**. (**d**, **e** RR Wise)

fluids have accumulated. Escape is unlikely due to the downward pointed trichomes, the wax crystals, and their slippery surface.

Even larger organisms, such as mice, have been found to lose their grip and to fall prey to the digestive system of the pitcher plant. After 2–3 weeks the entire mouse will become digested, including the bones. There are over 100 species of pitcher plants including hybrids and cultivars, but the common names do not imply any evolutionary relationships among the organisms.

While the pitcher plant represents a unique type of carnivorous plant, recent studies have shown an even more amazing adaptation in its coevolution with bats. In the forests of Borneo, a tropical pitcher plant, *Nepenthes hemsleyana*, feeds on bat guano and thus does not need to carry out its own digestive processes. This is accomplished by a mutualistic relationship with bats in which the pitcher plant has a structure called a "reflector" that echoes acoustic signals from the bats to reveal the plant's location. The bats are attracted to the pitcher plant and are rewarded with a stable, spacious, and parasite-free roosting site. The bats in turn reward the pitcher plant with their feces that is digested by the plant secretions within the pitcher (Grafe et al. 2011). While not technically

■ **Fig. 13.2**   **f** A general view of the spoonleaf sundew plant (*Drosera intermedia*), one of the multiple species that grow in wet, acidic environments including bog-like regions with poor nutrient soils. This specimen was photographed in east central Florida. Scale bar = 1 cm. (RR Wise)
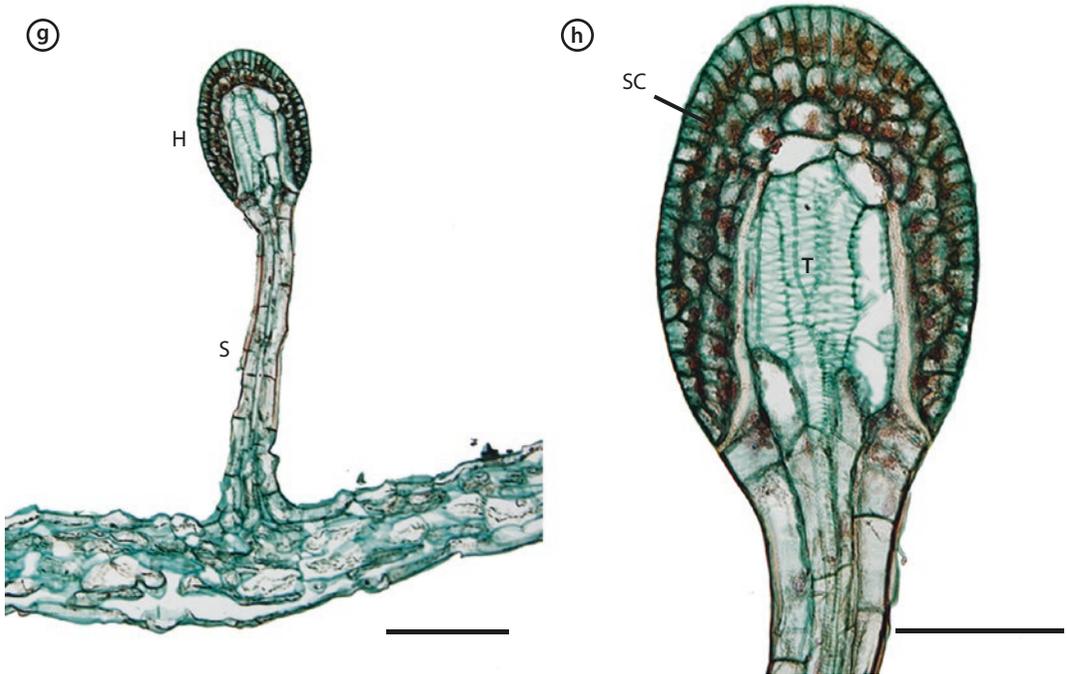
■ **Fig. 13.2**   **g** Tentacles (or gland) in sundew (*Drosera* sp.) consist of a stalk (S) of various lengths and a head (H). **h** An outer layer of secretory cells (SC) surrounds a group of tracheids (T). Scale bars = 100 μm in **g** and 50 μm in **h**. (**g, h** RR Wise)

carnivory, this relationship uses many of the same features as found in the insect-trapping pitcher plants.

Other carnivorous plants include the sundew plant (■ Fig. 13.2b and f), which also exhibits passive entrapment by virtue of producing a modified leaf with many secretory trichomes (■ Fig. 13.2g, h) that

⬛ Fig. 13.2   i Flowering and above-water view of the swollen bladderwort (*Utricularia inflata*) carnivorous plant from North Carolina, USA. Flowers are approximately 8–10 cm. **j** Beneath the water, bladderlike pouches trap the prey. Scale bars = 5 cm in **i** and 1 mm in **j**. (**i** ,**j** B Rice, ▶ sarracenia.com)

generate both attractants and digestive fluids at the surface. Small organisms, usually insects or spiders, are attracted and are trapped by sticky secretions produced by the trichomes, which may infold somewhat and digest the prey in situ.

Not all carnivorous plants are found in bogs. In fact, the great bladderwort (*Utricularia macrorhiza*) plant (⬛ Fig. 13.2i, j), a carnivorous species, has been found in the freshwaters of Lake Michigan along the Chicago shoreline by small sandy dunes, which are nutrient depleted. It appears as floating stems with bright yellow flowers above the waterline, but most of the plant is underneath the water where bladderlike pouches are filled with water. On the pouches are protruding hairs that serve as trigger-like mechanisms for catching prey. If aquatic invertebrates hit the hairs, water shoots out of the bladders and creates a vacuum-like effect internally. When the water rushes back into the pouches, it carries the prey (usually water fleas, zooplankton, and other small aquatic insects) along, where they remain until digested.

Box 13.2   Evolutionary Connections Between Plant Carnivory and Defense

Carnivorous plants lack a highly developed root system due to the harsh acidic conditions in which they live, such as in acidic bogs. These plants are known for trapping insects with modified leaves to supplement their nutritive needs. Insects are trapped and subsequently broken down via secretion of digestive enzymes. The plant digestive response occurs within 2 h following detection of insect movements within the trap. By utilizing the mRNA that was expressed within cells, researchers discovered that the movements of the insect within the Venus flytrap lead to the production and secretion of enzymes including chitinases, proteinases, and hydrolases that digest the hard chitin exoskeleton. This induction of hydrolase

activity is similar to the plant defensive response to herbivory. Venus flytraps also respond to triggering by an insect, in a similar fashion that noncarnivorous plants respond to stress by producing jasmonic acid. The use of the molecular genetics of mRNA and the analysis of protein expression indicated that genes controlling carnivorous plants such as the Venus flytrap are related to the defense genes of noncarnivorous plants. Reference: Bemm et al. (2016).

13.3 Internal Secretory Structures Include Oil Cavities, Resin Ducts, and Laticifers

In contrast to external structures, internal secretory structures include secretory cavities and canals (ducts), laticifers, and idioblasts. These structures are found in tissues such as xylem, phloem, cortical, and pith parenchyma where they remain within the cytoplasm and may contain oils, latex, crystals, and resin.
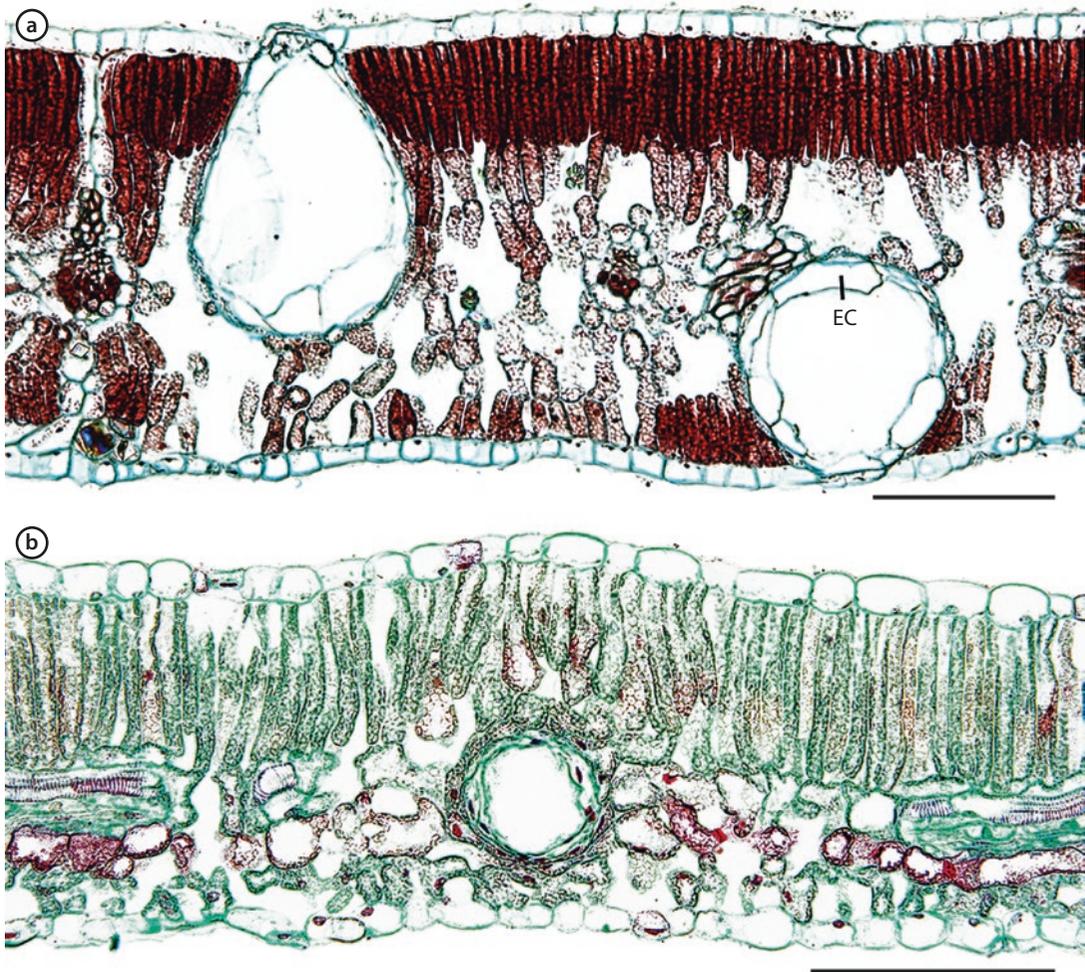
13.3.1 Oil Cavities

Oil cavities within leaves, such as in members of the Myrtaceae (i.e., *Eucalyptus* sp.) and Rutaceae, are large, spherical, isolated intercellular spaces that are the sites of internal secretion and storage. They may be found throughout the plant and, in leaves, may be part of the epidermis (◘ Fig. 13.3a) or the mesophyll (◘ Fig. 13.3b). The cavities, which are filled with oils or other secretions, are lined by epithelial cells, the sites of oil synthesis. These secretions are also termed volatile or ethereal oils and are aromatic, oily substances and upon extraction are termed "essential oils" (refer to ► Sect. 13.5). The oils can be present in nearly any portion of a plant depending upon the species. Many oils are produced by plants to serve as important antiherbivory chemicals.
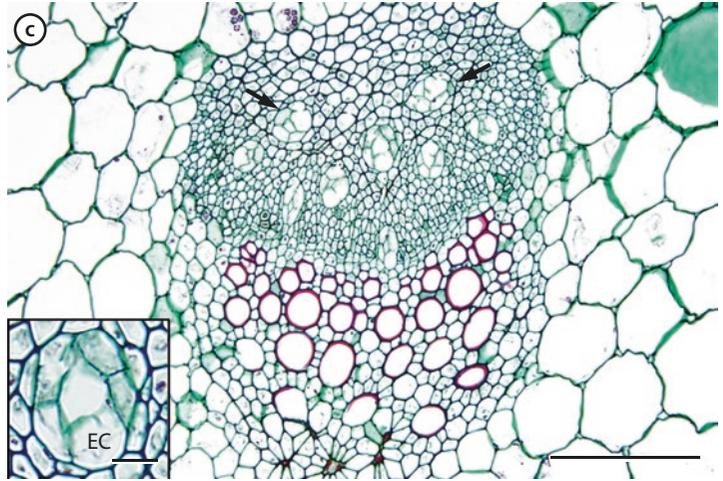
13.3.2 Resin Ducts

In contrast to the isolated nature of secretory cavities, **resin ducts** (or canals) are extended structures that may run the entire length of a leaf or stem. They are filled with secretion and lined by a layer of epithelial (secretory) cells. Such ducts may be found in the cortex, in primary and secondary phloem, in pith, or in the secondary xylem of stems and roots; they may also develop in leaves (◘ Fig. 13.3c) and flower parts. Resin ducts are similar to other plant secretory structures such as colleters and oil glands that produce

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☐ **Fig. 13.3** **a** Epidermal oil cavities in a eucalyptus (*Eucalyptus* sp.) leaf. **b** A mesophyll oil gland in a cotton (*Gossypium hirsutum*) leaf. Note the epithelial cells (EC) lining the cavities that would contain oil within a living leaf and the red-stained nuclei in the cotton epithelial cells. The oil was extracted during specimen preparation; thus, the cavities appear empty. Scale bars = 100 μm in both panels. (**a**, **b** RR Wise)

mainly terpenes, i.e., lipophilic substances that provide defense against insects and fungi. Resins are released from cells into canals. They are common in gymnosperm leaves (☐ Fig. 13.3d) and stems (☐ Fig. 13.3e) and in response to injury (☐ Fig. 13.3f). These are the resins that were extracted and used in the production of pine tar (refer to ☐ Fig. 15.2).

Essential oils are involved in both external and internal secretion in plants. Some plants, such as many in the mint family (Lamiaceae), often exude essential oils externally from glandular trichomes, but in some cases, the oils are stored in a subcuticular space prior to secretion.

Fig. 13.3   c Cross-sectional view of a vascular bundle from celery (*Apium graveolens*) petiole, depicting nine small resin ducts (two are indicated with *arrows*) in the phloem. The resin ducts are rosettes of epithelial cells surrounding the **resin canals** (inset). The elongation of the petiole has ceased, and the secretion completed. When viewed with electron microscopy, the epithelial cells appear to be in a highly vacuolated, inactive state. Scale bar = 100 μm in main panel, 10 μm in inset. (RR Wise)
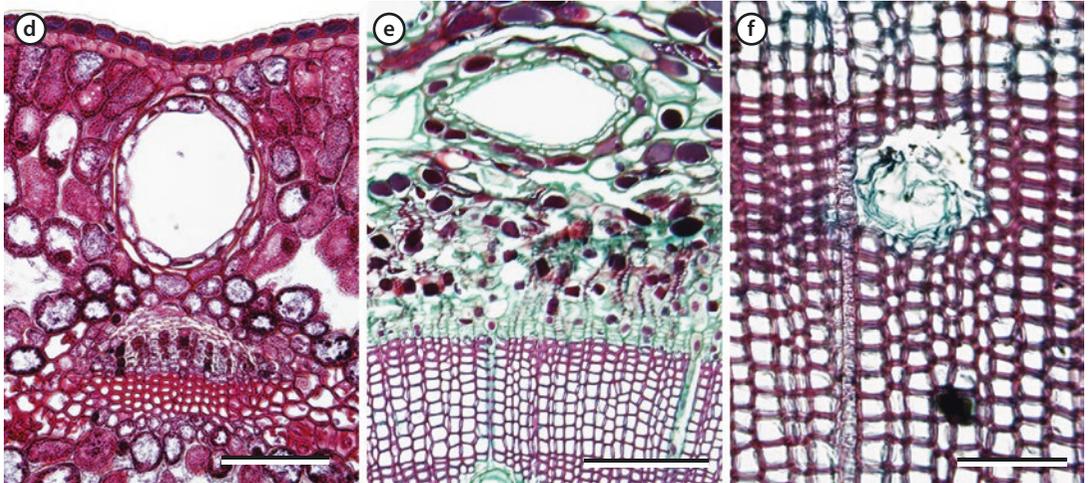

Fig. 13.3   d–f Resin ducts in **d** red cedar (*Juniperus virginiana*) leaf, **e** red pine (*Pinus resinosa*) stem, and **f** damaged lodgepole pine (*Pinus contorta*) stem. Scale bars = 50 μm in **d**, 100 μm in **e**, and 50 μm in **f**. (**d–f** RR Wise)

13.3.3   Laticifers

Laticifers are a special type of internal secretory system. Like resin ducts, they can be quite long, but they are differentiated from ducts in that they produce milky substances, primarily **latex**. Laticifers are either chains of fused cells whose cross-walls are digested in the center or single cells with nearly unlimited growth. The first are termed **articulated laticifers** (a.k.a. **laticiferous vessels**) (■ Fig. 13.3g); the second are **non-articulated laticifers** (a.k.a. **laticiferous cells**)
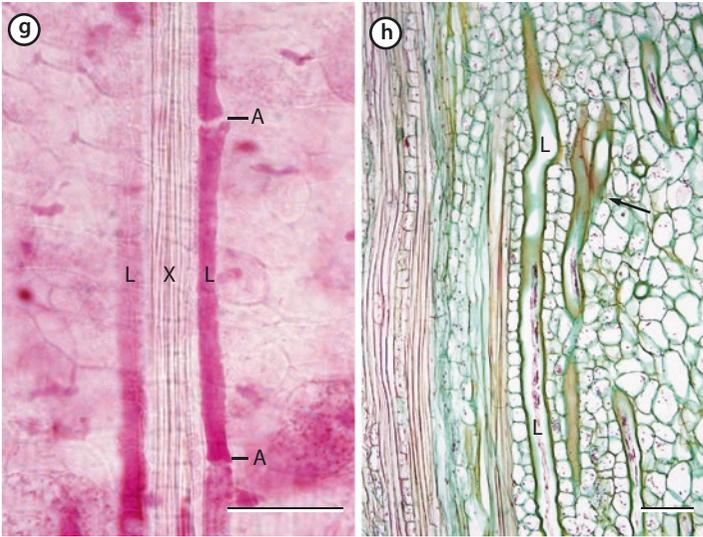
◘ **Fig. 13.3** **g** Articulated (A), anastomosing (connected cells) laticifers (L) lying on either side of a xylem strand (X) in a banana leaf (*Musa* sp.). The laticifers are stained red. The term "anastomosing" implies that the adjacent laticifers fuse with each other to form one long secretory structure. **h** A longitudinal section of *Euphorbia* sp. stem laticifers (L) with one showing a branch visible as a "fork" (*arrow*). Non-articulated anastomosing laticifers characterize all of the Euphorbiaceae. Scale bars = 50 μm in **g** and 100 μm in **h**. (**g**, **h** RR Wise)

(◘ Fig. 13.3h). Non-articulated laticifers grow **intrusively** (pushing aside neighboring cells). They undergo mitoses that are not accompanied by cytokinesis. As a result, a multinuclear (coenocytic) cell is formed. Both articulated and non-articulated laticifers may be branched (i.e., anastomosed). Latex is a typically a milky fluid, but it can also be clear, brown, or orange. Latex is composed of both organic (alkaloids, terpenoids such as those in rubber particles, tannins, etc.) and inorganic substances (crystals) in an aqueous phase. The latex is a powerful defense against herbivores. Plants that contain latex are found within the Euphorbiaceae and the Apocynaceae that includes the dogbanes, milkweeds, and other plant families.

Some insects utilize plant defenses for their own benefit. Monarch butterflies (*Danaus plexippus*) are migratory insects within North America. Monarch caterpillars consume milkweed leaves and thus ingest latex that contains cardiac glycosides that are toxic to many other insects. The insect sequesters the toxin within the body, which renders it as distasteful to many potential predators. Predators with previous experience with eating monarchs learn to avoid them by cueing in on the butterfly's distinctive aposematic coloration. Thus, the monarch uses the products of plant defense for its own defense.

Often there is a question about how to distinguish between euphorbia (Euphorbiaceae) and cacti (Cactaceae) that have evolved via convergent evolution. One general distinction between the plant families is the presence or absence of latex. A small cut or prick of the plant will show either a watery fluid (cactus) or a "milky white" latex (euphorbia). While both may have spines, cacti typically have multiple ones that are on raised circular disks called areolas,

whereas euphorbs have paired spines but no areolas. Cacti are typically found in arid regions of the Americas; alternatively, euphorbs are found worldwide in multiple environments. Some euphorbs lack succulence and have broad leaves. This includes the poinsettia (*Euphorbia pulcherrima*), castor bean (*Ricinus communis*), and the economically important rubber tree (*Hevea brasiliensis*).
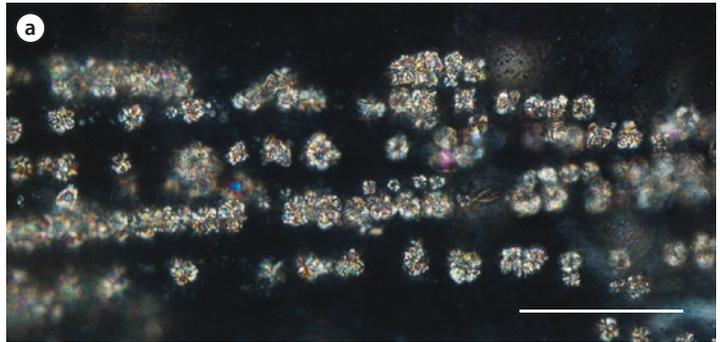
13.4 Idioblasts Are Internal Secretory Cells That Contain Crystals, Cystoliths, or Tannins

Crystals, cystoliths, and tannins are found in unique individual and isolated cells termed idioblasts. "Idio-" is Latin for distinct or separate, and idioblasts are so named because they are uniquely different in structure and function from the surrounding cells or tissues of plants. Idioblasts may be found in any plant organ and in any tissue.

13.4.1 Crystal Idioblasts

Crystals are common features of many plants and plant organs (◘ Fig. 13.4a). The vast majorities are composed of calcium oxalate, but calcium carbonate, magnesium carbonate, and calcium malate crystals can be found as well (Franceschi and Nakata 2005). When calcium carbonate is found, it is usually in association with cell wall material in a cystolith (refer to ▶ Sect. 13.4.2).

Although calcium oxalate (CaOx) crystals may appear to be in the cell wall or even the cuticle, their formation is always within the vacuole(s) of the cell. Calcium is an important regulator of many cellular enzymes and functions; therefore its concentration must be tightly controlled. Significant evidence exists to support the hypothesis that crystal formation is a method for the plant to sequester Ca^{+2} into a non-soluble, nonphysiological form and then remobilize it if needed (Franceschi and Nakata 2005). In addition, crystals have well-known antiherbivory effects. The leaves of dumb cane (see below) when eaten release sharp, pointed crystals that can

◘ **Fig. 13.4   a** A paper birch (*Betula papyrifera*) leaf shown using polarized light. Druse crystals are aligned with the vasculature, forming rows of diamond-like jewels. Scale bar = 50 μm. (RR Wise)

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lead to a severe numbing of the mouth and throat and a temporary loss of speech.

Calcium oxalate crystals can take a variety of forms, and form is used as the most common method of categorizing crystals (tissue location is the other). All crystals are formed in the cell vacuole. **Druse** crystals are isodiametric with many pointed facets (◙ Fig. 13.4b, c). **Raphide** and **styloid** crystals are both **acicular**, meaning needle-shaped (◙ Fig. 13.4d). They differ in that styloids are solitary, while raphides occur in bundles of up to several dozen individual crystals. Raphides are present in specialized cells called
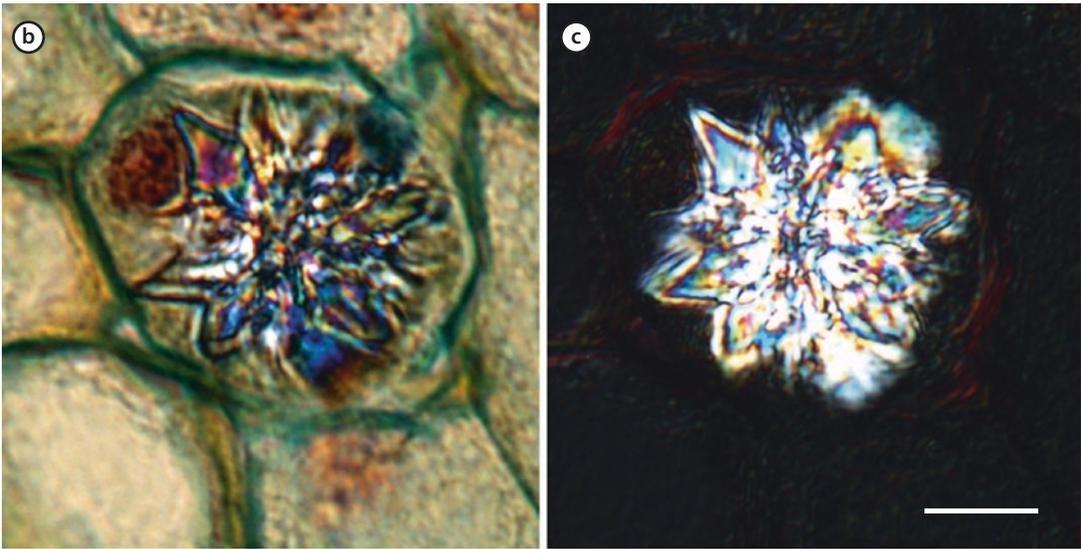
◙ **Fig. 13.4** **b**, **c** Druse crystal in the stem of ginkgo (*Ginkgo biloba*) viewed under brightfield **b** and polarized light **c** illumination. Scale bar = 10 μm for both panels. (**b**, **c** RR Wise)
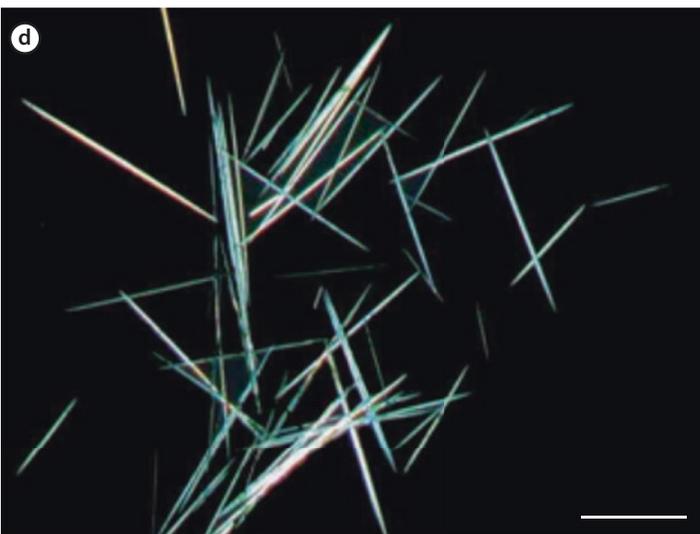
◙ **Fig. 13.4** **d** Polarized light of isolated acicular crystals designated as raphides from dumb cane (*Dieffenbachia seguine*). Ingestion can cause a very sore throat and temporary speechlessness when swallowed. Scale bar = 25 μm. (RR Wise)
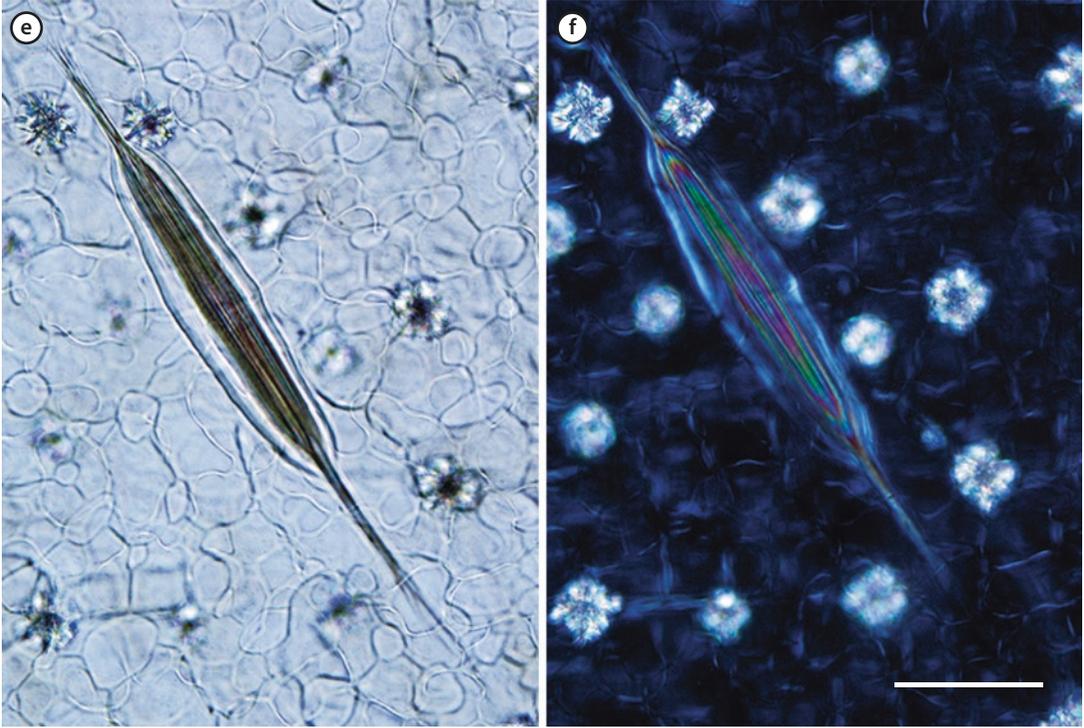
■ **Fig. 13.4   e**, **f** Raphides in a biforine cell from a dumb cane (*Dieffenbachia* sp.) leaf. Styloid crystals are being extruded from both ends of the biforine. Note also the numerous druse crystals in the background. **e** Viewed with bright-field light microscopy. **f** Viewed with polarized light. Scale bar = 50 μm for both panels. (**e**, **f** RR Wise)
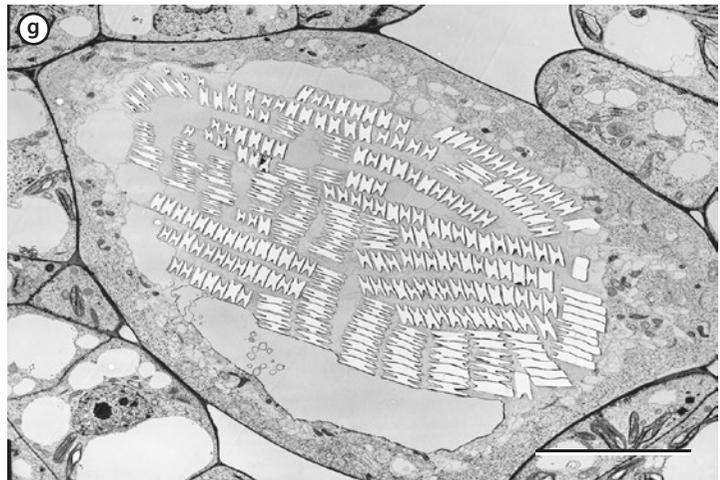
■ **Fig. 13.4   g** Raphides in the vacuole of a water lettuce (*Pistia stratiotes*) leaf. The raphides are lost during sample preparation leaving empty spaces in the tissue section. Scale bar = 10 μm. (Image courtesy of Gayle Volk and Vincent Franceschi)

biforine cells (■ Fig. 13.4e–g) that are capable of ejecting the raphide crystals upon disruption, causing the symptoms that gave dumb cane its name. **Crystal sands** appear as clusters of small, individual cube-like particles scattered throughout the cell cytoplasm
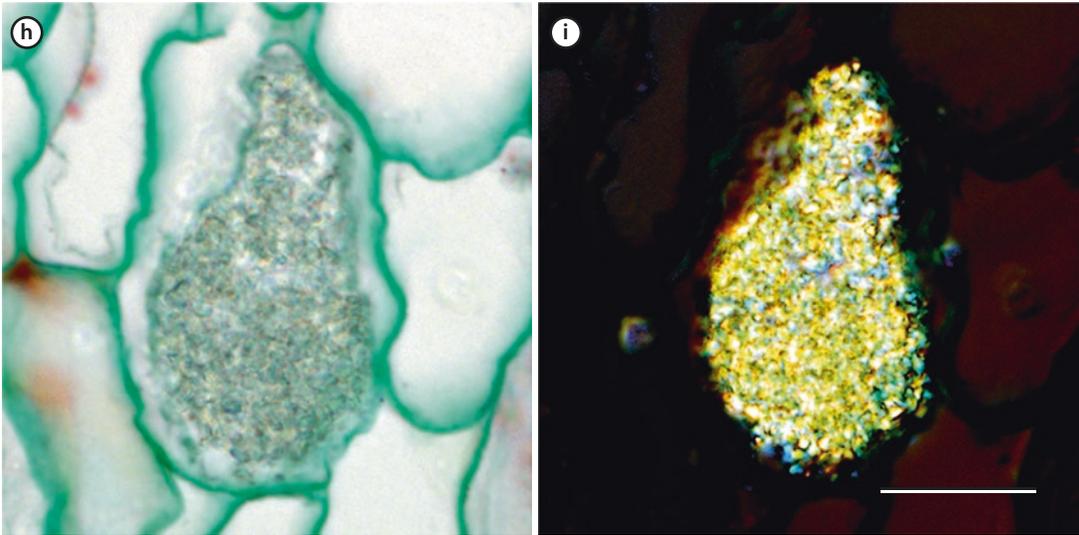
■ **Fig. 13.4**   **h, i** Brightfield **h** and polarized light **i** images of crystal sand in tobacco (*Nicotiana tabacum*) root. Scale bar = 10 μm for both panels. (**h, i** RR Wise)
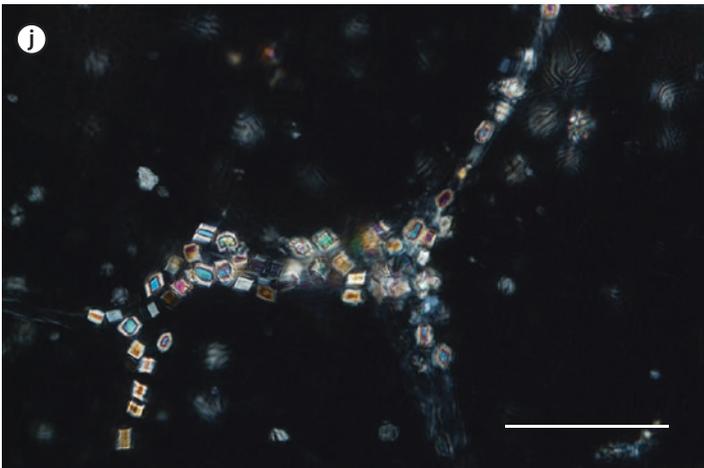
■ **Fig. 13.4**   **j** Polarized light image of prismatic crystals from a quaking aspen (*Populus tremuloides*) leaf. The crystals lie along leaf veins, which cannot be seen in polarized light. Scale bar = 50 μm. (RR Wise)

(■ Fig. 13.4h, i). **Prismatic crystals** are large and sometimes with pointed ends and usually only occur as one to several per cell (■ Fig. 13.4j). All crystals exhibit birefringence such that light is refracted when illuminated with polarized light in the light microscope, an effect seen in some of the micrographs in this section.

13.4.2   Cystoliths

Lithocysts (literally "rock box") are large epidermal cells containing amorphous calcium carbonate in a cellulose matrix; the cellulose core arises from and remains connected to the primary cell

wall (■ Fig. 13.4k). Lithocysts may extend inward towards the leaf mesophyll and do not project above the surface of the leaf as is the case with trichomes. The calcium carbonate concretion is called a **cystolith** (or "box rock"). Cystoliths are found in less than a dozen of the 620 angiosperm families, and vary in structure (■ Fig. 13.4l–o). Their function and that of the calcium carbonate inclusions remain cryptic. However, plants are known to sequester calcium in a number of insoluble forms, which may be related to the need to keep intercellular calcium levels low. As evidence of this, experiments using varying soil calcium levels, and therefore the amount of Ca^{+2} available to be taken up by the plant, demonstrate a relationship between Ca^{+2} uptake and lithocyst development. Although they are undoubtedly involved in calcium storage and regulation, cystoliths differ from calcium oxalate crystals in that they store amorphous calcium carbonate as opposed to crystalline CaOx (hence the lack of cystolith birefringence), and they are extracellular (cell wall or apoplastic), while CaOx crystals are intracellular (vacuole or symplastic).

The elemental composition of a cystolith can be imaged using XRMA (■ Fig. 13.4p). ■ Figure 13.4q shows that the cystolith has much higher levels of calcium than the surrounding cells and that the cellulose stalk is high in silicon. If the X-ray microanalyzer had been used to image the carbon or oxygen of the carbonate, those elements would not have stood out against the backdrop of the abundant carbon and oxygen in the surrounding leaf tissue; the entire field of view would have been yellow.
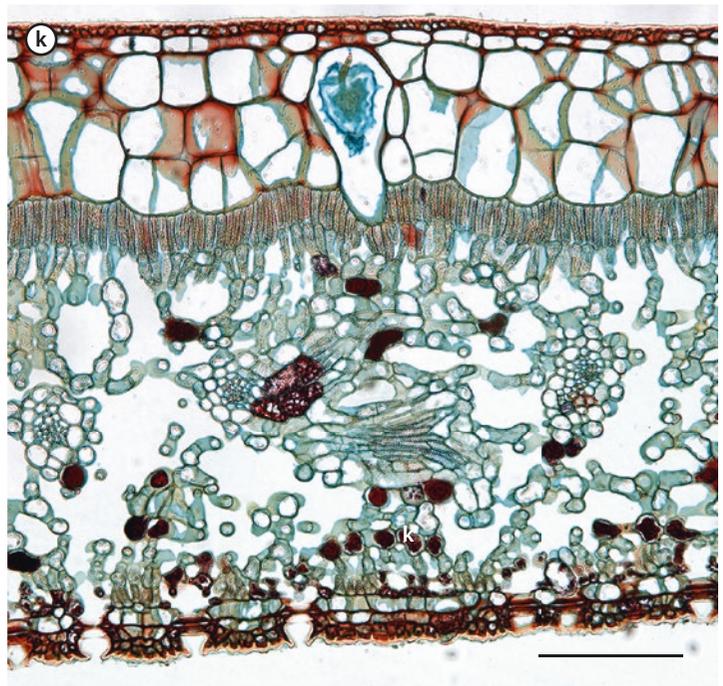
■ **Fig. 13.4   k** A lithocyst in the adaxial, multiple-layered epidermis of a fig (*Ficus* sp.) leaf. Note how the cystolith is attached to the cell wall by a small stalk composed of cellulose. Scale bar = 125 μm. (RR Wise)
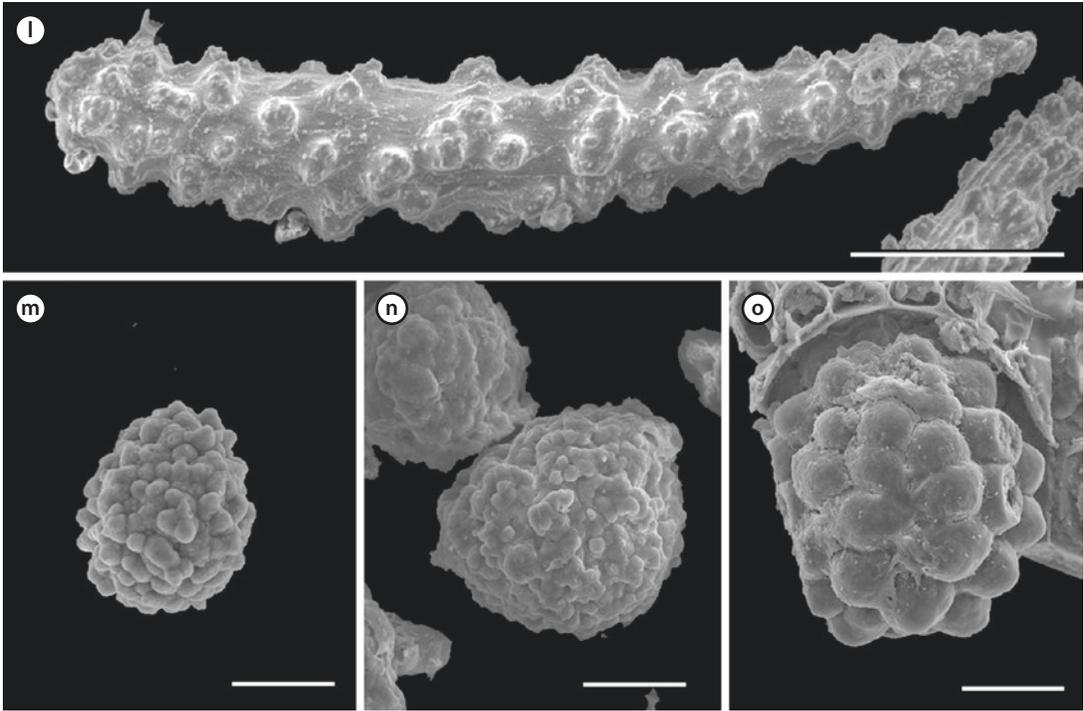
◘ Fig. 13.4   Cystoliths from **l** Mexican petunia (*Ruellia simplex*), **m** creeping fig (*Ficus pumila*), **n** white mulberry (*Morus alba*), **o** hops (*Humulus lupulus*). Scale bars = 50 μm in **l** and 25 μm in **m–o**. (**l–o** RR Wise)
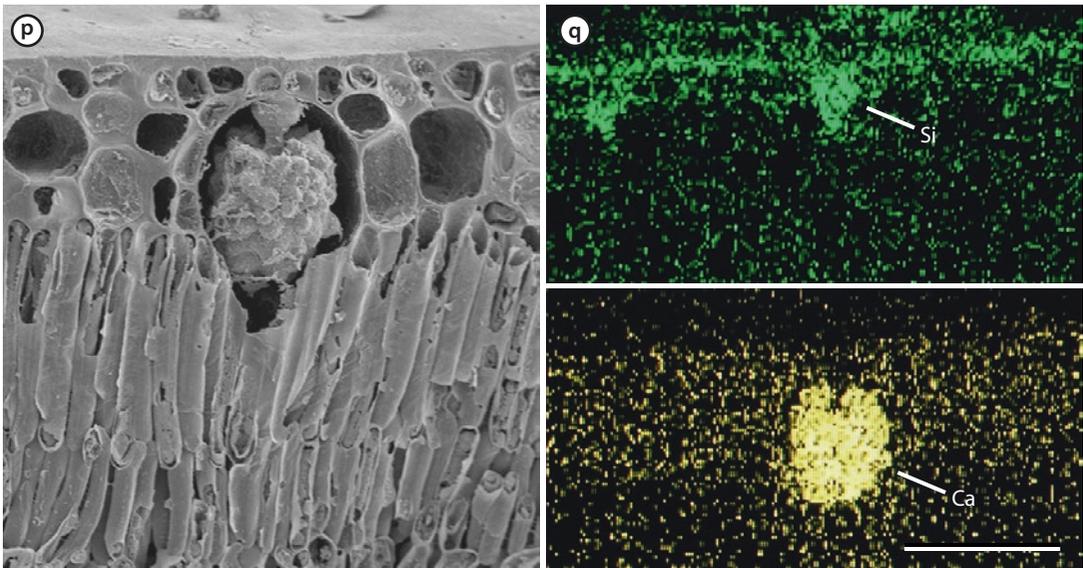
◘ Fig. 13.4   **p**, **q** A lithocyst in the epidermis of a fiddle leaf fig (*Ficus lyrata*) leaf. **p** The scanning electron micrograph shows the size and morphology of a cystolith within a lithocyst. **q** X-ray microanalysis images of the same area indicates that the cystolith contains high levels of calcium (Ca, *highlighted in yellow*) suspended by a silicon-rich stalk (Si, *green*). Scale bar = 50 μm. (**p**, **q** Nicholas Gabel)

13.4.3   **Tannin-Containing Idioblasts**

Tannin compounds are widely distributed in many species of plants (Mole 1993), where they play a valuable role in protection from predation, and perhaps also as pesticides, and in plant growth regulation. Tannins are localized within the vacuoles of specialized cells and stained black in both light (◼ Fig. 13.4r) and electron microscopy (◼ Fig. 13.4s). The astringency from the tannins is what causes the dry and "pucker" feeling in the mouth following the consumption of unripened fruit or red wine. Likewise, the destruction or modification of tannins with time plays an important role in the ripening of fruit and the aging of wine.
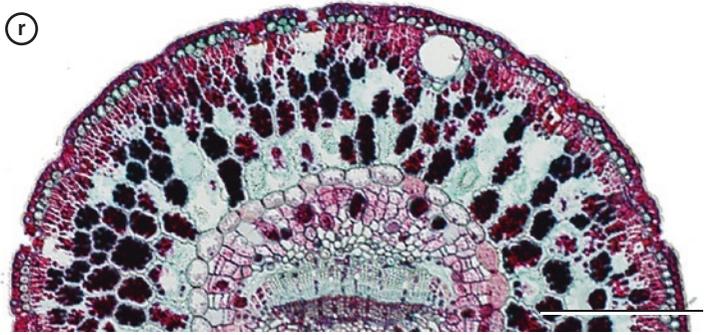
◼ **Fig. 13.4   r** A portion of single-leaf piñon (*Pinus monophylla*) leaf with many large tannin-filled cells. A large resin duct can be seen near the epidermis in the 1:00 position. Scale bar = 250 μm. (RR Wise)
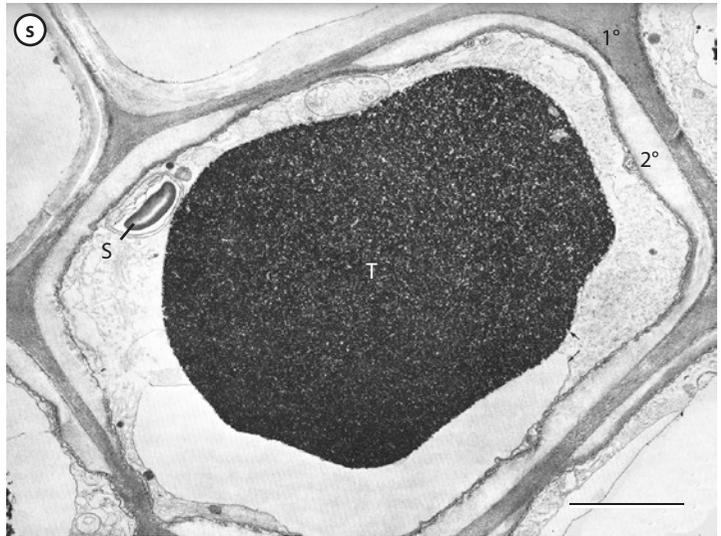
◼ **Fig. 13.4   s** Tannin cell in the vascular parenchyma of an eastern white pine (*Pinus strobus*) needle visualized with transmission electron microscopy. The dark inclusion (T) in the vacuole represents a product of tannin (a phenolic compound) reaction with the fixatives used in specimen preparation. Primary (1°) and secondary (2°) walls are indicated. Scale bar = 10 μm. (Image from: Ledbetter and Porter (1970), with permission)

13.5   Essential Oils Are Valuable Plant Extracts

Essential oils (the word "essential" meaning an embodiment of the essence of the plant) are extracts of any plant part that are used in a variety of applications including food additives, perfumes, drugs, and medicines (Burt 2004) (◘ Fig. 13.5a, b). While there are many types of plant extracts (think tea and coffee) and no clear lines between the different types, an essential oil typically contains true oils produced by internal or external secretory structures (Guenther 1948) (◘ Fig. 13.5a). Essential oils and other plant extracts have been used by humans for thousands of years and continue to play important roles today. Essential oils are typically extracted via distillation, organic solvents, supercritical CO_2, or a process called cold pressing which avoids the use of heat and solvents (Soto et al. 2004) (◘ Fig. 13.5b). The legalization of medical and recreational marijuana in many areas of the USA has driven an acceleration of the development of small- to medium-scale tetrahydrocannabinol (THC) extraction technologies, some of which can be quite dangerous in the hands of do-it-yourselfers (Hughes 2015).

13.6   Toxic Oils Often Cause Severe Dermatitis

The bane of countless trekkers throughout many wildlife regions of the USA (exceptions are California, Alaska, and Hawaii) has been plants that produce highly toxic oils. These plants commonly include poison oak, poison ivy, and poison sumac that are members of the genus *Toxicodendron* within the Anacardiaceae. These plants contain toxic oil, primarily urushiol, that is found within secretory canals of the phloem. This compound is found within the sap of most, if not all, plant structures and serves as an allergen that can cause a skin rash in sensitive individuals (also known as urushiol-induced contact dermatitis).

Urushiol is a mixture of several closely related aromatic (ring) organic compounds, which varies in composition by species. Those with longer side chains of unsaturated alkyls tend to produce stronger reactions. Upon absorption in the skin, urushiol becomes recognized by the immune system's dendritic cells and then migrates to lymph nodes where they stimulate the migration of T-lymphocytes into the skin and produce rashes and extreme irritation.

A variety of compounds have been found in the plant *Gelsemium elegans*, commonly known as "heartbreak grass" (◘ Fig. 13.6). The toxic compounds (largely alkaloids) are primarily found in the underground rhizome. Ingesting a solution of extracts of *Gelsemium* and alcohol is fatal, sometimes in a matter of seconds. It acts by paralyzing the respiratory centers, causing tremors, paralysis of extremities, convulsions, urination, defecation, and uncontrolled salivation. Death is brought about by paralysis of the spinal cord, near complete loss of muscular power and brain damage. In very small doses, studies have shown that extracts can wipe out tumor
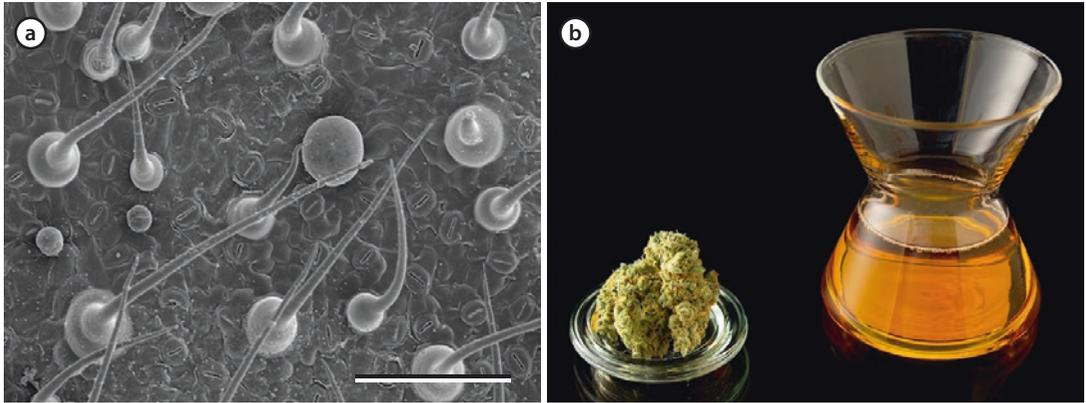
■ **Fig. 13.5**   THC-producing glands on the surface of a marijuana (*Cannabis sativa*) leaf. Image **b** shows extraction products. Scale bar in **a** = 15 μm. (**a** RR Wise; **b** AR Wise, Avitas Agriculture, Seattle, WA)

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■ **Fig. 13.6**   Heartbreak grass (*Gelsemium elegans*) grows as a vine in southeastern and southwestern USA, as well as in southern China near rivers and streambeds. Careful minute administration of extracts provided pain relief in the nineteenth century for some individuals, but that is no longer used for obvious reasons. Scale bar = 2 cm. (CF Crang)

cells linked to leukemia and cancer of the liver, lungs, breast, and colon. Some people who have consumed honey containing traces of *Gelsemium* toxins have died within hours. ■ Table 13.1 provides a partial list of toxic plants and the causes of their toxicity

■ Table 13.1	A partial listing of toxic and dangerous plants	
Common name	**Scientific name**	**Cause of toxicity**
Castor oil plant	*Ricinus communis*	Ricin from seeds
Suicide tree	*Cerbera odollam*	Cerberin from seeds
Little apple of death	*Hippomane mancinella*	Toxic milky sap
Rosary pea	*Abrus precatorius*	Abrin in seeds
Dumb cane	*Dieffenbachia* sp.	Raphides of calcium oxalate
Angel's trumpet	*Brugmansia* sp.	Atropine and scopolamine
Oleander	*Nerium oleander*	Cardiac glycosides
Hemlock	*Conium maculatum*	Coniline from leaves, seeds, and roots
Wolf's bane	*Aconitum lycoctonum*	Aconitine neurotoxins and cardiotoxins

13.7   Chapter Review

■ **Concept Review**

13.1 *External secretion involves moving substances outside of the plant.* Plants secrete to the exterior a large variety of oils, resins, salts, nectars, and toxins from a wide range of specific structures.

13.2 *Carnivorous plants have evolved external secretory structures as a mechanism for nutrient acquisition.* Carnivory in plants is a strategy for acquiring minerals in nutrient-deficient environments by capturing and digesting small animals, usually insects, in leaf traps or with sticky secretions. The prey is then digested, and the nutrients are absorbed by the leaf.

13.3 *Internal secretory structures include oil cavities, laticifers, and resin ducts.* Internal secretory products include oils, latex, and resins. They are diverse in both chemistry and function.

13.4 *Idioblasts are internal secretory cells that contain crystals or tannins.* Idioblasts are cells that appear different or out of place, as compared to surrounding cells. Many contain calcium oxalate (in several different crystal shapes), calcium carbonate (found in cystoliths), or tannins (located in the vacuole).

13.5 *Essential oils are valuable plant extracts.* For thousands of years, the products of internal and external secretory structures—typically called essential oils—have been extracted and used by humans for food additives, drugs, and medicines.

13.6 *Toxic oils often cause severe dermatitis.* The secretions of multiple plant species contain a variety of toxic oils that can cause serious allergic reactions and skin irritation.

■ **Concept Connections**

? 1. Insert the terms below into the following concept map. Every term will be used once and only once (except for "deter herbivory" which will be used five times).

Creosote	Idioblasts	Resin ducts
Crystal sand	Laticifers	Salt
Crystals	Lithocysts	Secreted to surface
Cystoliths	Nectar	Stinging hairs
Deter herbivory (use five times)	Nectaries	Stored internally
Digestive enzymes	Oil cavities	Styloid
Druse	Prismatic	Tannin bodies
Glandular trichomes	Raphide	Water
Halophytes	Reduce transpiration	Water balance
	Resin	

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Secretory structures
— two types →
- internal
- external

internal
- products are → [ ]
- four types:
  - [ ] may contain → essential oils → used to → [ ]
  - [ ] secrete → [ ] → used to → [ ]
  - [ ] secrete → latex → used to → [ ]
  - [ ] three types:
    - [ ] contain → calcium carbonate
    - found in → [ ]
    - [ ] used to
    - [ ] used to
  - five types:
    - [ ] contain → calcium oxalate
    - [ ] → [ ]
    - [ ] → [ ]
    - [ ] → [ ]
    - [ ] → [ ]

external
- products are → [ ]
- six types:
  - [ ] can secrete → [ ] used in → carnivory
  - colleters → can secrete → [ ] used to → [ ]
  - [ ] secrete → toxins → used to → [ ]
  - [ ] secrete → [ ] used to → reward pollinators
  - [ ] secrete → water → used to → [ ]
  - salt glands → secrete → [ ] adaptation for → [ ]

- **Concept Assessment**

? 2. Single-celled laticifers that are branched are said to be
   a. articulated.
   b. non-articulated.
   c. anastomosed.
   d. both articulated and anastomosed.
   e. both non-articulated and anastomosed.

? 3. Epithelial cells of *Apium* resin ducts are densely cytoplasmic.
   a. true.
   b. false.

? 4. Peltate digestive glands are likely to be found in
   a. *Dionaea.*
   b. *Dracaena.*
   c. *Drosera.*
   d. *Drosophyllum.*
   e. *Pinguicula.*

? 5. Which secretory structure is most likely derived from the epidermis?
   a. resin duct.
   b. tannin cell.
   c. laticifer.
   d. druse-containing cell.
   e. colleters.

? 6. Epithem cells are
   a. modified epidermal cells.
   b. modified vascular bundle cells.
   c. a kind of transfer cell.
   d. glandular trichomes.
   e. individual units of laticifers.

? 7. Trichomes that secrete a sticky substance typically attract
   a. pollinators.
   b. predators.
   c. prey.
   d. people.
   e. water for secretion.

? 8. Hydathodes have stomata.
   a. true.
   b. false.

? 9. Raphides develop in
   a. chloroplasts.
   b. nuclei.
   c. endoplasmic reticulum.
   d. vacuoles.
   e. more than one of the above.

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❓ 10. Lithocysts contain
   a. druses.
   b. raphides.
   c. prismatic crystals.
   d. tannins.
   e. cystoliths.

❓ 11. Latex is produced by
   a. glandular trichomes.
   b. laticifers.
   c. vacuoles.
   d. nectaries.
   e. resin ducts.

- **Concept Applications**

❓ 12. Plants are often not very nice to their distantly related zoo-logical cousins. Compile a list of the structures plants use to deter herbivory, and explain how each helps to protect the plant. Even when plants offer a sweet reward for the attentions of a bird or insect, it is only to serve their own needs. What secretory structures and secretions do plants use to attract and reward animals? What benefit(s) do the plants gain?

❓ 13. Carnivorous plants are found in soils with low-nutrient environments and use carnivory to acquire minerals (mostly nitrogen) that are not available in the soil. Explain the additional observation that carnivorous plants are usually found in high-light environments.

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