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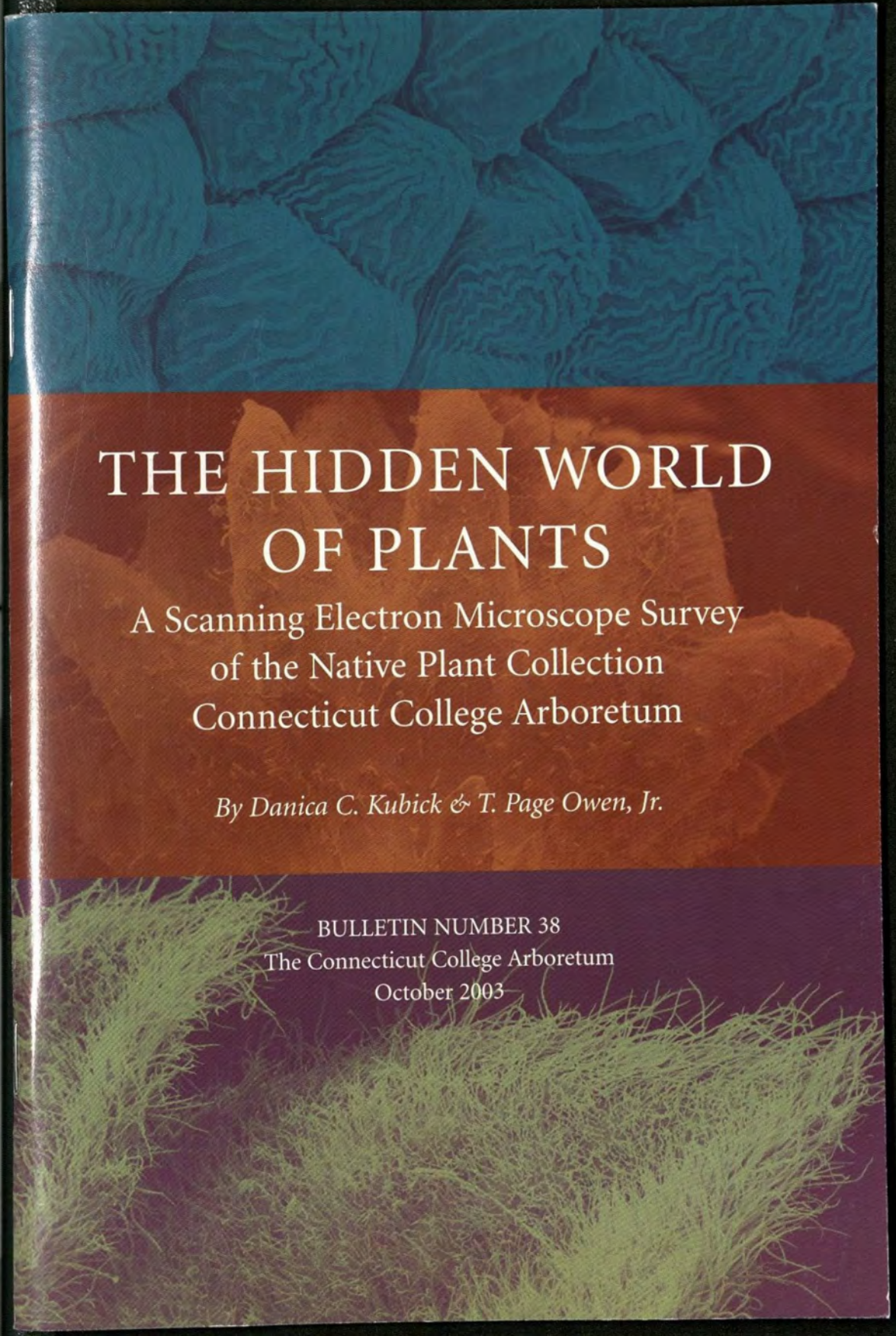

THE HIDDEN WORLD OF PLANTS

A Scanning Electron Microscope Survey of the Native Plant Collection Connecticut College Arboretum

By Danica C. Kubick & T. Page Owen, Jr.

BULLETIN NUMBER 38
The Connecticut College Arboretum
October 2003

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FOREWORD

THIS PUBLICATION FOLLOWS in the tradition of showcasing the results of student/faculty research projects done primarily in the Connecticut College Arboretum. Previous bulletins have explored the Arboretum's Native Plant Collection, its reptiles and amphibians, its birds, as well as special habitats like tidal marshes, freshwater wetlands and estuaries.

Author Danica Kubick, a *magna cum laude* biology graduate in the class of 2000, originated this project as a summer internship to learn how to use the scanning electron microscope. Working with Botany Professor T. Page Owen, Jr., Danica chose as her subject woody plants in the Arboretum's Native Plant Collection. The resulting images are as beautiful as they are informative of nature's design. The photographs and accompanying text are intended to be an introduction to the functions and capability of this type of microscope, and to plant surface structures that are just beyond the range of human vision. "The Hidden World of Plants" reveals what seem like alien landscapes within the most common trees and shrubs. It also shows how the Arboretum can provide an endless stream of educational projects for lab as well as field-based teaching and research.

Glenn D. Dreyer
Charles and Sarah P. Becker '27 Director

ACKNOWLEDGEMENTS

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INTRODUCTION

IN OUR DAILY OBSERVATIONS of nature, plants are admired for beautiful fruits and flowers, brilliant autumn foliage, and their capacity to create and restore natural beauty to virtually any landscape. Plants, like animals, are complex and dynamic organisms, with biological functions that are highly organized at the cellular and molecular levels. Scanning electron microscopy has emerged as an important technique for relating the structures of an organism to its physiological function. This project began as a scanning electron microscope study of the "hidden world of plants" and developed into a microscopic picture gallery of the specialized structures and surfaces of specimens in the Native Woody Plant Collection of the Connecticut College Arboretum. The micrographs in this bulletin not only show the relevance of scanning electron microscopy to the study of structure and function, but they also inspire an appreciation for the beauty of the plant world, and how that beauty is present from the microscopic level all the way through to the more familiar entire plant body.

The development of the electron microscope in the 1930s profoundly influenced the study of biological structure, especially the cell (see Bozzola and Russell 1999 for a complete overview). Since then, the electron microscope has become one of the most important and widely used tools of modern science. Not only does the electron microscope have a magnification capability thousands of times greater than the light microscope, but the images it creates have a much higher resolution, allowing scientists to view viruses and molecules such as DNA, as well as very small organisms, with increased clarity. Indeed, virtually all organelles (specialized parts within a cell) were discovered or examined in detail using the electron microscope. The electron microscope set the stage for experiments designed to relate cell structure with function, and to examine how cell structure changes under different experimental conditions; these experiments have revolutionized our knowledge of the cell. Electron microscopy technology is becoming more advanced with computer-assisted imaging and image enhancement. As the electron microscope becomes more versatile through technological advancements, it will play an ever-increasing role in our understanding of biological structures and whole organisms.

THE SCANNING ELECTRON MICROSCOPE

THERE ARE TWO TYPES of electron microscopes – the transmission electron microscope (TEM) and the scanning electron microscope (SEM). The TEM typically creates a two-dimensional image by transmitting electrons through a very thin (60 – 80 nanometers thick) section of specimen; thus one usually examines the inside of cells using the TEM. With the SEM used in this study, one can observe three-dimensional features of recognizable samples, even whole organisms. A three-dimensional image is produced when a narrow, high-energy beam of electrons is scanned over the organism, secondarily creating new low energy electrons from the sample surface (Figure A). In most SEMs, a heated tungsten filament emits the electrons in the electron beam. The SEM has an electron detector that collects the secondary electrons and generates an electrical signal. The signal is processed and transformed into pixels corresponding to the scanned point on the sample, which are then displayed on a computer monitor to produce an image. The brightness of a pixel is directly proportional to the number of secondary electrons coming from the surface of the specimen. The pixels blend into a continuous image in which differences in contrast give the impression of depth and a three-dimensional appearance to the image. Contrast is created because regions that generate a large amount of secondary electrons appear brighter than those that generate less. SEM images have a very high resolution and a large depth of field (the depth of the specimen that is in focus) at very low or very high magnifications, especially compared to a light microscope. Central to the proper functioning of the SEM is a vacuum system that removes air molecules that can obstruct the movement of high-energy electrons to and from the specimen, as well as low-energy secondary electrons to the detector.

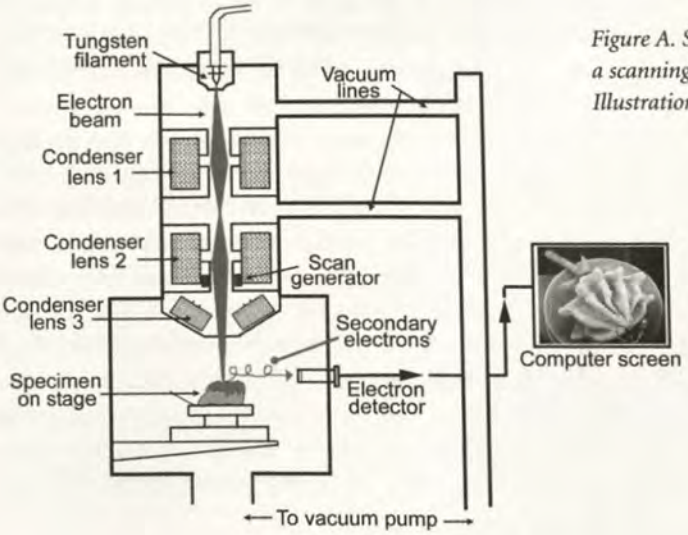

Figure A. Simplified diagram of a scanning electron microscope. Illustration by Owen.

Another use of the SEM is for compositional analysis of specimens. The identity, amount and location of elements in a sample can be determined by monitoring X-rays generated from the interaction between the electrons and the specimen (Kessel and Shih 1974). Thus, the SEM can be used as an analytical as well as an imaging tool.

SPECIMEN PREPARATION

Before being loaded on the specimen stage in the SEM, each sample undergoes a specific preparation procedure. First, the specimen is chemically preserved ensuring that the structure of the tissue remains unaltered from the living state. Preservation of a specimen occurs in a glutaraldehyde solution followed by one with osmium tetroxide. Glutaraldehyde serves to cross-link the components of the cell, particularly proteins, so the structure of the cell is maintained by an interconnecting meshwork. Osmium tetroxide adds density and contrast to the specimen. To prevent damage, a buffer is used with both fixations to stabilize the pH of the specimen.

The next processing step is dehydration; the water in the cells is replaced with a dehydrating agent such as ethanol or acetone. The specimens in this study were dehydrated in an acetone dilution series and then 100% ethanol. After dehydration, the specimens cannot be allowed to air dry; under these conditions, biological structures tend to collapse and surface details are destroyed. The specimen drying technique used in this study was critical point drying, in which the ethanol in the specimen was replaced with pressurized, liquid carbon dioxide. Inside the critical point dryer, the carbon dioxide reaches its critical point (a specific combination of temperature and pressure), which causes its transition from the liquid phase to the gas phase, without damaging the sample. The gas is slowly released from the chamber of the critical point dryer and the result is a dry, but very fragile and brittle specimen.

The dried specimen is then glued onto an aluminum mount and coated with a thin layer of gold. The gold coat supplies the secondary electrons; it also serves to ground the specimen, which prevents the buildup of high voltage static charges, and to conduct away heat that could harm the specimen. The metal is commonly applied with a sputter coater. In the vacuum chamber of the sputter coater, ionized inert argon gas molecules and electrons strike a negatively charged gold target with such force that some atoms from the gold target are released. The gold atoms bounce around in the chamber with the ionized gas molecules and electrons and in a very random pattern, striking the specimen's surface. The specimen gradually becomes coated with a uniform and thin layer of the gold. The coated and mounted specimen is then ready for the SEM (LEO 435VP). Samples are placed on a stage that can be moved in horizontal vertical planes, and can also be tilted and rotated.

THE CONNECTICUT COLLEGE NATIVE WOODY PLANT COLLECTION

THE PLANT SPECIMENS used to make the electron microscope images in this bulletin came from the Native Woody Plant Collection of the Connecticut College Arboretum. This collection is a 25-acre area that features trees and shrubs native to Eastern North America and hardy in Southeastern Connecticut. The collection is a result of the ongoing efforts of the Arboretum to cultivate and display native plants (Harvey and Dreyer 1996). The Native Woody Plant Collection is bordered to the west by Williams Street and the college campus, to the east by Bolleswood Natural Area, to the north by Gallows Lane and to the south by a chain-link fence. Currently, the collection contains approximately 320 different, accessioned plant taxa (species, subspecies and varieties). Each tree and shrub in the collection is labeled with a metal tag that includes its botanical name and accession number.

SURFACE STRUCTURES

In order to help the reader better understand the SEM micrographs featured in this bulletin, a short description of the outer structures of plants follows. Figure numbers in parenthesis indicate the images that correspond to the descriptions. Those interested in additional detail may refer a number of publications that were the primary sources for this summary (Cutter 1978, Esau 1953 and 1960, Lott 1976, Raven et al. 1999, Rudall 1992).

THE EPIDERMIS

The epidermis is the outer layer of cells of the primary plant body; it is present on stems, roots, leaves, flowers, fruits and seeds (1-14). Its surface is in direct contact with the environment; consequently, it has developed specialized structures that function in plant processes that involve the external environment. Specializations on the aerial plant body, including stomates, trichomes (hairs) and wax deposits, are discussed below. The epidermis is typically a single layer of cells with square or sometimes elongated shapes that have straight or undulating cell walls (7).

THE CUTICLE

The cuticle, a layer composed of cutin (a fatty substance), lipids (fats, oils and related substances) and wax, covers the epidermis of the majority of the aerial plant body (4, 7,

18-19, 27). Its primary function is the prevention of water loss. The cuticle is typically not smooth, but appears to have ridges and folds of various lengths and arrangements. These surface features often radiate from trichomes and stomata. The pattern of cuticle deposition, along with the shape of epidermal cells, can have taxonomic applications.

In several plants, conspicuous deposits of wax form over the cuticle; this is referred to as epicuticular wax. The wax is synthesized by the epidermal cells, secreted through their outer cell walls and deposited on the surface. Wax deposits vary in shape, size and arrangement and come in the form of flakes, granules, filaments and sheets (5, 21). Epicuticular wax forms mostly on leaves and fruits; the whitish "bloom" often seen on fruits and leaves is the result of this wax. Bayberry fruit is a well known example. The function of these deposits is to resist fungal infection by limiting water contact. Plants that have surface wax are much less susceptible to herbicides and fungicides than plants that have a smooth cuticle. In carnivorous pitcher plants, epicuticular wax on the inner surface of the pitcher creates a slippery surface so that insects are more likely to fall in and less likely to climb out. If epicuticular wax is rubbed off, it will grow back in its original form, often within 24 hours.

STOMATA

Gas exchange is critical for respiration and photosynthesis – the life processes of the plant. Higher plants, such as Gymnoperms and Angiosperms, have evolved specialized structures called stomata for the purpose of gas exchange. Stomata are small pores in the epidermis of aerial structures, usually leaves (2, 3). The term stomata comes from the Greek word "stoma," which means mouth. A stoma is surrounded by two kidney-shaped guard cells (5-7) that control the opening and closing of the pore. Characteristic of guard cells are their unevenly thickened cell walls, which enable them to change their shape according to internal fluctuations in cell water pressure. As the guard cells absorb water, they become turgid; in this state, the stoma's pore is open. The pore is closed when the guard cells are in a less rigid state. The guard cells are typically the only epidermal cells that are photosynthetic.

Stomata are most abundant on leaves, but also frequently occur on stems and flower parts. Stomata may occur on both sides of the leaf but typically occur more frequently on the lower side; this prevents water loss because there is less exposure to sunlight and wind on the lower surface of the leaf. Esau (1953) estimates that the number of stomata on the surface of a dicot leaf (net-veined, broadleaved plants) ranges between 1,000 – 100,000 per square centimeter. Some stomata may occur at a level even with epidermal cells; others may be raised above or sunken below the surface of the epidermis.

In leaves with parallel venation, such as monocots like grases and lilies, and the needles of conifers, stomata are arranged in parallel rows with the long axis of the leaf (8). In most monocots, the stomata are long and thin, and the opening is narrow. In

dicots, the stomata are scattered and appear randomly arranged (7). Stoma of conifers are typically deeply sunken (9). Sunken stomata function to minimize water loss during transpiration by trapping moist air between the epidermis of the needle and the guard cell. In conifers, a heavy cuticle on the surface of the needle further reduces water loss; this cuticle extends over the sunken stomata and into the cavity above the guard cells (Lott 1976). Sunken stomata are an adaptation in northern conifers, which have leaves (needles) that are evergreen and remain attached through the winter. In the north, winter temperatures are often too low for roots to function in absorbing water and conifer leaves have evolved sunken stomata to reduce water loss (Pielou 1988).

TRICHOMES

Trichomes are epidermal hairs that have a variety of forms and functions. The word trichome is of Greek origin and means "growth of hair." Trichomes are formed by the outgrowth of epidermal cells and are often classified by the type and number of cells they contain (10-17, 20, 22-26). Trichomes can be single or multicellular, glandular (15-17) or non-glandular, branched (10-11) or unbranched (12-13), or even shield shaped with the attachment at its center, referred to as peltate (22-23). They are present on all parts of the plant, although they vary in form and density on different organs. Some remain attached to the plant throughout its life and some fall off early in development. Trichomes often have a characteristic form within species or groups of plants and can therefore be used for identification purposes. For example *Rhododendron* (26) and *Cannabis* can each be identified by their characteristic trichomes.

Trichomes serve a variety of functions and many have evolved as adaptations to habitat. For example, root hairs are unicellular trichomes that function in absorbing water. Dense coverings of hairs on leaf surfaces trap moist air, which reduces water loss. Increased leaf pubescence, or hairiness, serves a protective function against insects (12); many studies have linked mortality of insect larvae to increased trichome density. Hooked hairs that impale insects are another defensive mechanism.

Glandular trichomes (16-17), external secretory structures, have a wide array of specific functions in plants. They have a head region consisting of secretory cells, which sits atop a stalk; both the head and the stalk can be unicellular or multicellular. A raised cuticle covers the head region; secretions accumulate between the cuticle and the head region. Some glandular trichomes secrete sticky substances that trap insects; others secrete stinging chemicals that are repellant or toxic to insects. The glandular trichomes of stinging nettle (*Urtica dioca*) are specialized stinging hairs, whose tips break off when contacted by an outside body; the sharp point of the stiff hair penetrates the body and releases a toxic chemical. Glandular trichomes of carnivorous plants secrete digestive juices. On flowers, they secrete fragrant chemicals to attract insects for pollination. Secretions of some glandular trichomes may also reduce water

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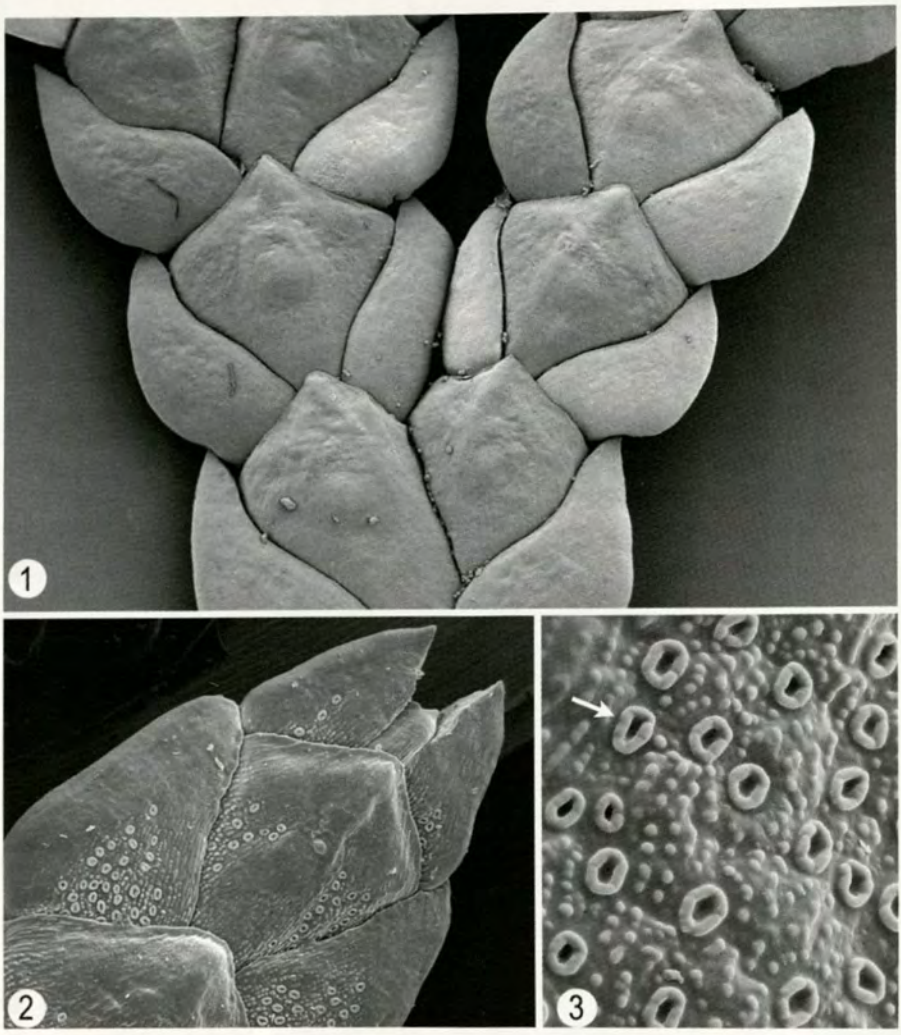

PLATE 1

PLATE 1

1. Branchlet of eastern arborvitae (*Thuja occidentalis*), a conifer with prominent, overlapping, scale-like leaves.
2. Tip of the eastern arborvitae branchlet; the larger, white, circular structures are stomates.
3. Section of the eastern arborvitae branchlet at a higher magnification. Guard cells surrounding the stomatal pores (arrow) and ridges in the waxy cuticle are visible.

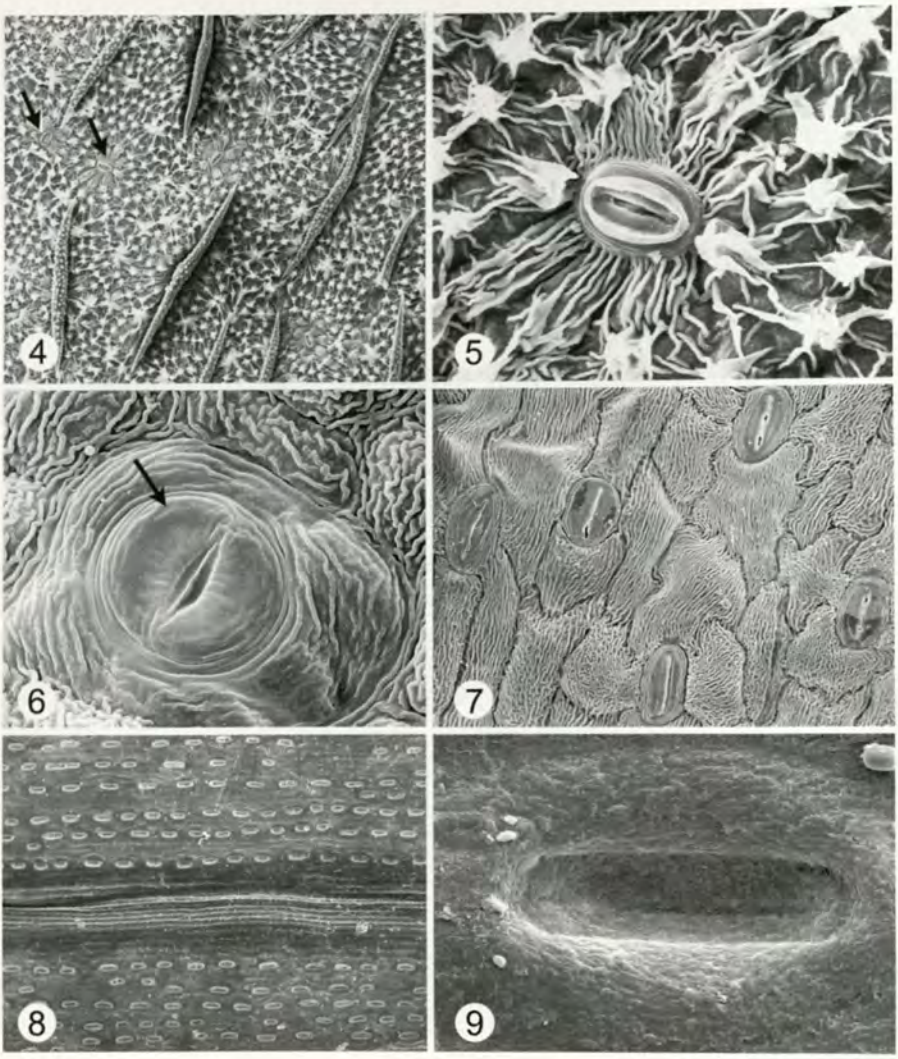

PLATE 2

PLATE 2

4. Lower side of a flowering dogwood (*Cornus florida*) leaf with large cuticular ridges and a meshwork of asterisk-like epicuticular wax surrounding small stomata (arrows).

5. Stoma of a flowering dogwood leaf at a higher magnification. Epicuticular wax radiates from the stomal complex, which is partly open and surrounded by two kidney-shaped guard cells.

6. Stoma on a "Pink Puff" azalea (*Rhododendron bakeri x R. arborescens*) bud showing guard cells (arrow). Note the elaborate pattern of the epidermal wax.

7. Stomata of a northern bayberry (*Myrica pennsylvanica*) flower petal. The epidermal cells are covered with striations of epicuticular wax and are in the typical puzzle-like arrangement of a dicot epidermis.

8. Sunken stomata in vertical rows on an eastern hemlock (*Tsuga canadensis*) needle.

9. Higher magnified image of the sunken stomata on an eastern hemlock needle.

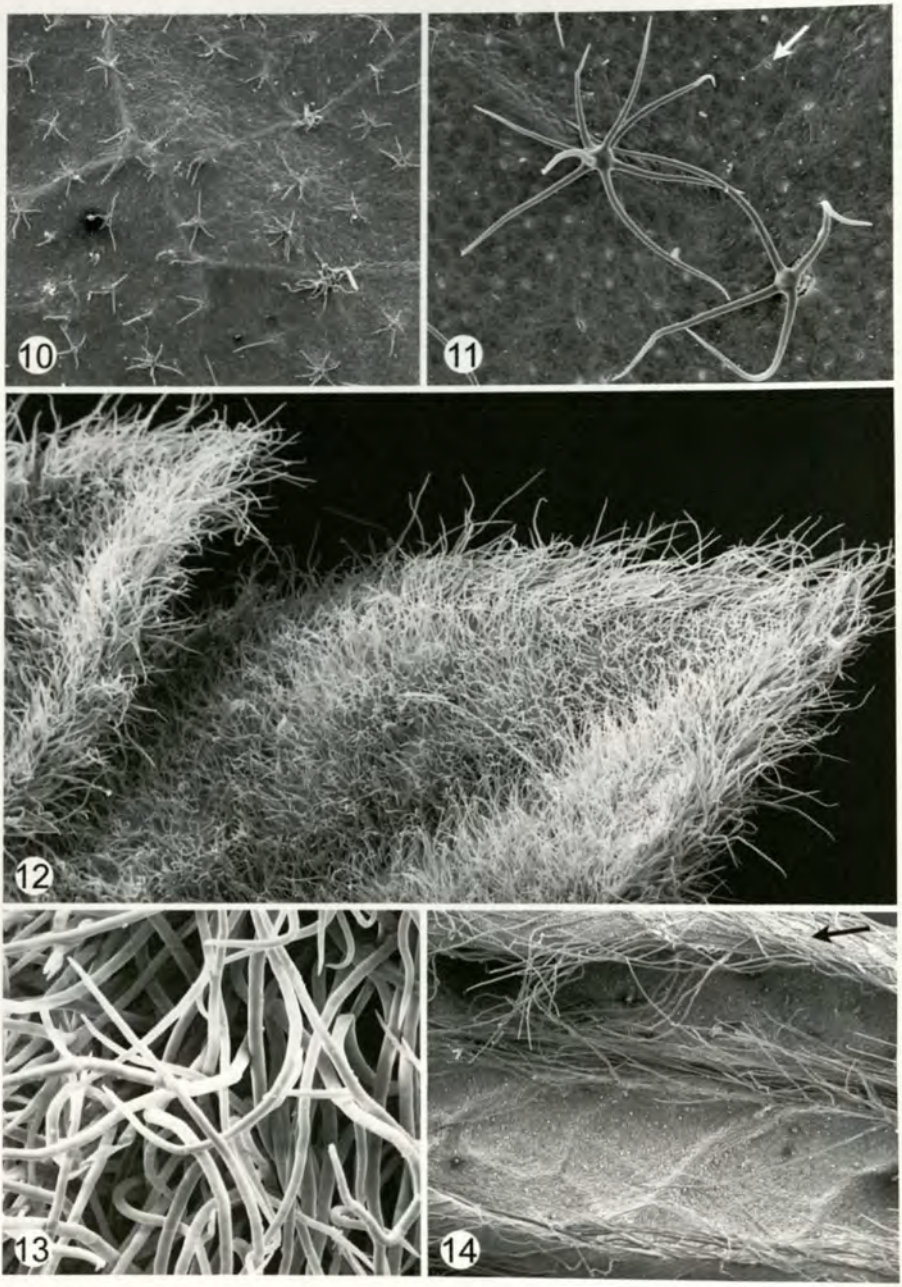

PLATE 3

PLATE 3

10. Branched and star-shaped hairs, or trichomes, on the leaf from a tulip tree (*Liriodendron tulipifera*).

11. Branched hairs and stomates (arrow) on a tulip tree leaf.

12. Pubescence on an immature sassafras (*Sassafras albidum*) leaf. These hairs may protect against the plant from being eaten by insects and other animals. The density of the hairs decreases as the leaf grows.

13. Sassafras leaf pubescence at a higher magnification. The hair density is such that the underlying leaf surface cannot be seen.

14. Lower side of a shrubby cinquefoil (*Potentilla fruticosa*) leaf showing a decreased density of hairs compared to the upper surface (arrow). Since the upper leaf is exposed to direct sun, an increased amount of covering hairs should be advantageous in decreasing the evaporation of water from the leaf. This hair density is not needed on the lower surface and would decrease air flow through stomata.

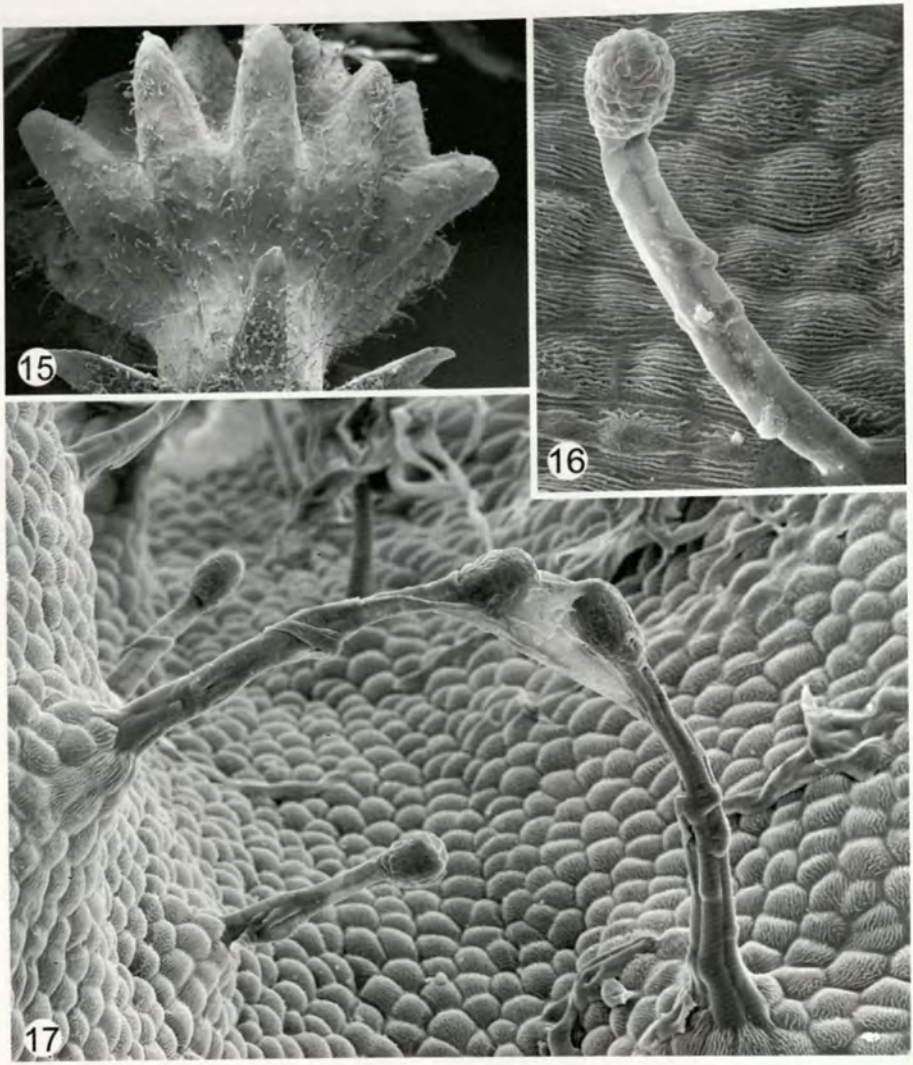

PLATE 4

PLATE 4

15. A mountain laurel (*Kalmia latifolia*) flower bud, with glandular trichomes on the surface which may secrete fragrant chemicals that attract insects for pollination.

16. Higher magnification of a prominent glandular trichome on a mountain laurel bud. Note the striated pattern of the epicuticular wax in the background.

17. Heads of two glandular trichomes on a mountain laurel flower bud bound together by a sticky secretion.

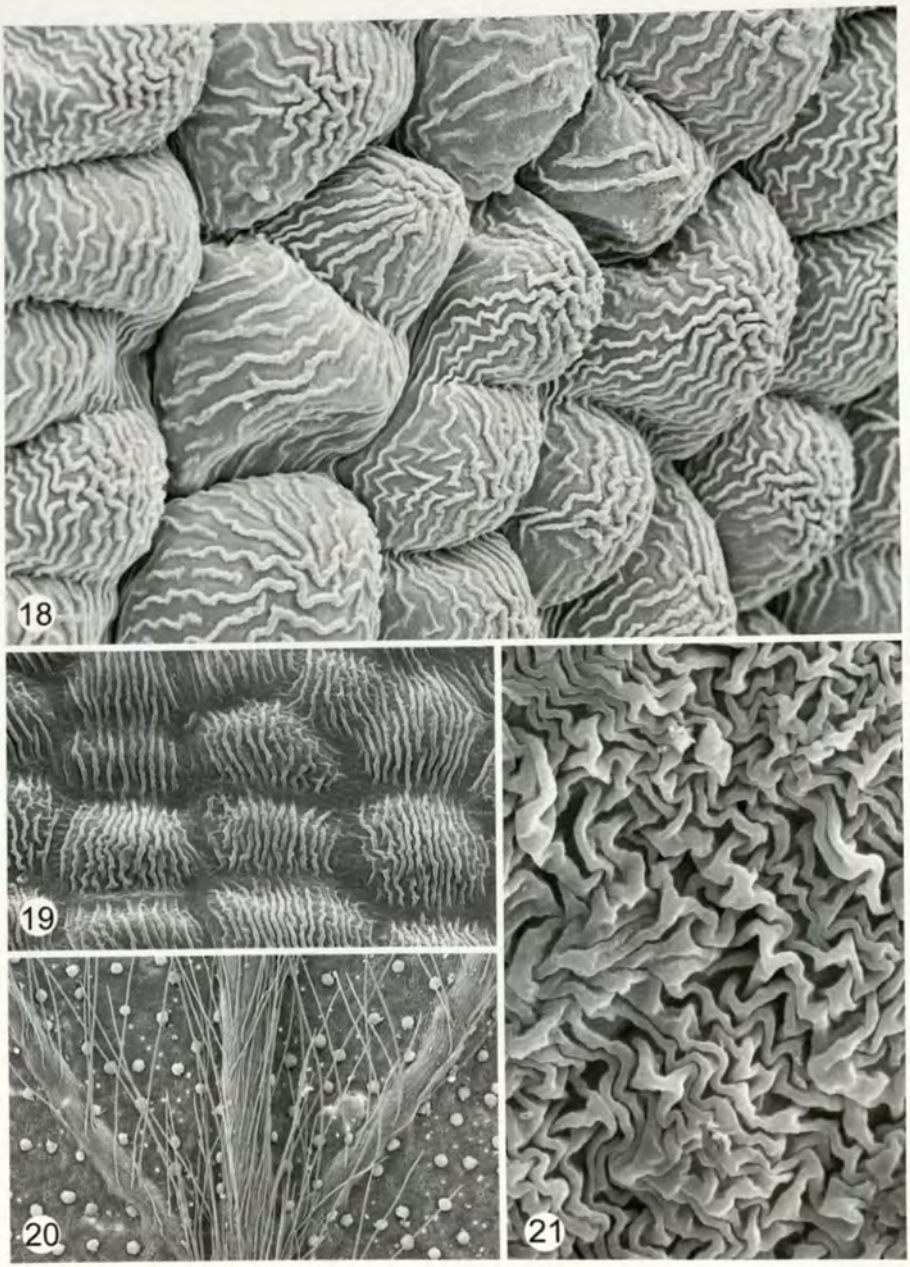

PLATE 5

PLATE 5

18. Small, protruding papillate cells and distinctive striations of the epicuticular wax on a mountain laurel (*Kalmia latifolia*) flower bud.

19. Epicuticular wax striations from a petal of a mountain laurel flower. These waxes may contribute to the way light reflects from the petal surface for attracting pollinators.

20. Leaf of black birch (*Betula lenta*) with hairs over the veins and granules of epicuticular wax on the flat leaf surface.

21. Wax on the petal of an inkberry (*Ilex glabra*) flower.

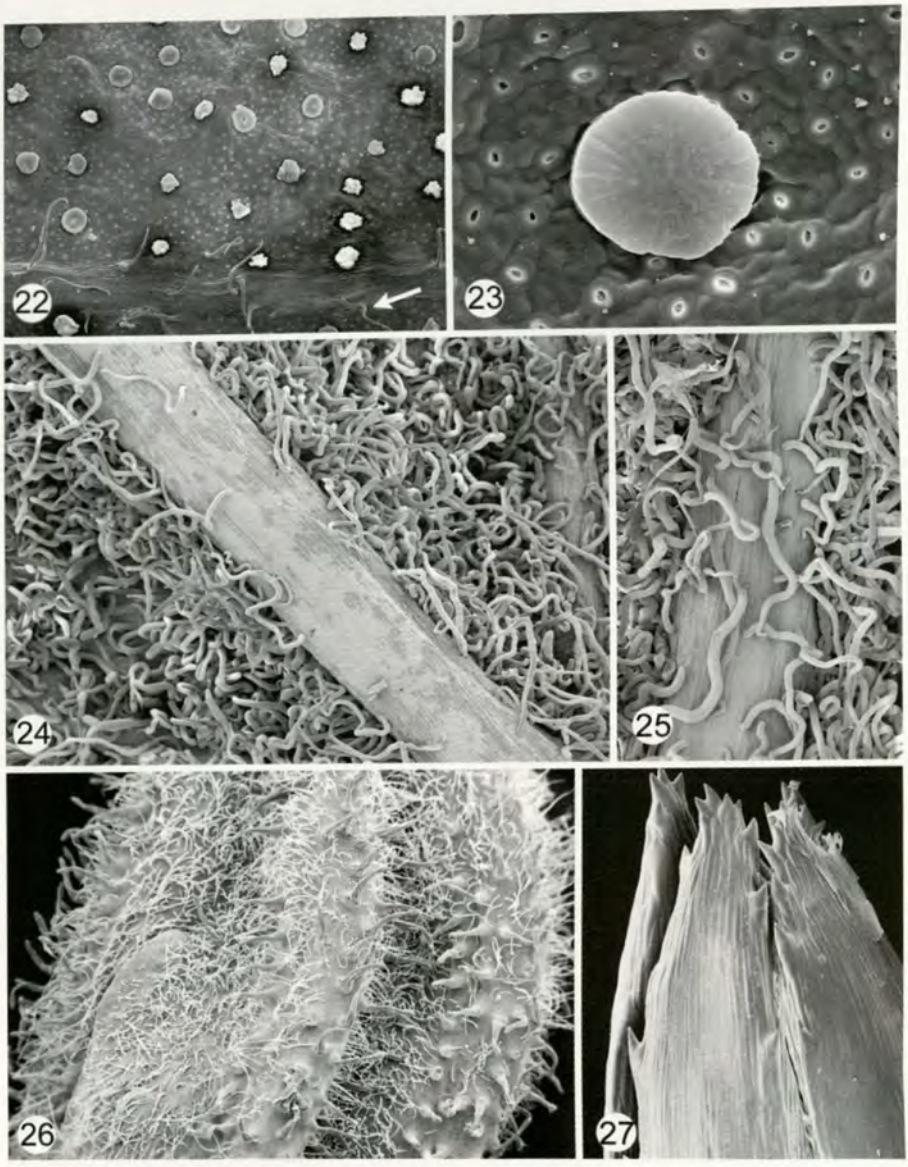

PLATE 6

PLATE 6

22. Sunken trichomes (flat, round structures) and unicellular hairs (arrow) on a northern bayberry (*Myrica pensylvanica*) leaf. The tiny white holes are stomata.

23. Higher magnification of a sunken trichome on a northern bayberry leaf. The hair is surrounded by stomata.

24. Extreme pubescence (hairiness) on the immature leaf of a red maple (*Acer rubrum*). The central leaf vein runs diagonally across the image.

25. Covering hairs along the central vein of a red maple leaf.

26. Glandular trichomes and covering hairs on a "Pink Puff" azalea flower bud (*Rhododendron bakeri x R. arborescens*).

27. Tips of emerging white pine needles (*Pinus strobus*) showing a ridged cuticular pattern.

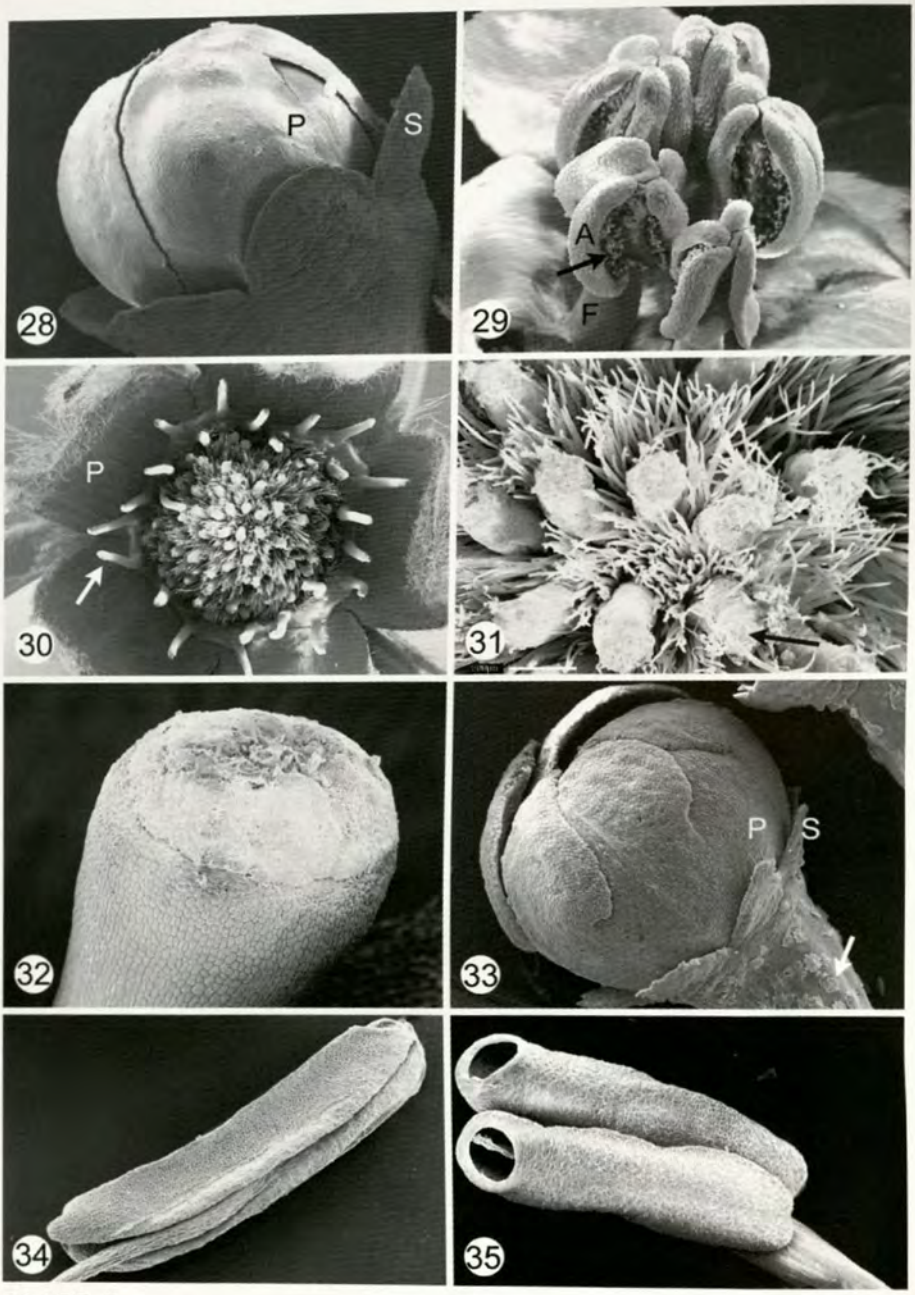

PLATE 7

PLATE 7

28. Flower bud of inkberry holly (*Ilex glabra*) with opened sepals (S) and closed petals (P).

29. Opened male inkberry flower with five stamens. Each anther (A) sits atop a filament (F). The bi-lobed anthers have longitudinally dehisced, or opened, to permit the escape of pollen grains (arrow).

30. Flower of shrubby cinquefoil (*Potentilla fruticosa*) with five petals (P) tipped with thin hair, and a whorl of sterile anthers (arrow). Numerous carpels emerge from a densely hairy base.

31. Higher magnification of a shrubby cinquefoil flower. The carpels (arrow) are simple in shape and are surrounded by numerous hairs.

32. Stigma of a mountain laurel (*Kalmia latifolia*) flower. The tip has openings for the passage of secretions that stimulate pollen germination.

33. Flower bud of smooth withe-rod (*Viburnum nudum*) with small sepals (S), closed petals (P) and flat trichomes on the pedicel or flower stalk (arrow).

34. Bi-lobed anther of sweet azalea (*Rhododendron arborescens*).

35. Stamen of rosebay rhododendron (*Rhododendron maximum*). Each anther of the stamen has two cavities where the pollen develops and is eventually released.

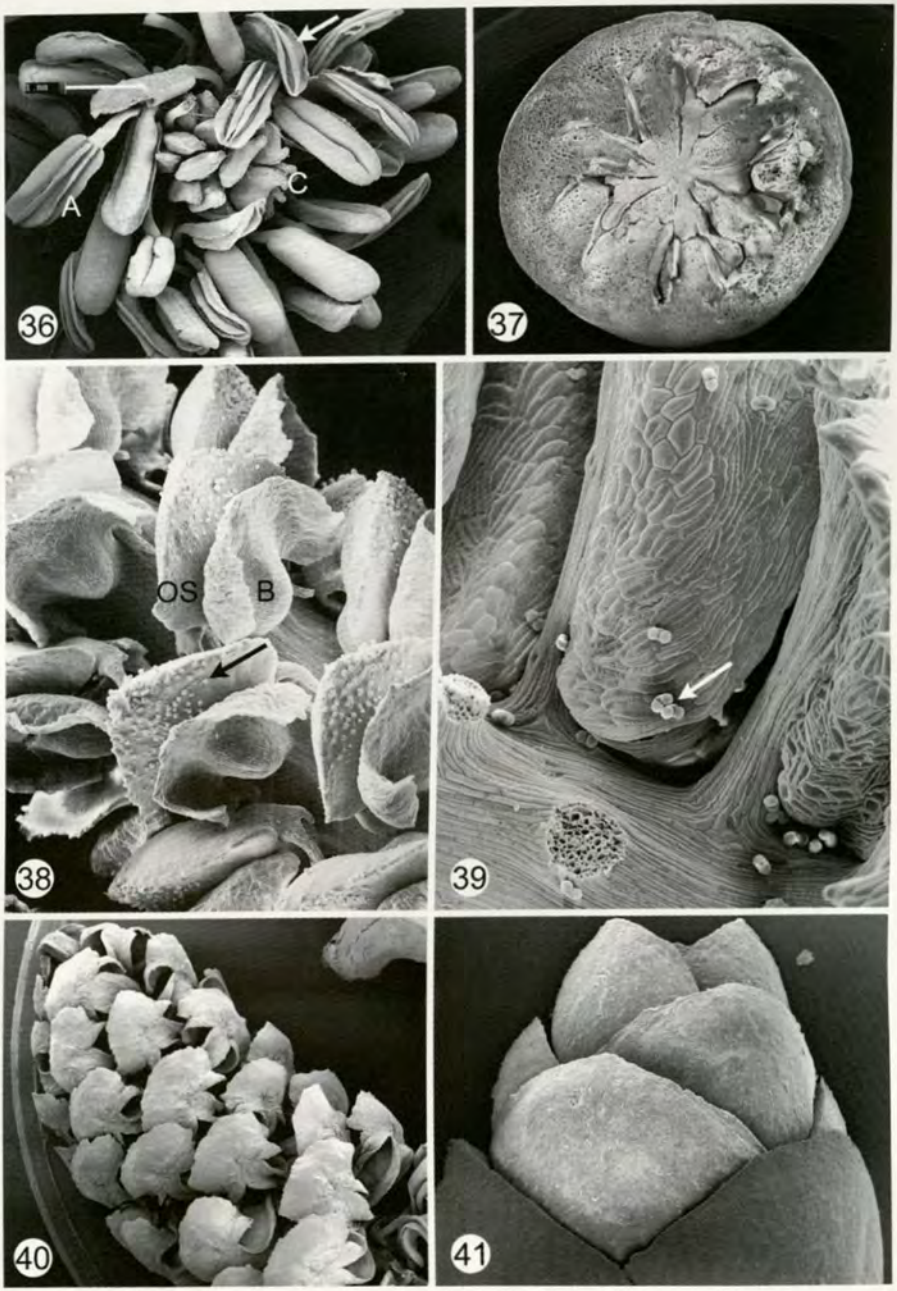

PLATE 8

PLATE 8

36. Anthers (A) and carpels (C) of a shrub yellow root (*Xanthoriza simplicissima*) flower. Most of the anthers have dehisced (arrow) to release their pollen.

37. Cross-section of a lowbush blueberry (*Vaccinium angustifolium*) ovary with five united carpels. Each carpel contains two ovules attached to an axile placenta.

38. Ovuliferous scales (OS) on which ovules develop, surrounding bracts (B), and pollen (arrow) in a young female white pine (*Pinus strobus*) cone. The pollen will fertilize the egg within the ovule to produce an embryonic plant.

39. Pollen-bearing cone of white pine showing microsporophylls on a central axis and pollen grains (arrow) with bladder-shaped wings that aid in wind pollination.

40. Ovulate cone of a pitch pine (*Pinus rigida*).

41. One-year-old female ovulate cone of a white pine (*Pinus strobus*) showing closed ovuliferous scales.

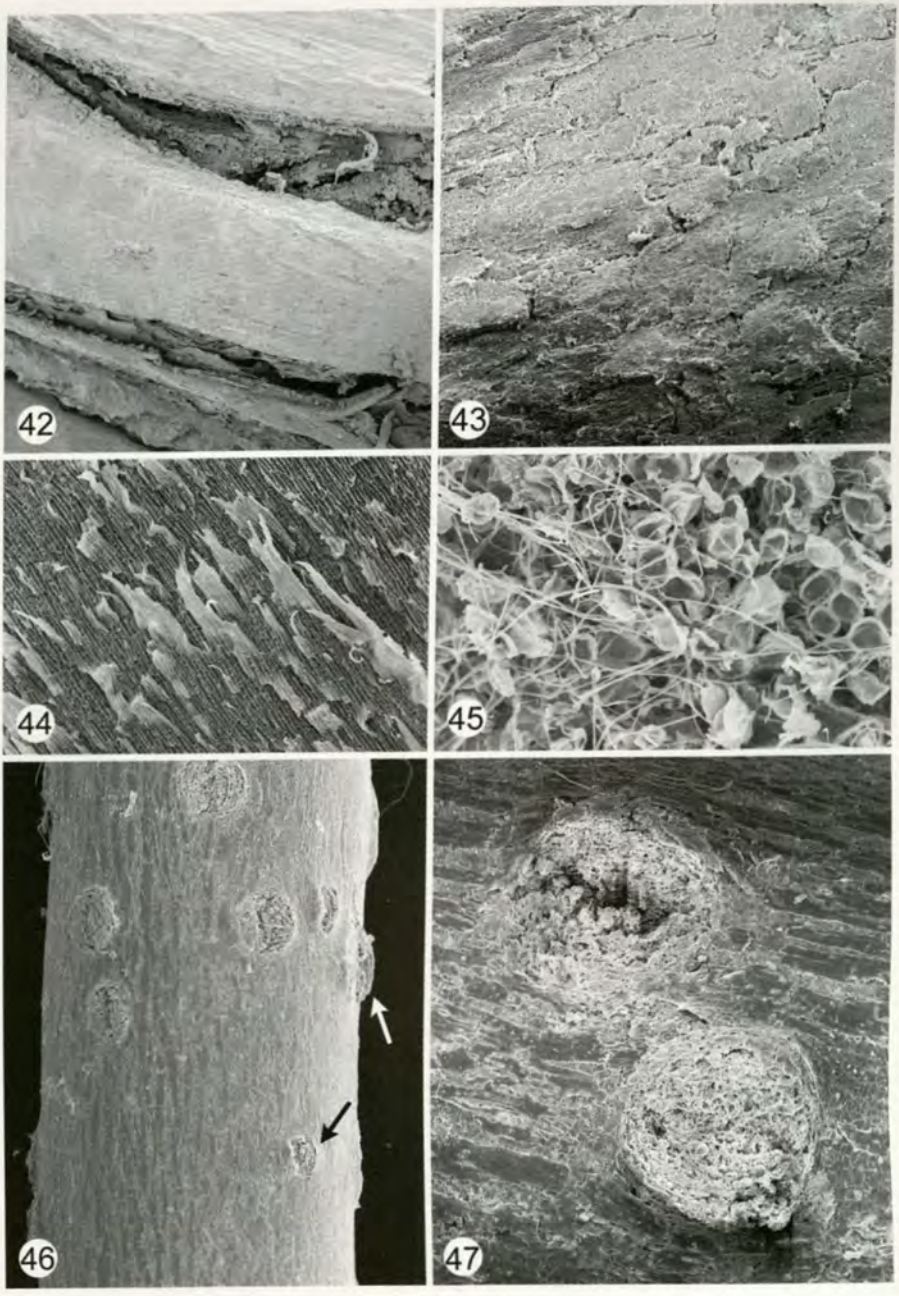

PLATE 9

PLATE 9

42. Scale bark of pitch pine (*Pinus rigida*) showing overlapping periderms.

43. Ring bark of American beech (*Fagus grandifolia*), in which successive periderms form in concentric rings.

44. Flaking thin, papery sheets of periderm on the ring bark of paper birch (*Betula papyrifera*).

45. Rough surface of flowering dogwood bark (*Cornus florida*).

46. Lenticels (arrows) on the bark of wild black cherry (*Prunus serotina*).

47. Loosely packed cells in the lenticels of wild black cherry permit gas exchange through the thick bark.

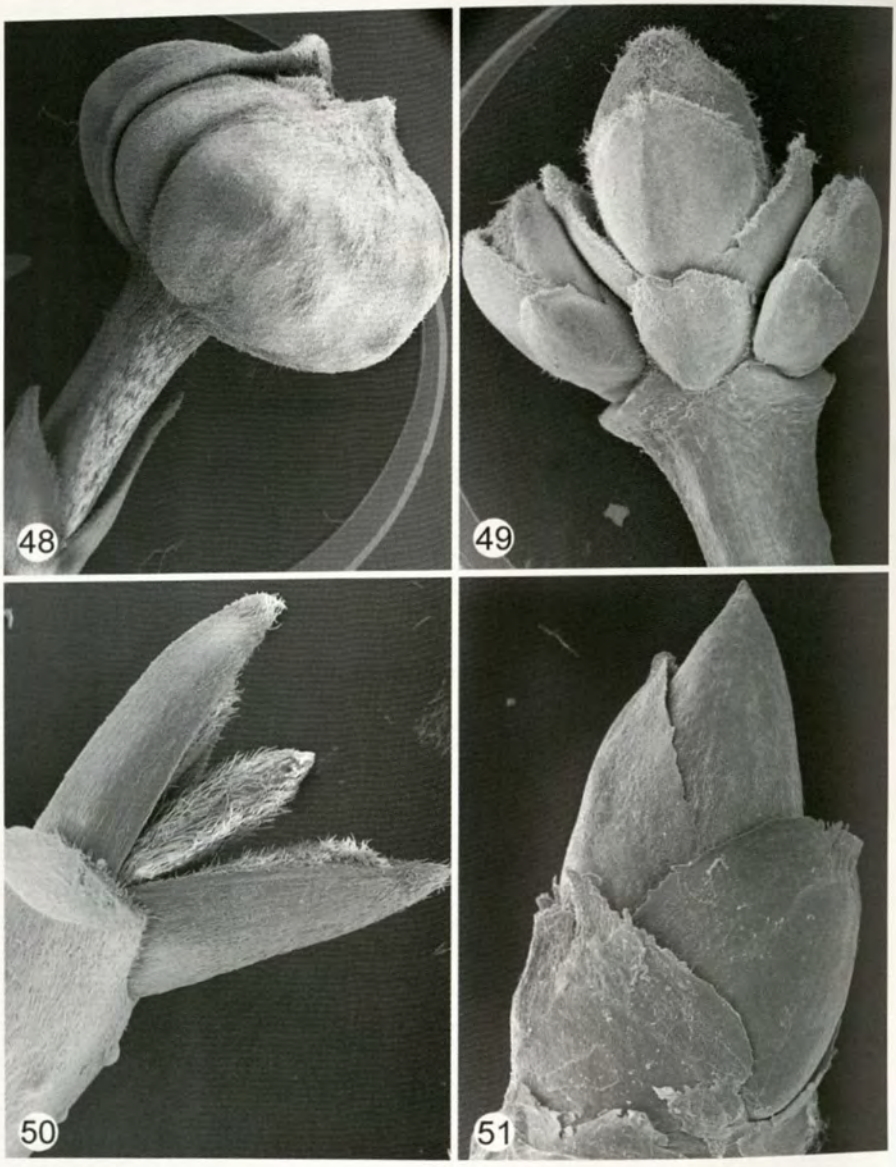

PLATE 10

PLATE 10

48. Flower bud of flowering dogwood (*Cornus florida*), which is much larger than the leaf bud. The bud has emerged from the winter bud and its bud scales.

49. Three red maple (*Acer rubrum*) winter buds that are breaking dormancy. There are more than four bud scales on each bud. They are rounded, typical of red maple.

50. Leaf bud of flowering dogwood with separating bud scales and emerging leaf primordia.

51. Winter bud of wild black cherry (*Prunus serotina*) with four scales, typical of the genus.

continued from page
loss. Humans have learned to use secretions from glandular trichomes for things such as fragrances and drugs. Nicotine in tobacco (*Nicotiana*), tetrahydrocannabinol in marijuana (*Canabis*), and mint extract are all examples of secretions from glandular trichomes.

Trichomes are often specialized to suit the environment of the plant. In arid environments, plants typically have increased leaf pubescence, which enables the leaf to reflect more sunlight and thus minimize water loss through evaporation. In saline environments, glandular trichomes are adapted to secrete salt to prevent it from reaching a toxic level in the plant.

REPRODUCTIVE STRUCTURES

THE FLOWER

The flower is the reproductive structure in Angiosperms (flowering plants). With over 200,000 species, flowering plants have evolved a great diversity of morphological and physiological characteristics. They vary by size, color, scent, amount, arrangement, and differentiation of structures, development of fused structures, and method of pollination.

Generally, the flower is made up of four whorls of extensively modified leaves (Figure B). The outermost whorl, collectively called the calyx, consists of individual sepals that protect the developing bud (28, 33, 48). Inside the calyx is the corolla,

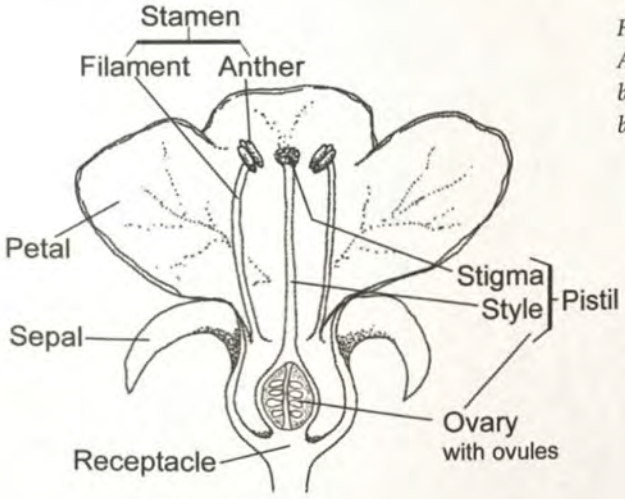

Figure B. Diagram of typical Angiosperm flower showing basic structures. Illustration by Owen after Poincelot.

which consists of a whorl of individual petals (30). Petals are often the most brightly colored of all the flower parts, functioning to attract insects. The surface of petals can be smooth or papillate. Papillae (small hairs) are thought to direct light into the petal for photosynthesis; they may also be striated with epicuticular wax (19, 21), which may further guide light into the petal. Petals and sepals may also have trichomes and stomata. Together, the sepals and the petals are referred to as the perianth, and they make up the sterile part of the flower.

The inner two whorls are the reproductive or fertile structures of the flower (29-31). The androecium (literally "house of man") consists of stamens (29, 34-35), which are the pollen producing structures. Each stamen has an anther borne atop a slender, cylindrical filament. The anther is typically bi-lobed and each lobe contains two pollen sacs (35) that produce pollen grains. One of the two cells in the pollen grain, the generative cell, divides into sperm cells.

The central whorl, the gynoecium (literally "house of woman") is comprised of one or more carpels (36-37). Carpels may be separate, fused or partly fused. The enlarged, basal region of the carpel is the ovary, the middle region is typically an elongated style and the upper part is the stigma (32). The epidermal cells of the stigma are secretory with elongated papillae; the sticky secretions function to trap pollen. The style has specialized tissue that guides the pollen tube, which grows from the pollen grain on the surface of the stigma, down to the ovary. Within the ovary are ovules that contain the egg. The ovule is connected to the ovary wall by the placenta, from which the ovule originated and to which it remains attached until maturity (37). The arrangement of placentae and ovules in the ovary is referred to as placentation and is another example of variation in flowers. After fertilization occurs, the ovule becomes the seed, and the ovary becomes the fruit.

It is important to recognize that many exceptions exist to the basic four-whorled arrangement of the flower. Flowers that do not have four whorls are considered incomplete, as opposed to flowers that do have four whorls, which are called complete. If the same flower has both male and female parts, then it is referred to as perfect (the majority of flowers are perfect). If it lacks one of the reproductive whorls, then it is imperfect and said to be staminate or carpellate. When a single plant has both male and female flowers, it is monoecious ("one house") and if male and female flowers are on different plants, the plant is referred to as dioecious ("two houses"). Flowers sometimes occur in aggregations, as opposed to being borne singly; clusters of flowers are called inflorescences.

THE STROBILI OF CONIFERS

Conifers, like pine, spruce and fir, are the most abundant and widespread of Gymnosperms alive today. Characteristic of the Gymnosperms, conifers produce

naked seeds on the surface of modified leaves called sporophylls (38-40). The reproductive structures of conifers, or "cones," are technically known as strobili, which consist of many sporophylls grouped on a stem. There are two types of cones – the pollen-bearing cone (male) and the ovulate cone (female). In pines and most other conifers, both types of cones are on separate branches on the same tree.

The pollen-bearing cones are small, usually one-half to one inch long, and consist of scale-like "microsporophylls" (literally small seed leaves) (39) that are spirally arranged on a central stalk. The tops of the microsporophylls are specialized to prevent the drying out of the pollen-producing center of the cone; they have a thick cuticle and are closely pressed against one another (38). Two pollen sacs are attached to the lower side of the microsporophyll. Conifers are wind pollinated; as soon as the pollen matures, the microsporophylls separate and release the pollen into the air (38-39). Conifers produce enormous amounts of pollen; the yellow film that covers our cars in the spring is conifer pollen.

Ovulate (female) cones are developed by the time pollen is released from the pollen-producing cone (38). Ovulate cones are larger and much more complex than pollen-producing cones. They consist of special scales that bear two ovules on the upper surface near the center of the cone. In the spring, the scales separate so that pollen can blow in (40), and then they close up to protect the developing ovule (41). It takes two seasons for the ovule to develop into the seed, and, during this time, the ovulate cone increases its size and becomes the typical woody cone we are all used to seeing on pine and other conifers.

FEATURES OF THE WOODY PLANT

BARK — THE PERIDERM

Unlike soft-stemmed herbaceous plants, woody plants continually increase in stem girth. This is known as secondary growth since the elongation of shoots and roots is considered primary growth.

As secondary growth progresses in the stems and roots of woody plants, the epidermis, along with underlying tissues, is sloughed off and replaced by another protective layer called the periderm (Figure C); this process occurs within the first year of growth. The periderm is composed of three layers (Figure D). The middle layer, the phellogen or cork cambium, gives rise to the inner and outer layers. The outer layer, the phellem, is commonly referred to as cork. It is dead at maturity and the cell walls are full of waxy material, which makes it an ideal protective tissue. The innermost layer, the phellogen, is composed of living tissue. As the circumference of the stem or

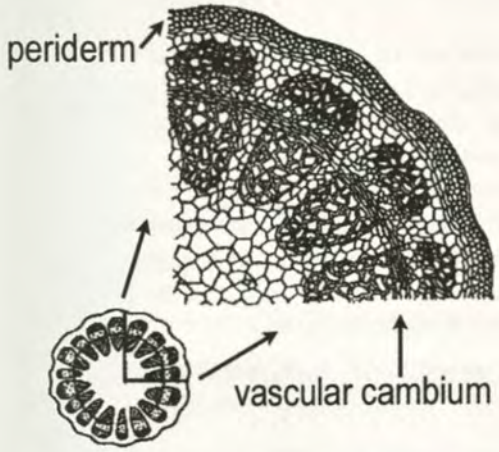

Figure C. Typical cross section of a woody plant stem showing tissues that produce radial growth and bark.

root increases, new periderms are produced to the inside of the original periderm to accommodate this growth; this leads to the buildup of dead tissue (Esau 1960). The common term "bark" refers to all of the tissue outside the vascular cambium. The pattern of periderm development influences the appearance of bark. If the newly formed peridems develop in overlapping layers, the bark appears scaly or shaggy (42) and is referred to as scale bark seen, for example, in Shagbark Hickory (*Carya ovata*). Less common is ring bark, in which the periderms form complete rings around the stem (43, 44). A typical example of ring bark is the American Beech (*Fagus grandifolia*). The pattern, color, and thickness of bark can often be used to identify species of woody plants.

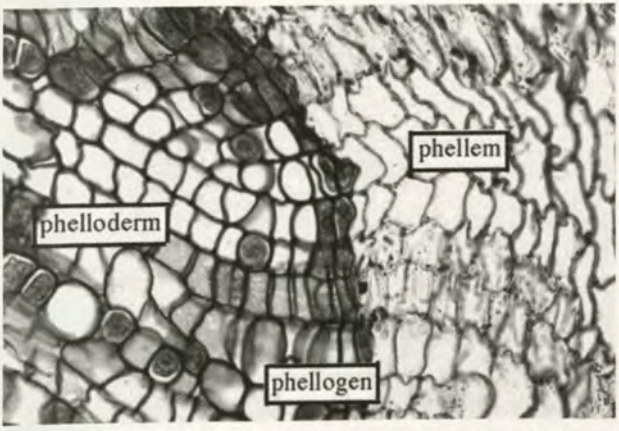

Figure D. Microscopic view of the three types of tissue that form the periderm, or bark, in woody plants.

LENTICELS

Stems and roots with secondary growth have an outer layer of cork cells impermeable to gas and water. Consequently, woody stems and roots have areas of specialized periderm tissue that enable gas exchange between the outside environment and the cells beneath the cork; these are called lenticels (46-47). A lenticel is a mass of loosely packed, permeable cells. The numerous spaces between these cells permit the flow of gases. Lenticels typically form below stomata; during secondary growth they penetrate the epidermis and create protrusions on the surface of the stem or root. Lenticels appear as raised circular or horizontal regions on the surface of the periderm and small dots on the surface of fruits, such as apples and pears.

WINTER BUDS

Winter buds are critical to the survival of both herbaceous and woody plants that live in temperate regions where the winters are characterized by low temperatures. Winter buds are enclosed by one or many bud scales, which are modified leaves that prevent drying and damage to the bud from low temperatures (48-51). The bud scales may be covered in hairs or resins to further protect the developing bud. The number, arrangement, and color of bud scales may be used for winter woody plant identification. Winter buds of most deciduous plants require cold temperatures to come out of dormancy (48), which is why, for example, apple and peach trees cannot grow in regions where the winters are not cold.

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