Secretory Structures of Aromatic and Medicinal Plants

A Review and Atlas of Micrographs

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Key to images on front cover:

Top to bottom: Wormwood,
Peppermint, Marjoram, Rosemary,
Greek Oregano, Lavender
Background: Eucalyptus leaf

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PREFACE

Aromatic and medicinal plants are used in the food, flavour, perfumery, pharmaceutical and healthcare industries. Their use is expected to increase every year due to a consumer-led trend towards natural foods, food and cosmetic additives and complimentary medicine including aromatherapy. Many branches of industry are searching for alternative, cleaner antimicrobial, antibiotic, antioxidant and crop-protection agents. The possibility of utilising volatile oils is being investigated as it has been known since antiquity that they possess biological activities. During the last decade many books have been written about herbs and spices, chemical constituents found in various plant families and their uses.

However, very few research articles deal with the description of the sites where these chemicals are produced, either on the surface of the plants or internally. There is a distinct lack of illustrations which would help the reader to visualise these anatomical structures. An early acquaintance with micrographs of secretory tissues increases the appreciation of the relationship between the plant and its biochemical products.

This book is a source of useful terms and concepts for description of a variety of secretory structures. It does not cover the subject exhaustively but presents numerous examples and examines a few in detail. The reader is made aware of the endless variability in anatomical form and will therefore be better prepared to interpret the structure of other plant species and relate them to those described in this book. An exhaustive list of references collected over the last ten years gives the reader guidance for scientific approach to this area. Use of increasingly more advanced methods of microscopic studies has resulted in remarkable insight into plant anatomy, differentiation and development.

All photomicrographs are original, prepared by Microscopix from authentic plants and material. My botanical and phytochemical interest, directed towards research on aromatic plants, unavoidably influenced the presentation of individual plant species. The problems of classification are not resolved and the order of plant presentation is not related to taxonomy. The plants are presented in alphabetical sequence of their common names, supporting interpretations and conclusions that have been placed in the text. This method of organisation is simple, coherent and quickly permits the reader access to specific plates.

This book aims to be useful to both students and scientists with an interest in aromatic and medicinal plants and may be a valuable resource to all those involved in the research, development, cultivation, marketing and uses of these crops.

Dr. K. P. Svoboda
May 2000

'Apricots are ripe
With moonlight dripping
On each fruit'

Haiku by Shibata Hakuyojo

PLATE 1

Mobile distillation unit being used for chamomile oil extraction (Norfolk, Anglian Essential Oils Ltd.)

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INTRODUCTION

Plants and their extracts have been used for centuries to relieve pain, aid healing and kill bacteria and insects. They have also been employed in perfumery, cosmetics and religious rites. Plant chemistry became an established discipline in universities at the end of the nineteenth century and since then many new structures have been discovered. The number of natural products obtained from plants has now reached over 100 000 and every year new chemical compounds are being discovered. Although their functions in plants have not been fully established, it is known that some substances have growth regulatory properties whilst others are involved in pollination and seed dispersal. Many are important as antifungal and antiherbivore agents with further compounds being involved in the symbiotic associations in plants. Detailed information on individual plant chemicals is available in the *Dictionary of Natural Products* and the *Phytochemical Dictionary.*

The complex nature of these chemicals, which are usually produced in various types of secretory structures, is also influenced and controlled by genetic and ecological factors and significantly, by the mode of extraction from the plants. The type of secretory structure is an important characteristic of a plant family. Detailed anatomical description of these structures is relevant to the market value of the plants, the verification of authenticity of a given species and for the detection of substitution or adulteration. It also provides a guide to the method of processing.

Microscopical investigation of plant structures is an important part of the complex biological research process which includes plant growth and development, genetics and breeding. There is endless variability in form and structure; observing these with the microscope allows us to discover Nature in one of its most powerful forms.

Plant material received for these investigations was examined fresh or as chemically-fixed and stained sections for light microscopy (LM), chemically-fixed and critical point dried (CPD) for scanning electron microscopy (SEM) or cryogenically fixed for cryo-SEM. No single technique was ideal for all purposes since each had its own limitation and risk of introducing artifacts but by employing several methods these difficulties were reduced to give a clearer understanding of the structures. For LM, thin transverse sections (T/S) were cut from wax-embedded material and stained to provide colour contrast, however, the involved chemical processes invariably caused some damage to the sample. This was alleviated by examining fresh, unstained sections either by differential interference contrast (DIC) or, if sufficient contrast was attainable, bright field illumination (BF) where no chemical or staining processes were employed. SEM allowed high magnifications together with improved depth of field giving an overall view of the structures. Since SEM is incapable of recording colour, all images produced using this method were manually enhanced using computer techniques.

PLATE 2

Collection of various mint species, experimental plots at Auchincruive

SECRETORY STRUCTURES IN PLANTS

Plant chemicals can be classed as primary or secondary metabolites, depending on whether or not they have an essential role in plant metabolism and are universally present in all plants. Primary metabolites include sugars, amino acids, nucleic acids and the chlorophylls. Secondary metabolites make up all the remaining plant chemicals from alkaloids to phenols.

Essential oils and other secondary plant metabolites are found in a wide range of plant species including annual, biennial or perennial herbaceous plants, evergreen or deciduous shrubs and trees. The ecological and evolutionary role of these secondary metabolites has been associated with defence against animals, healing of plant organ wounds, protection from harmful insects, resistance to microbial attacks and attraction of insects and animals for pollination. Several species and varieties of plants, mostly those of commercial interest, were investigated systematically and in depth. Recently, various studies concerned with secretory structures and factors influencing their development have been undertaken by research groups in biological and pharmacological departments.

Secretion is a common feature of living cells and involves the discharge of substances to the exterior (exotropic secretion) or into special intercellular cavities (endotropic secretion). These are specialised cells and the secreted material may contain various salts, latex, waxes, fats, flavonoids, sugars, gums, mucilages, essential oils and resins. It has been assumed that these products are biosynthesised *in situ* and direct evidence for the biosynthetic capacity of gland cells has become available relatively recently with the development of procedures for gland isolation. These methods have yielded definitive proof of the presence of enzymes specifically within gland cells.

Trichomes present on the leaf surface and other secretory tissues can be examined using light, scanning and transmission electron microscopy which enables detailed observation of major stages in the development of secretory cells, including their membrane system and nuclei, the overall size of the gland and the amount of material released into the subcuticular cavity.

Essential oils, with or without accompanying resins and gums, are most commonly found in special secretory structures either on the surface of the plant or within the plant tissues. The type of structure is family or species specific. This can be useful in identification of plant material and verifying the authenticity of the plant source in the case of suspected adulteration.

SECRETORY CELLS

The most simple secretory structure is a single secretion-containing cell where it is only the actual content that distinguishes it from adjacent non-secretory cells. However, it may also be larger than the other cells or have a thick cuticularized lining. This cell type is found in many different plant tissues: in the leaf parenchyma of lemongrass (*Andropogon* spp.), bay (*Laurus nobilis*), citronella (*Cymbopogon nardus* and *C. winterianus*) and patchouli (*Pogostemon patchouli*), in the seed coat of cardamom (*Elettaria cardamomum*), in the rhizome of ginger (*Zingiber*

officinale) [Plates 42-44] and turmeric (*Curcuma longa*), in the fruit wall of pepper (*Piper nigrum*), capsicum and chillies (*Capsicum annum*), in the perisperm and embryo of nutmeg (*Myristica fragrans*) [Plates 63 & 64], in the bark of cassia (*Cassia angustifolia*) and cinnamon (*Cinnamomum zeylanicum*) and in the root of valerian (*Valeriana officinalis*).

OSMOPHORES

Osmophores are areas of flower tissues with secretory cells differing structurally from the adjacent cells (e.g. isodiametric cells in orchids).

SECRETORY CAVITIES

These cavities are more or less spherical structures that can be formed in two ways: the parenchyma cells can separate one from another leaving intercellular spaces called lumina or lacuna, or an actual cell can disintegrate leaving a cavity within the tissue. These spaces are lined with secretory cells or an epithelium that produces the essential oils. In high oil yielding plants several layers of these secretory cells are formed. The cavities continually enlarge and some become filled with cells with thin, convoluted walls which also store the oil produced from within their plastids. Included in this group are fruits and leaves of plants in the *Citrus* family (*C. aurantifolia, C. aurantium, C. bergamia, C. sinensis, C. limon*) [Plates 20-22] as well as *Eucalyptus* spp. [Plates 34 & 35] and buchu leaves. Citrus peel oils are confined in oblate to spherical-shaped oil cavities (glands), sometimes called oils sacs, that are located irregularly in the exocarp of the fruit [Plate 22]. These cavities have no walls and are embedded at different depths in the flavedo (the coloured outer portion or skin of the fruit). The glands of grapefruit lie deeply in the flavedo and those of mandarin are likely to be nearer the surface. Fruits and leaves of these plants are covered by a thick cuticle which is waterproof and also the primary means of water conservation. Being shiny and reflective it is capable of deflecting some of the excess solar radiation in tropical and subtropical regions; it also reflects ultraviolet light, thereby protecting the DNA from the mutagenic effects of sunlight. It is an excellent protection against fungi and bacteria since they have no enzymes capable of digesting cutin. Secretory cavities are also present in the flower buds of cloves (*Syzygium aromaticum*) [Plates 23-26] , the fruit walls of pimento (*Pimenta dioica*), and in the elongated cavities in the bark of myrrh (*Commiphora molmol*), benzoin (*Styrax benzoin*) and frankincense (*Boswellia* spp.) [Plates 36 & 37].

SECRETORY DUCTS

Ducts are elongated cavities. They can often branch to create a network extending from the roots through the stem to the leaves, flowers and fruits. They are composed of an epithelium which surrounds a central cavity. Several predisposed cells within the parenchyma undergo asynchronous division and in doing so they expand the initial space in the middle where the cells are all adjacent to form a cavity. Some of these cells forming the wall of the cavity will change into secretory epithelial cells. The oils are biosynthesised within their leucoplasts and move via the endoplasmic reticulum into the cavity. These cavities then become joined to form ducts. They can be found in all of the Umbelliferae family including anise (*Pimpinella anisum*), fennel (*Foeniculum vulgare*), dill (*Anethum graveolens*), coriander (*Coriandrum sativum*), cumin

(*Cuminum cyminum*) [Plates 27-30], parsley (*Petroselinum crispum*) and angelica (*Angelica archangelica*). In the case of celery (*Apium graveolens*) they can branch to create a network extending from the roots, through the stem to the leaves, then to the flowers and finally to the fruits where they are known as vittae (*sing.* vitta). They are also present in the Pinaceae [Plates 13-15], Compositae, Hypericaceae and Coniferae families. The resin ducts in the xylem of Coniferae can reach 4-10 cm in length with between 2 and 7 ducts per leaf.

GLANDULAR TRICHOMES

Glandular trichomes are modified epidermal hairs and can be found covering leaves, stems, and even parts of flowers such as the calyx in many plants of the Labiatae family. These include basil (*Ocimum basilicum*) [Plates 5 & 6], lavender (*Lavandula* spp.) [Plate 53 & 54], marjoram [Plates 61 & 62] and oregano (*Origanum* spp.) [Plates 68-72], mint (*Mentha* spp.) [Plates 73 & 74] and thyme (*Thymus* sp.). The secretory cells are attached by a single stem or basal cell in the epidermis. The outer surface of the gland is heavily cutinized. A toughened cuticle in which no pores or perforations are present, usually completely covers the trichome [Plate 7]. The essential oils accumulate in subcuticular spaces and it is thought that they diffuse outwards through the cuticle. The glandular cells differ from normal plant cells in that they have a very large nucleus and a dense protoplasm that lacks a large central vacuole. There are numerous plasmodesmata across the walls of the gland cells especially between the stalk cell and the collecting cell. In the very young gland the intracellular organisation is almost identical to that of the adjacent cells but as the secretory cells develop complex changes occur. The membrane system progressively degenerates and in the fully-developed glands only a fine granular cytoplasm remains.

Cells in the multicellular heads usually have nuclei with double the normal numbers of chromosomes (endopolyploidy) and in fully-mature glands, mitochondria are the most abundant organelles which might reflect a high energy requirement. There is also a well-developed endoplasmic reticulum. Essential oils accumulate in the subcuticular cavity [Plates 32, 70 & 92]. All these changes in the glands occur at a very early stage of the leaf development and the glandular hairs are fully-formed by the time the leaves are about 5 mm long. The formation and transformation of the essential oils, however, takes place continuously from the formation of the gland until senescence. The essential oil biogenetic precursor isopentenyl pyrophosphate is, with high probability, synthesised in the leucoplasts.

There are two main types of glands that can exhibit minor variations:

(i) Peltate glands with one basal cell, a short stalk and a large six- to eight- celled head [Plates 61, 84 & 86].

(ii) Capitate trichomes with either -

a) one basal cell, a short monocellular stalk and a two-cellular head [Plates 72 & 85].

or

b) one basal cell, a multicellular stalk and a small globose, unicellular head [Plate 67].

In every species there are distinctive variations in the size and shape of the glands. For example, yarrow (*Achillea millefolium*) secretory trichomes of the floret produce azulene and occur mainly in the corolla lobes of the ray and disk florets and also on the leaves. When a floret reaches 0.25mm, fully-mature trichomes are present having developed from protodermal cells. They have 10 cells including a pair of basal cells, a pair of stalk cells and 3 pairs of glandular cells. In *Cannabis sativa* a variety of glandular trichomes occur, including bulbous (small glands with a single-celled head and a unicellular stalk), capitate-sessile (a gland with a head of 8 or more cells on a very short stalk) and capitate-stalked (similar to previous type but with a substantial multicellular stalk). These glands are considered to be the main location of the narcotic cannabinoids.

It is possible to isolate an individual gland from the leaf surface and analyse its content for chemical composition and presence of specific enzymes.

EPIDERMAL CELLS

Essential oils obtained from flowers are not usually secreted by glandular hairs but merely diffuse through the cytoplasm, the cell walls and the cuticle to the outside. The yield of essential oils from these species is generally very low. Examples include rose (*Rosa* spp.), 0.075% (w/v), acacia (*Acacia* spp.) 0.084% (w/v) and jasmine (*Jasminum* spp.) 0.04% (w/v).

Buds of a number of plant species (e.g. *Aesculus, Alnus, Betula, Populus, Prunus* and *Rhamnus*) also secrete lipophilic substances, mainly flavonoid aglycones mixed with essential oils. Secretion here occurs from epidermal cells which are covered by a cuticle. The secreted material is first eliminated into a space formed between the outer walls of the cells and the cuticle covering them, forming a blister that subsequently bursts.

CONCLUSION

Plants have provided man for hundreds of years with many of the basic and important materials required for day-to-day living, including oxygen, food, clothing and timber, as well as being a source of compounds such as oils, resins, rubbers, gums, dyes, pesticides and drugs. Plants can be considered as biochemical factories that have been evolving their programmes over the last 400 million years. Researchers have been elucidating chemical pathways and various industrial applications of these products, and anatomical description is one of the most important aspects of economical uses of these plants. It is also important to highlight the need to safeguard and conserve the diversity of our global flora and to contribute with research into careful exploitation of plant resources.

PLATE 3

Echinacae angustifolia, experimental plots at Auchincruive

PLATE 4

Takeda, Japanese pharmaceutical company herb garden, Osaka

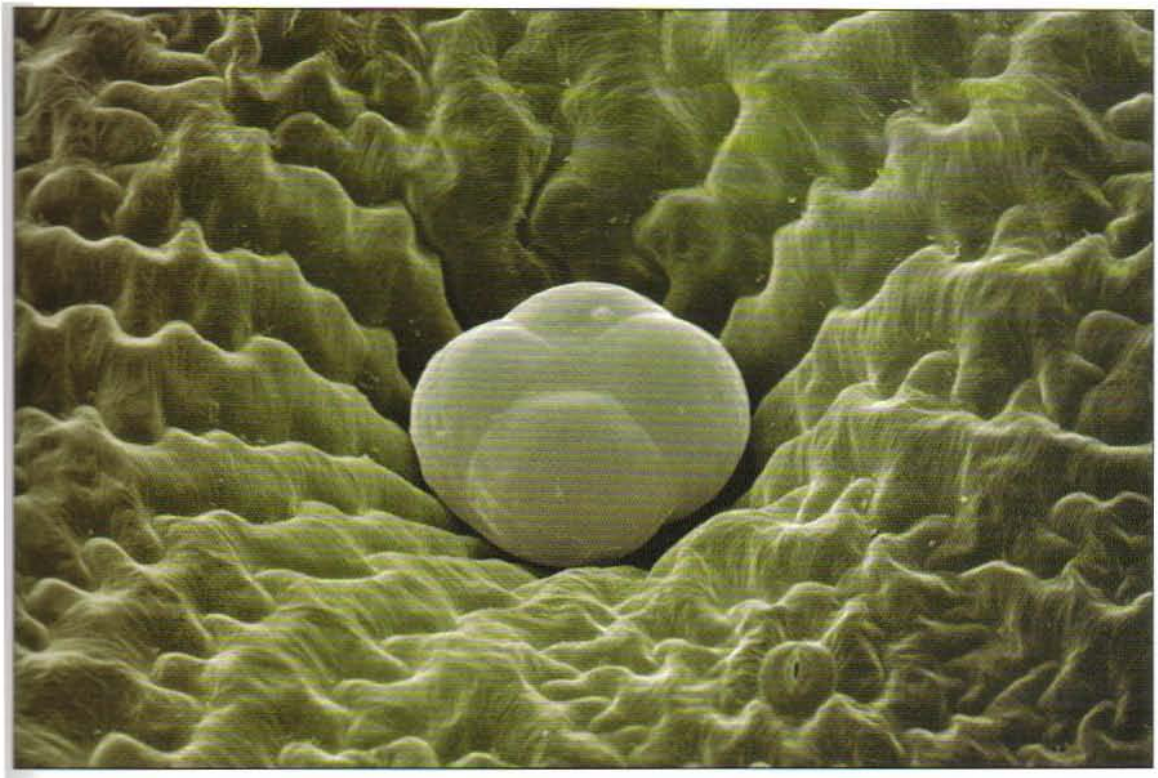


Plate 5: Sessile secretory gland on lower leaf surface covered by turgid, intact cuticle (SEM, CPD) [x559].

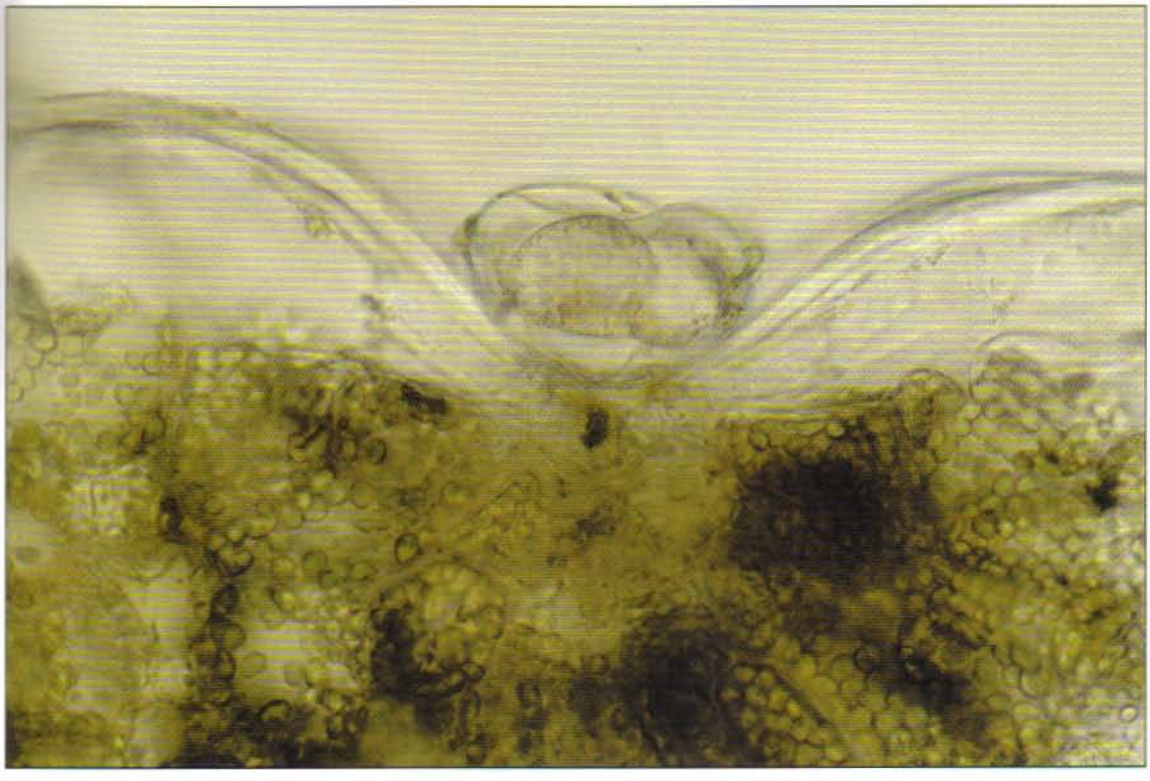


Plate 6: Leaf (T/S) showing sessile secretory gland with collapsed, ruptured cuticle. Chloroplasts visible in the underlying parenchyma (LM, BF, fresh, unstained) [x575].

BOG MYRTLE - *Myrica gale*

Plate 7: Sessile secretory gland on lower leaf surface covered by turgid, intact cuticle (SEM,CPD) [x607].

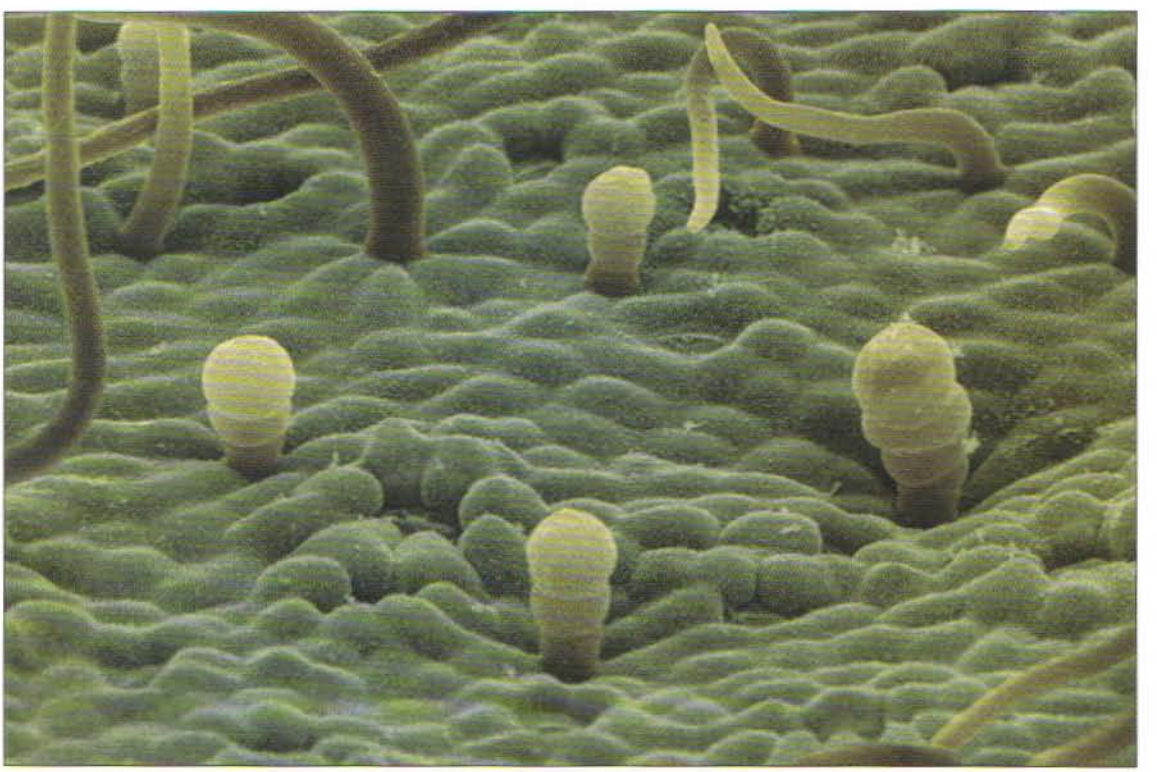


Plate 8: Stalked glands and non-secretory trichomes on lower leaf surface (SEM,CPD) [x600].

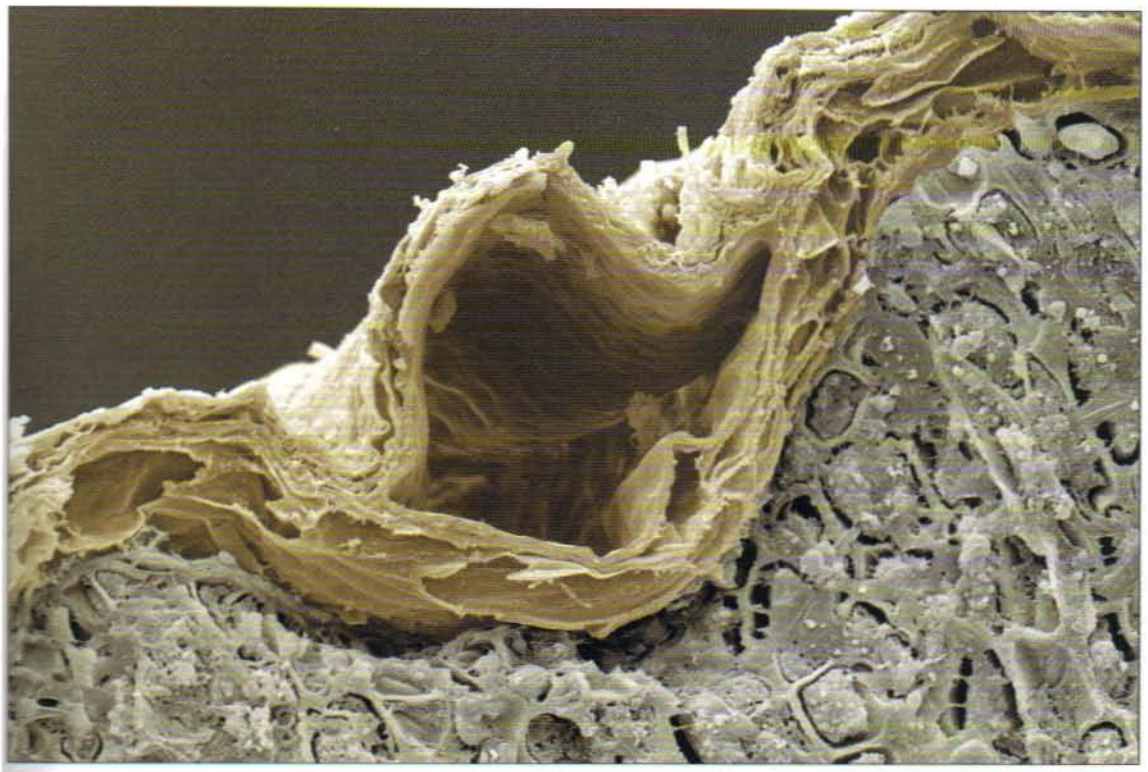


Plate 9: Seed (T/S) showing detail of primary vitta (SEM, CPD) [x406].

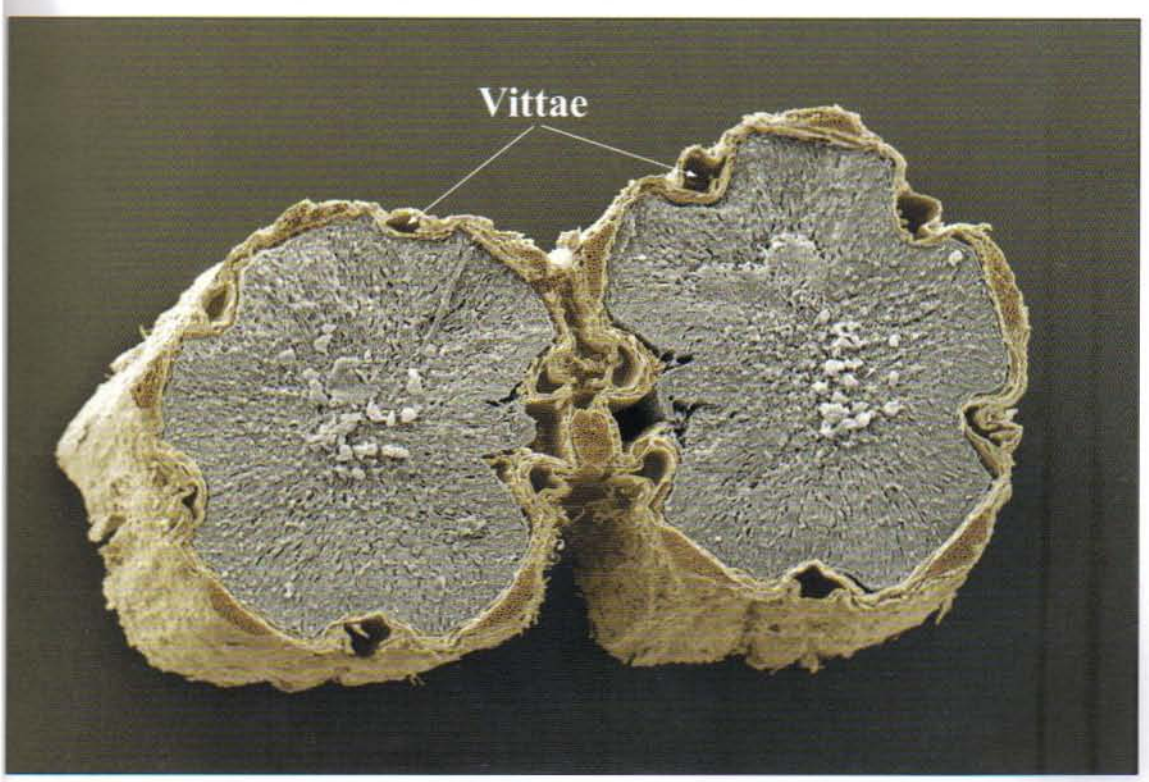


Plate 10: Seed pair (T/S) showing 4 primary and 2 commissural vittae (SEM, CPD) [x48].

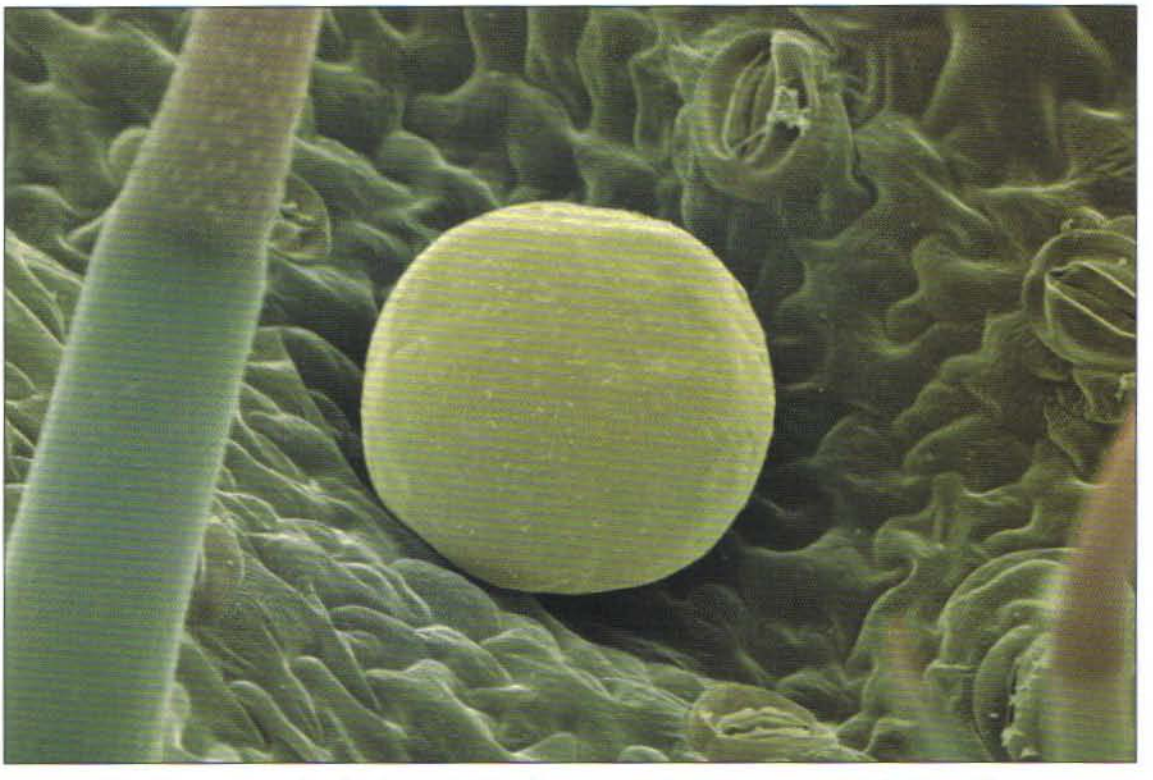


Plate 11: Sessile secretory gland on lower leaf surface covered by turgid, intact cuticle. Part of non-secretory hair visible in foreground (SEM, CPD) [x948].

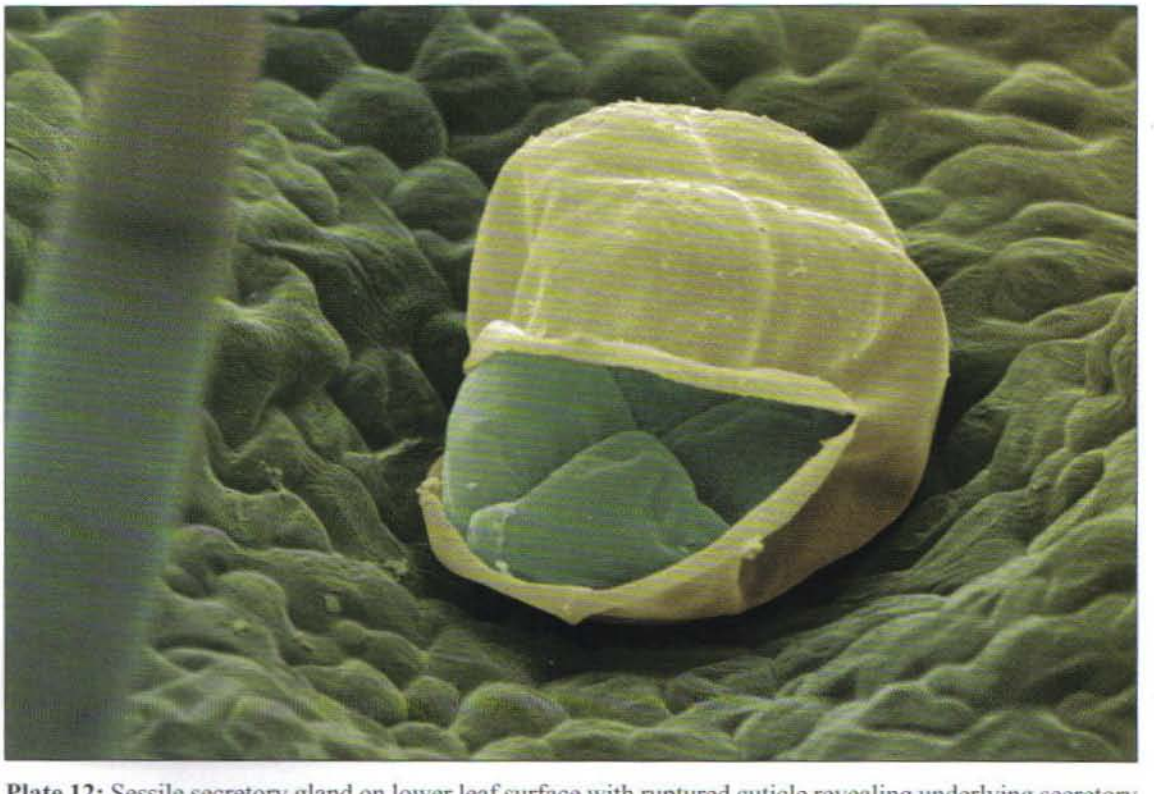


Plate 12: Sessile secretory gland on lower leaf surface with ruptured cuticle revealing underlying secretory cells (SEM, CPD) [x1,250].

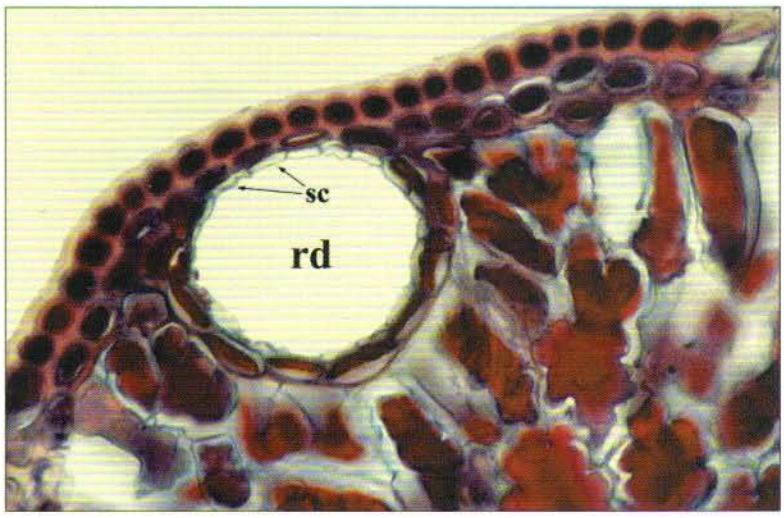


Plate 13: Needle (T/S) of *C. atlantica* with detail of resin duct (rd). Duct is lined with epithelium of secretory cells (sc) (LM, BF, stained with safranin and fast green) [x333].

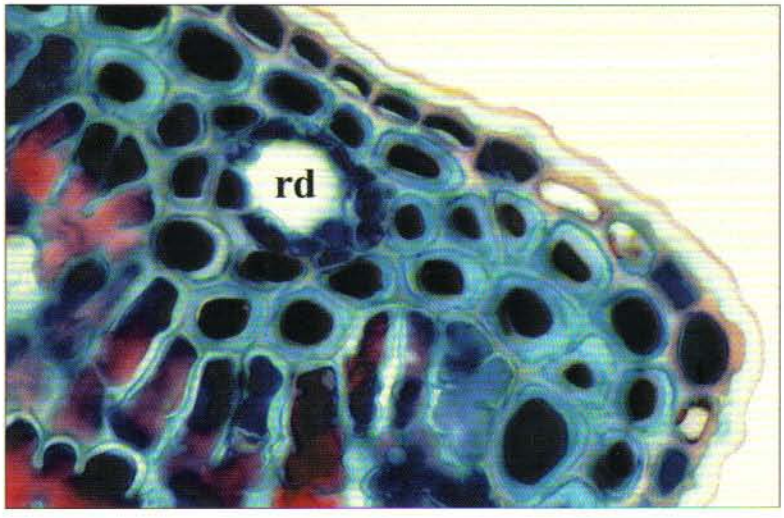


Plate 14: Needle (T/S) of *C. brevifolia* with detail of a narrow resin duct (rd) (LM, BF, stained with safranin and fast green) [x325].

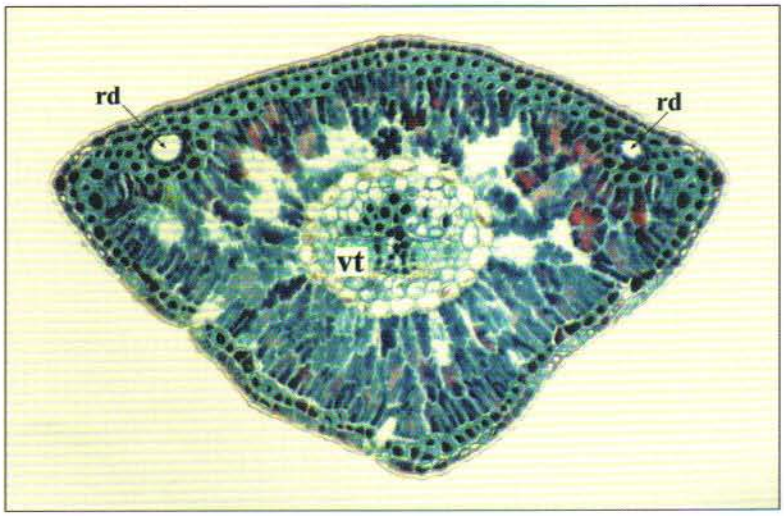


Plate 15: Wax-coated needle (T/S) of *C. atlantica* showing 2 well-formed resin ducts (rd), parenchyma and centrally-located vascular tissue (vt), xylem and phloem (LM, BF, stained with safranin and fast green) [x64].

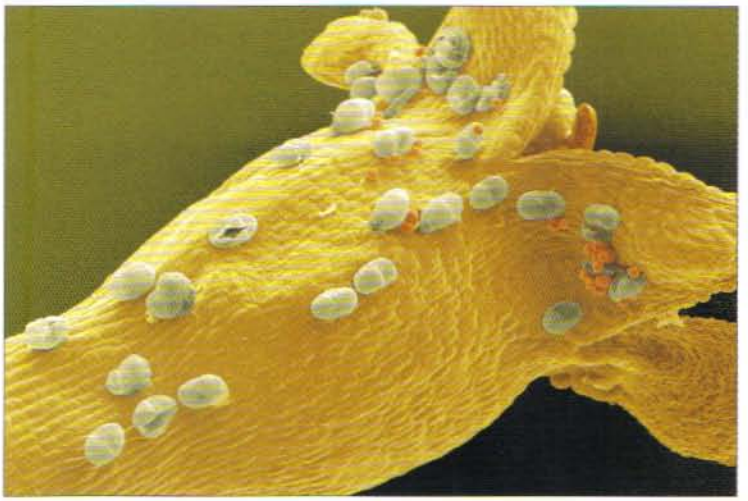


Plate 16: Individual floret from composite flower covered with sessile secretory glands (SEM, CPD) [x83].

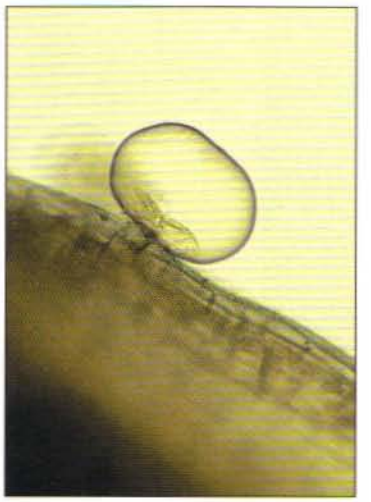


Plate 17: Detail of sessile secretory gland on floret surface with oil-filled subcuticular space resulting in fully-extended cuticle. Secretory cells visible at base of gland structure (LM, BF, fresh, unstained) [x297].

Plate 18: Upper leaf surface with sessile secretory glands and non-secretory trichomes (SEM, CPD) [x144].

Note: Chamazulene, produced in the oil during distillation by thermal decomposition of matricin, is responsible for the blue colouration of the extracted oil - in its raw state the oil is virtually colourless.

Plate 19: Developing ovule of fully-matured flower covered with sessile secretory glands (SEM, CPD) [x72].

Plate 20: Detail of secretory cavity (T/S) in the flavedo of orange fruit peel (SEM, CPD) [x96].

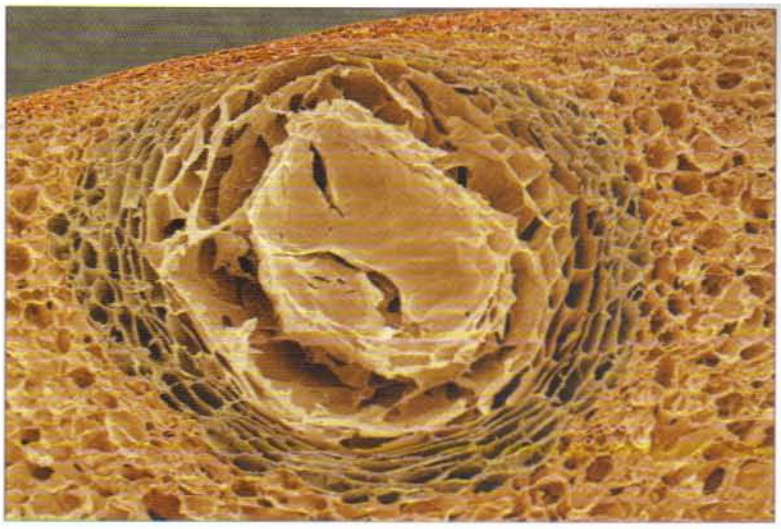


Plate 21: Secretory cavities (T/S) in the flavedo of orange fruit peel (LM, BF, stained with safranin and fast green) [x40].

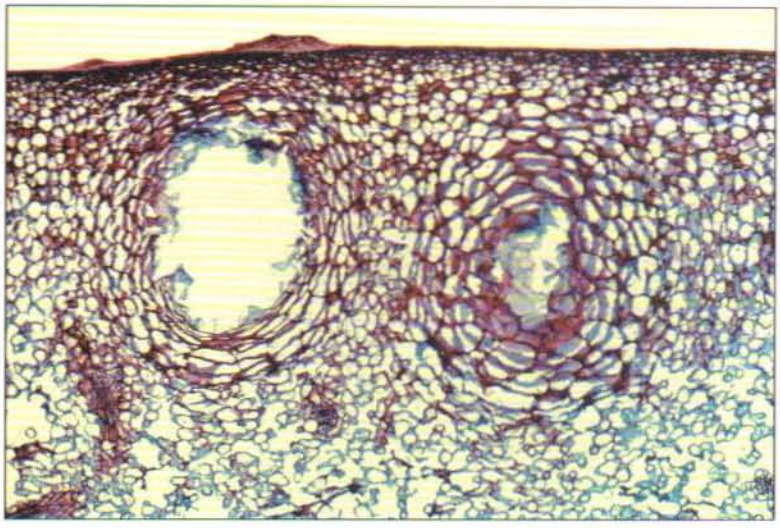
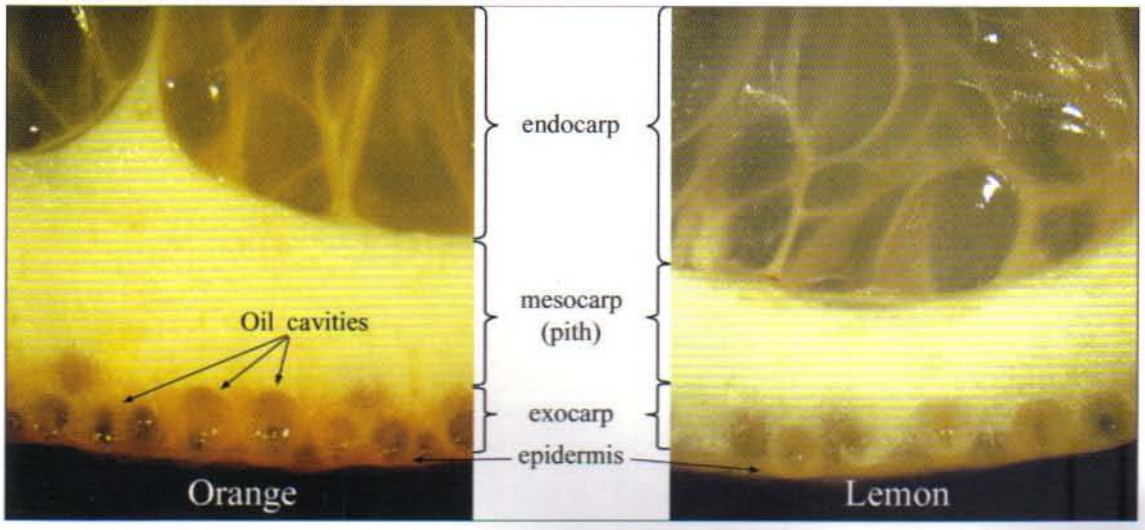


Plate 22: Orange and lemon (T/S) showing general structure of a citrus fruit with oil cavities located in the exocarp (LM, incident illumination, fresh, unstained) [x6].



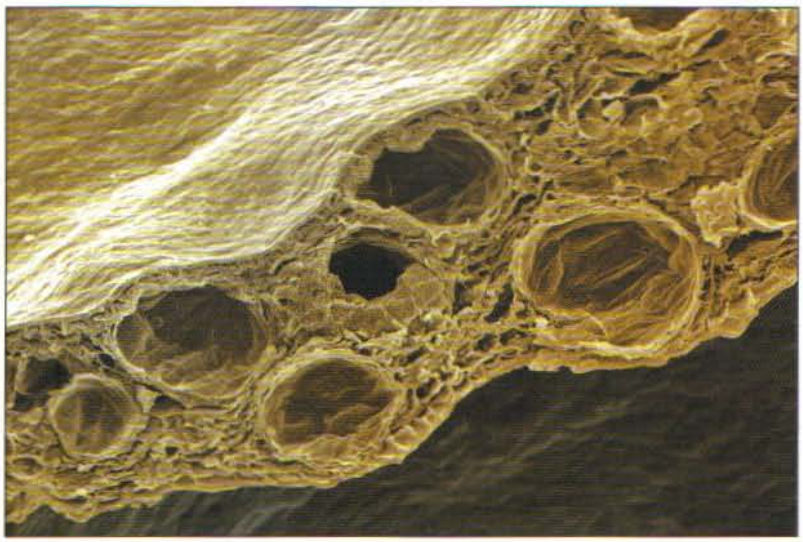


Plate 23: Dried petal (T/S) showing prolific occurrence of endogenous oil glands (SEM, CPD) [x224].

Plate 24: Detail of an endogenous oil gland (T/S) in dried petal (SEM, CPD) [x338].

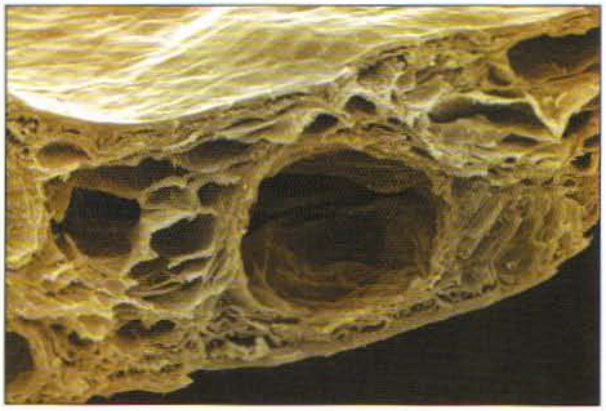


Plate 25: Dried stem (T/S) showing the distribution of endogenous oil glands beneath the surface (SEM, CPD) [x37].

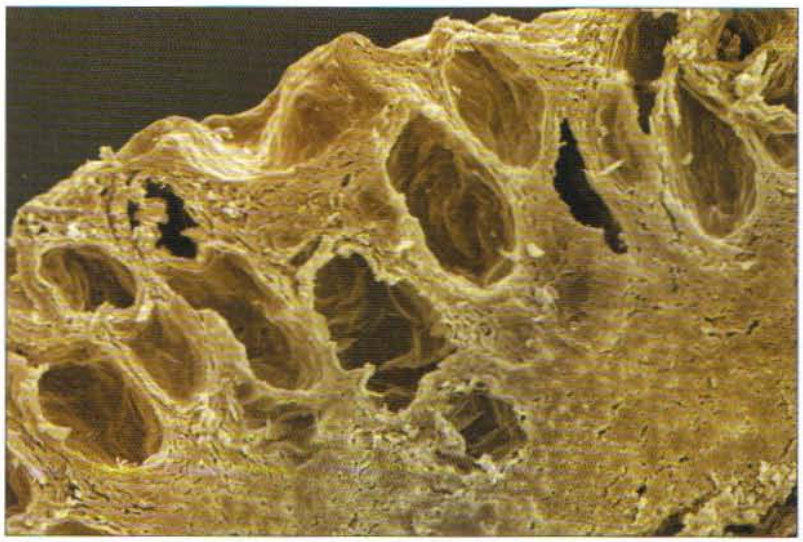
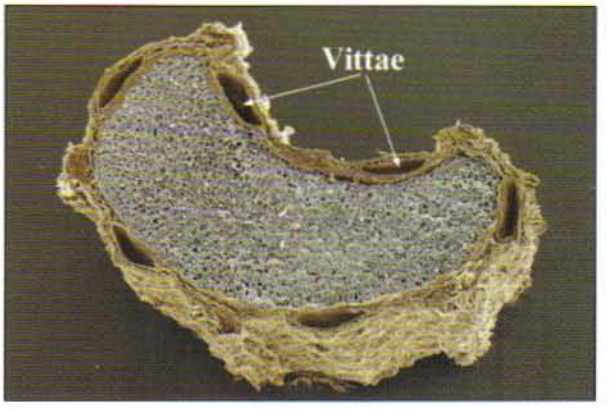


Plate 26: Detail of endogenous oil glands (T/S) in dried stem (SEM, CPD) [x139].

Plate 27: Detail of seed pair (T/S) with carpophores and commissural vittae (SEM, CPD) [x91].

Plate 28: Seed pair (T/S) (SEM, CPD) [x23].



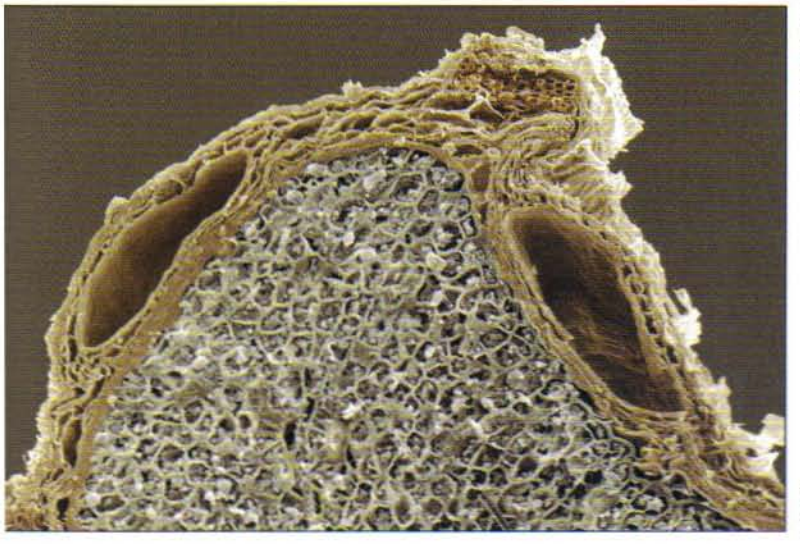


Plate 29: Seed (T/S) showing 4 primary and 2 commissural vittae situated beneath the seed coat (SEM, CPD) [x39].

Plate 30: Seed (T/S) showing detail of vittae (SEM, CPD) [x147].

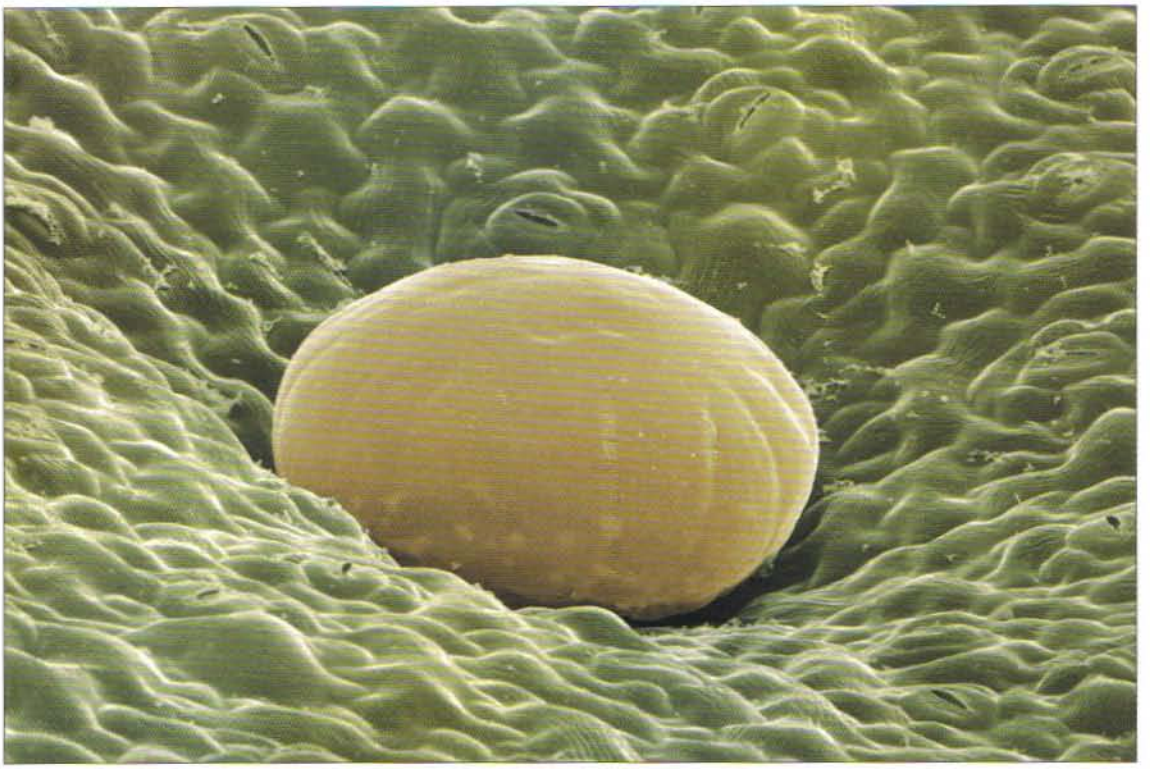


Plate 31: Sessile secretory gland on lower leaf surface; stomata visible on epidermis (SEM, CPD) [x790].

Plate 32: Sessile secretory gland on calyx (T/S) with oil-filled subcuticular space resulting in fully-extended cuticle. Secretory cells visible at base of gland structure. Non-secretory trichomes present on right hand side (LM, BF, fresh, unstained) [x305].

PLATE 33

Detail of dragonhead flower showing distribution of secretory glands [x20]

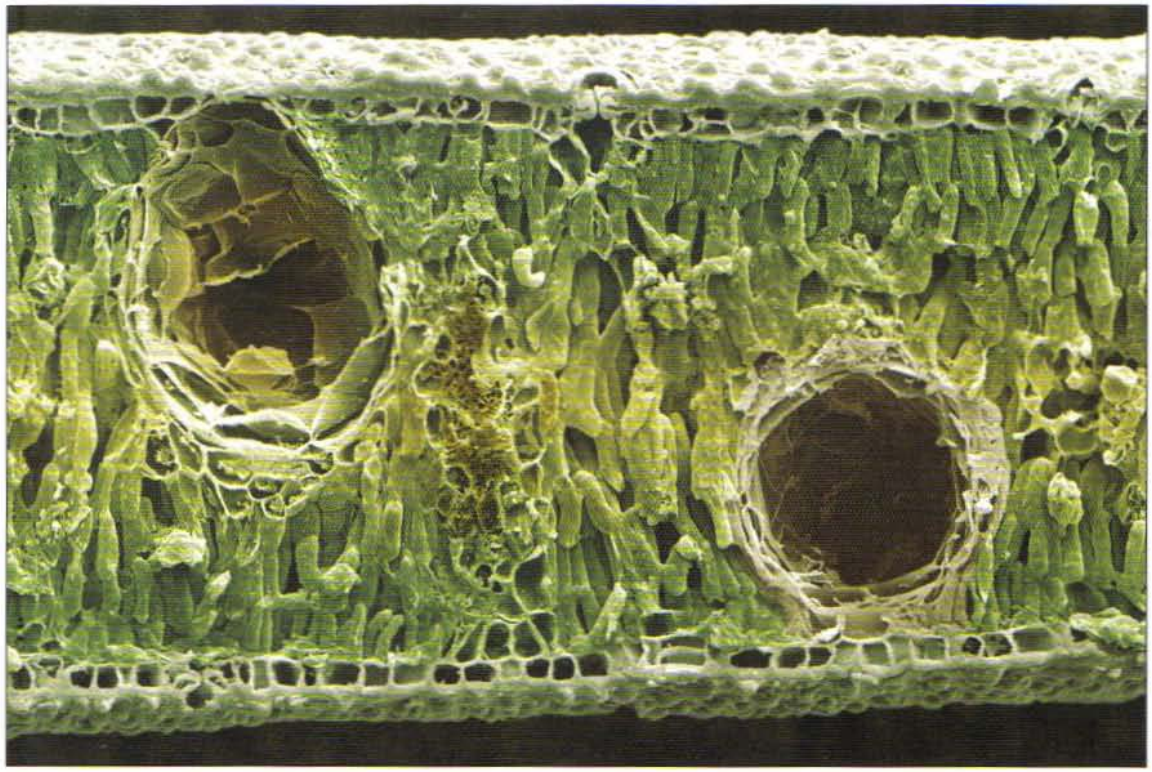


Plate 34: Leaf (T/S) showing secretory cavities. Oil removed by chemical treatment during preparation of tissue for microscopy (SEM, CPD) [x236].

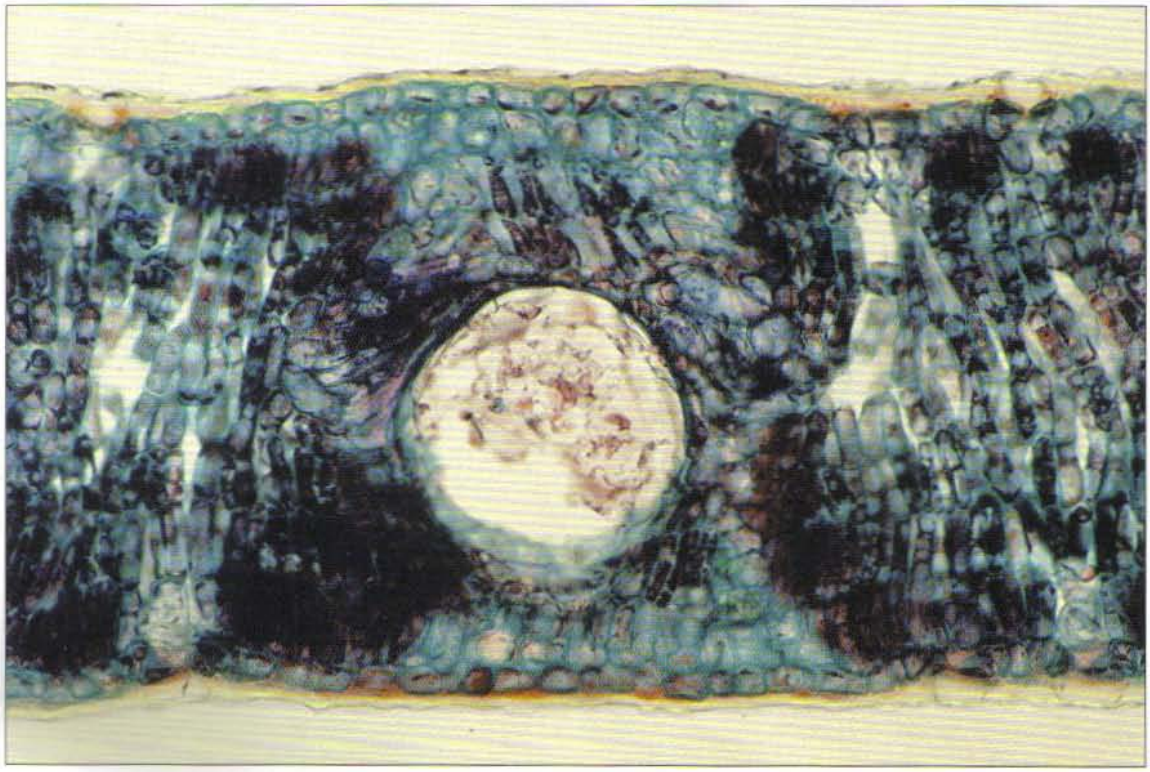


Plate 35: Leaf (T/S) showing secretory cavity (LM, BF, stained with safranin and fast green) [x231].

Plate 36: Five year old stem (T/S). Xylem and bark tissues clearly visible with resin globules oozing from ducts (cryo-SEM) [x128].

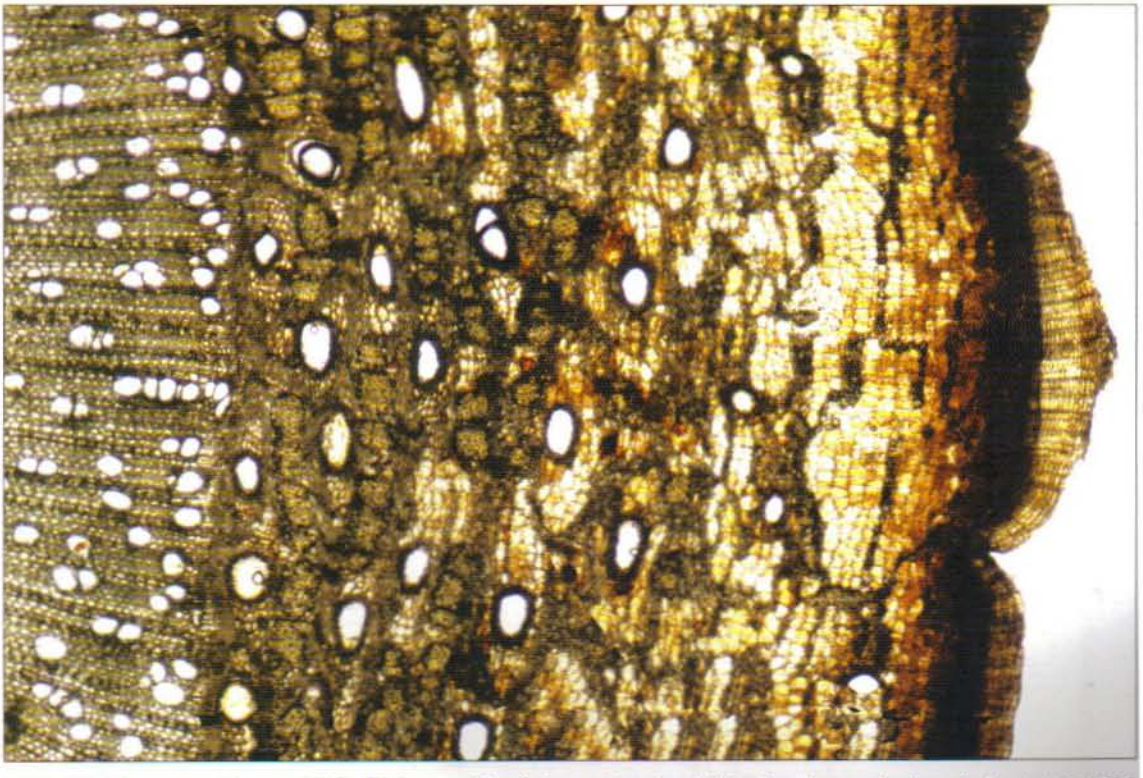


Plate 37: Five year old stem (T/S). Xylem and bark tissue clearly visible showing resin ducts in bark (LM, BF, fresh, unstained) [x47].

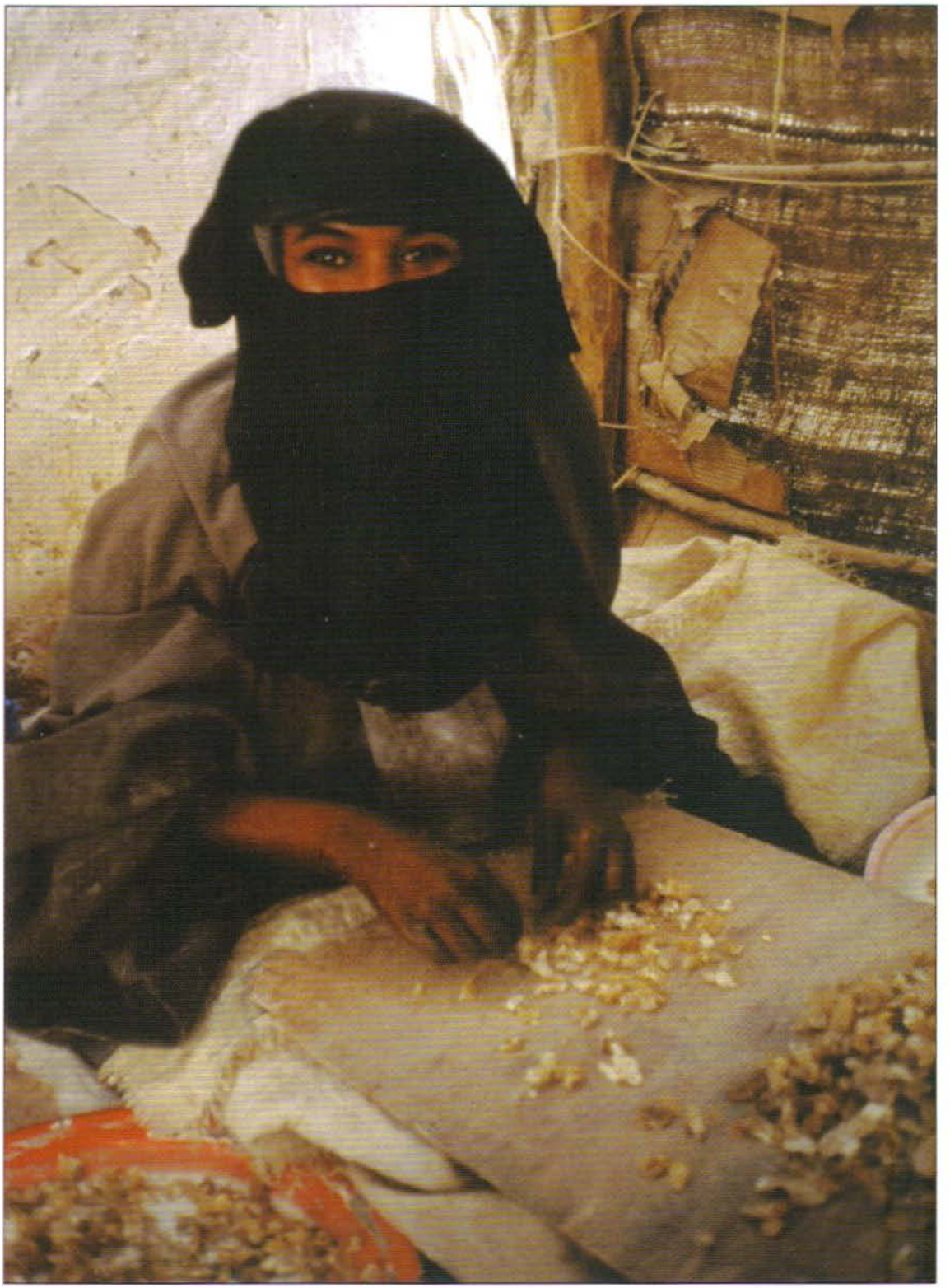
FRANKINCENSE- *Boswelia carteri*

Plate 38: Resin sample, maydi grade 3-4, sorted by local Somalian collectors.

Plate 39: Resin sample, maydi grade 1-2, sorted by local Somalian collectors.

Plate 40: Freshly-collected myrrh (*Commiphora myrrha*) resin.

PLATE 41



A young Somalian woman grading (1-6) freshly-collected resin for traders

GINGER - *Zingiber officinale*

Plate 42: Rhizome (T/S) showing oil globule oozing from secretory cell. Starch granules also clearly visible (cryo-SEM and etched) [x600].

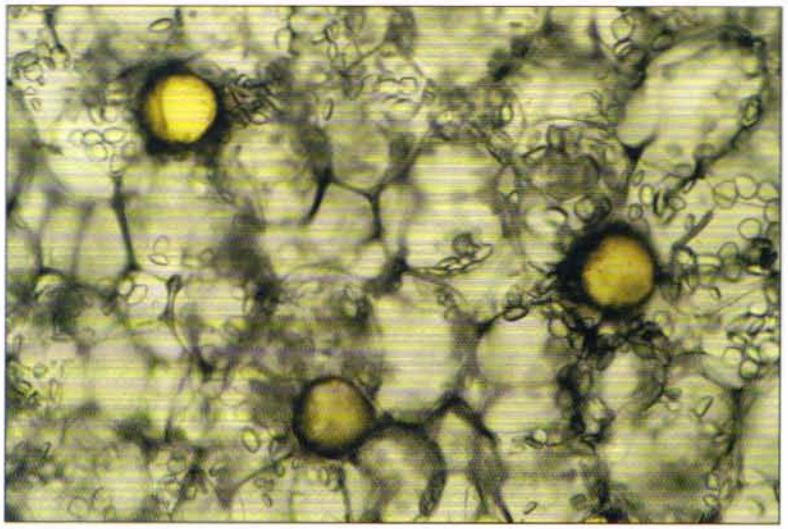


Plate 43: Rhizome (T/S) showing oil globules in secretory cells of parenchyma tissue. Starch granules abundant (LM, BF, fresh, unstained) [x205].

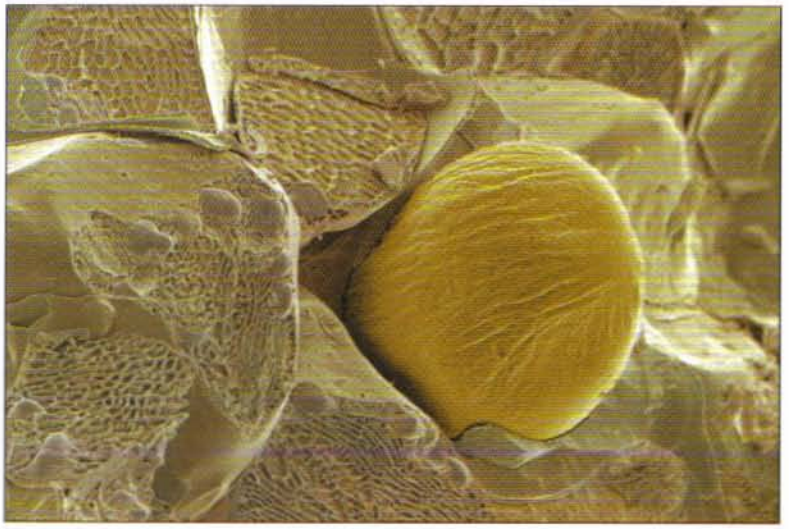


Plate 44: Rhizome (T/S) showing oil globules within membrane of secretory cell (cryo-SEM and etched) [x813].

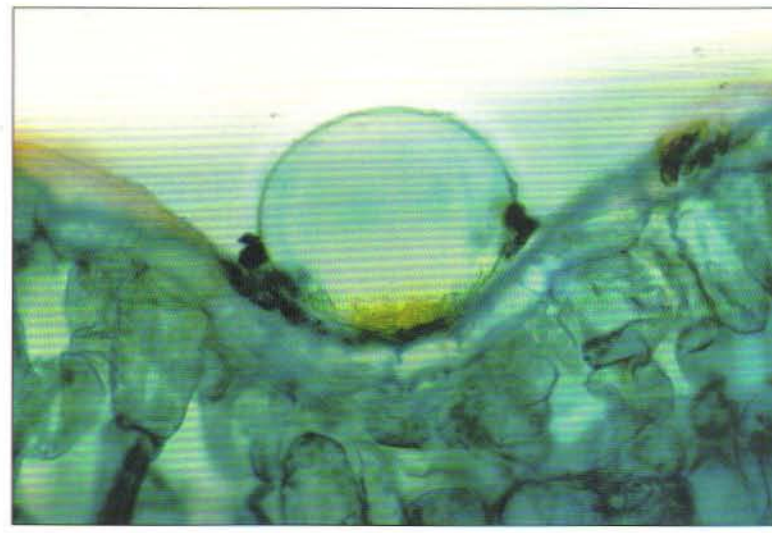


Plate 45: Leaf (T/S) showing sessile secretory gland on upper surface with oil-filled subcuticular space resulting in fully-extended cuticle (LM, BF, stained with safranin and fast green) [x411].

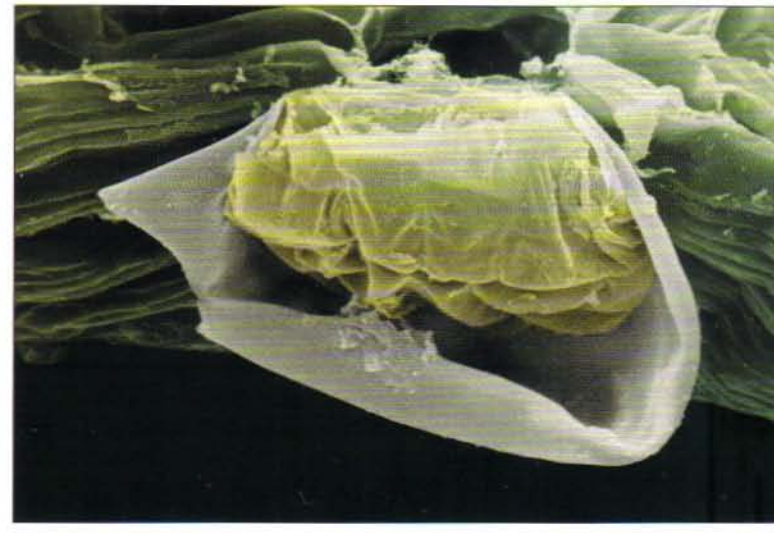


Plate 46: Sessile secretory gland with ruptured cuticle on lower leaf surface. Fresh material was dried at 80°C to demonstrate the destructive effect of high drying temperatures (SEM, CPD) [x1,069].

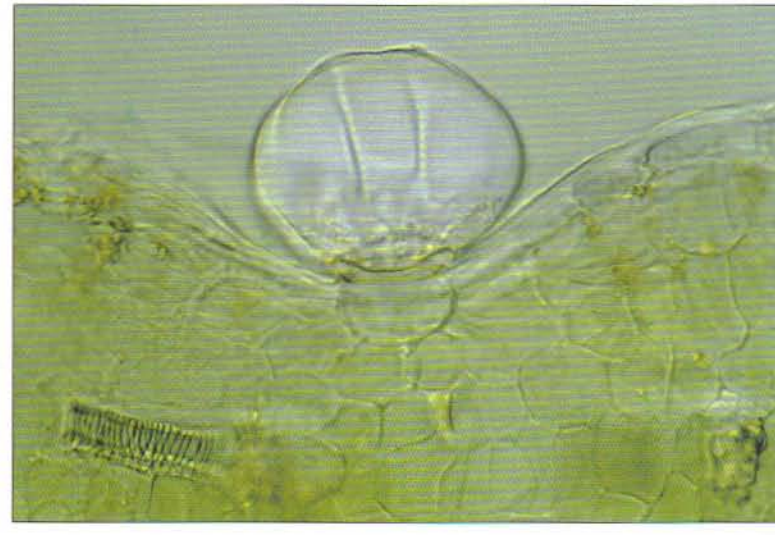


Plate 47: Leaf (T/S) showing sessile secretory gland on upper surface with oil-filled subcuticular space resulting in fully-extended cuticle (LM, DIC, fresh, unstained) [x400].

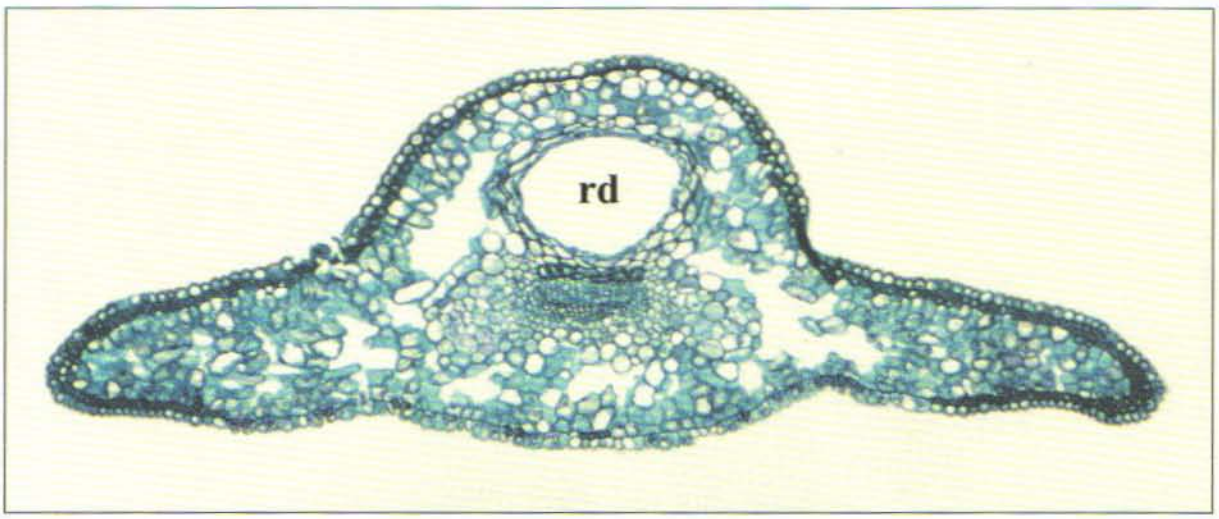


Plate 48: Needle (T/S) showing central resin duct (rd) (LM, BF, stained with safranin and fast green) [x67].

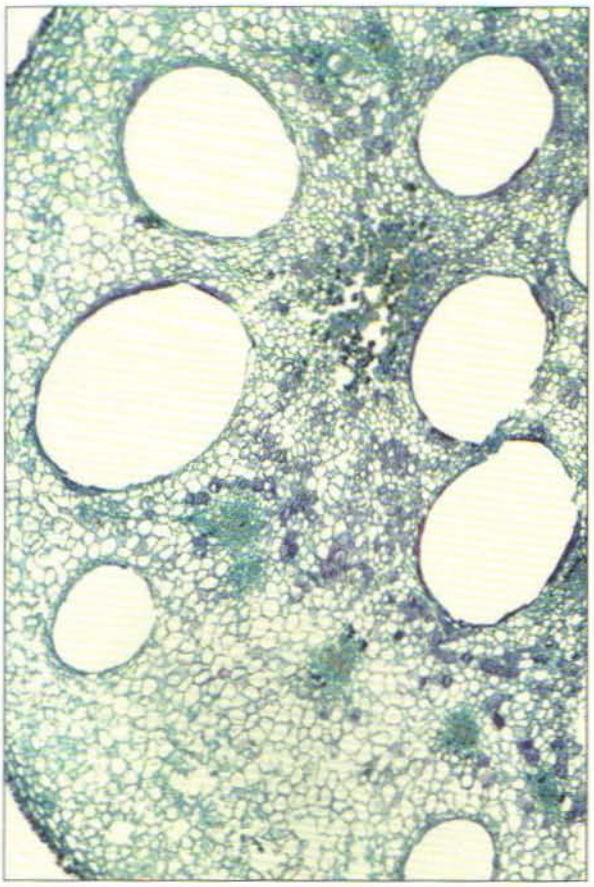


Plate 49: Green berry (T/S) showing secretory cavities (LM, BF, stained with safranin and fast green) [x44].

Plate 50: Ripe berry (T/S) detail of epithelium-lined secretory cavity (LM, BF, stained with safranin and fast green) [x200].

Plate 51: Sessile secretory gland on lower leaf surface; stomata visible on epidermis (SEM, CPD) [x1,325].

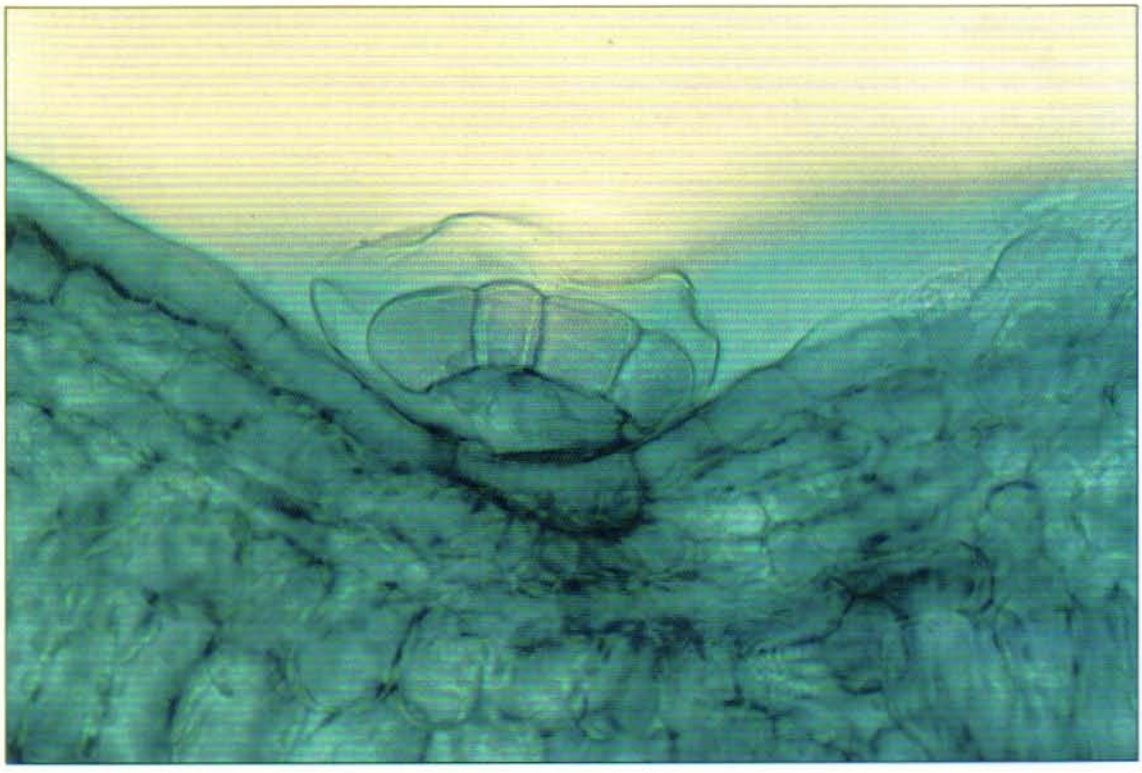


Plate 52: Detail of sessile secretory gland on lower leaf surface (T/S) with single basal cell, 4 secretory cells and oil-filled, partially-extended subcuticular space (LM, BF, stained with fast green) [x600].

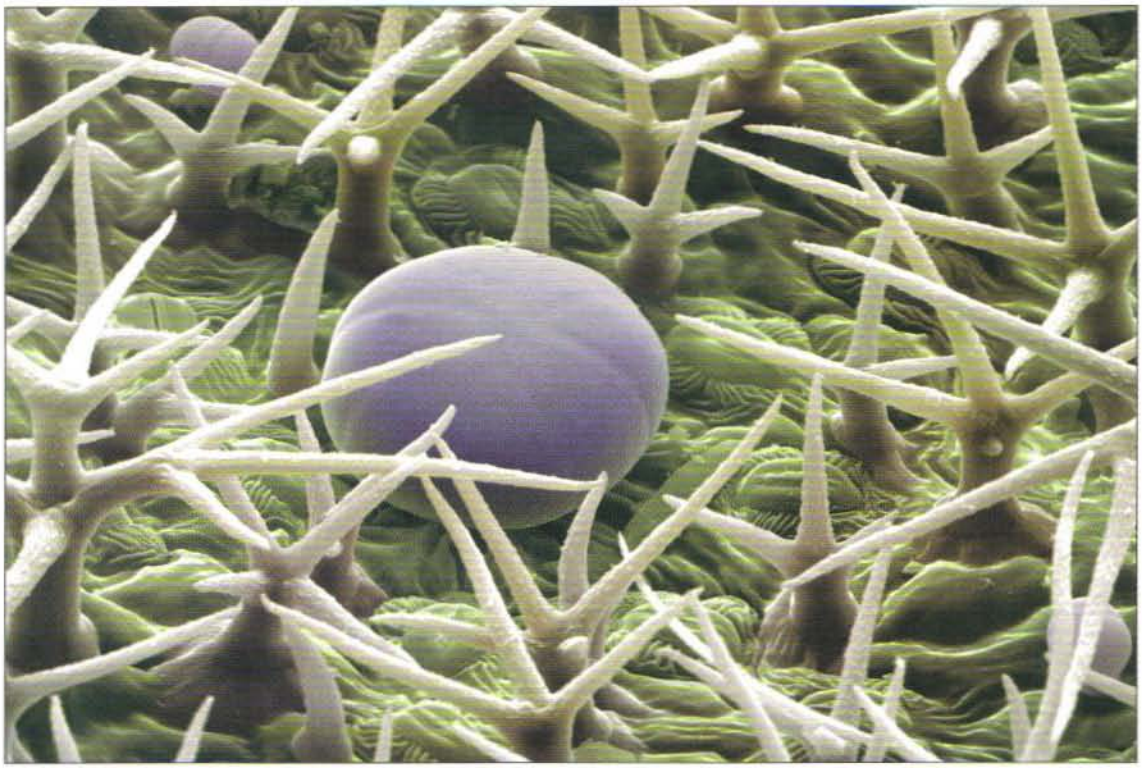


Plate 53: Detail of lower leaf surface showing sessile secretory gland and non-secretory trichomes associated with water conservation (SEM, CPD) [x638].

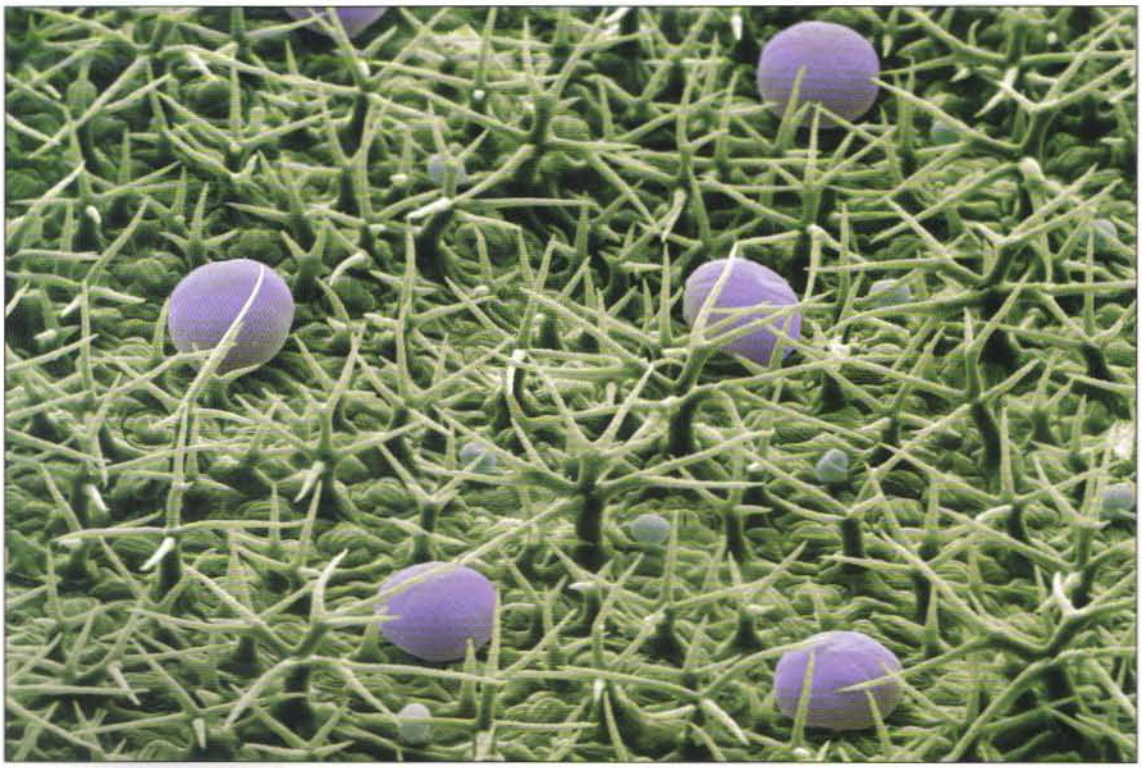


Plate 54: Lower leaf surface showing two types of sessile secretory glands and dense covering of non-secretory trichomes (SEM, CPD) [x251].

Plate 55: Leaf (T/S) showing sessile secretory gland on lower surface (LM, BF, fresh, unstained) [x375].

Plate 56: General view of lower leaf surface showing sparse distribution of sessile secretory glands. Extremely low density of trichomes (<10 per mm^2) is responsible for low yield of volatile oil in this species (LM, incident illumination) [x41].

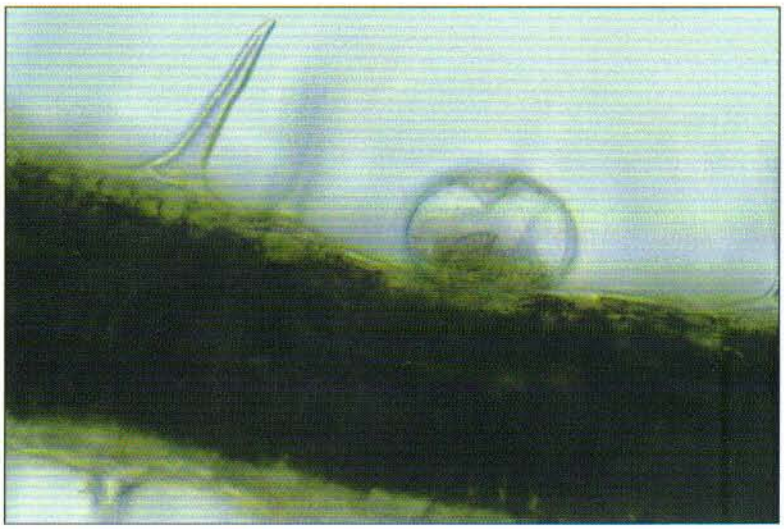
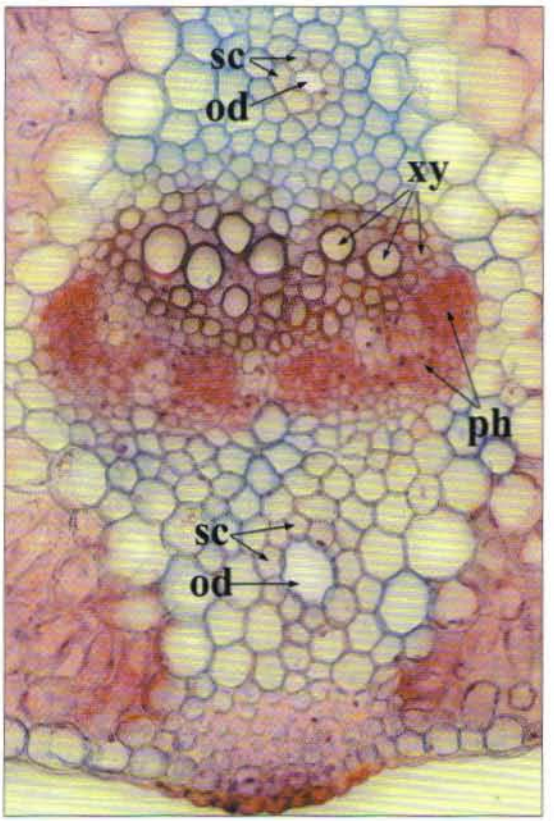
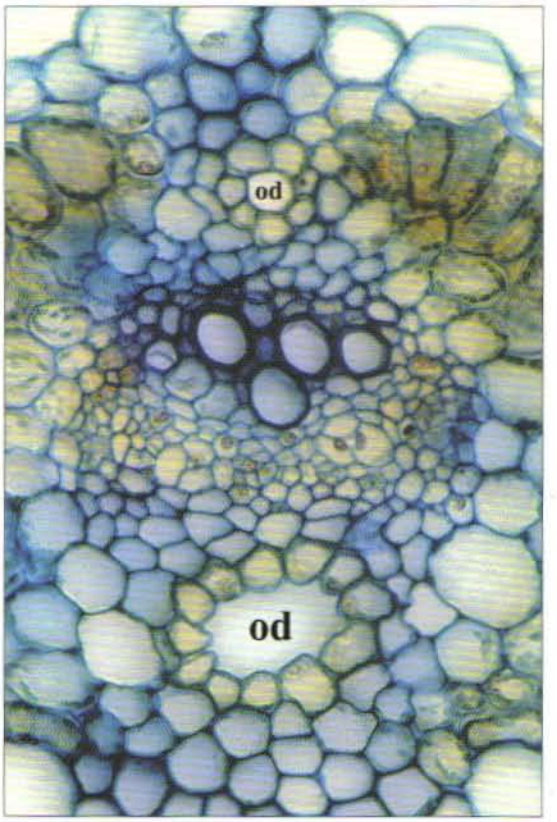


Plate 57: Young leaf (4 weeks old) (T/S) with well-developed sessile secretory gland filled with oil. Non-secretory hair also present on upper surface (LM, DIC) [x370].





Plates 58 & 59: Leaf at midrib (T/S) showing two oil ducts lined with secretory cells. Xylem, phloem and cambium form the midrib vascular tissue (LM, BF, stained with safranin and fast green by two different techniques) od - oil duct; ph - phloem; sc - secretory cells; xy - xylem [x414; x410].

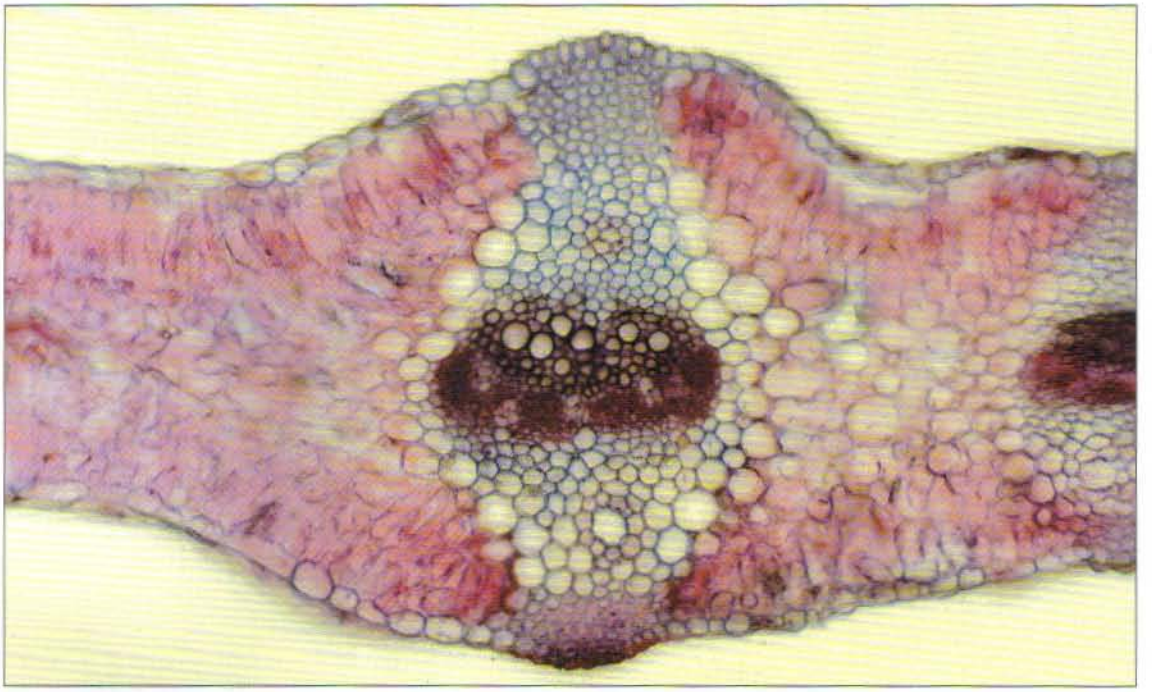


Plate 60: Overall view of leaf at midrib (T/S) with two oil ducts clearly visible (LM, BF, stained with safranin and fast green) [x290].

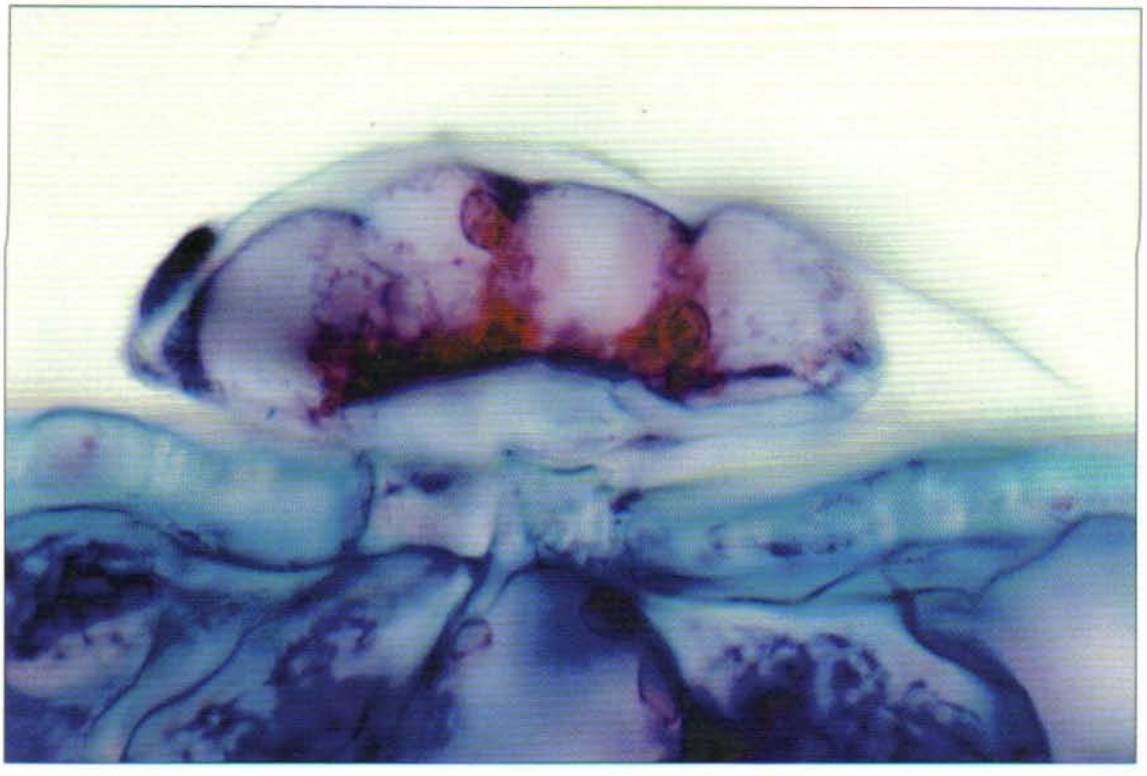


Plate 61: Sessile secretory gland on lower leaf surface (T/S). Four secretory cells clearly visible beneath ruptured cuticle (LM, BF, stained with safranin and fast green) [x1,887].

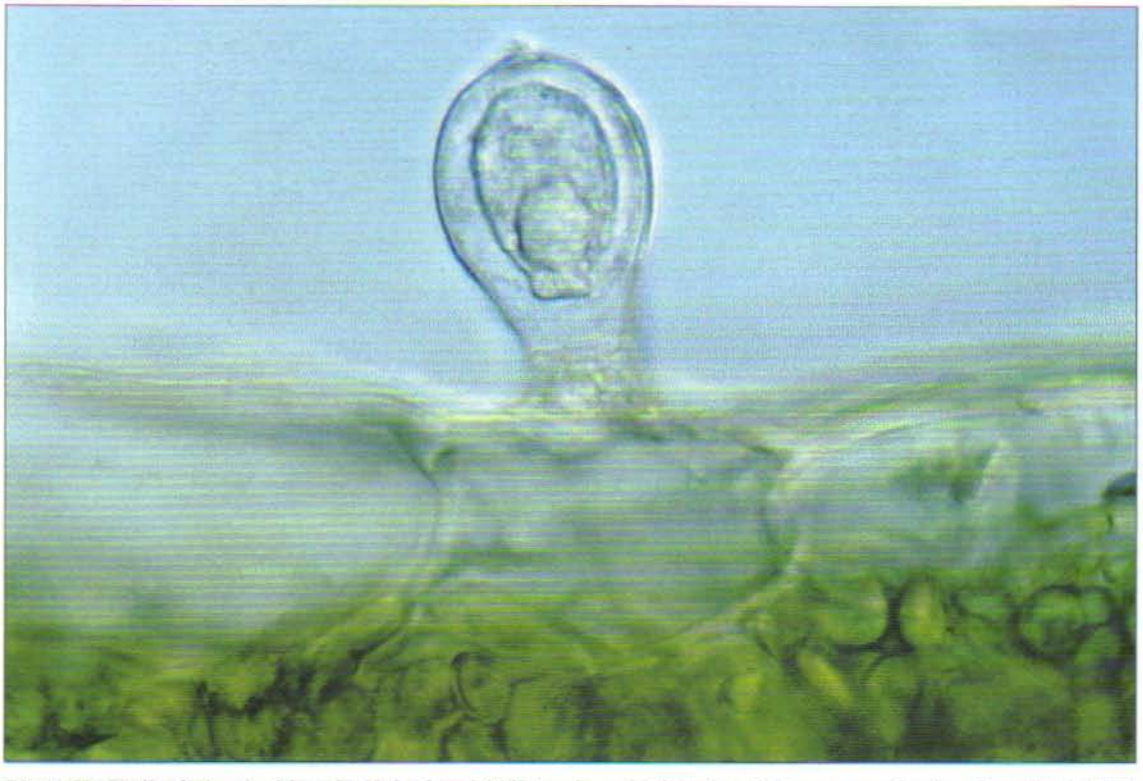


Plate 62: Stalked gland with unicellular head (T/S) and turgid, intact cuticle on lower leaf surface (LM, DIC, fresh, unstained) [x1,800].

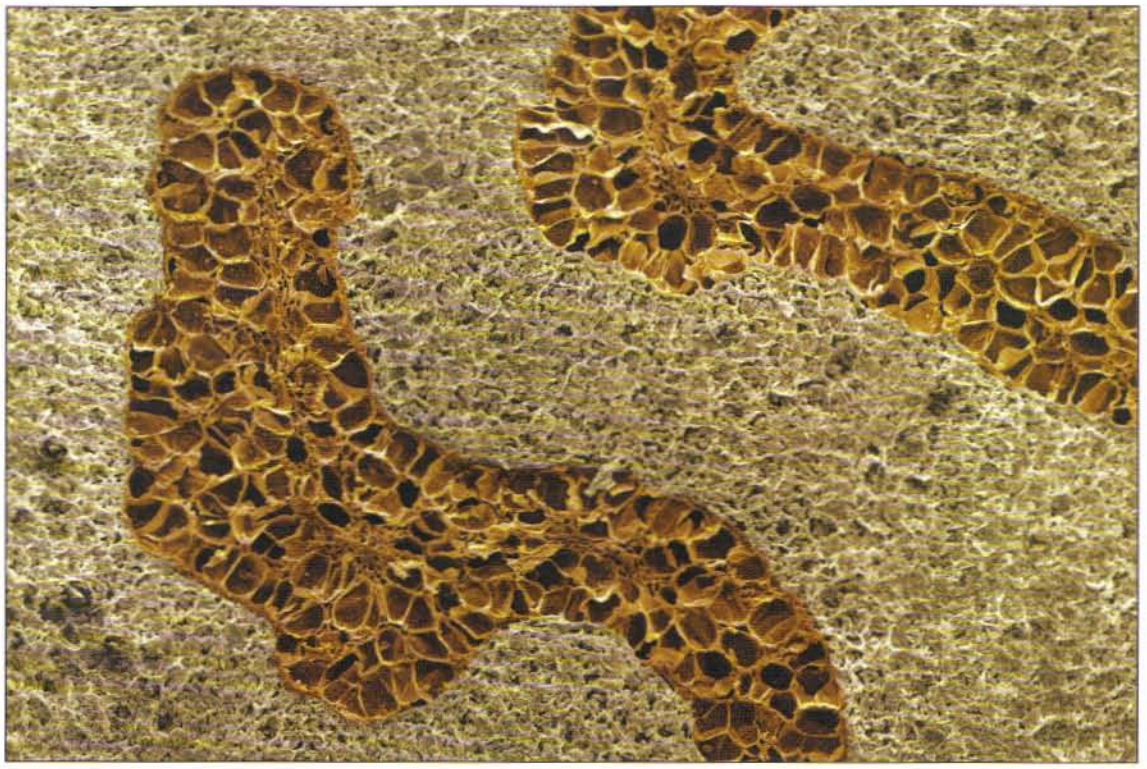


Plate 63: Embryo (T/S) showing inner perisperm and secretory cells. Preparation for CPD process has removed all oil from cells (SEM, CPD) [x79].

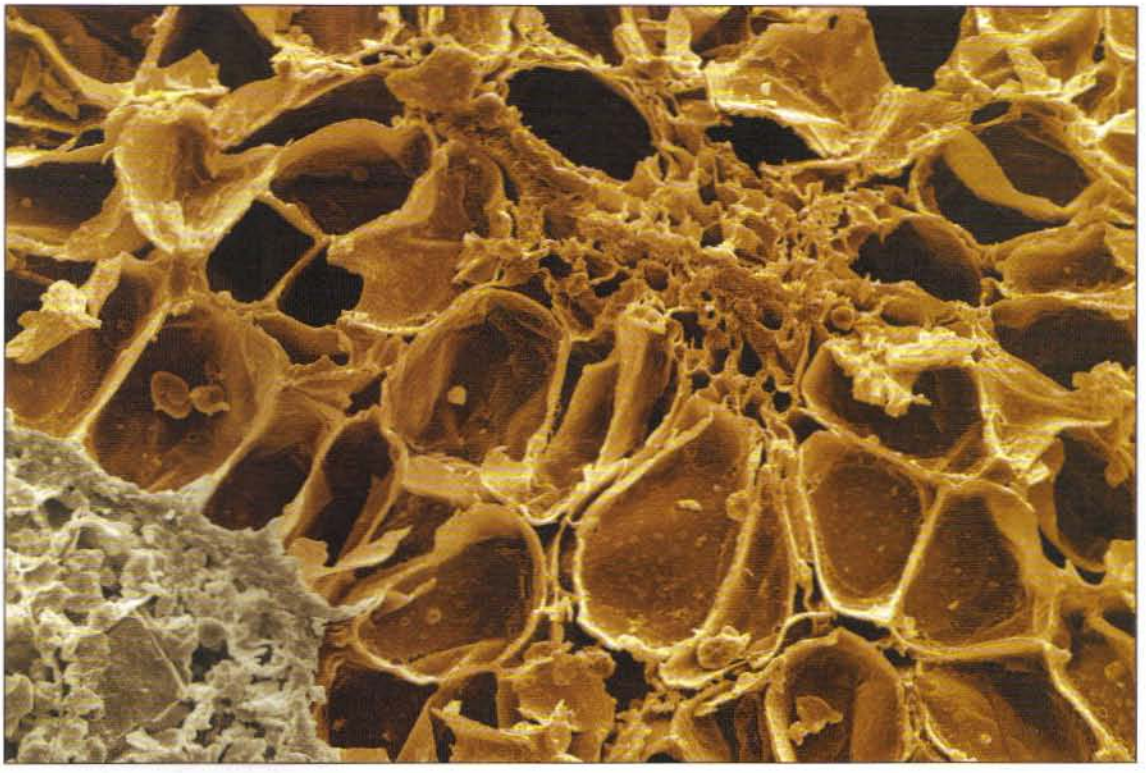


Plate 64: Detail of secretory cells (T/S) in embryo (SEM, CPD) [x380].

Plate 65: Stalked glandular trichomes on upper leaf surface (LM, incident illumination, fresh, unstained) [x100].

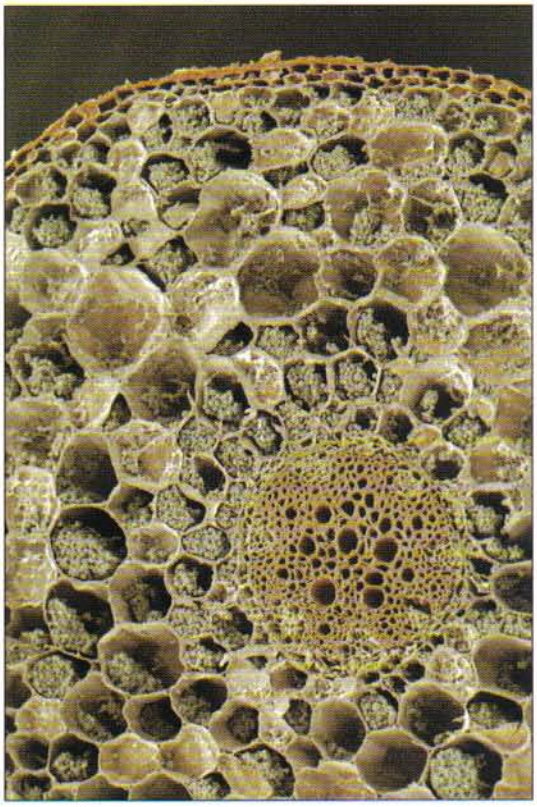


Plate 66: Root (T/S) showing cortex parenchyma cells filled with starch grains (SEM, CPD) [x67].

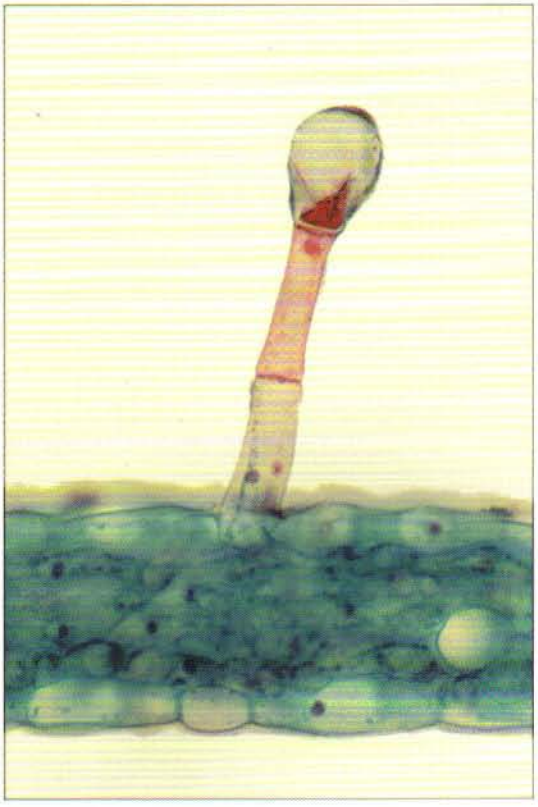


Plate 67: Leaf (T/S) showing stalked glandular trichome with unicellular head (LM, BF, stained with safranin and fast green) [x205].

Plate 68: Sessile secretory gland on lower leaf surface. Impression of cell sutures not visible on cuticle surface due to distention by oil secretions (SEM, CPD) [x1,245].

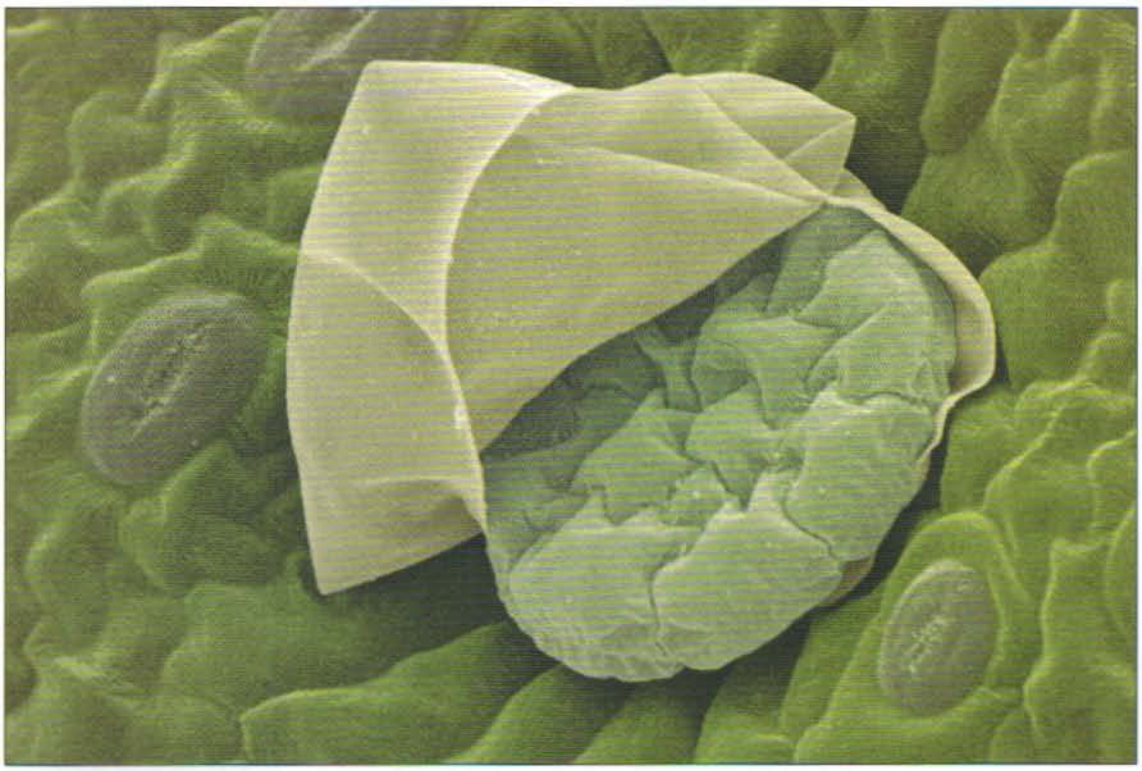


Plate 69: Sessile secretory gland on lower leaf surface with ruptured cuticle revealing individual secretory cells. Neighbouring stomata clearly visible (SEM, CPD) [x1,230].

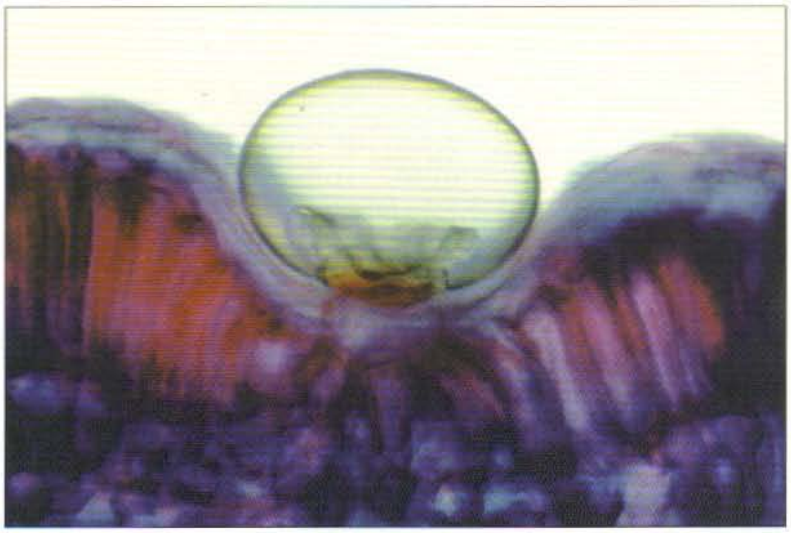


Plate 70: Leaf (T/S) showing sessile secretory gland on upper surface with oil-filled subcuticular space resulting in fully-extended cuticle. Pallisade parenchyma visible beneath epidermis (LM, BF, stained with safranin and fast green) [x420].

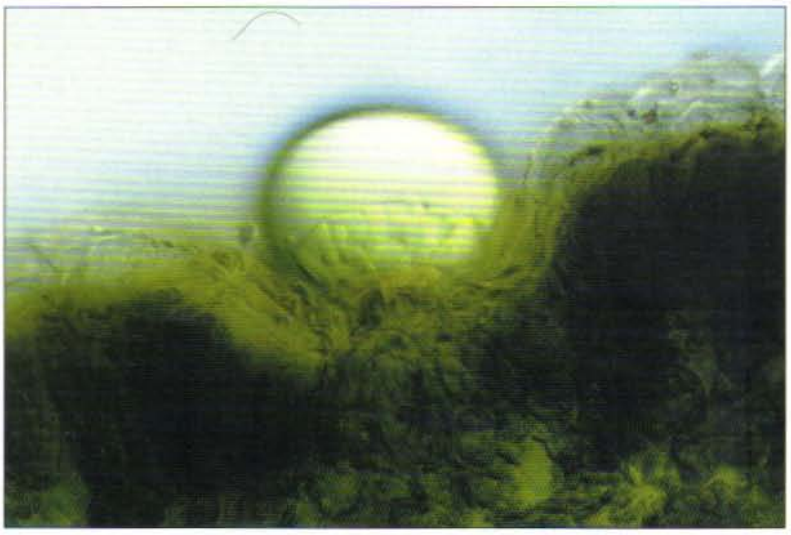


Plate 71: Sessile secretory gland (T/S) on upper leaf surface with oil-filled, fully-extended intact cuticle (LM, DIC, fresh, unstained) [x420].

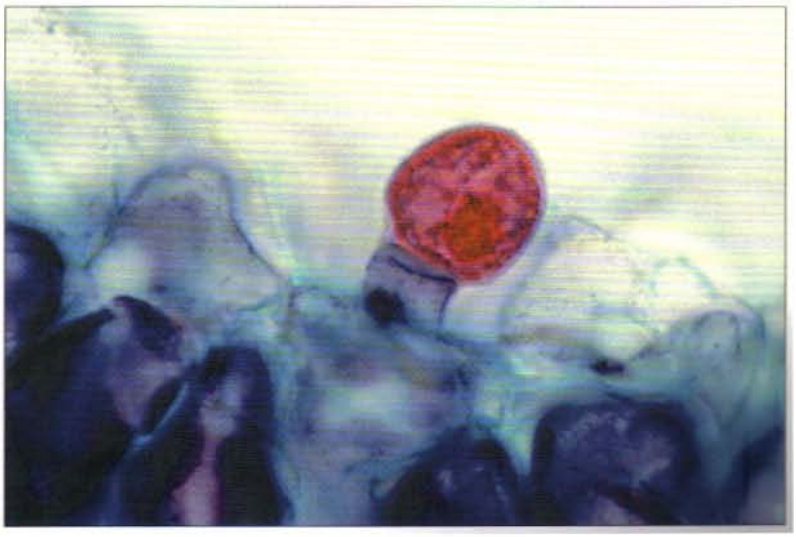


Plate 72: Stalked glandular trichome (T/S) with unicellular head on upper leaf surface (LM, BF, stained with safranin and fast green) [x420].

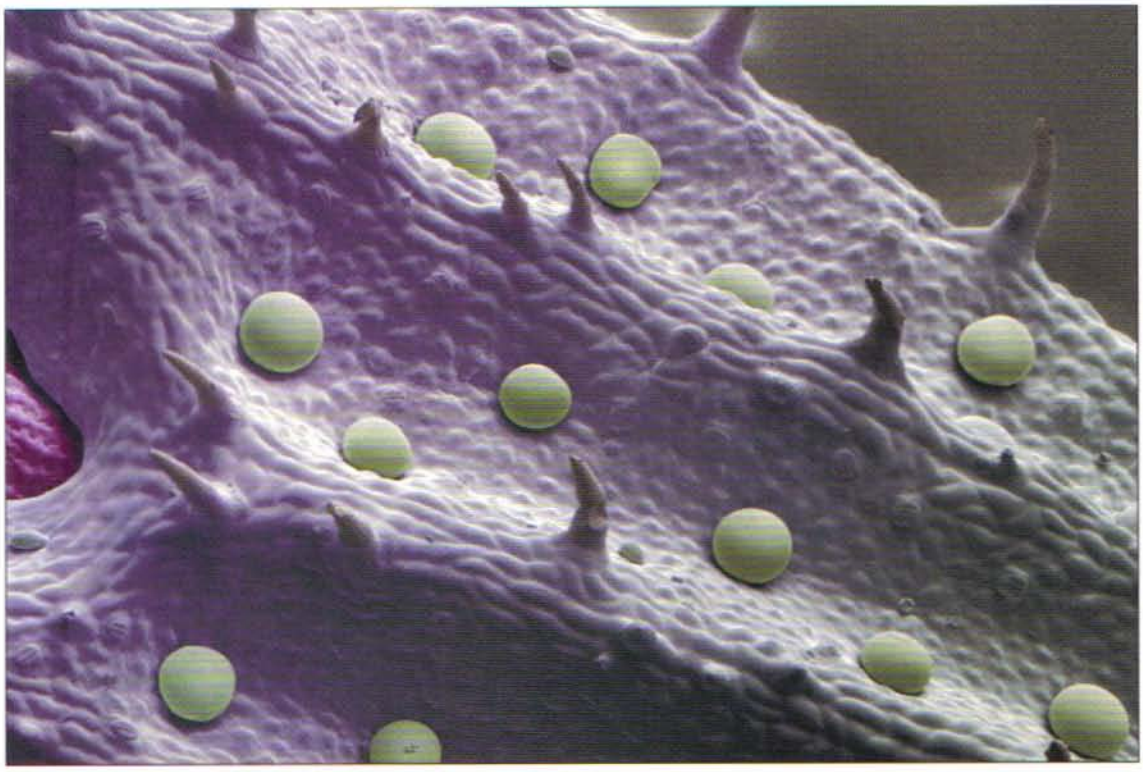


Plate 73: Turgid sessile secretory glands and non-secretory trichomes on calyx surface (cryo-SEM) [x137].

Plate 74: Detail of sessile secretory glands and non-secretory trichomes on calyx surface (cryo-SEM) [x465].

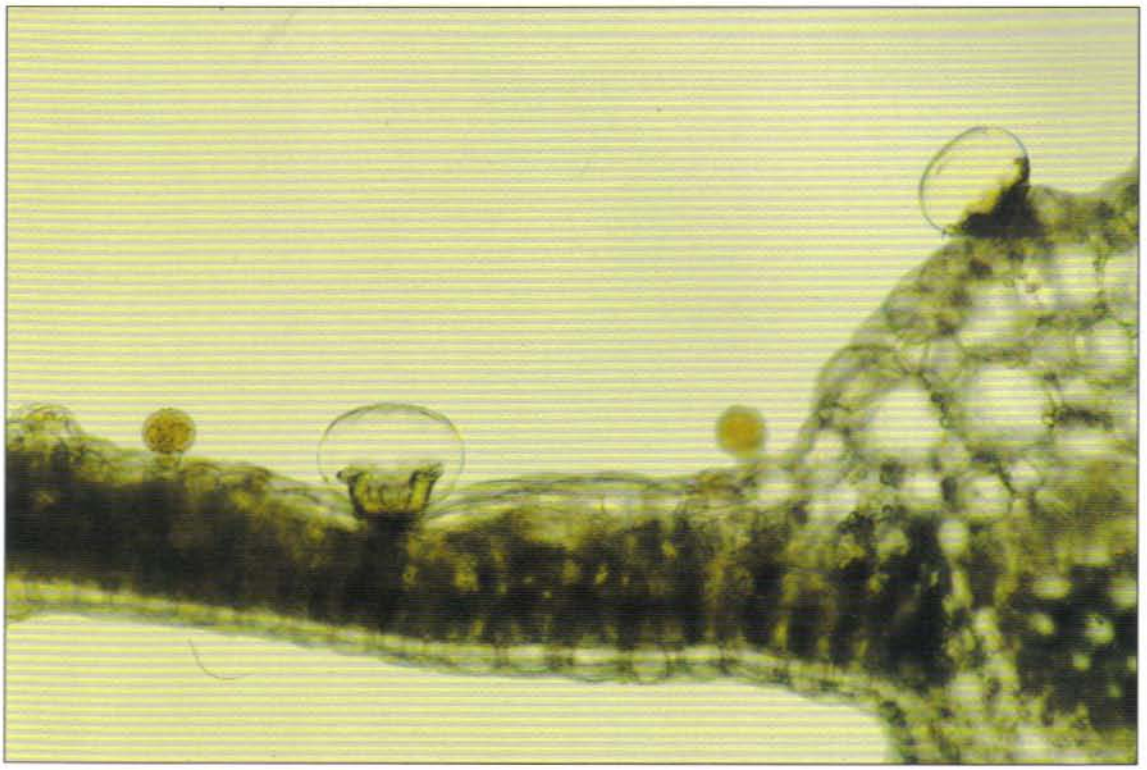


Plate 75: Leaf (T/S) showing 2 types of secretory glands on lower surface: a) multicellular with oil-filled subcuticular space resulting in fully-extended cuticle b) stalked with unicellular head (LM, BF, fresh, unstained) [x283].

Plate 76: Leaf (T/S) showing stalked secretory glands on upper and lower surfaces and single non-secretory trichome on lower (LM, BF, fresh, unstained) [x285].

PLANTAIN - *Plantago psyllium*

Plate 77: Whole seed after soaking in water for several hours showing resultant swollen, mucilaginous coating (LM, DIC) [x24].

Plate 78: Detailed structure of mucilaginous coating after soaking in water for several hours (SEM, freeze-dried) [x1,570].

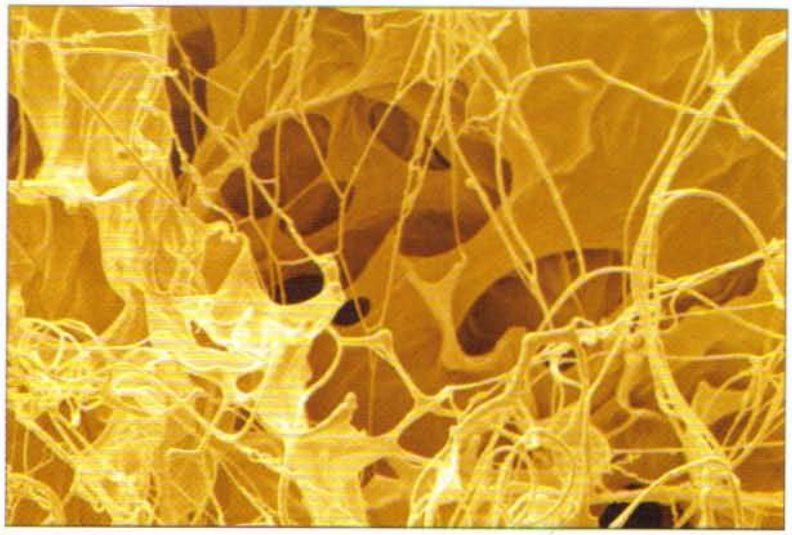


Plate 79: Detail of mucilaginous coating (T/S) attached to seed testa (SEM, freeze-dried) [x266].

Plate 80: Contextual view of whole seed (T/S) and its mucilaginous layer after imbibition (SEM, freeze-dried) [x41].

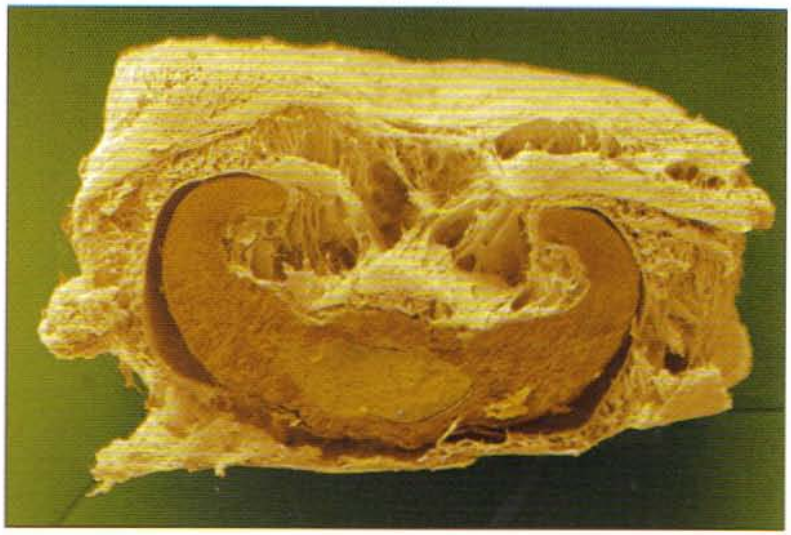


PLATE 81

Agastache foeniculum at Auchincruive herb garden

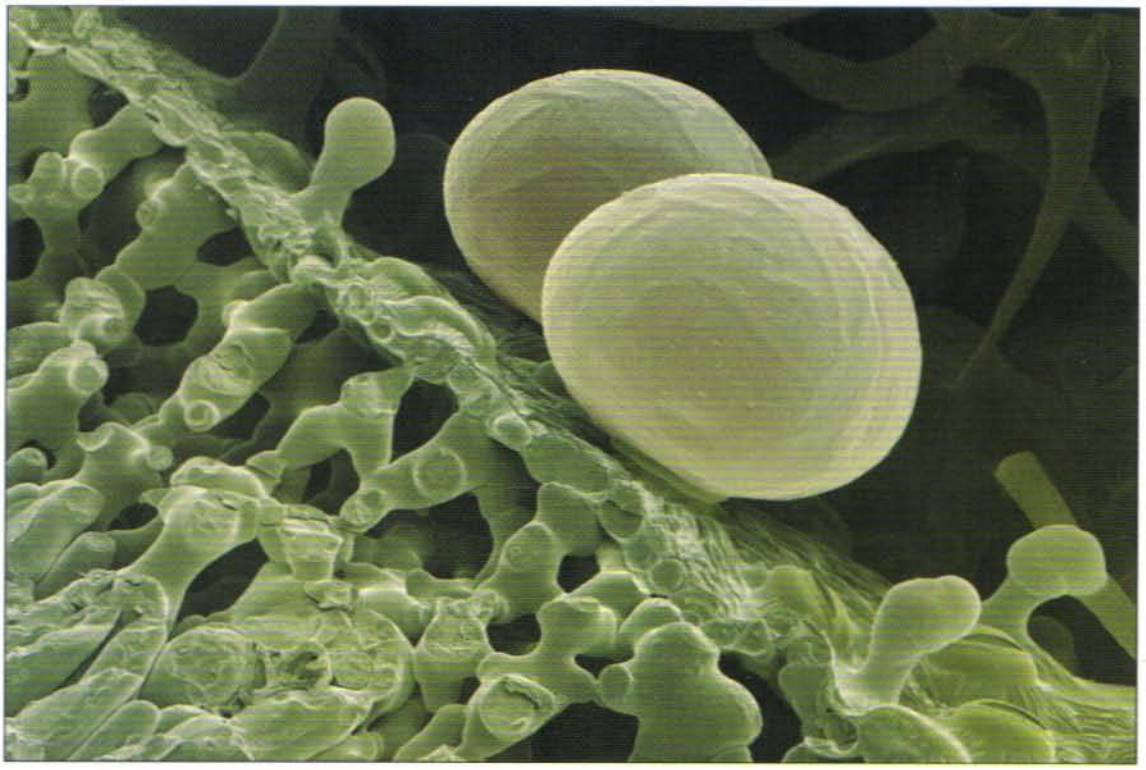


Plate 82: Detail of freeze-fractured leaf to reveal spongy mesophyll and secretory glands on lower surface (cryo-SEM) [x615].

Plate 83: Lower surface of leaf showing both sessile and stalked secretory glands together with non-secretory trichomes associated with water conservation and imparting a glaucous appearance (cryo-SEM) [x287].

Plate 84: Detail of sessile secretory gland (T/S) showing basal cell and 4 distinct secretory cells loosely covered by cuticle. Epidermis and underlying pallisade parenchyma clearly visible (LM, BF, stained with safranin and fast green) [x1,250].

Plate 85: Detail of stalked secretory gland (T/S) with unicellular head on lower leaf surface (LM, BF, fresh, stained with light green) [x1,250].

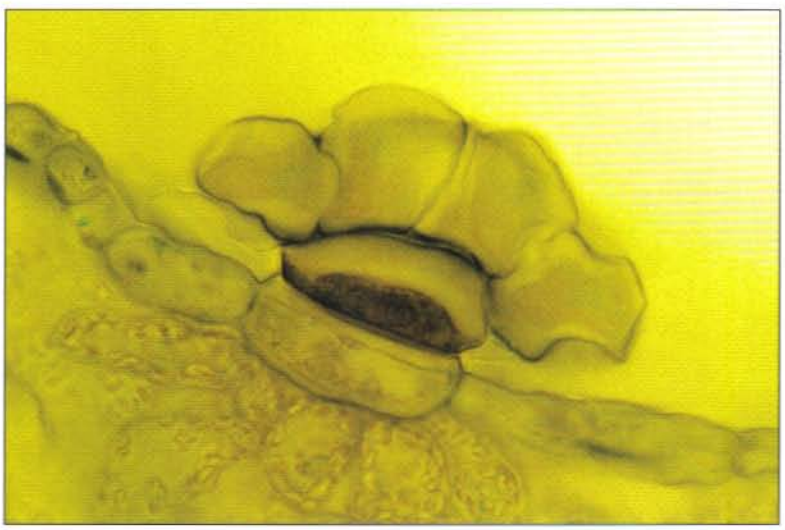


Plate 86: Detail of sessile secretory gland (T/S) on lower leaf surface showing basal cell and 4 secretory cells (LM, BF, stained with light green) [x1,250].

Plate 87: Detail of sessile secretory gland with turgid, intact cuticle on lower leaf surface. Single basal cell visible (cryo-SEM) [x1,540].

Plate 88: Sessile secretory glands with turgid, intact cuticles on lower leaf surface. Single closed stoma visible (cryo-SEM) [x812].

PLATE 89

Experimental plot of tansy grown for volatile oil with high thujone content (Auchincruive)

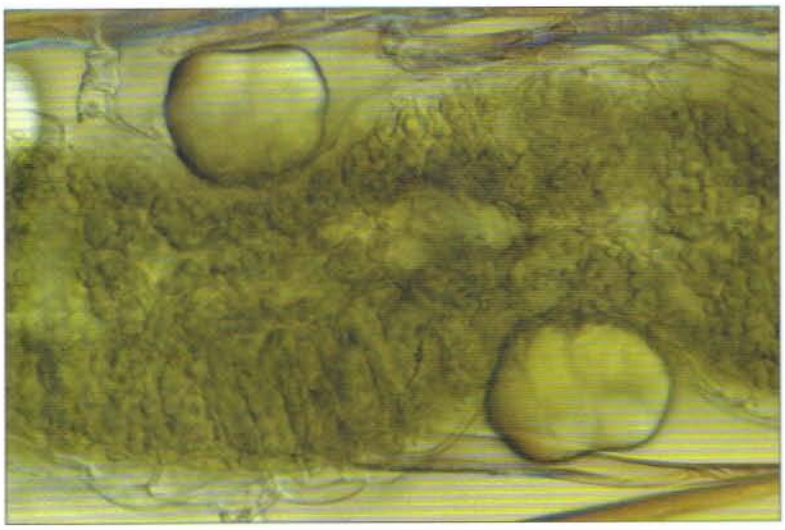


Plate 90: Leaf (T/S) showing sessile secretory glands with oil-filled subcuticular space resulting in fully-extended cuticle (LM, DIC, fresh, unstained) [x416].

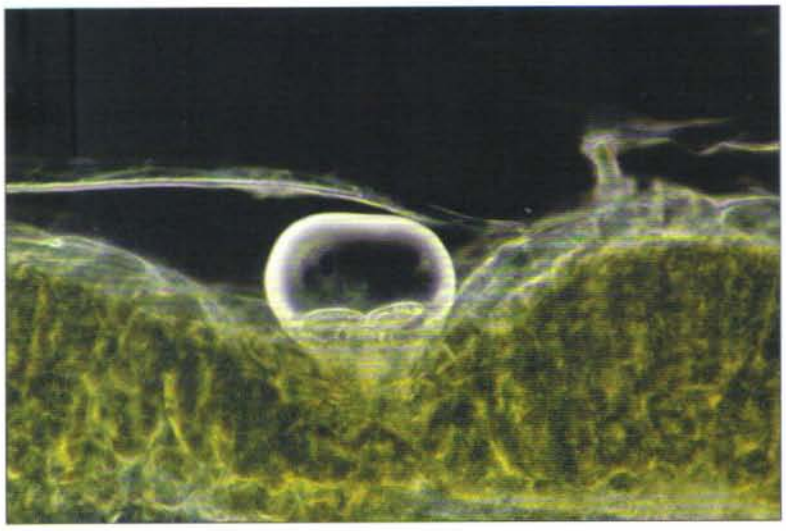


Plate 91: Leaf (T/S) showing sessile secretory gland on upper surface with oil-filled subcuticular space resulting in fully-extended cuticle (LM, dark ground illumination, fresh, unstained) [x416].

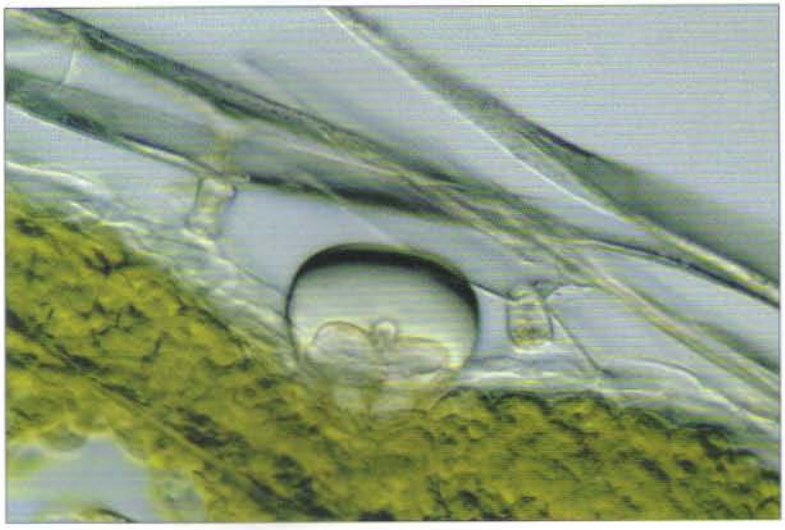


Plate 92: Leaf (T/S) showing sessile secretory gland on lower surface with oil-filled subcuticular space resulting in fully-extended cuticle. Non-secretory trichomes clearly visible (LM, DIC, fresh, unstained) [x416].

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PLATE 93

Street market with herbs and spices, Seoul, Korea

LIST OF PLANT SPECIES USED IN AROMATHERAPY

LATIN NAME	ENGLISH NAME
Abies spp.	Fir
Achillea millefolium	Yarrow
Allium sativum	Garlic
Allium sepa	Onion
Alpinia galanga	Galangal root
Ammi visnaga	Khella
Amyris balsamifera	Amyris
Anethum graveolens	Dill
Angelica archangelica	Angelica
Aniba rosaeodora	Rosewood
Anthoxanthum odoratum	Flouve
Apium graveolens	Celery seed
Artemisia annua	Wormwood sweet
Artemisia arborescens	Mugwort greater
Artemisia dracunculus	Tarragon
Betula spp.	Birch
Boswellia carteri	Frankincense
Bursera delpechiana	Linaloe berry
Cananga odorata	Ylang Ylang
Canarium luzonicum	Elemi
Carum carvi	Caraway
Cedrus spp.	Cedarwood
Chamaemelum spp.	Chamomile Roman
Cinnamomum camphora	Camphor
Cinnamomum zeylanicum	Cinnamon leaf
Cistus ladaniferus	Cistus
Citrus aurantifolia	Lime
Citrus aurantium	Bitter orange (peel)
Citrus aurantium	Neroli bigarade (flower)
Citrus aurantium ssp. *amara*	Petitgrain (leaf)
Citrus aurantium ssp. *bergamia*	Bergamot (peel)
Citrus aurantium ssp. *bergamia*	Petitgrain bergamier
Citrus limon	Lemon
Citrus paradisi	Grapefruit
Citrus reticulata var. *Mandarin*	Mandarin
Citrus reticulata var. *Tangerine*	Tangarine
Citrus sinensis	Sweet orange
Commiphora myrrha	Myrrh
Commiphora erythraea	Opopanax
Coriandrum sativum	Coriander
Cuminum cyminum	Cumin seed
Cupressus sempervirens	Cypress
Cymbopogon citratus	Lemongrass citratus
Cymbopogon flexuosus	Lemongrass flexuosus
Cymbopogon martini	Palmarosa
Cymbopogon nardus	Citronella
Cyperus rotundus	Turmeric
Daucus carota	Carrot seed
Elletaria cardamomum	Cardamon
Erigeron canadensis	Fleabane
Eucalyptus spp.	Eucalyptus
Ferula galbaniflua	Galbanum
Foeniculum vulgare	Fennel
Gaultheria procumbens	Wintergreen
Helichrysum angustifolium	Curry plant
Humulus lupulus	Hop
Hypericum perforatum	St. John's wort
Hyssopus officinalis	Hyssop
Illicium verum	Anise star
Inula graveolens	Inula
Jasmimum officinale	Jasmine

LATIN NAME *(cont.)*	ENGLISH NAME *(cont.)*
Juniperus communis	Juniper
Lantana camara	Lantana
Laurus nobilis	Laurel leaf
Lavandula spp.	Lavender
Lavandula x *intermedia 'super'*	Lavandin
Leptospermum scoparium	Manuka
Leptospermum (Kunzea) ericoides	Kanuka
Levisticum officinale	Lovage
Lippia citriodora	Verbena true
Litsea cubeba	May chang
Matricaria spp.	Chamomile German
Melaleuca alternifolia	Tea tree
Melaleuca leucadendron	Cajuput
Melaleuca quimquenervia	Niaouli
Melissa officinalis	Melissa
Mentha citrata	Mint bergamont
Mentha pulegium	Pennyroyal
Mentha spp.	Mint
Myristica fragrans	Nutmeg
Myroxylon pereirae	Peru balsam
Myroxylon balsamum	Tolu balsam
Myrtus communis	Myrtle
Nardostachys jatamansi	Spikenard
Nepeta cataria	Catnip
Ocimum spp.	Basil
Origanum spp.	Oregano
Pelargonium spp.	Geranium
Petroselinum sativum	Parsley seed
Picea mariana	Spruce (black)
Pimenta dioica	Pimento berry
Pimenta racemosa	Bay
Pimpinella anisum	Aniseed
Pinus sylvestris	Pine
Piper cubeba	Cubeb seed
Piper nigrum	Black pepper
Pogostemon patchouli	Patchouli
Prunus amygdalus	Almond
Pseudotsuga spp.	Fir douglas
Ravensara aromatica	Ravensara
Rosa centifolia	Rose otto
Rosmarinus officinalis	Rosemary
Salvia lavandulaefolia	Sage Spanish
Salvia officinalis	Sage
Salvia sclarea	Clary
Salvia triloba	Sage cretan
Santalum album	Sandalwood
Satureja hortensis	Summer savory
Satureja montana	Winter savory
Satureja thymbra	Savory thyme-leaved
Styrax benzoin	Benzoin
Syzygium aromaticum	Clove bud
Tagetes glandulifera	Tagetes
Thuja occidentalis	Thuja
Thymus spp.	Thyme
Tilia europaea	Linden blossom
Tsuga canadensis	Eastern hemlock
Turnera diffusa	Damiana
Valeriana officinalis	Valerian
Vetivera zizanioides	Vetiver
Viola odorata	Violet leaf
Vitex agnus-castus	Chaste-tree
Zingiber officinale	Ginger

GLOSSARY

Aglycone the non-carbohydrate portion of a glycoside.

Azulene cyclopentacycloheptene [$C_{10}H_8$], insoluble in water, intensely blue with naphthalene odour; precursor to chamazulene in plants.

Calyx the sepals collectively, forming the outer whorl of the flower.

Carpophore the part of a flower axis to which carpels are attached. The extension of the stem which divides into two and to which each single seed is attached (Umbelliferae).

Commissural face the inner surface of a seed pair to which both seeds are attached.

Critical point (drying) the temperature and pressure of a substance at which the densities of the liquid and gaseous states are identical. At this point there is no meniscus and artifacts caused by surface tension are avoided.

Cryogenic fixation a method of mechanical fixation avoiding chemical artifacts where a specimen is quickly frozen at a very low temperature, usually -210^{0}C in Nitrogen slush and examined microscopically in the frozen state.

Cuticle an outer skin or pellicle, sometimes referring to the epidermis as a whole, especially when impermeable to water; (bot.) layer of waxy material, cutin, on the outer wall of epidermal cells in many plants, making them fairly impermeable to water.

Cutin a wax-like or fatty substance impregnating epidermal walls of plant cells and also forming a separate layer, the cuticle, on the outer wall of the epidermis in plants making the surface impermeable to water.

Cytoplasm all the living parts of a cell inside the cell membrane and excluding the nucleus.

Endocarp the innermost layer of pericarp of fruit, usually fibrous, hard or stony, as the "stone" enclosing the seed in plums, cherries, etc.

Endoplasmic reticulum (ER) extensive, convoluted internal membrane in cells, continuous with the outer nuclear membrane and enclosing a continuous internal space (lumen). Involved in the synthesis and transport of membrane proteins and lipids and of material destined for secretion from the cell.

Epithelium sheet of cells tightly bound together, lining any internal or external surface in multicellular organisms. Epithelia variously serve protective, secretory or absorptive functions.

Essential oils mixtures of various volatile oils derived from benzenes and terpenes found in plants and producing characteristic odours. Having various functions such as attracting insects or warding off fungal attacks.

Flavedo the outer layer, or rind, of pericarp in citrus fruits.

Glycoside any class of compound which on hydrolysis gives a sugar and a non-sugar residue.

Isopentenyl pyrophosphate biogenetic precursor of terpenes [C_5H_8].

Lacuna space or cavity.

Leucoplast(id) colourless plastid that develops into chloroplasts, etc.

Lignin a hard material found in walls of cells of xylem in plants, a very variable cross-linked polymer which stiffens the cell wall.

Lipophilic relating to or having a strong affinity for fats and other lipids.

Lumen internal space of any tubular or sac-like organ or sub-cellular organelle.

Mesocarp the middle layer of the pericarp e.g. comprising the flesh of fruits such as plums and cherries.

Mitochondria organelles in the cytoplasm of eukaryotic cells, having a double membrane, important for energy production and genetic coding.

Parenchyma soft plant tissue composed of thin-walled, relatively undifferentiated cells which may vary in structure and function.

Pericarp the tissues of fruit that develop from the ovary wall, comprising an outer skin, sometimes a fleshy mesocarp and an inner endocarp.

Perisperm in some seeds, a storage tissue formed by proliferation of the nucleus rather than the endosperm.

Phloem the principal food-conducting tissue of vascular plants extending throughout the plant body. It is composed of elongated conducting vessels and sieve tubes (in angiosperms), both containing clusters of pores (sieve areas) in the walls through which the protoplasts of adjacent cells communicate. Sugars and amino acids are the main nutrients transported via the phloem. Parenchymatous companion cells closely associated with the conducting elements are involved in the delivery to- and uptake of- material from the phloem.

Plasmodesmata cytoplasmic threads running transversely through plant cell walls and connecting cytoplasm of adjacent cells.

Plastid one of a class of cytoplasmic organelles, including chloroplasts, found in plants and eukaryotic algae. Bounded by a double membrane and containing DNA.

Proliferation increase by frequent and repeated reproduction; increase by cell division.

Protoplast the living component of a cell, i.e. the protoplasm not including any cell wall.

Rhizome thick horizontal stem, usually underground, bearing buds and scale leaves and sending out shoots from above and below.

Secondary metabolites compounds produced by plants and microbes, e.g. antibiotics, alkaloids, and flower pigments that are not essential to the growth of the organism.

Secretory tissues cells and tissues that secrete substances such as digestive enzymes, polypeptide hormones, neuro-transmitters or complex material such as mucus, slime, fragrances, etc.

Senescence advancing age; the complex ageing processes that eventually lead to death.

Thujone [$C_{10}H_{16}O$] a toxic constituent of many essential oils. A colourless liquid practically insoluble in water.

Tracheid a type of water-conducting xylem cell present in all vascular plants with lignified secondary cell wall usually containing spiral thickening or bordered pits.

Trichome any of various outgrowths of the epidermis in plants including branched and unbranched hairs, vesicles, hooks, spines and stinging hairs; a hair tuft.

Xylem the main water-conducting tissue in vascular plants extending throughout the whole plant, involved in storage, support and the transport of minerals and nutrients. Xylem is composed of tracheary elements: tracheids and (in angiosperms) vessel elements. Both are elongated, hollow cells with thickened, usually heavily-lignified walls and lacking protoplasts when mature. They are joined end-to-end to form a continuous, conducting tube.

INDEX OF SPECIES

ENGLISH NAMES

LATIN NAMES

PLATE 94

Statue of a street seller with various herbs, essential oils and perfumes
(Perfumery Museum, Grasse, South of France)

KATERINA PAVLA SVOBODA

Dr. K. P. Svoboda lectures on plant anatomy, plant breeding and biotechnology at the Scottish Agricultural College (SAC), Auchincruive. She is also responsible for research on aromatic and medicinal plants including botany, physiology, chemotaxonomy and the production of secondary metabolites and their application. During the last 10 years she has published 73 refereed and general articles on aromatic and medicinal plants and has contributed over 70 papers and posters to national and international conferences. She has travelled extensively in the course of her work and in 1992 spent a year in Japan.

TOMAS GALEN SVOBODA

T. G. Svoboda is a first-year student at Medical University, Dundee. He has an interest in aromatic plants and essential oils and has worked at a chamomile farm in Norfolk running a large-scale distillation plant there. He has now finished his project at SAC on the phytochemical investigation and genetic fingerprinting of chamomile, and during this time also contributed to several papers on various other aromatic plants.

ANDREW SYRED

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