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Secretory Tissues and Factors Influencing their Development

By

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Summary

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Some secretory tissues occur normally in certain plants, while in others they may be formed only in response to external stimuli. In some plants the production of secretory tissues proceeds in any case and is only intensified by external factors. Injuries, pathogens and exogenous growth substances effect the formation of resin and gum ducts. Ethylene appears to be the most important factor. In the epithelial duct-cells the resin is synthesized mainly in the plastids, although other cell organelles may also be involved in this process. The gum is produced by the Golgi apparatus. The existence of an evolutionary trend in the development of the secretory tissues from scattered cells to organized ducts and cavities and culminating in glandular trichomes, is suggested.

Zusammenfassung

FAHN A. 1988. Sekretgewebe und Faktoren, die ihre Entwicklung beeinflussen. – Phyton (Austria) 28 (1): 13–26, 8 Abbildungen. – Englisch mit deutscher Zusammenfassung.

Manche sekretorische Gewebe kommen in Pflanzen normalerweise vor, während andere erst als Antwort auf äußere Stimuli gebildet werden. In manchen Pflanzen werden Sekretgewebe auf jeden Fall gebildet, äußere Faktoren wirken nur verstärkend. Schädigungen, Krankheitserreger und exogene Wuchsstoffe bewirken die Ausbildung von Harz- und Gummigängen, Ethylen erscheint als der wichtigste Faktor. In den Epithelzellen der Harzgänge wird das Harz hauptsächlich in den Plastiden

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synthetisiert, wenngleich auch andere Organelle daran Teil-nehmen können. Gummi wird im Golgiapparat gebildet. Es wird angenommen, daß ein entwicklungsgeschichtlicher Trend in der Entwicklung des Sekretionssystems von zerstreutliegenden Zellen zu organisierten Gängen und Höhlungen, culminierend in den Drüsenhaaren, vorliegt.

Introduction

On the basis of their origin and location, the secretory tissues can be divided into two main types:

1. Secretory tissues which occur on plant surfaces (e. g. glandular trichomes) and usually exude the secreted substances directly to the outside of the plant (exogenous secretion).

2. Secretory tissues which occur inside the plant body and secrete into specialized intercellular spaces (endogenous secretion). The intercellular spaces may develop schizogenously or lysigenously or by a combination of these two. In some cases, as for instance in the laticifers, the secreted material is accumulated inside the cells.

The glandular trichomes are constant features characteristic of many plant species and develop without external stimuli. The question whether external factors may influence their density on the plant surfaces has not yet been studied.

The inner secretory tissues, such as ducts and cavities, are also characteristic of certain plants, but their development may or may not depend on external factors, such as injuries and pathogens, or on physiological stresses. This paper will deal with the influence of external as well as of internal factors on the development of secretory tissues. Possible evolutionary trends in the development of secretory tissues will also be discussed.

Resin ducts

In the wood of the *Pinaceae,* resin ducts are regarded as a normal feature in the genera *Pinus, Picea, Larix* and *Pseudotsuga,* whereas in the species *Abies, Cedrus, Tsuga* and *Pseudolarix* they were reported to develop only as a result of injury (Figs. 1 and 2).

Fig. 1. Cross-section of the secondary xylem of *Cedrus libani,* showing a tangential row of traumatic resin ducts. Bar = 1 mm.

Fig. 2. Cross-section of the secondary xylem of *Pinus halepensis,* showing scattared normal resin ducts. Bar = 1 mm.

Fig. 3. Cross-section of a stem 1½ year-old *Pinus halepensis* plant, just below the region of application of 0.3% NAA, showing the wood increment (IN) and the large number of resin ducts which developed during a period of 6 weeks. Bar = 1 mm.

Fig. 4. As in Fig. 3, but without NAA treatment. Bar = 1 mm. (Figs. 3 and 4 from FAHN & ZAMSKI 1970.)

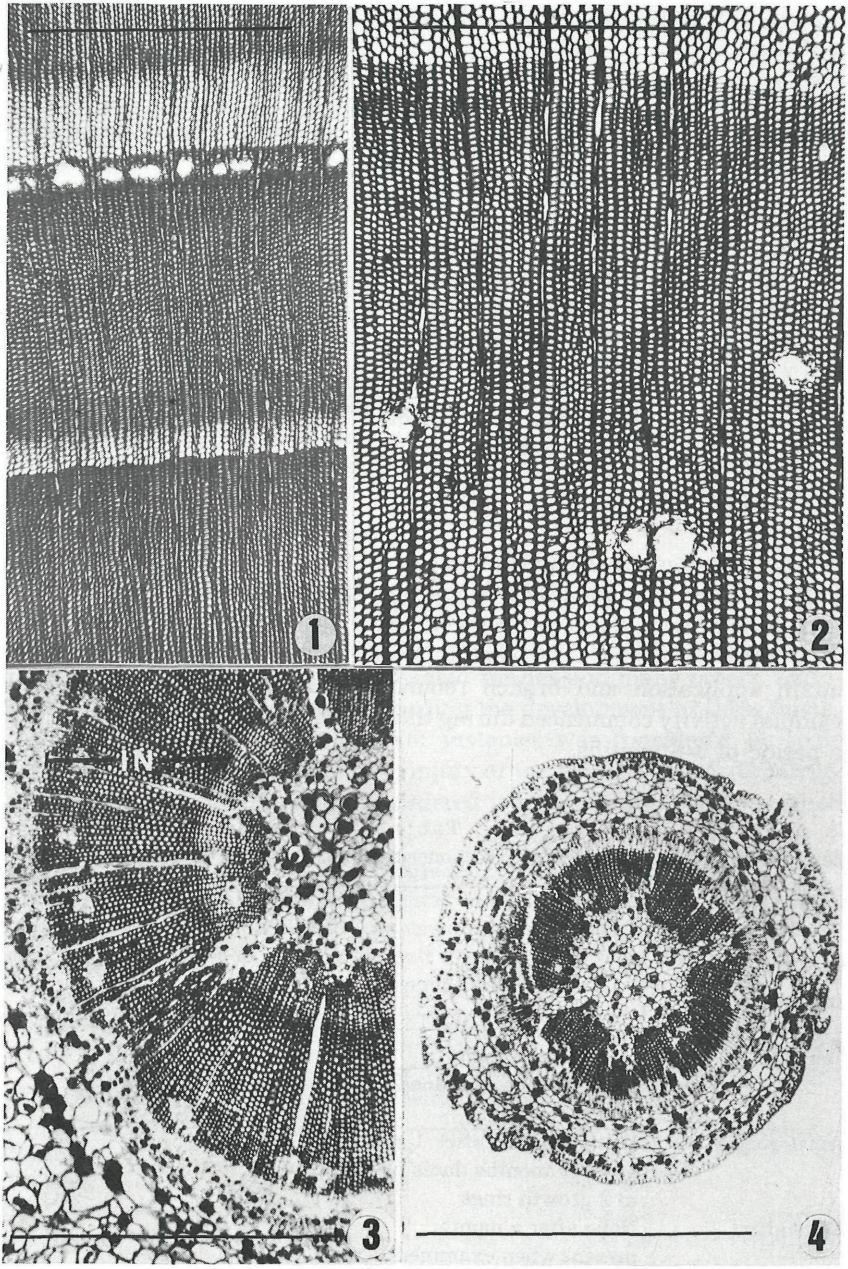

Table 1
Duct formation in *Cedrus libani* in response to wounding. (Adapted from FAHN & al. 1979.)

Month of treatment	Duct formation	Maximal length of ducts in mm	
		Above treated area	Below treated area
January	None after a month; a few when examined after 3 months	5	4
April (end)	After a month in some samples; later in the majority	>50	>57
May–August	After a month in all samples	43	23
December	None after 1 and 2 months; later in some samples	16	2.5

An investigation carried out on *Cedrus libani* some time ago (FAHN & al. 1979) revealed that not only wounds, but also exogenous auxin induced the formation of resin ducts in the secondary xylem of this plant (Tables 1 and 2). Ducts were formed, if the cambium was active within the period between auxin application and branch removal. Ducts were also formed when cambial activity commenced during the period of the experiment, even after a period of 3–4 months.

Table 2
Duct formation in *Cedrus libani* in response to NAA. (Adapted from FAHN & al. 1979.)

Month of treatment	Duct formation	Maximal length of ducts in mm	
		Above treated area	Below treated area
January	None after a month; present when examined after 6 months	30	24
April–August	Ducts present after 1 month; after 10 months ducts present in 2 growth rings	63	>30
December	None after a month; present when examined after 7 months	25	44

In *Pinus* where duct formation occurs normally in the secondary body, wounding, exposure to wind or the application of growth substances caused an increase in the number of the secondary resin ducts (FAHN & ZAMSKI 1970) (Figs. 3 and 4, Table 3).

It seems possible that the so called normally occuring ducts of the secondary body of *Pinus* also develop as a result of external stimuli, but their sensitivity thershold is much lower than that of *Cedrus,* for instance.

The manner of resin production

The resin which contains a variety of terpenes is synthesized by the secretory cells; in the case of resin ducts, by their epithelial cells. The cell organelles most commonly involved in the synthesis of resin and other lipophilic substances are the plastids. The latter are often surrounded by a periplastidal ER. Other organelles which have been reported to play a role in the synthesis of lipophilic materials, in resin ducts and in other secretory tissues, are the ER, Golgi vesicles, mitochondria and in some cases even the nuclear envelope (Fig. 5) (FAHN & EVERT 1974, FAHN & BENAYOUN 1976, BENAYOUN & FAHN 1979, FAHN 1979, JOEL & FAHN 1980, WERKER & FAHN 1981, BOSABALIDIS & TSEKOS 1982).

Gum ducts

Gum duct formation is known to occur in many plants, e. g. in the *Prunoideae, Brachychiton, Citrus, Acacia* species and many others. Different views have been expressed regarding the development of these ducts.

Gummosis in the *Prunoideae* for instance, was considered by some authors to be primarily a response to injury or to pathogen attack (CERUTI & SCURTI 1954 a, b), while others considered it to be a natural phenomenon

Table 3

Effect of the application of growth substances on wood increment and duct formation in *Pinus halepensis*. The plants were grown under long-day high-temperature conditions from 15 May 1968 to 10 July 1968 and treated when 3 years old. 10 plants were used for each treatment. (Adapted from FAHN & ZAMSKI 1970.)

Treatment	Width of wood increment in number of tracheids	Number of vertical resin ducts in the new increment
0.1% IAA	39 ± 3.2	22 ± 3.5
0.1% NAA	73 ± 7.1	46 ± 9.4
0.1% GA	10	3 ± 0.3
0.1% Kinetin	10	5 ± 1.0
Control (lanolin only)	10	4 ± 1.6

which is intensified by injury or pathogen infection (GROSCLAUDE 1966, MORRISON & POLITO 1985).

Gummosis in *Citrus* may serve as an example of secretory duct development caused by external factors only. Gum ducts in *Citrus* trees develop in response to fungal and viral diseases. The well known "brown rot" gummosis of *Citrus* trees is caused by the fungus *Phytophthora citrophthora* (SM. & SM.) LEON. When *Citrus* trees were artificially infected with this fungus gum ducts were formed (GEDALOVICH & FAHN 1985 a).

The manner of gum production

Different views were expressed regarding the way the gum is produced. Many authors attributed gum formation to cell wall decomposition. The cell walls which according to these authors are transformed into gum may be of cells of mature xylem (VANDER MOLEN & al. 1977, MAGNANO DI SAN LIO & al. 1978, MATARESE PALMIERI & al. 1979) or of cells in specialised parenchyma groups which differentiate in the cambium and later disintegrate and form the gum and duct lumen (TSCHIRCH 1889, BUTLER 1911, GROOM 1926, GHOSH & PURKAYASTHA 1959, SKENE 1965, STÖSSER 1979). However, in *Citrus* and also in some other plants it has been shown that gum production results from the synthetic activity of secretory cells (CATESSON & al. 1976, CATESSON & MOREAU 1985, MOREAU & al. 1978, GEDALOVICH & FAHN 1985a, MORRISON & POLITO 1985).

When *Citrus* plants were infected with the fungus *Phytophthora citrophthora,* gum ducts started to develop schizogenously in the cambium (GEDALOVICH & FAHN 1985 a). Many active dictyosomes occured in the epithelial cells of the ducts (Fig. 6). The gum was found to be secreted first into the space between the plasmalemma and the cell wall facing the duct lumen. Part of the gum later also appeared on the outside of the cell wall (Fig. 6). With the continuing development of the xylem the gum ducts became embedded in it and the activity of the epithelial cells ceased. The cell wall of many epithelial cells broke and the gum still present in the cells was released (GEDALOVICH & FAHN 1985 a).

Another type of gummosis is the occlusion of vessels with gum-like material. This may occur in response to physiological stresses arising from wounding or infection. The vascular occlusions in the roots of cassava (*Manihot esculenta* CRANTZ) were suggested to develop in response to wounding and to be intensified when roots were stored in low humidity (RICKARD & GAHAN 1983). In a number of investigated plants, e. g. *Dianthus caryophyllus* L., *Ulmus campestris* L. and *Ailanthus excelsa* ROXB., it was reported that the vascular occlusions developed in response to infection by fungi (CATESSON & MOREAU 1985, SHAH & BABU 1986).

In *Dianthus* it has been shown that as a result of infection, the vessel contact cells acquire secretory functions. They secreted carbohydrates,

glycoproteins and polyphenols into the damaged vessels and occluded them. It was suggested that the polysaccharides and the glycoproteins were secreted through the Golgi apparatus and the polyphenols were synthesized by the ER (CATESSON & al. 1976, CATESSON & MOREAU 1985).

In *Ailanthus excelsa,* according to SHAH & BABU 1986, the vascular occlusions contain polysaccharides, lipids, protein, phenolics, lignin and probably also pectins. All the inclusion components except lignin and pectin were postulated by these authors to be produced by the vessel contact cells. RICKARD & GAHAN 1983, suggested that the lignin-like response of the occlusions in the cassava vessels obtained by histochemical tests, were probably produced by condensed tannins with lignin-like properties.

It should be emphasized that the mechanisms of secretion, as can be learned from ultrastructural studies, are similar in all anatomical types of secretory tissues, i. e. in secretory cells (idioblasts), in glandular trichomes and in secretory ducts and cavities, regardless of their way of development. The involvment of the various cell compartments in the process of secretion depends only on the secreted substance.

The effect of ethylene on duct formation

Experiments involving application of ethrel, 1-amino-cyclopropan -1-carboxylic acid (ACC) and auxins to branches of *Citrus* trees showed that these substances cause the formation of gum ducts in a manner similar to that caused by the fungus *Phytophthora citrophthora* (GEDALOVICH & FAHN 1985 b). Ethrel was found to be the most effective substance. Ethrel 0.05% in water induced the formation of gum ducts of the same length as those formed after infection with the fungus, that is 3–5 cm above and below the infected or treated wound. When higher concentrations of ethrel were used, much longer gum ducts were formed (up to 15 cm). The rate of cambial activity affected the response of the branches to ethrel and to a greater extent in response to auxin. While there was almost no response to auxin during the periods of low cambial activity, ethrel caused the differentiation of many ducts except during December and January. Infection with the fungus during these months also failed to cause the formation of gum ducts.

Stem segments artificially infected with the fungus were found to release ethylene. As gum ducts were also formed in response to ACC, which is a precursor of ethylene in higher plants and not in fungi, it seemed that the production of ethylene by the infected stem tissue was the direct factor influencing the gum duct production in the *Citrus* trees.

Recently, YAMAMOTO & al. 1987 found that the flooding of *Pinus halepensis* seedlings caused an increase in the formation of the longitudinal resin ducts in the secondary xylem and that the flooding also stimulated ethylene production by the immersed stems. YAMAMOTO & KOZLOWSKI 1987 a repored that 1% ethrel also stimulated an increase in the number of resin ducts in the xylem of seedlings of this species.

In seedlings of *Pinus densiflora* flooding did not induce the formation of resin ducts, however ethrel did so (YAMAMOTO & KOZLOWSKI 1987 b).

It should be mentioned that many effects previously considered to be induced directly by auxin are now known to be a result of auxin induced ethylene formation (ABELES 1973, JONES & KENDE 1979, YANG & al. 1980, IMASEKI & al. 1982). The effect of auxin on the formation of resin ducts in *Pinus halepensis* observed by FAHN & ZAMSKI 1970, and in *Citrus* by GEDALOVICH & FAHN 1985 a, b, may thus be a result of auxin induced ethylene formation.

Evolutionary considerations

Secretory structures have often been taken in consideration in taxonomic studies, however only little attention has been paid to the evolutionary aspects of these structures. Phylogenetic trends in the evolution of nectaries were suggested by some authors (see FAHN 1979). Evolution of terpenoid secreting tissues was discussed by DENISSOVA 1975.

Resin ducts in the secondary plant body

In all conifers resin ducts are present in the primary tissues. However, in the *Pinaceae* they are also present in the secondary tissues. In this family, as has been mentioned previously, plants of some genera produce resin ducts in the secondary tissues without external stimuli, while in other genera the resin ducts are formed only in response to outer factors.

PENHALLOW 1907 considered the development of resin ducts in the secondary xylem of the *Pinaceae* as specialization. He suggested that in the primitive condition parenchyma cells were scattered throughout the secondary xylem. Then these cells became aggregated and resin cysts, such as those found in *Abies* and *Tsuga,* were formed. From cysts resin ducts such as those occuring in *Pinus* were derived.

JAIN 1976 supported PENHALLOW'S view on the basis of a study of the wood structure of the *Pinaceae* in the eastern Himalaya and data of other authors concerning fossil gymnosperm wood. According to these data no ducts were found in woods from the Carboniferous, Permian and Triassic strata. The first vertical resin ducts were seen in coniferous woods of the Mid Jurassic stratum. In these fossil woods only a few resin ducts were observed in tangential series. In a number of *Protopiceoxylon* forms of somewhat later age (Upper Jurassic and Lower Cretaceous) scattered resin ducts have been reported to occur in addition to those occuring in tangential series. JAIN further stated that with the exception of "the doubtful *Pityoxylon eiggense",* pine-like woods have not been recognized in strata below the Lower Cretaceous. In *Pityoxylon* too, the resin ducts are in tangential series, indicating therefore, a possible relation to *Larix, Pseudotsuga* and *Picea.* (In *Pinus* the vertical ducts are always scattered). The fossil data thus

indicate that the localization and restricted distribution of resin ducts preceded the scattered and widely dispersed type, such as found in *Pinus* (Fig. 2). The vertical resin ducts of *Cedrus, Abies, Tsuga* and *Pseudolarix* that develop in response to outer stimuli, occur in tangential rows (Fig. 1).

Secretory trichomes

With regard to terpenoid secreting tissues, DENISSOVA 1975 suggested a classification according to their progressive evolution. She distinguished four types of terpene secreting tissues and deduced that they originally evolved from unspecialized parenchyma cells. These types are: I. endogenous secretory tissues with intracellular accumulation of secreted material; II. schizogenous endogenous secretory tissues with extracellular accumulation of secreted material; III. secretory tissues with schizo-lysigenous lumen; IV. exogenous glandular structures (glandular trichomes).

In the various organs of many pteridophyts occur secretory ducts, which usually secrete mucilage or gums. In some pteridophytes the terminal cell of the hairs may become glandular (OGURA 1972). In the rhizome and leaf bases of *Dryopteris* species, glandular hairs occur situated in intercellular spaces. These hairs secrete phloroglucinol derivatives (HUURRE & al. 1979). In some *Dryopteris* species such hairs occur also on the epidermis of the rhizome. It is of interest to mention that in *Dryopteris fragrans* (L.) SCHOTT, the inner glandular hairs are sparse but the rhizome epidermis is densely covered by glandular hairs (WIDEN & BRITTON 1969). This may perhaps indicate the existence of a trend shifting these hairs from the inside of the plant to the outside.

The occurrence of resin ducts in conifers is well known, however, glandular hairs are rare and were reported to occur only on juvenile leaves of *Pinus cembra* and *P. lambertiana* (NAPP-ZINN 1966).

In the dicotyledons all types of secretory tissues are very common, including glandular trichomes. However, the latter do not occur in most of the woody Ranales.

In some dicotyledonous families, e. g. in the *Rutaceae* and *Myrtaceae* oil cavities occur in the cortex of the stems and in the leaves. In *Eucalyptus citriodora* HOOK *(Myrtaceae)* and *Dictamnus albus* L. *(Rutaceae)* trichomes that include oil cavities are present. BROCHERIOU 1976 suggested that the oil-cavity bearing emergences of young leaves of *Eucalyptus citriodora* preceded in evolution the oil cavities occurring within the leaves. DENISSOVA 1976 expressed an opposite view regarding the evolution of the oil-cavity bearing trichomes. She suggested that the *Dictamnus* glands have developed phylogenetically from oil cavities occurring within organs of the *Rutaceae*. I am inclined to accept DENISSOVA'S view also in relation to emergences of *Eucalyptus citriodora*.

Glandular trichomes of a number of plant species were suggested to have developed phylogenetically from non-glandular trichomes (c. f. FEDOROWICZ, in UPHOF 1962, FAHN & SHIMONY 1977, FAHN 1979). In *Avicennia marina* (FORSSKAL) VIERH. glandular and non-glandular trichomes are present. Both types of trichome were found to initiate and develop similarly up to the stage of a three-celled primordium. From this stage differences between the two types start to appear (FAHN & SHIMONY 1977). The non-glandular trichomes of *Avicennia* species vary in the number of cells, from 3 to 5. The number of cells in the glandular trichomes of *A. marina* is 11 to 17. It has therefore been suggested that the phylogenetic sequence proceeded from very few celled to several celled non-glandular trichomes and then to glandular trichomes.

In some species of the *Labiatae* (e. g. *Phlomis* spp. and *Rosmarinus officinalis* L.) there occur both branched non-glandular trichomes and similar trichomes in which one of the branches carries a glandular head (Figs. 7 and 8) (cf. AZIZIA & CUTLER 1982; WERKER & al. 1985).

In summary, the following trends in the evolution of the secretory tissues are suggested:

1. During the course of evolution secretory tissues developed first inside the plant organs. 2. In the primitive condition only secretory idioblasts or groups of such cells were scattered among the cells of the ordinary tissues. 3. Later secretory ducts and cavities developed. 4. Conifers with resin ducts that differentiated in response to outer stimuli preceded those in which ducts differentiated in the normal course of development. 5. The glandular trichomes are the most recently evolved secretory structures.

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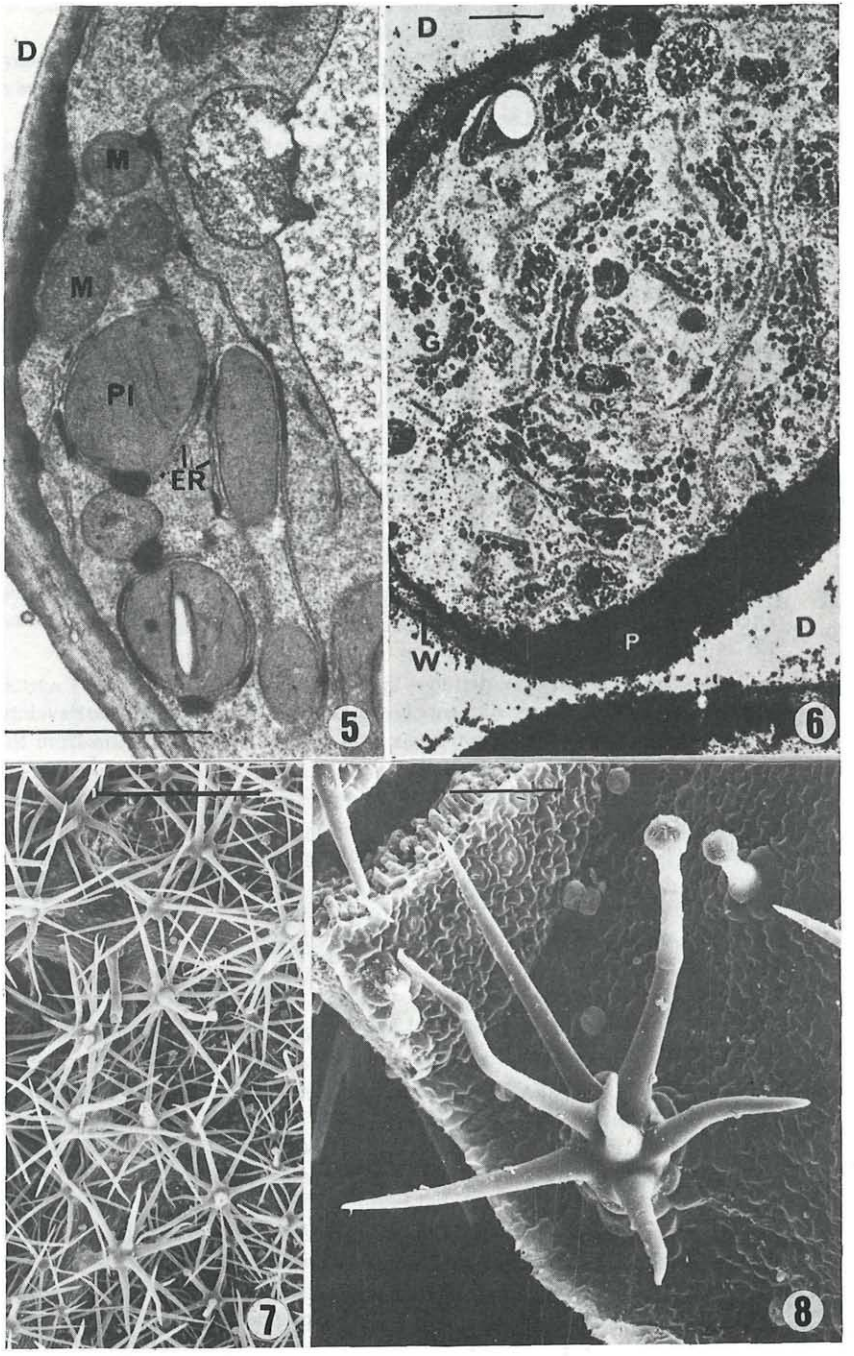
Fig. 5. Electron micrographs of a portion of an epithelial cell of a resin duct of *Pinus halepensis,* showing ER profiles associated with mitochondria (M), plastids (Pl) and plasmalemma. Osmiophilic droplets occur at the places where the ER approaches the organelles and inside free ER portions. Bar = 1 μm.
(From BENAYOUN & FAHN 1979.)

Fig. 6. Electron micrograph of an epithelial cell of a gum duct of *Citrus volkamariana* PASQUALE, stained for polysaccharides with periodic acid and silver-methenamine. D = duct lumen, G = dictyosome, P = polysaccharide eliminated from the cytoplasm, W = cell wall. Bar = 1 μm.

Fig. 7 and 8. Scanning electron micrographs of leaf trichomes of *Phlomis viscosa* POIR. Fig. 7. Branched glandular and non-glandular trichomes. Bar = 0.5 mm. Fig. 8. A branched trichome with a glandular head at the end of one of its branches. Bar = 0.1 mm.



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