

ARCHITECTURE
AND INNER STRUCTURE
OF THE
Coriandrum
sativum L.

JÚLIA SZUJKÓ-LACZA

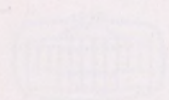


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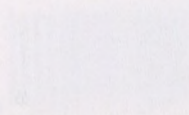
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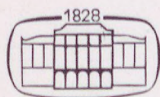
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CONTENTS

Origin, history and distribution of coriander	I	Root	34
Systematic position and relatives of coriander	I	Stem (main axis)	37
Review of literature	3	Leaf	46
Numerical coding system correlating morphological and anatomical features	12	Leaf sheath	46
Architecture of the coriander	15	Petiole	48
Seedling	15	Leaf lamina	49
The fully developed plant	15	Schizocarp	55
Stem	15	Megasporogenesis	58
Leaves	18	Embryo development	71
Compound umbel	20	Calyx tooth	79
Development of compound umbel, umbellet and pistil	20	Carpophore	80
Development of petals	22	Petals	82
Inner structure of the coriander	34	Microsporogenesis	85
Radicle	34	Summary	93
Hypocotyl	34	Outer structure	93
Cotyledon	34	Inflorescence-flower	93
		Inner structure	94
		Secretory system of the plant	95
		Transfer cells of the reproductive organ	96
		References	97
		Subject index	107

ORIGIN, HISTORY AND DISTRIBUTION OF CORIANDER

The *Coriandrum sativum* is mediterranean in origin. Its name had already appeared in the Sanskrit literature. It was mentioned at the beginning of the Egyptian New Empire (1800 BC) in the Papyrus anasi III. H.1 as 'Š3wt'. Its fruit was referred to as 'Pr.T.Šwt'. It is also mentioned as a kind of spice in later papyri (Papyrus anasi IV. 811. VI. 15,11; P. nansing 11,5; P. Harris I. 72.10; P. Sallier II-VIII; Ebers papyrus 47613-8108). Its Coptic name is 'bershain' (Helck and Eberhard (eds): *Lexicon der Ägyptologie* Vol. 2: 594-595 [1977]). It is known from Schweinfurt's (1900) *Pflanzenreste in ägyptischen Gräbern* that the fruit of coriander belonged to the Egyptian grave goods. Coriander apparently was a sacrificial gift. Ancient Greek and Latin authors still mentioned it as *Coriandrum*. According to Pliny the Elder (23-79 AD), the Egyptian coriander was one of the best aromatic spices (*Historiae Naturalis*).

The coriander served as a basic component of the special drink 'Eau de Carmes', made by the Carmelites, that was very popular in the 17th century (Redgrove 1933). First records concerning its cultivation come from the 16th century. Lippay (1664) wrote about its cultivation and use as well as its basic morphological features.

Its name is known by every European language, an argument for the fact that it had already been well known everywhere earlier than mentioned above. In Hungary, for instance, it had a folk name (*cigánypetrezselyem* = 'gipsy parsley') as early as in 1578; moreover, it had an even earlier name, *zobragbori*, in the 15th century (Priszter 1991).

SYSTEMATIC POSITION AND RELATIVES OF CORIANDER

The coriander belongs to the Apioideae subfamily of the Apiaceae (Umbelliferae) family of the Umbelliferae or Araliales order of the Dicotyledonopsida class of the Angiospermatophyta branch. The family is widespread throughout the world but they mostly live in the Northern hemisphere (R. Soó 1964, in Boros 1964). Tutin describes 110 genera and 412 species in Europe (Tutin 1968).

The Apiaceae (Umbelliferae) family is divided into the following three subfamilies: Hydrocotyloideae, Saniculoideae (each with two subsections), and Apioideae. The latter subfamily is the richest containing eight subsections; Coriandreae is the third section, with one genus and one species, the *Coriandrum* (Willis and Airy Shaw 1973). The other species originally assigned to this genus was

moved to the closely related *Bifora* genera and is known as *Bifora testiculata* (L.) Roth.

The *Coriandrum sativum* L. was described by Linné (1753). Its closest relative is the *Bifora* genus, consisting of two species, whose leaves and fruits are similar to those of the coriander.

SYSTEMATIC POSITION AND RELATIVES OF CORIANDER

The coriander belongs to the Umbellales subfamily of the Umbellales family of the Umbellales order of the Umbellales class of the Umbellales division of the Umbellales kingdom. The family is widespread throughout the world, but it is especially common in the tropical and subtropical regions. In these regions, it is found in the following areas: India, China, Japan, and the Philippines. The coriander is a perennial plant, but it is usually grown as an annual. It has a thick, fleshy root and a woody stem. The leaves are finely divided and have a characteristic odor. The flowers are small and white, and they are arranged in a flat-topped cluster. The fruits are small and round, and they are covered with a thin, waxy coating. The coriander is a very important spice in many cuisines, and it is used in a wide variety of dishes. It is also used in traditional medicine for a variety of ailments.

REVIEW OF LITERATURE

Sieler (1870) was one of the first to classify Umbelliferae species on the basis of appearance of organs in the carpel primordia. He has set up three groups. In his first typification the stamen primordia are the first to develop, then the petal and the sepal appear (if they exist), and the carpel is the last to develop. In the second type stamens and petals come into existence simultaneously. In the third type an alternate appearance of stamens and petals precedes the development of carpel primordia.

According to Payer (1853), Umbelliferae species are characterized by organogenesis that occurs in an acropetal order.

The first embryological work on Umbelliferae was written by Håkansson (1923), which was followed by Kordyum's (1967) elaboration. Gupta (1970) provides a good summary of the relevant results of the European and Indian embryological schools.

Inner secretory glands of flowers (tapetum, hypostase, endothel, or integumentary tapetum, obturator) as well as outer secretory glands and nectar-producing organs of flowers, their anatomy and functioning time, especially in the case of species known as good bee forages, were already under intensive investigation in the middle of last century. The following writings are the most important summaries of the results: Behrens (1879), Bonnier (1879), Fahn (1952, 1979), Frei (1955), Percival (1961), Esau (1977), Gulyás (1975) and Findlay (1988).

In the case of the Umbelliferae family and Apioideae subfamily, numerous species have already been subjected to disc or stylopodic examinations (Martel 1905, Jurica 1922, Håkansson 1923, Boros and Szujkó-Lacza 1970, Szujkó-Lacza 1975b, Magin 1983).

According to Magin (1983), the disc develops on the top of the epigynous flower in the case of each species that belongs to the Apioideae. Its vertical anatomical structure is also uniform: under the transformed stomata in the epidermis the nectary and the normal parenchyma can be found, connected with the vascular tissues. Szujkó-Lacza (1975b) described the special pattern of nectary parenchyma cells of the *Pimpinella anisum* disc.

The first publication on postfloral nectar secretion is presumably due to Dauman (1932), and Snepf (1969) was the first to provide a broad summary of the ultrastructure of secreting cells. Since then data concerning several species have been published. We refer the reader to Vassilyev's (1969, 1971) summary on nectar secretion.

Presently, the behaviour of the stigma is regarded not only to be an organ of fertilization, but its activity is also correlated with nectar production. In certain

species there is a close relationship between petal abscission and style functioning (Lowell et al. 1987).

In species that belong to the Umbelliferae and other families such as Rosaceae, after pollination the stamens and then the petals dry up, but styles keep on growing, and stigmas also keep on producing nectar (Szujkó-Lacza 1975a, b, 1983, 1987, Szujkó-Lacza and Kordyum 1990). These species appear to be characterized by the lack of the customary interrelations.

Nowadays, numerous articles or chapters of books are devoted to the structure of stigma and style; the interaction between pollen grain and stigma; the behaviour of pollen tube(s), as well as such related topics as the self- or cross-fertilization of cultivated species and convarieties, with special respect to such factors of the question as honey, seed, and crop productivity. We refer the reader in physiological function of the pistil to sources that include: Mattison et al. (1974), Heslop-Harrison (1975, 1978), Heslop-Harrison and Shivanna (1977), Kuruvilla and Shah (1988).

The newer literature classifies the stigma (and style) as:

Stigma:

- a. papillate,
 - a₁. with one-cell-row (unicellular) papilla,
 - a₂. with more-cell-row (compound) papilla (Capus 1978),
- b. non-papillate,
- c. with holes on its surface (Vasil and Johri 1964, Rougier et al. 1978),
- d. secreting on its surface (Rosen and Thomas 1970, Heslop-Harrison and Shivanna 1977),
- e. with a dry surface (Heslop-Harrison and Shivanna 1977).

The style can be classified as follows:

- a. either its interior is non-canalized,
- b. or there are one or more pollen tube-conducting channels in its centre (Guéguen 1900, Kuruvilla and Shah 1988).

Furthermore, there are observations concerning style secretion. J. and Y. Heslop-Harrison (1982a) analysed the secretion of stigma and style in *Trifolium pratense*. Miki-Hirosige et al. (1987) described the cytological revelation of canal cavity-secreting cells in *Lilium longiflorum*. Guéguen (1900) was probably one of the first researchers to publish comparisons concerning stigma and stigma surface.

Owens et al. (1984) described the structure of stigma papilla cells characteristic to Commelinaceae species on the basis of their observations aided by photo-microscopes as follows: cells with only one nucleus, a great vacuole and a peripheral cytoplasm. The cytoplasm is mostly located at the base of the cell, while the vacuole towards its apex. The ultrastructure of papillate stigma cells in *Lilium* species is described by Vassilyev (1970), and Miki-Hirosige et al. (1987). The relationship between structure and function in *Lilium* is discussed by Rosen and Thomas (1970) and in *Crocus* by J. and Y. Heslop-Harrison (1982a).

Kandasamy and Kristen (1987) distinguished three zones on the papillate stigma: the papillate epidermal layer, the subepidermal secretory zone, and the parenchymatous base tissue. With the aid of new technical possibilities, J. and Y. Heslop-Harrison (1982b) provided an elaborated description on the stigma cuticle, and the development and role of the pellicle. The ontogeny and secretory activity of stigma cells in the *Lycopersicum peruvianum* were discussed by Ruogier et al. in 1978, and the stigma organization in the *Trifolium pratense* was described by J. and Y. Heslop-Harrison in 1983.

Jensen and Fischer (1969) described in cotton the relation of structures of style and stigma to the pollen tube. Kuruvilla and Shah (1988) revealed the stigma-style development and the histochemistry of the *Mandhuca indica*, with special respect to the interaction between the pollen grains and the pistil. The mechanism of pollination in *Medicago sativa* was observed by Brink and Cooper (1963).

Knox (1984) provides a good summary of observations concerning the interaction between pollen and stigma.

Owens et al. (1984) were the first to re-examine Heslop-Harrison and Shivanna's stigma classification (wet or dry). According to Owens et al. (1984), the variability has something to do with the structure of the stigma and the style, the viscosity of the secreted fluid, the permeability of the cuticle, and environmental factors. (As had been verified by numerous previous examinations, there is a correlation between factors of the habitat and the production of nectar or its chemical composition.)

According to the classification of Heslop-Harrison and Shivanna (1977), the species that they examined, members of the Umbelliferae family, belong to the group of species with 'dry' stigmas. Detecting their stigma development, however, Szujkó-Lacza and Kordyum (1990) were led to the conclusion that *Aethum graveolens* L., *Coriandrum sativum* L. and also *Pimpinella anisum* L. (members of the Apioidae subfamily), belong to the group of secreting species (Szujkó-Lacza 1975b). In these species secretion begins only after double fertilization taking place in the embryo sac.

The chemical composition of secreted materials was examined by Kandasamy and Kristen (1987) in *Nicotiana sylvestris*, and Sedgley and Schofield (1980) in *Citrullus lanatus*. Their results led them to conclude that the stigma exuded lipids, polysaccharides, and proteins. In both species an esterase activity of papillae was found.

Dalmer (1880, in Tilton and Horner 1980) was the first to assume that the transmitting tissues, such as stigma, style, and obturator, bore some connection with the pollen tube, or provided it with nutrients. Tilton and Horner (1980) argue that the transmitting tissues of *Ornithogalum caudatum* are morphologically of the same origin; they play a role in the provision of the pollen tube with nutrients and the facilitation of the growth of the pollen tube chemotactically. Other authors hypothesize, however, that the pollen grain contains enough nutrients for the pollen tube and the cells in it to get into the ovule. Having

examined pollen tube growth in *Lilium longifolium*, Reiss and Herth (1978) pointed out a Ca^{2+} gradient in the pollen tube, which refers to a physiological relation between the pollen tube and the surrounding tissues. Cruden and Lyon (1985), however, rejected the idea that the pollen has enough nutrients on the basis of the lack of correlation between the volume of pollen grains and the length of styles. However, they observed a positive correlation between stigma holes and pollen grain size in species that belong to the Umbelliferae family. Style length and pollen grain size did not correlate in this family either.

As for the special literature, we offer Kroh and Helsper's (1974) review on data concerning transmitting tissues and pollen tube growth. Vasil's summary on the physiological-histological relations between the growth of stigma, style, and pollen tube was also published in 1974. Kronstedt et al. (1986) published new results in this topic concerning the *Strelitzia reginae*.

Finally, the economically important aspect of compatibility and incompatibility also belongs to this group of questions.

With respect to the influence of self- and cross-fertilization on yield, the question of compatibility and incompatibility is an economic expression of the interaction between pollen grain and stigma. Mattison et al. (1974) remark that the protein membranes forming on the surface of stigma papillae are potential places of incompatibility. See also J. Heslop-Harrison's (1975, 1978) summaries for the relevant experimental results.

Perhaps Guéguen (1900) was the first to pay attention to the structure of the style as a pollen tube conducting tissue. The classification of Capus (1978) is based upon the existence or lack of the style channel(s) for the pollen tube. Tilton et al. (1984) published important observations concerning the stigma and style cells, among the transmitting tissues of the *Glycine maxima*. They stated in both types of styles existed a great number of axillary orientated channels. Channels were full of exudates of surrounding cells and the exudate could serve as a nutrient source, or to play a conducting role for the pollen tube.

The compact style structure, containing vascular bundles and oil ducts, in *Anethum graveolens* and *Pimpinella anisum*, two species that belong to the Apioidae subfamily of the Umbelliferae, was described by Szujkó-Lacza (1975b).

A peculiarity to the Umbelliferae family is carpophore, which can be identified among the mature fruit (schizocarp) only by means of cross-sections (Jackson 1933). Boros and Szujkó-Lacza (1970) observed in dill (*Anethum graveolens*) that the two mericarps, when mature, almost 'fluttered' on the carpophore separated in two at its upper one-third.

Jackson (1933) intended to reveal the origin of the carpophore by examining species of the 24 genera of the three subfamilies of Umbelliferae. Earlier the carpophore used to be regarded as an axis (Jackson 1933) whereas others considered it a component of the carpel. According to Jackson (1933), the carpophore is a growth peculiar to the Apioidae within the family while in the

Hydrocotyledoneae and Saniculoideae subfamilies it is reduced or absent. In the Apioideae, the carpophore bundle is separated in two halves at the upper one-third. These parts consist of lignified protoxylem and metaxylem elements, the latter transporting the nutrients.

The bundle is surrounded by parenchyma cells with thin walls. At the base of the carpophore there are cells with thickened and lignified walls. In the carpophore of the ripened schizocarp the basal part mostly consists of thick-walled fibres, specialized from the metaxylem elements. In the bifurcated region of the carpophore halves there are also fibres. Having fibrillated to a great extent, the mericarps are separated from the carpophore and fall down. The mericarps part from the carpophore at the stele of the receptacle. In young schizocarps the inner part of the carpophore is not perfectly separate from the mericarp.

Tseng (1967) argues that phylogenetically the carpophore used to be a marginal bundle. In more developed species of the Umbelliferae family, however, this marginal bundle together with the surrounding tissues turns into a carpophore-like structure, which is not separate from other tissues of the schizocarp. In extreme cases, the carpophore becomes free, and the highest degree of differentiation occurs when the carpophore divides into two as in *Anethum graveolens* (Boros and Szujkó-Lacza 1970).

Pollen grain genesis is simultaneous with a permanent change of surrounding tissues such as the tapetum, middle layer(s) and epidermis. Strasburger (1882), and somewhat later Duggar (1899), were the first to describe the nuclear division of the mitotic cells typical of cells of tapetum. Tischler (1906) observed amitosis at the second cell nucleus division in *Ribes* hybrids. Here tetraploid nuclei developed as a result of fusion of diploid tapetum cell nuclei. In *Wistroemia indica*, huge cell nuclei were observed in certain tapetum cells as a result of fusion of nuclei (Winkler 1906). Thara (1910, in Geitler 1953) reported a repetition of mitotic nuclear divisions and fusion of nuclei in tapetum cells of *Morus indica*. Bonnet (1912), in *Fuchsia*, observed a tetraploid and two diploid nuclei within a single tapetum cell. Campini (1925) mentions tapetum cells with two and four nuclei in *Nolana*, and Meyer (1925) found tetra-, hexa-, and octoploid nuclei in *Leontodon autumnalis*.

A simultaneous observation of the behaviour of cells of the sporocytic tissue and the process of tapetum cell divisions and fusions was carried out by Gates and Rees (1921), Maheshwari (1929), and Mascré and Thomas (1930). Smith (1933) examined simultaneously the development of anther wall, middle layer, tapetum cells, and sporocytic tissues in *Galtinia candicans*.

The behaviour of the tapetum layer began to be paid attention when Geitler introduced the concept of endomitosis in 1948, defined (Geitler 1953) as follows: 'reduplication of chromosomes with subsequent separation of centromeres inside the nuclear membrane'.

During the last decades (Geitler 1953) the endomitosis of tapetum cells with

a secreting function (Schnarf 1929) in the course of microsporogenesis was under intensive investigation. It is in this tissue where the existence of endomitosis was verified and defined as the phenomenon during which more separate nuclei with distinct degree of ploidy may come into existence in one and the same cell. Geitler in 1938 and 1939 (Geitler 1948) was the first to study the entire cycle of endomitosis, in Heteropterae. Brown (1949) observed the same phenomenon in tomato tapetum cells. Carniel (1952, 1962) called attention to bridges between nuclei. Turala (1958) executed simultaneous observations on tapetum and pollen mother cells of *Cucurbita pepo*. Similar way was followed in *Pisum banksiana* anthers by Dickinson and Bell (1976). Trela (1958) outlined three steps of endomitotic polyploidization. According to Trela (1958), the differentiation of tapetum cells involves two mitotic divisions and the prevention of cytokinesis, and their mitosis mostly corresponds to the meiosis of pollen mother cells in prophase. Wunderlich (1954) created types of tapetum cells according to the number of nuclei on the basis of data available in the contemporary special literature.

According to Gupta (1964), tapetum cells in species of the Umbelliferae family have two nuclei. Kordyum (1967), however, observed more than two nuclei in tapetum cells of several species.

Endomitosis, as a possibility, has also often arisen in connection with cells of endosperm tissues of flowering plants storing reserves.

The endosperm is a fairly homogeneous tissue; in addition to anomalies observed in its cytological behaviour, its nutrients storing ability attracted attention.

Ways of endosperm development were classified by Maheshwari (1950), Esau (1977), and others as follows: the endosperm may be of cellular, nuclear, or helobial type, the latter being regarded either as a sub-group of the nuclear type or an independent type.

The first evaluation of endosperm development is presumably due to Brink and Cooper (1947). Further results were published by: Maheshwari (1950), Wardlaw (1955), Poddubnaya-Arnoldi (1964), Singh (1964), Davis (1966), Rutishauser (1956), Swamy and Krishnamurty (1973).

The species in which the endosperm becomes cellular (with cell walls) without delay show lesser variability than those in which the cellular (secondary) endosperm goes through a long phase of development compared with embryo development. A high percentage of plants containing seeds belong to the slowly developing endosperm group. In the *Capsella bursa-pastoris*, for instance, the endosperm and embryo development are parallel (Schulz and Jensen 1974), whereas in other species, such as *Grevilla robusta* (Brough 1933), *Trillitium undulatum* (Swamy 1948), *Anethum graveolens* (Szujkó-Lacza 1978), the embryo was observed to be prevented from developing until the endosperm was in the coenocytic stage (with free endosperm nuclei). From a cytological point of view, this phenomenon is to be regarded as a permanent caryokinesis, which is followed by

cytokinesis only after reaching the nucleus number characteristic of the species in question.

Triploid first endosperm nuclei come into existence after the polar cells' fusion and fertilization with microgametes. In the embryo sac this kind of fusion is the most often occurring and most general form (Esau 1977). Polyploidy may take place also later in the secondary endosperm tissue but it is irregular. Neuman (1934) was the first to establish that in endosperm tissues of the *Acacia baileyana*, cells with 4n, 7n, and 8n chromosomes occur together. Most researchers attribute this phenomenon to endomitosis (Rutishauser 1956). Others, however, argue for the fusion of these cells (Gupta 1964, Gorindappa 1955, Raju 1952, 1956, Steffen 1956, Szujkó-Lacza 1975a). Brodsky and Urugaeva (1977) made a fairly strong criticism of the approach where exclusively endomitosis was assumed: "The terms endomitosis and especially endomitotic polyploidy are used in the literature much more frequently than they actually deserve. Geitler drew a sharp distinction between directly observed endomitosis and its assumed effects, that is, patterns of polyploid cells of unknown origin. Later on, such vague cases were referred to as endomitotic polyploidy. Reliable patterns of endomitosis have not been observed in many such cell populations. This is true of all definitive mammalian tissues and many invertebrate tissues."

The endosperm in the Umbelliferae family belongs to the nuclear type but high oil content is a special character of its stored nutrients. The volatile oil content of the fruit is only partially of endosperm origin, oil canals of the mesocarp also contribute to it. All in all, in tapetum cells developed by endomitosis there can be observed more nuclei, separate or linked with bridges but undoubtedly detectable.

In endosperm cells of also different ploidy there are at most two or three nucleoles in a single nucleus, and the phenomenon that a common cell wall develops around two nuclei and their cytoplasms only takes place in the course of cell wall biogenesis. In the last phase of the coenocytic stage of the endosperm tissue there is often only one nucleus but it is huge, 10–12 µm in diameter.

Nowadays, the process of endosperm cell wall biogenesis is under intensive investigation, with the aid of TEM. Numerous details of this process have been revealed in various species. In *Triticum vulgare* (Butterose 1963), *T. aestivum* (Mares et al. 1975, 1977, Morison and O'Brien 1976, Fineran et al. 1982, Orel and Slaraev 1987), *Stellaria media* (Newcomb and Fowke 1973), *Helianthus annuus* (Newcomb 1973), *Haemanthus catherinae* (Newcomb 1978), *Cytinus hypocistis* (Ponzi and Pizzolongo 1984), *Quercus gambellii* (Singh and Mogensen 1976) published results of endosperm formation. Morre and Mollenhauser (1974) stated functional integration between Golgi apparatus and endoplasmic reticulum (e.g. 'endomembrane conception').

Popova and Szujkó-Lacza's (1990) results describing the behaviour of endosperm in two species that belong to the Umbelliferae, *Anethum graveolens* and *Coriandrum sativum*, are novel in comparison with other species.

There is an entirely different view of endosperm development in dicotyledonous plants. Wunderlich (1954) took a phylogenetic approach to this problem. Wunderlich (1954) and Esau (1977) claim that the origin of endosperms of the three different types (nuclear, cellular, helobial) are all divergent. According to Swamy and Ganapathy (1957), who analysed previous data with statistical methods, endosperm evolution is characterized by a changing developing tendency, from 'cellular' to 'nuclear'. A fact that seems to serve as an argument against this conclusion is that giant-cell algae are in a coenocytic stage in their entire cycles of development. It is likely that Newcomb (1978) also transferred this concept from algae to the free nuclei endosperm stage.

Embryology was summarized by Maheshwari (1950) and Johri (1984). Tilton and Lersten (1982) produced an annotated bibliography on the anatomy of reproductive organs of the angiospermae. Nevertheless, the most essential work in this area is supposedly the series 'Comparative embryology of flowering plants', launched by Poddubnaya-Arnoldi, whose last volume until Brunelliaceae-Tremendaceae had already been edited by Batygina et al. (1985).

In addition to endopolyploid tapetum cells covering the sporophytic tissue (e.g. pollen mother cells) in the anther and the tissue of the endosperm, which is also often held to be endopolyploid, there are numerous publications on integumental tapetum or endothelial cells. Kapil and Tiwari (1978) provide the entire terminological synonymics. The inner epidermal layer(s) of the one- or twofold integument is (are) called the integumental tapetum, whose cells are lengthened in radial direction and often include polyploid nuclei. Guignard (1893) and his followers attributed a dissolving function to the integumental tapetum or endothelial cells. According to this hypothesis, when the embryo and the embryo sac appear, this series of cells secrete certain enzymes, which dissolve the parenchyma cells of the surrounding integument. Much later histochemical examinations have proved that endothelial cells at a certain stage bear a rich hydrolitic enzyme content (protease, amylase) (Kapil and Tiwari 1978). Newcomb and Steeves (1971) think that the integumental tapetum metabolizes the saccharides moving towards the embryo sac.

Håkansson (1923) and Adata and Shah (1952) claim that in the Umbelliferae family the presence of the integumental tapetum is general. According to Szujkó-Lacza's (1970, 1978) observations, in the species *Anethum graveolens*, *Pimpinella anisum* (Apiioideae subfamily), and *Prunus armeniaca* (Szujkó-Lacza 1983) the endothelial cells contain large nuclei, their cytoplasm stain strongly, and they dissolve simultaneously with the appearance of the coenocytic state. Agarwal and Gupta (1976) argue that no significant difference was observed in polysaccharide content in the ovule of the *Foeniculum vulgare* (which also belongs to the Apiioideae), between the integumental tapetum and the surrounding cells. They observed a high polysaccharide content in endothelial cells only during the period when the embryo was developing.

In the Umbelliferae, the schizocarp is characterized by a very special morpho-

logical and anatomical structure. Roth (1977) devoted a separate chapter in her book to the description of the pericarp in the Umbelliferae, based upon her own examinations and publications of Baumann (1946) and Tseng (1967). The pericarp generally consists of three layers: an outer one-cell-layer exocarp, which corresponds to the epidermis, a multiple-cell-layer mesocarp, which often resembles parenchyma, and a one-cell-layer endocarp, which is prosenchymatous or also parenchymatous. The mesocarp involves the vascular bundles and the oil ducts associated with them. There are contradictory explanations of the origin of vascular bundles and oil ducts and their accommodation inside the mesocarp (Baumann 1946 vs. Tseng 1967). Baumann derives the Umbelliferae fruit from the Araliaceae, by reduction.

NUMERICAL CODING SYSTEM CORRELATING MORPHOLOGICAL AND ANATOMICAL FEATURES

In order to record outer morphological and inner anatomical factors simultaneously, I have assigned code numbers to the observed phases during the ontogeny of the coriander.

The first version of such an ontogenetic code system, an assignment of code numbers to phases of ontogeny, was used by Szujkó-Lacza and Fekete (1973). I applied this method, with slight modifications (Szujkó-Lacza 1976) for the purpose of a simultaneous description of outer morphological changes and the concomitant anatomical stages. Here I follow the same method. In this code system the development of a plant consists of the following stages: germination and seedling development begin with 11, the development of basal and stem leaves begin with 21, the appearance of flower buds seed development and fruit ripening begin with 31, and the drying-up of individual organs and the plant begin with 41 (Szujkó-Lacza and Kordyum 1990).

Detailed codes are:

Anabiotic phase: 11.0 = dormant seed = schizocarp. Juvenile phase: 21.1 = the radicle appears in the thickened neck of the stylopodium. 21.2.1 = cotyledons appear; 21.2.2 = cotyledons are fully developed. 21.2.3 = the first rosetting leaf appears. 21.2.4 = the first ovate cuneate three lobed leaf has developed. 21.3.1 = the second rosetting leaf appears. 21.3.2 = the pinnatifid leaf lamina has developed. 21.4.1 = the third rosetting leaf has appeared. 21.4.2 = the leaf in the rosette with the longest petiole and segmented laminae has developed. 22.1 = at the shoot apex the first (4th) stem leaf, which comes from the first node, appears, its petiole is shorter than leaves in the rosette, and its lamina is deeply segmented. 22.3 = the second stem leaf appears; the imparipinnate lamina consists of three leaflets. The first internode has already developed while the second one is just growing. 22.4 = the second stem leaf has developed. 22.5 = the third stem leaf appears. 22.6 = the third stem leaf consisting of 5 segments is fully developed, the second internode has already ceased to grow while the third one is still growing above it. 23.1 = the fourth stem leaf appears with the first lateral branch in its axil. 23.2 = the fourth stem leaf of an imparipinnate segmented lamina has developed. 24.1 = in the case of the further stem leaves the most apparent phenomenon is the reduction of the petiole; a lateral branch comes from the axil of each further stem leaf, whose inflorescence spreads longer than the main umbel of the terminal shoot.

Adult phase: 23.1-31.1 = the main branch is pseudodichotomic, the inflorescence appears on the stem; its colour is green, and individual flowers are closely covered by darker green calyx teeth. 31.1.2 = the outer ray flowers are 4 mm and

the inner ones are 2 mm in length; the inflorescence is green, calyx teeth have erected, the longest ones are 2 mm in length. 31.1.1.3 = the pedicel, the uppermost internode, is 30 mm, secondary inflorescence axes are 6–7 mm, petioles on individual flowers are green and closely cover stamens 31.2 = a half petal of each outer flower is lengthened, tapering, and as if it were twirled. 31.2.2 = inflorescence axes of the third order (pedicels) are lengthened, two petioles are lengthened on each outer flower and they stick together forming a boat. Petals are light green and propeller-shaped. 31.3.1 = the inflorescence axis of the second order of the outer umbellet is 7–12 mm, while the inflorescence axes of the third order are 2–5 mm long. On the main axis the collenchyma is light, the clenchyma is green but there are no ribs and furrows on it. The curve of the filament is visible between the two petals of the outer flowers, the two stigma surfaces are light lilac and the stigmas closely stick together. 31.3.1.2 = the length of the inflorescence axes and pedicels have not changed. The gynoeceum of an outer flower is 0.5 mm long, petals are pink and 2–2.5 mm long. Some are just opening. Styles moved farther from each other, the calyx teeth, alternating with petals, are green, spear-pointed, and 1 mm in length. 31.4.1 = the gynoeceum is 1 mm, calyx teeth are 1.5 mm, petals on outer flowers are pink and 4 mm long. Stigmas of inner flowers are light pink with two parallel one-mm-long green styles. Filaments are curved, anthers are covered by petals that have not lengthened. 31.4.2 = the white filaments have lengthened but they are still strongly reclinate. 32.1 = the diameter of the ovary has increased, ray petals of outer flowers have opened; out of filaments alternating with petals, some have erected. Certain anthers have dehisced while other anthers are still closed. Pollen grains are light pink, styles are also whitish pink. Stigmas are lilac, calyx teeth differ from each other in length. 32.3.2 = the outer ovary is 2 mm long. Length of the styles is the same. Styles are farther apart from each other. Outer petals are 3 mm long, the stylopodium is cone-shaped and light green with nectar drops on its surface. Inner flowers lack stigmas or stamens. 32.3.3 = several petals are abscised, stamens dried and fallen, the ovary is 3 mm long, 2.5 mm wide. Ovary with the stylopodium together is 3.5 mm. Styles are 3.5 mm long and diverging, and the darkened stigma is like a croissant, with pollen grains on its surface. Inner flowers are strongly degenerate. 32.3.4 = the schizocarp is 3 mm long as well as wide. Petals have dried out and abscised. The inclination of styles is 70–80°. 32.3.6 = the schizocarp is 4 mm long and wide. Dried petals abscised. Schizocarps on lateral branches are 2–3 mm long. 32.3.7 = schizocarps in the main umbel are 4–5 mm long while those on lateral branches are 3 mm. The inclination of style schizocarps of the main umbel is 180°.

From adult phase to senescence: 33.1–41.1 = schizocarps are yellowish or light green, 4 mm long, 3–4 mm wide, with dried and abscised styles. Schizocarps are spherical, only the calyx teeth differ in length. On average there are 10 fruits in an umbel, which are so close to each other that the lack of absent or sterile flowers is not apparent. On lateral branches, however, there are only 3 or 5, or

at most 7 fruits. The first stem leaf has dried out and abscised while the second and third ones are yellowish green. 33.2.1-41.2 = ripening light yellow schizocarps are 4-5 mm long and 4 mm wide. Stem leaves are drying out. 33.2.2-42.2.2 = surfaces of sphere-shaped yellowish green fruits are bright, their diameter somewhat increased. Upper stem leaves are also drying out. 33.2.3-42.2.3 = the colour of the ripening fruit is light brown, stem leaves are dry.

ARCHITECTURE OF THE CORIANDER

SEEDLING

21.1 The radicle appears.

21.2.1 The cotyledons are visible.

21.2.2 The cotyledons have developed and the shoot apex appeared between them (Fig. 1a).

It is erect and colourless. The young root is 20–30 mm long, with very thin lateral roots.

The hypocotyl is light green, 12 mm in length and 1.5–2.0 mm in diameter.

Its cotyledons are petiolate with entire margins, the lamina is elliptical and narrows into the petiole (Fig. 1a).

Two lateral bundles branch from the midrib of the lamina at an angle of 2–3°; later they are parallel with the midrib (acrodrom type).

The cotyledon's petiole is 11 mm long on average, the lamina is 5 mm wide and 16 mm long.

THE FULLY DEVELOPED PLANT (21.2.3–23.2)

The number of base leaves can range from 1 to 5. They come from the same node as cotyledons (Fig. 1a). The most frequent number of stem leaves is 6 but it may range to 9 in certain cultivars (Figs 1a, b).

STEM

The stem is erect and divided by internodes. The cotyledons and base leaves are attached to the first node, stem leaves to upper nodes. Lateral shoots emerge from axils of the upper leaves (Figs 1a, b). The stem is characterized by a smooth surface. It is green, or pinkish in certain cultivars. Stem height is cultivar-specific and ranges from 40 to 60 cm (Table 1).

The length of the first internode varies widely with a minimum of 18 mm, a maximum of 45 mm, and an average of 30.3 mm. The length of the second and the third internodes is also variable depending on the planting distance and on the cultivar.

Internode length reaches its maximum at the fourth internode but occasionally as soon as at the third internode (Fig. 1a). The first significant lateral branch usually appears at the axil of the fifth stem leaf. The largest difference between succeeding internodes is between second and third internode, and later, in the

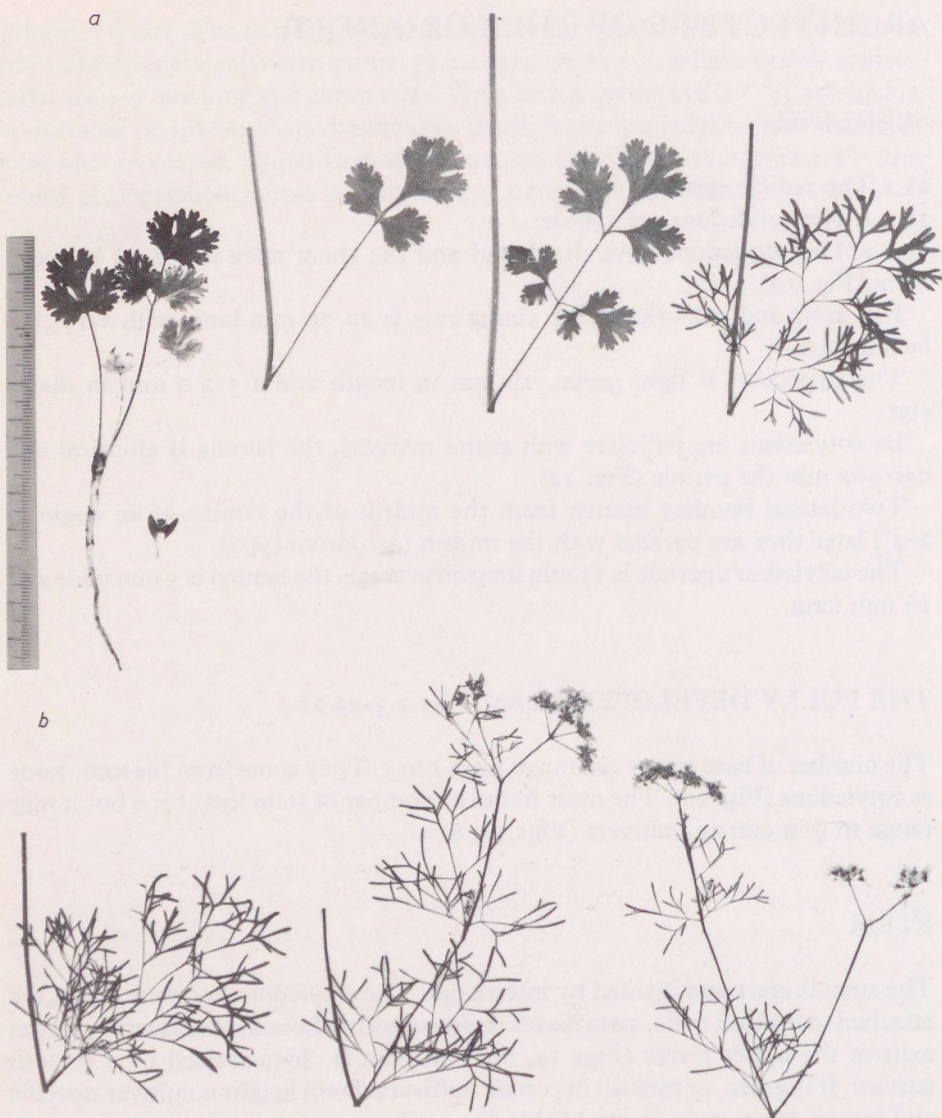


Fig. 1. Internode- and leaf-length distribution in the *Coriandrum sativum* L. Change of internodes (a, b) and leaves in the coriander (photo: I. Rácz)

case of later succeeding internodes, this difference shows a significantly decreasing tendency (Table 1).

A diameter of 2.2–2.5 mm is characteristic of the first four internodes, and there is a regular decreasing tendency in the case of upper internode diameters (Table 1).

Table 1. Quantitative characters of leaves and internodes in the *Coriandrum sativum* L.

Leaves										Internode		Leaf-internode connection				
leaf type	No.	petiole length	differences between succeeding leaves	blade length, mm	difference	blade width, mm	difference	width/length	total length, mm (blade + petiole), mm	blade/petiole length	length, mm	difference in length	diameter	length of petiole/length of internode + petiole)	whole leaf length/inter-nodal length (blade + petiole)	reciprocal value
cotyledon		11.0		16.0		5.0		0.31	27.0	1.40						
rosetting	1.	48.0		19.0		19.0		1.00	67.0	0.39						
rosetting	2.	70.0	22.0	25.5	0.5	26.9	7.9	1.05	95.0	0.36						
stem	1.	83.8	13.8	35.1	9.6	37.4	10.5	1.06	118.9	0.41	30.3		2.5	2.7	3.90	0.26
stem	2.	65.8	-18.0	50.1	15.0	45.3	7.9	0.90	115.9	0.76	40.9	10.6	2.4	1.6	2.80	0.35
stem	3.	28.5 ⁺	-37.3	66.2	16.1	48.5	3.2	0.73	94.7	2.32	74.5	33.6	2.4	0.3	1.20	0.97
stem	4.	9.5 ^{&}	-19.0	67.8	1.6	64.8	16.3	0.95	77.3	7.13	82.2	7.7	2.2	0.1	0.90	1.06
stem	5.	7.5	-2.0	59.9	7.9	78.5	13.7	1.47	67.4	7.98	62.5	-9.7	1.9	0.1	1.07	0.92
stem	6.	6.7	-1.4	49.3	-10.6	65.3	-13.2	1.32	55.4	8.80	56.7	-5.8	1.6	0.1	0.97	1.23

Note: the seventh stem leaf has developed only in 30% of specimens and 10% of specimens had 9 leaves. +: only the leaf sheath has remained; &: location of side shoot appearance in 70% of specimens.

LEAVES

The 2-5 base leaves growing from the first node, which is the same as that of the cotyledons. The base leaves constitute a more or less developed rosette (Fig. 1a). These leaves are called rosetting leaves. The petiole of the first base leaf is long with poorly developed leaf sheaths and a three-lobed ovate-cuneate lamina (Fig. 1a). The leaf base is erect, the marginal part is irregularly toothed and anastomosed with pinnated venation (craspedromous, reticulatus). The second rosetting leaf also has a long petiole, and its lamina is imparipinnate. Between the first and the second segments there is no lamina rachis. The leaf base, the marginal part, and its venation are similar to those of the first rosetting leaf. The petiole of the first stem leaf coming from the second node is shorter than the internode that originates in the same point (Fig. 1a). The lamina is segmented. The lower segments are petiolate and there is a lengthened rachis between the first and the second segments (Fig. 1a). The second stem leaf coming from the third node is petiolate, its lamina is twice imparipinnate, both pinnates are petiolate, and in the case of the first one even the middle leaflet is petiolate (Fig. 1a). The lamina of the middle leaflet narrows into the petiole at the bottom. The lamina of the apical segment is divided into lobes, its teeth are still wide, and its surface is covered by a wrinkled cuticle (Fig. 2). Only the leaf sheath has remained from the petiole of the third stem leaf coming from the fourth node (Fig. 1a). The entire leaf (petiole + lamina) is shorter than the internode that originates in the same node (Table 1). The lamina is entirely divided, pinnules are linear filiform with apiculate apices (Fig. 1a).

The three leaflet pairs of the imparipinnate lamina as well as the apical leaflet are petiolate. The rachis between the first and the second leaflet pairs is longer

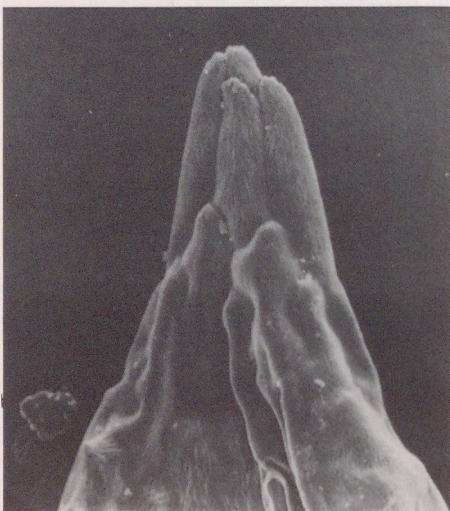
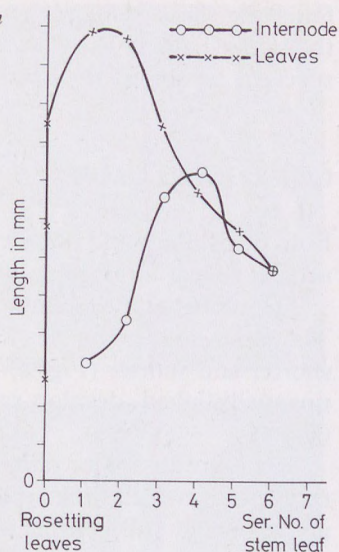


Fig. 2. Leaflet tooth from second stem leaf (SEM $\times 400$, photo: E. Gondár)

Fig. 3. Internode and leaf-length distribution in the *Coriandrum sativum*



than that between the second one and the third one (Fig. 1a). The proportion of the length of the fourth stem leaf that originates from the fifth node to that of the internode that originates from the same node is 0.9 (Table 1), and every pinnule of the leaf lamina is petiolate. Lateral branches usually develop from axils. The growth of a lateral branch is in correlation with a decrease in leaf length and the maximum of internode length (Table 1). Internode length shows somewhat inclined normal distribution (Fig. 3).

Stem leaves that originate in the sixth and seventh node do not change further in shape; pinnules and leaflet rachises become similar to each other but they reduce in size. Both the leaf and the internode that originates from the same node become shorter but lateral branches grow from all axils (Fig. 1b). As for the structure of the leaf lamina, there is an obvious tendency of surface reduction, which is facilitated by the development of lateral branches. Lateral branches may grow also from lower axils but these usually remain undeveloped.

The reduction of a leaf lamina, and its direction of morphological change, can be predicted on the basis of the lamina of the leaf situated just under the given leaf, that predicts whether the leaf will be cleft, divided, or pinnate. It is to be noted that in new large-bodied and late ripening cultivars, 4 or 5 stem leaves may develop. In this case the development of petioles and laminae follows the same pattern as that of the first-third stem leaves, described above.

The phenomenon refers to the relation between internode reduction and rosette development.

If lateral branches consist of more internodes, the shape of leaves that have developed on them follows the shape of leaves on the main branch in the

following sense: the leaf that originates in the first node of a lateral branch is of the same shape as the leaf on the main branch that originates in the node that succeeds (is above) the one in which the lateral branch originates.

COMPOUND UMBEL

Both main stems and non-degenerate lateral branches end in umbels. Bracts are usually absent; bracteoles, if any, consist of simple linear pinnate or cleft lobes.

The umbel and the umbellets involve many rays. The outer rays are longer. The inner rays (peduncles), which develop along a very reduced spiral, become shorter and shorter (Fig. 4). Outer flowers of the umbel, which are deeply and unequally lobed, develop earlier than the inner flowers (with inflected petals) (Fig. 4).

Sepals are absent, or rather, they have grown together with the fruit wall; only calyx teeth, which differ in length, have remained. Calyx teeth are simple and apiculate and still conspicuous even on the mature fruit. Petals alternate with calyx teeth. Outer radiate flowers are asymmetric (Fig. 5).

DEVELOPMENT OF COMPOUND UMBEL, UMBELLET AND PISTIL

23.2-31.1.1 Flower buds have appeared on the pseudo-dichotomic stem. Their colour is green, and inclining bracteoles cover them.

31.1.2 Outer flowers are 4 mm and inner ones are 2 mm long. The umbel is green and cumulous, with cca. 2-mm-long erect calyx teeth (Fig. 6).



4



5

Figs 4, 5. Compound umbel with open flowers and buds ($\times 8$, photo: E.B. Szikszai, rfl = ray flower)



Fig. 6. Umbel with straight calyx teeth ($\times 10$, photo: Zs.H. Hidas)

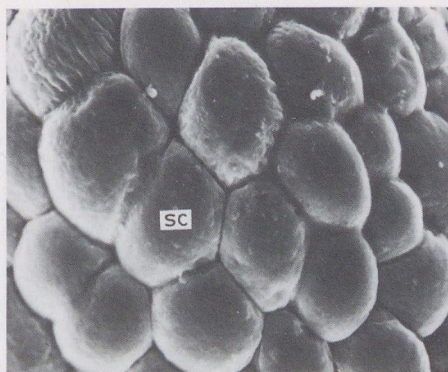


Fig. 7. Stigma surface in the closed flower bud (SEM $\times 4000$, photo: E. Gondár, sc= stigma cell)

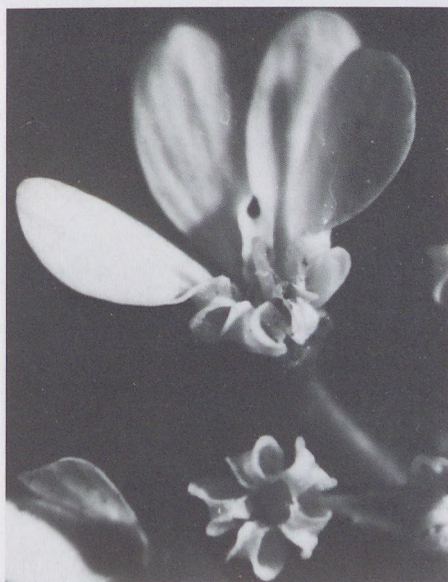


Fig. 8. Petal organization differences in the umbel ($\times 18$, photo: E.B. Szikszai)

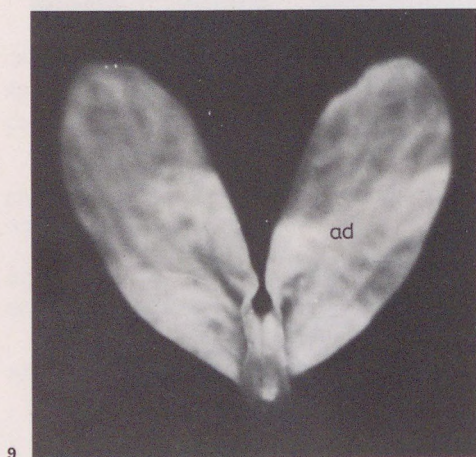
31.1.3 First and second order rays are 30 mm and 6–7 mm long, respectively. Petals of solitary flowers are green and they are inflexed on the ovary and the filaments. Styles in the closed flower are short and erect. The division of stigma cells is completed. Stigma cells are polygonal and their surface is usually smooth (Fig. 7).

31.2.1 A half petal of each outer flower is lengthened, apiculate, spindle-like.

31.2.2 Third order rays are longer than bracteoles. On each outer flower both petal halves have lengthened and stuck together forming a boat-like shape. The whole resembles a propeller, which is light-green or begins to become light (Fig. 5). Styles are short, surfaces of stigma cells are smooth, and their cell walls closely fit together (Fig. 7).

DEVELOPMENT OF PETALS

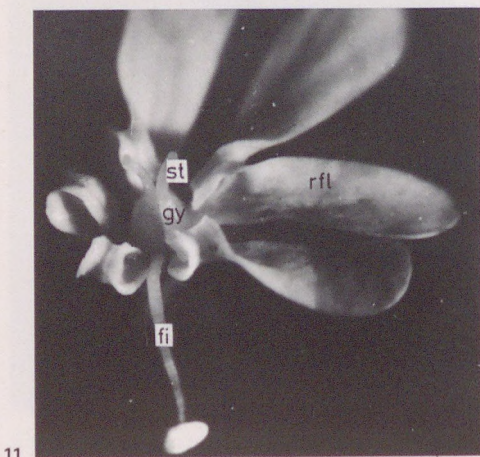
Among the flowers the outer, external, umbellets of an umbel are larger, deeply lobed, and 'radiate'. Moreover, the five petals of these flowers are different (Fig. 8). The petals are made up by two halves (Fig. 9) and the venation in the abaxial side is somewhat protuberant (Figs 9, 10). As for half petals, the long radiate ones have grown together to one-third of their length while the shorter non-radiate ones, the petals parallel with the ray, have grown together to their half length. Two of the five petals grow larger, they become pink and then whitish but remain reclinate (Fig. 8). One-half of the third petal is located in the clockwise order (Fig. 11), both halves of the fourth petal, and the opposite halves of the fifth petal lengthen (Figs 12*a, b*). Thus, beside the fully developed and lengthened fourth petal, only one-half of the third and the opposite halves of the fifth petal lengthen.



9



10



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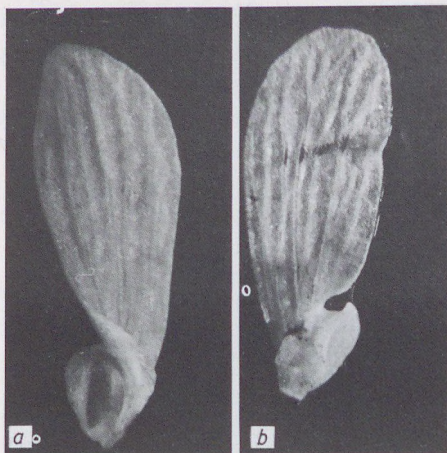
Figs 9, 10. Adaxial and abaxial sides of the 4th parietal petal ($\times 18$, photo: E.B. Szikszai, ab = abaxial, ad = adaxial)

Fig. 11. Differences between the petals in the ray flowers (rfl) of the compound umbel ($\times 18$, photo: E.B. Szikszai, fi = filament, gy = gynoecium, st = style)

Figs 12a, b. Adaxial and abaxial sides of the 5th petal in the ray flower ($\times 18$, photo: E.B. Szikszai)

Fig. 13. Protruding curved filaments (fi) between petals in an outer flower of the umbel ($\times 25$, photo: Zs.H. Hidas)

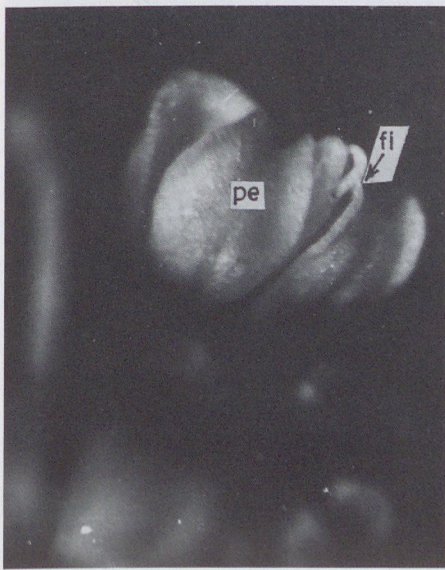
Fig. 14. Protruding curved filaments (fi) between petals (pe) in an inner flower of the umbel ($\times 18$, photo: E.B. Szikszai)



12



13



14

Thus, four halves of three petals form the 'radiate' petals (Fig. 8). The opposite halves of the third and fifth petals remain short and inflexed (Fig. 11). These differences in petal length in flowers correspond to the alternating calyx teeth. In inner flowers of the umbellet, however, petals do not become radiate and their asymmetry can scarcely be noticed.

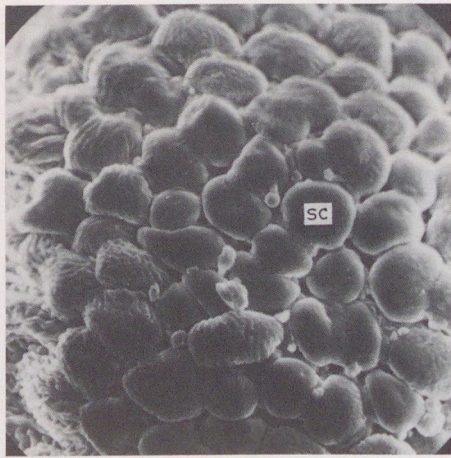
31.3.1 Second-order rays of the outer umbellet are 7–12 mm long while third-order rays are 2–5 mm. Surfaces of stems, umbels, and umbellets are smooth, they lack ribs and furrows, otherwise characteristic of the family. The part above the vascular bundle is lighter and that above the chlorenchyma is

bright green. The third, fourth and fifth petals of outer flowers are pink but still propeller-shaped. Among the reclinate petals there are bent filaments (Figs 5, 13, 14). The two styles stand close to each other (Fig. 15), the surface of the stigma is mauve. Stigma cells begin to become hemisphere-shaped with slightly wrinkled surface (Fig. 16).

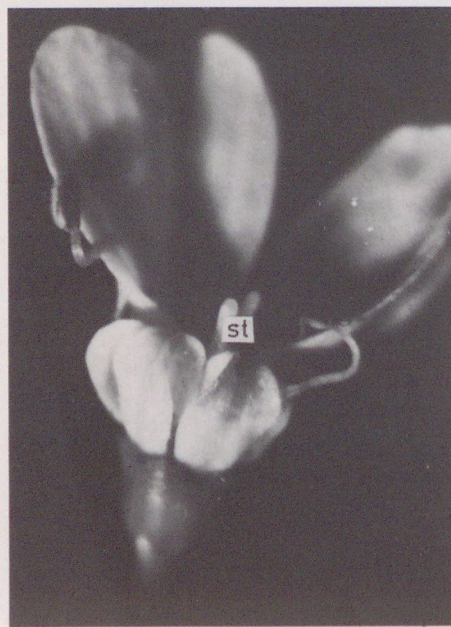
31.3.2 The length of second ordered rays has not changed. The gynoecium of an outer flower is cca. 0.5 mm long, the petals above it are 2–2.5 mm long and



15



16



17

Fig. 15. Two erect styles (st) ($\times 18$, photo: E.B. Szikszai)

Fig. 16. Spherical epidermal cells in the stigma in erect styles (SEM $\times 2000$, photo: E. Gondár, sc = stigma cell)

Fig. 17. Beginning of style (st) deviation ($\times 18$, photo: E.B. Szikszai)

Fig. 18. Appearance of the anther (a) between two neighbouring petals ($\times 18$, photo: E.B. Szikszai, fi = filament)

Fig. 19. Closed anthers (a) are lifted by filaments (fi) in the outer flowers ($\times 18$, photo: E.B. Szikszai)

Fig. 20. Pollen grains in the open anthers (a) ($\times 18$, photo: E.B. Szikszai)



18



19



20

pink, some of them are about to open. The two styles are almost parallel. Calyx teeth are green, lanceolate and cca. 1 mm in length.

31.4.1 The gynoecium is cca. 1 mm long and the shortest calyx teeth on it are 1.5 mm. The fourth petal of an outer flower is about 4 mm. The stigma is light pink and the 1 mm long styles are green. Filaments are still reclinate and covered by half petals (Figs 17, 18) or raising up.

31.4.2 There has been no change in gynoecium and calyx tooth length. Petals of radial flowers are whitish, and tops of neighbouring petals incline towards each other and touch while getting farther from each other in the middle. Styles are farther from each other. The filaments, which are white and lengthened, are still reclinate to a great extent (Fig. 19), or some of them have already risen above the petals (Fig. 20).

32.1 The diameter of the gynoecium has increased while its length has not changed. Radiate petals are already almost white (though in certain cultivars they retain their pink colour all way through). Neighbouring petals have reached their total length (Figs 19, 20) and separated farther from each other. The stamens alternating with the petals are already erect, some anthers have dehiscent (Fig. 21), pollen grains are light pink and sponge-like (Figs 22, 23, 24) with three germ pores. Above these pores a sphere-shaped (Fig. 23) or, in other cultivars, cone-shaped (Fig. 24) protuberance develops. The surface of the anthers is uneven and its exine is porous. The surface of the filament is longitudinally wrinkled covered with cuticle (Figs 25, 26) and above the connective element the cuticle contains a cable-like thickening (Fig. 27). The surface of the anther, at both the apical and the basal ends, is characterized by a papillate exothecium cell structure (Figs 28, 29, 30), which is covered by a wrinkled cuticle. At anther dehiscence exothecium cells along the stomium undergo a great transformation (Figs 31, 32, 33). These transformations include: the surface cells of the open anther become papillate (Fig. 33). The special cell wall thickening of the endothecium results in protuberances and cavities at the basal part of the cell (Figs 34, 35). The surface of the endothecium in the anther is tuberculate (Figs 35, 36). Pollen grains almost merge with the greatly wavy surface formed as a result of the cell wall thickening of the endothecium (Fig. 36). The sphere-shaped cell wall protuberances facili-



Fig. 21. Pollen grains (pg) in the anther (a) locules (SEM $\times 86$, photo: E. Gondár)

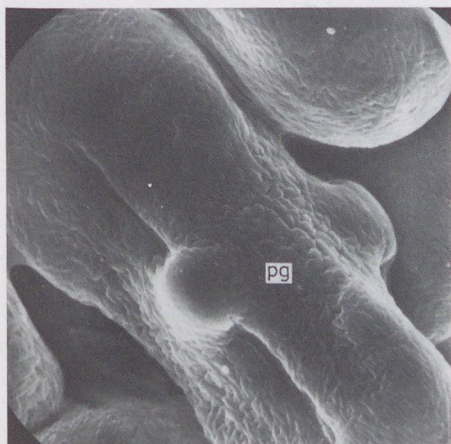
Fig. 22. Pollen grains (pg) of *Coriandrum sativum* (SEM $\times 1000$, photo: E. Gondár)

Figs 23, 24. Pollen grains (pg) of different cultivars of *Coriandrum sativum* (SEM $\times 4000$, photo: E. Gondár)

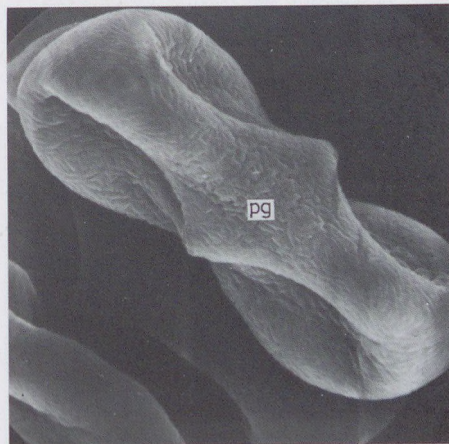
Figs 25, 26. Rugous cuticle on the filament (fi) surface (SEM, Fig. 25: $\times 480$, Fig. 26: $\times 2000$, photo: E. Gondár, a = anther, e = epidermis of filament, fi = filament)



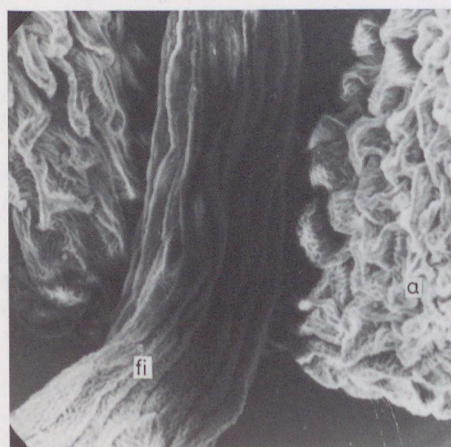
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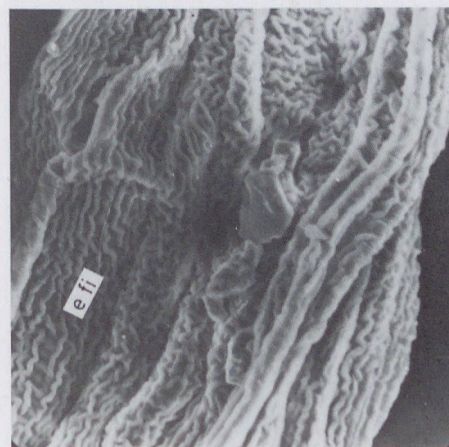
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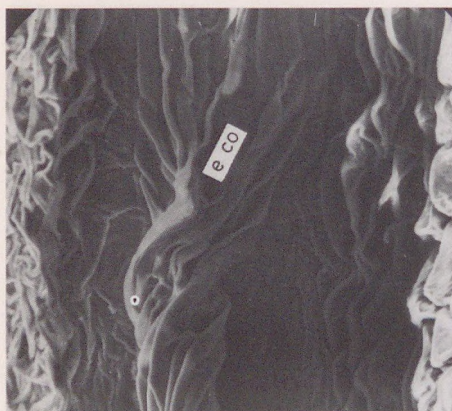


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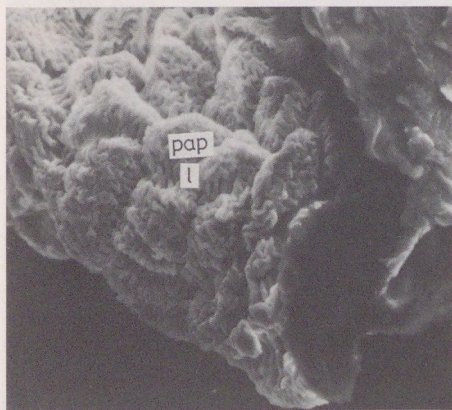


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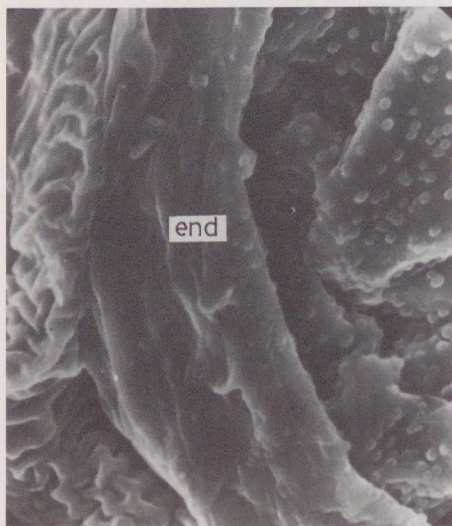
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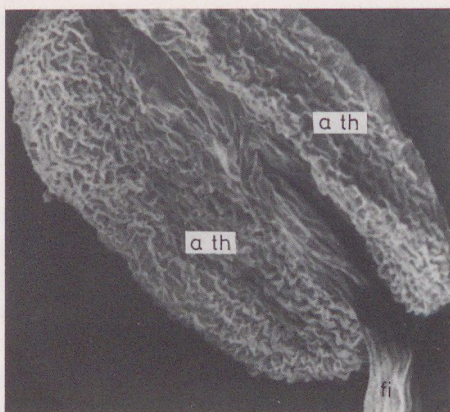
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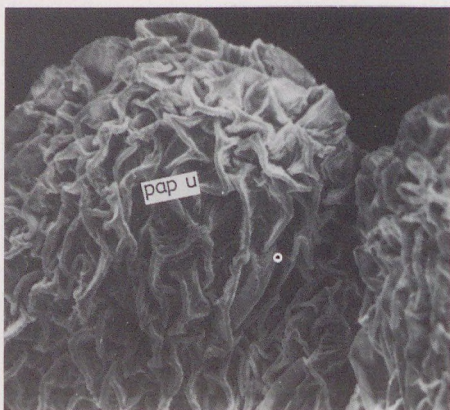


Fig. 27. Cable-like cells of filament between thecae (SEM $\times 480$, photo: E. Gondár, e co = epidermis of connective)

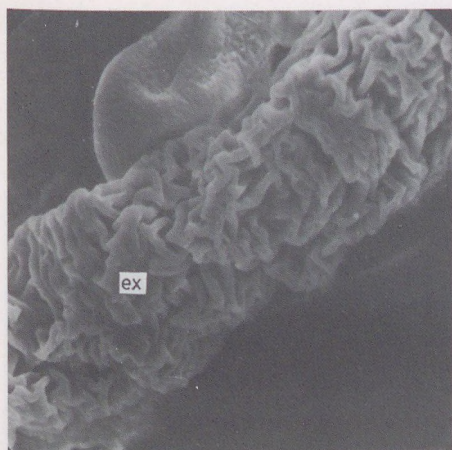
Fig. 28. Surface differences between filament (fi) and anther (SEM $\times 180$, photo: E. Gondár, a th = anther theca)

Fig. 29. Pattern of cell surface at the anther's apex (SEM $\times 1000$, photo: E. Gondár, l = lower, pap = papillae)

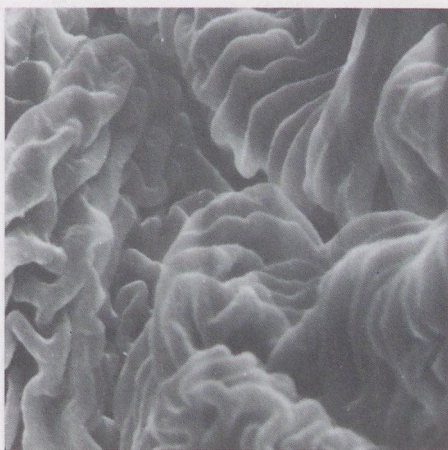
Fig. 30. Papillate surface (pap) of the middle part of the anther (SEM $\times 480$, photo: E. Gondár, u = upper)

Fig. 31. Tangential section of endothecium (end) along the stomium (SEM $\times 3000$, photo: E. Gondár)

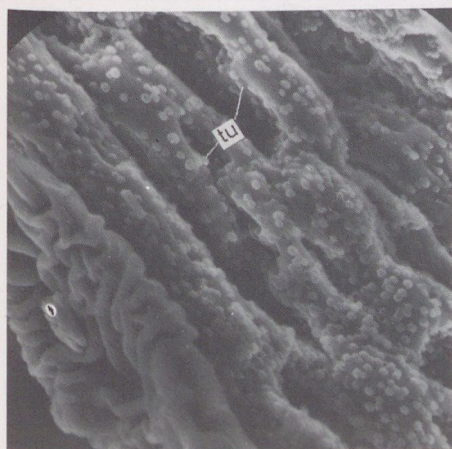
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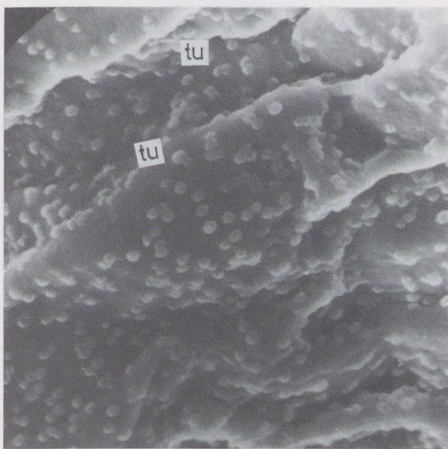
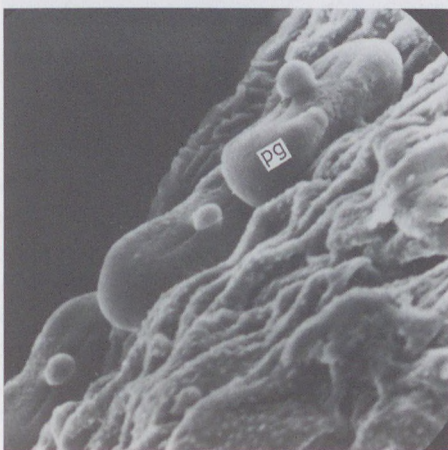


Fig. 32. Exothecium (ex) along the stomium (SEM $\times 2500$, photo: E. Gondár)

Fig. 33. Cuticle pattern in papillate exothecium (SEM $\times 6000$, photo: E. Gondár)

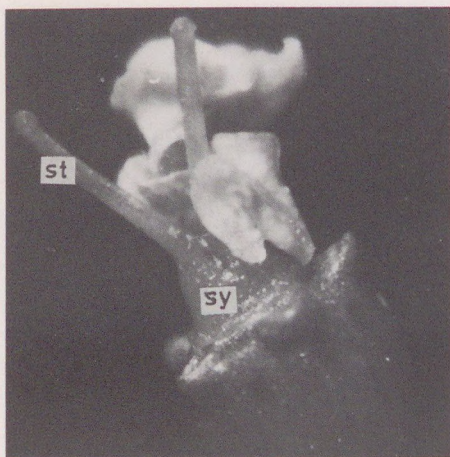
Figs 34, 35. Deep holes with tuberculate surface in the inner side of theca (SEM, Fig. 34: $\times 2400$, Fig. 35: $\times 3000$, photo: E. Gondár, tu = tuberculae)

Fig. 36. Pollen grains (pg) sitting close to the holes of the endothecium (SEM $\times 1300$, photo: E. Gondár)

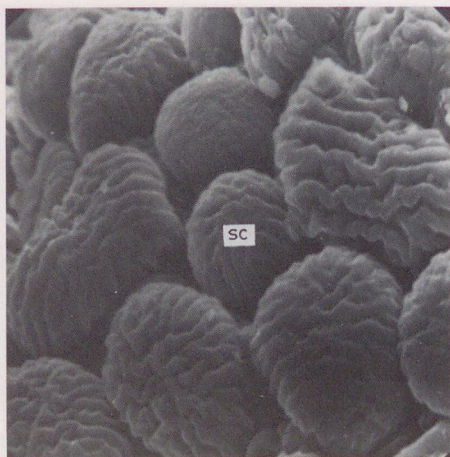


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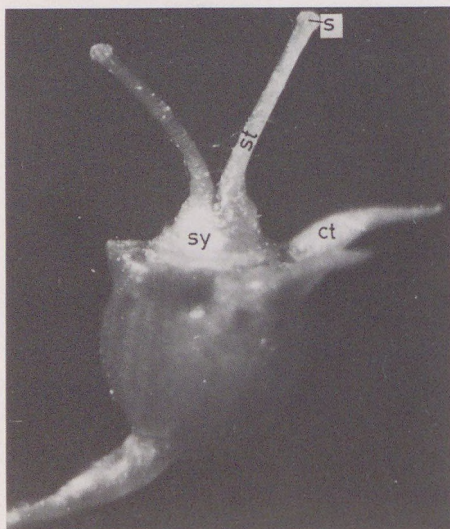


Fig. 37. Deviated styles (st) above the dome-shaped stylopodium (sy) ($\times 18$, photo: E.B. Szikszai)

Fig. 38. Wavy surface of papillate stigma cells (sc) (SEM $\times 3000$, photo: E. Gondár)

Fig. 39. Styles (st) deviated in $60-70^\circ$; pollen grains on the stigma (s) surface ($\times 18$, photo: E.B. Szikszai, ct = calyx teeth, sy = stylopodium)

tate pollen grains to separate from anther wall, or the content of cells of the middle layer can penetrate through these narrowed, tuberculate cell wall parts to the pollen grains. The middle layer is not perfectly homogeneous but consists of the two series of cells (see Fig. 154) that are the first to be absorbed.

32.3.2 The length of the outer pistil in the umbellet is 2 mm. The length of the styles which are farther from each other now is also 2 mm (Fig. 37). The stigma surface is wrinkled and composed of sphere-shaped cells (Fig. 38). Radial petals are 3 mm long. There are nectar drops on the surface of the stigma disc, which is cone-shaped (Figs 37, 39).

In the majority of inner flowers of an umbellet discs and styles are undeveloped while other flowers lack their stamens.

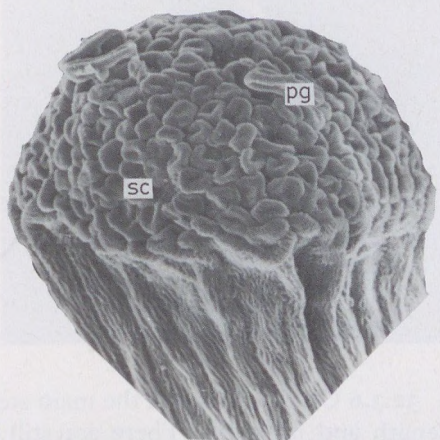
32.3.3 In outer flowers several petals and all stamens are absent, they have abscised. The ovary is 3.5 and 3 mm high with and without the disc, respectively, and 2.5 mm wide. The 3.5-mm-long styles are strongly diverging (Fig. 39), the stigma surface is like a croissant with pollen grains on it, its previous mauve colour has turned into transparent or quite dark (Figs 40, 41), and its cells are undulated (Fig. 42). Inner flowers, which lack styles or filaments, are characterized by a degenerate development.

32.3.4 Ovary length has not changed and the width is about 3 mm. All petals have dried out and abscised. The inclination of styles is about $100-110^\circ$ (Fig. 43). The stigma surface is covered by secreted material. The cells are deformed.

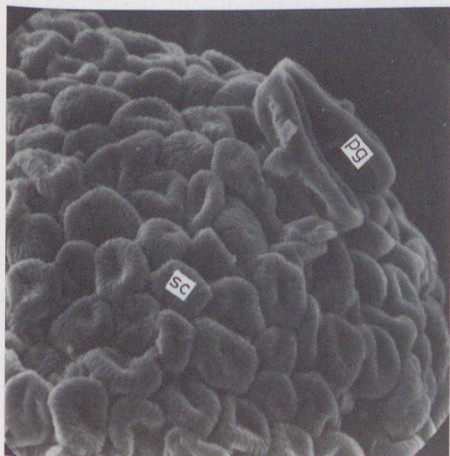
Fig. 40. Deepened stigma cells (sc) with pollen grains (pg) in phase 32.3.3 ($\times 480$, photo: E. Gondár)

Fig. 41. Open pollen grain (pg) on papillate stigma cells (sc) (SEM $\times 1000$, photo: E. Gondár)

Fig. 42. Last step of the change of stigma cells' (sc) surface (SEM, $\times 3000$, photo: E. Gondár, s sc = sunken stigma cell)



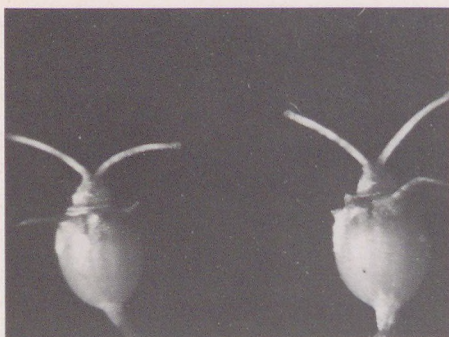
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Fig. 43. Styles deviated in $120-140^\circ$ ($\times 18$, photo: E.B. Szikszai)

Fig. 44. Difference of styles and stigmata according to flower position ($\times 18$, photo: E.B. Szikszai)

Fig. 45. Deviation of the dried styles (st) ($\times 18$, photo: E.B. Szikszai, ct = calyx teeth)

32.3.6 On outer rays of the main stem (Fig. 44) of the ovary is 4 mm both in length and in width. There are still pollen grains on the stigma surface. In compound umbels of lateral branches the stage of development described in 32.3.3 can be observed; ovary length ranges from 2 to 3 mm depending on the position inside the umbel (Fig. 44).

32.3.7 The length of schizocarps in umbels of lateral branches and the main stem is 3 mm and 4–5 mm, respectively. The inclination of styles in outer fruits of the main stem is almost 180° (Fig. 45).

33.1 Fruits on the main stem are green or yellowish-green. They are 4 and 3–4 mm in length and width, respectively.

Styles have partly or totally dried out and abscised. Schizocarps are almost sphere-shaped. Differences in calyx tooth length result in asymmetry (Fig. 45). There are 10 fruits in each umbellet; they are located closely together so the lack of abscised sterile flowers cannot be noticed. On lateral branches 3 or 5, or at most 7, fruits develop. In this phase of development (33.1) vegetative organs already begin to dry, which is assigned code number **42.1**, that is, lower leaves turn yellow.

33.2.1 Ripened fruits in the main umbel are light yellowish-green.

42.2 The schizocarp is almost sphere-shaped, its length is 4–5 mm, its width is 4 mm. Styles are dry and crumbling, base and lower stem leaves are drying.

33.2.2–42.2.2 Fruits are darker yellowish-green with bright surfaces. Their size has not changed. The middle stem leaf has become yellow or wilted.

33.2.3–42.2.3 Almost mature fruits in the main umbel are yellowish-brown while both fruits and leaves on lateral branches are light-green or slowly begin to change colour. Stem leaves on the main stem have dried.

43.1 Fruits are mature with the exception of those developed on lateral branches.

INNER STRUCTURE OF THE CORIANDER

RADICLE

Under the thin-walled, single-cell row rhizodermis, embedded in a cortex parenchyma layer, which consists of 5–6 cell rows, are: the central cylinder, an endodermis with a quite uncertain contour, the pericambium, and then the central vascular bundle, which consists of proto- and metaxylem elements. The diarch arrangement of vascular elements is characteristic of species of the Umbelliferae family.

HYPOCOTYL

Its epidermis consists of thick-walled cells, among which stomata develop. Parenchyma cells contain chloroplasts. Xylem elements in the central part form two groups.

COTYLEDON

The epidermis of the lanceolate dorsiventral cotyledon is rich in stomata on both sides. The palisade parenchyma consists of two cell rows and is followed by a transition cell row. The 3–4 cell rows of spongy parenchyma consist of isodiametrical cells that have lengthened in the direction opposite to the palisade cells. Xylem cells of the vascular bundles touch the palisade parenchyma cells and the volatile oil duct is associated with the phloem. Klotz in 1892 (cf. Napp-Zinn 1974) was the first to establish that the mesophyll of the coriander cotyledon consisted of more cell rows than that of stem leaves. Desphande and Joneja in 1962 (cf. Napp-Zinn 1974) observed a mesophyll of three cell layers in coriander cotyledon. Lassányi and Lörincz (1967) mentioned a discontinuous palisade layer and volatile oil components of cotyledons. Germination, as a function of the schizocarp, was examined by Augustin (1935).

ROOT

The development of the root from the diarch radicle is due to the wavy pericambium, which produces new phloem and xylem parts.

During the further growth, inside the breaking up rhizodermis cells the primary cortex cells also separate or suberize and serve as exodermis. Later this layer is almost totally replaced by the secondary periderm, which is a product of

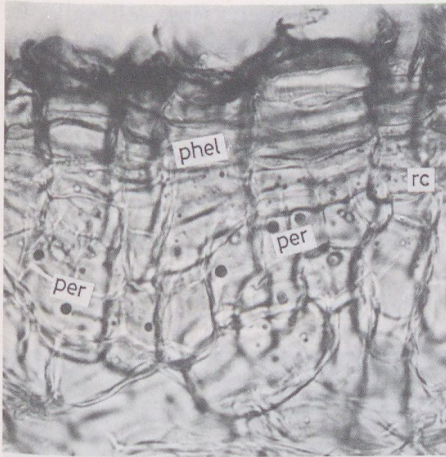


Fig. 46. Cross-section of periderm (per) in the root ($\times 350$, photo: E.B. Szikszai, rc = ray cell, phel = phellem)

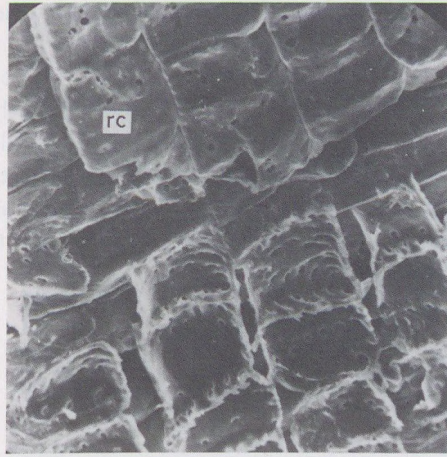
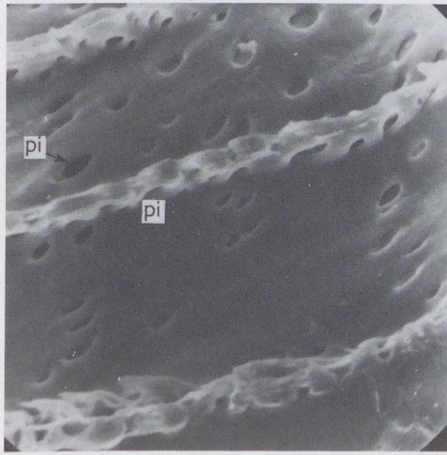
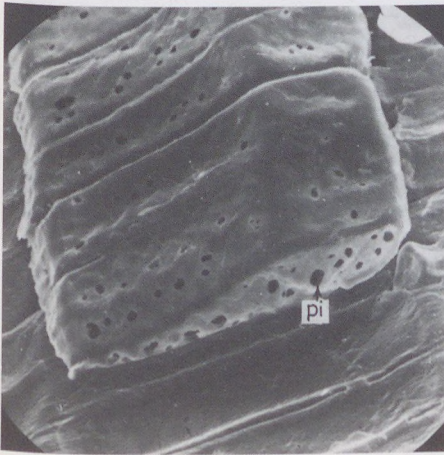


Fig. 47. Multiseriate and homocellular rays in the root (SEM $\times 600$, photo: E. Gondár, rc = ray cell)

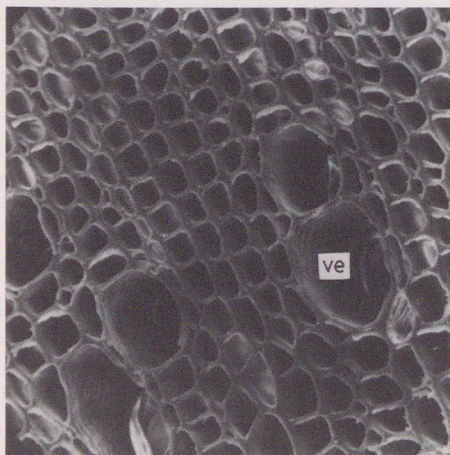


Figs 48, 49. Ray cells with solitary and clustered pits (pi) (SEM, Fig. 48: $\times 1000$, Fig. 49: $\times 4000$, photo: E. Gondár)

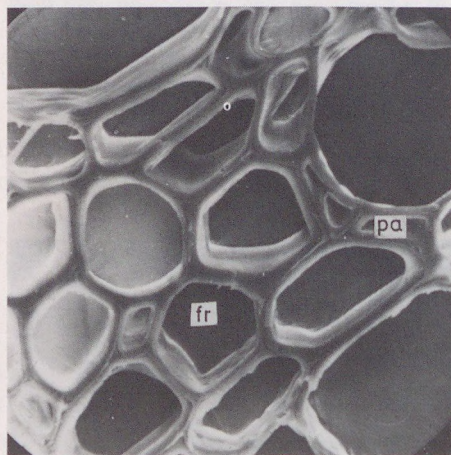
the dipleurically working paracambium (Fig. 46). There are several oil ducts among the newly formed periderm cells. Inward the paracambium produces a phelloderm similar to the cortex. The phloem is separated by medullary rays, which consist of several cell rows in depth (Fig. 47) and 1–3 rows in width (Fig. 46). Medullary ray cells are rhomboid (Fig. 48). Their cell walls are porous. Their pores are of different diameters, which make it possible to transfer metabolites from and to all directions (Fig. 49). Medullary ray cells mostly touch fibre

and parenchyma cell walls and sometimes immediately touch xylem cell walls. In the xylem, vessels consist of single-cell rows and are occasionally substituted by vessel groups and twin vessels (Fig. 50).

Walls of xylem parenchyma cells, which tightly fit together, have undergone a secondary thickening (Fig. 51). Similar process takes place in the cell wall of xylem fibres. Water transporting bundles are characterized by secondary cell wall thickening from the earliest annular and spiral tracheids (Figs 52, 53) up to tracheae with scalariform and pitted thickenings (Figs 54, 55), besides fibre elements also having walls with pores.



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Fig. 50. Transverse section of the root xylem with clustered and twin vessels (ve) (SEM $\times 1000$, photo: E. Gondár)

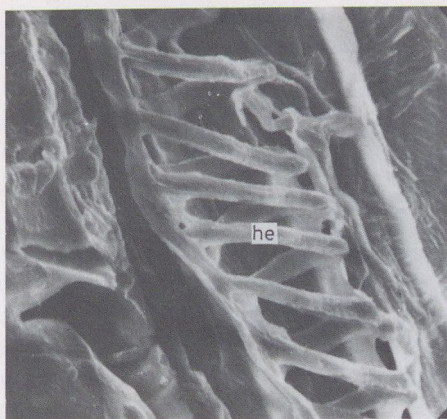
Fig. 51. Transverse section of xylem parenchyma (pa) and fibres (fr) with secondary thickened walls (SEM $\times 2000$, photo: E. Gondár)

Fig. 52. Annularly and helically thickened vessels in the root (SEM $\times 600$, photo: E. Gondár, an = annular)

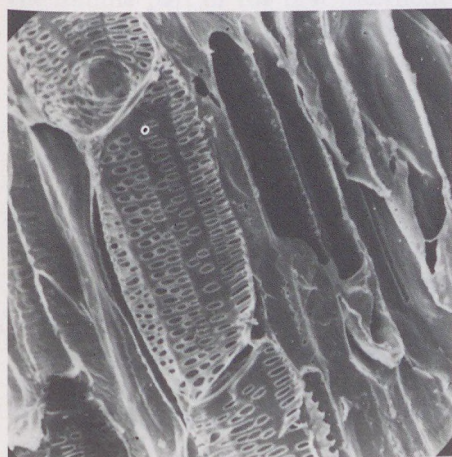
Fig. 53. Helically thickened vessel wall in the root (SEM $\times 1000$, photo: E. Gondár, he = helical)

Fig. 54. Scalariform secondary xylem elements with cell plate (SEM $\times 3000$, photo: E. Gondár)

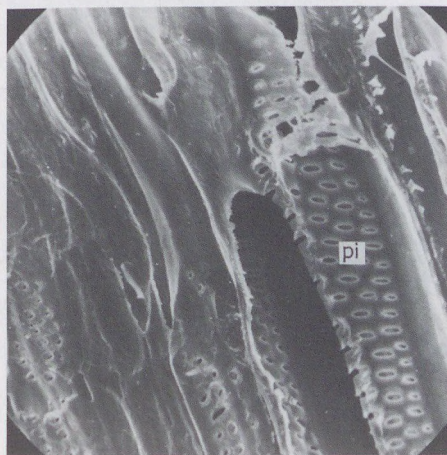
Fig. 55. Pitted vessels in the root xylem (SEM $\times 3000$, photo: E. Gondár, pi = pit)



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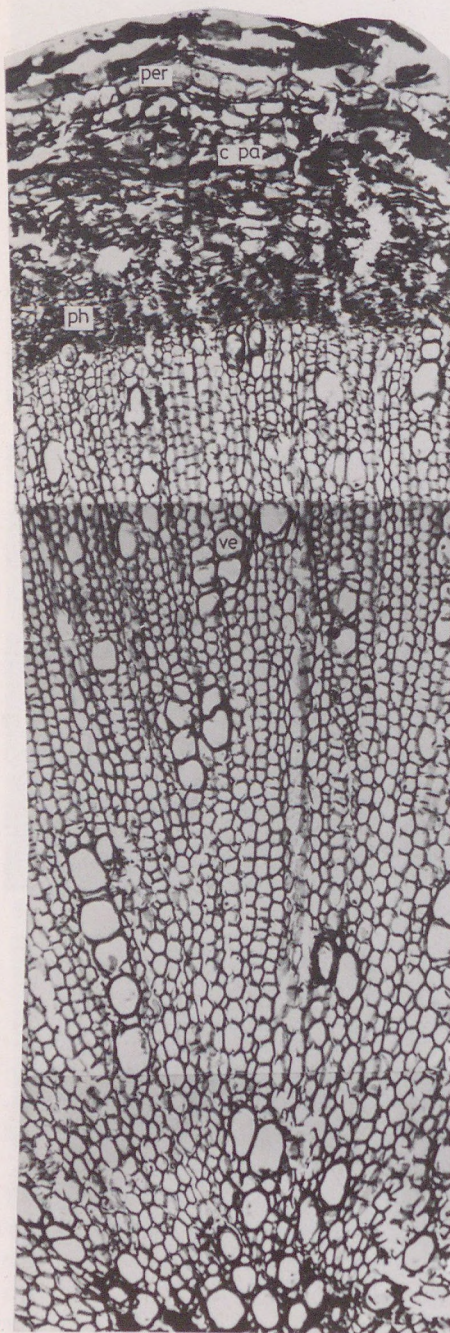


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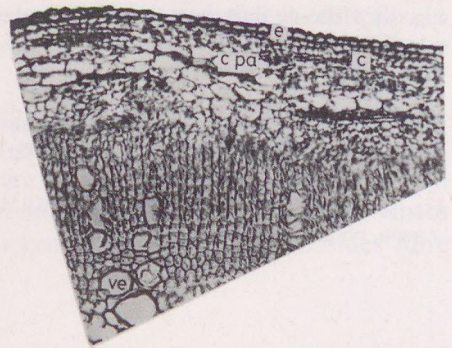
STEM (MAIN AXIS)

Previously Meyer (1937) and Mittal (1961) published data concerning the anatomy of vegetative organs of the coriander. The structure and function of the stem, which is divided into internodes, is subject to a (partial or total) spatial and temporal change.

23.1-31.3.1 The first internode at a young age, that is, at the beginning of bloom, is still intact. It has a continuous epidermis, cork parenchyma, narrow phloem and sclerenchyma, which is a supporting layer of 14-15 cell rows with the xylem embedded in it (Fig. 56). In the cortex, collenchyma alternates with chlorenchyma. Large diameter oil ducts are associated with phloem of vascular bundles. Near the inner boundary of cork parenchyma the interfascicular cambi-



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Fig. 56. Cross-section of the first internode in the young stem ($\times 150$, photo: E.B. Szikszai, c = collenchyma, c pa = cork parenchyma, e = epidermis, ve = vessel)

Fig. 57. Cross-section of the first internode at the base, with single, twin and clustered vessels in blossoming phase ($\times 150$, photo: E.B. Szikszai, c pa = cork parenchyma, per = periderm, ph = phloem, ve = vessel)

um can increase tissues in both the centrifugal and the centripetal directions (Figs 56, 57).

In the centre of the internode the pith tissue, which is made up of thin-walled polygonal cells, still occupies a fairly large area. Approaching the basal part of the internode from the middle, the proportion of cork parenchyma tends to increase. As a result of the activity of the interfascicular cambium (Fig. 57), in the cork parenchyma, cells and cell groups can be observed whose size shows a very wide variation (Fig. 57). From the older essential oil ducts located at the epidermis, quite young and small oil duct rows (or only one row) develop(s) toward the middle of the parenchyma cell groups. Water transporting elements (rows, vessel groups, twin vessel) and xylem parenchyma cells are radially arranged toward the centre. At the centre proto- and metaxylem elements, which are rather characteristic of the root, replace the still existing pith tissue (Fig. 57). The structure of the middle part of the first internode of a young fruiting plant is suitable for metabolite transport and supporting strength rather than assimilation. The epidermis is continuous but walls of its cells are thick, the chlorenchyma layer is compressed, and cell walls of the collenchyma layer are so thick that the stem surface is somewhat wavy but there are no ribs and furrows on it, that are often characteristic of other species of the Umbelliferae family. As a result of the activity of the fascicular cambium, xylems of fascicles touching the cork parenchyma have moved from the phloem in centripetal direction and the new xylem elements, in singles and more or less radially arranged, join the primary water transporting group. Xylem parenchyma cells of the primary bundles immediately touch the pith parenchyma (Fig. 58).

These processes are even more apparent in the cork parenchyma at the basal part of the first internode (Fig. 59). Fibre and parenchyma cells within the xylem of previously independent vascular bundles are of a small lumen and bear thick

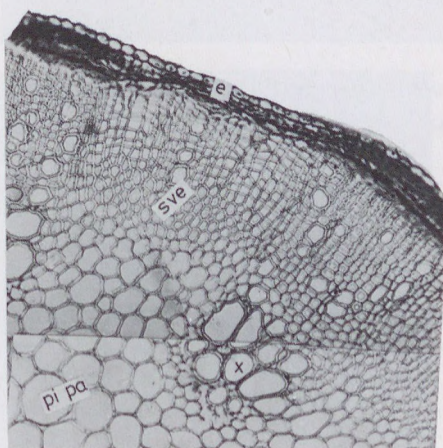
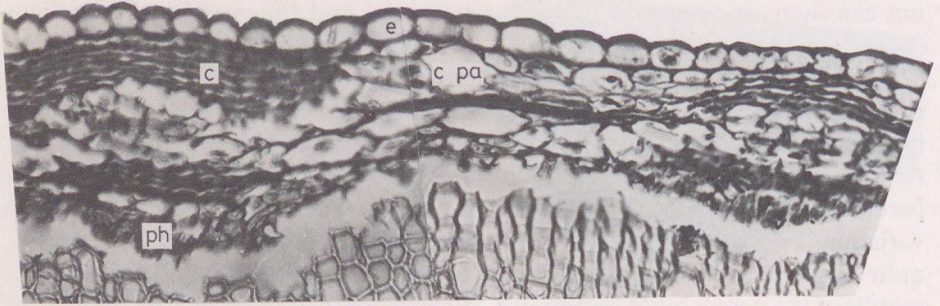


Fig. 58. Cross-section of the first internode at the middle part in blossoming phase ($\times 150$, photo: E.B. Szikszai, e = epidermis, pi pa = pith parenchyma, sve = solitary vessel, x = xylem)

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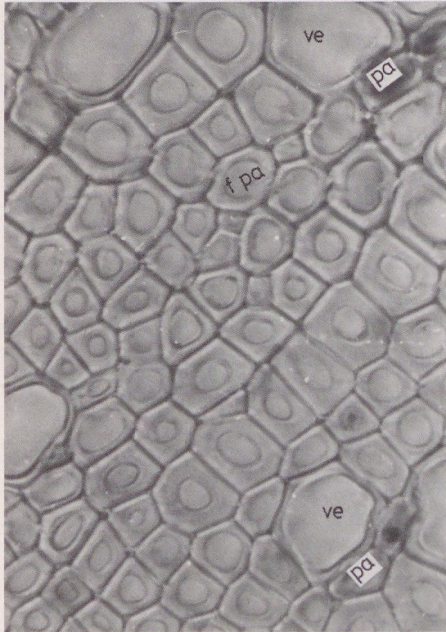


Fig. 59. Fascicular and interfascicular cambia in the cork parenchyma (c pa) of the first internode ($\times 350$, photo: E.B. Szikszai, c = collenchyma, e = epidermis, ph = phloem)

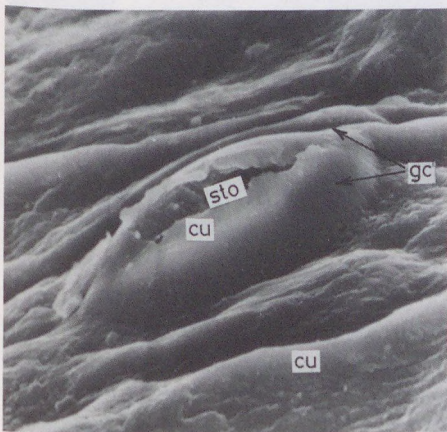
Fig. 60. Young parenchyma (pa) cells beside thick-walled xylem vessel and fibres ($\times 350$, photo: E.B. Szikszai, f pa = fibre parenchyma, ve = vessel)

walls (Fig. 60). Parenchyma cells containing cytoplasm and nuclei can be seen only beside tracheae.

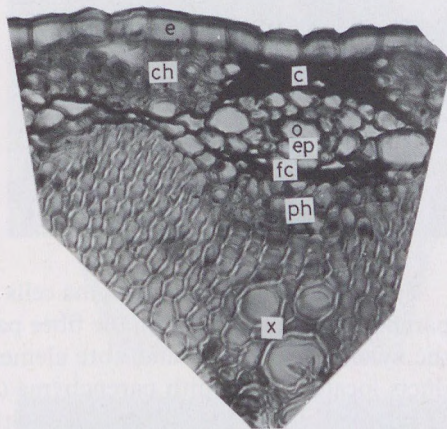
Occasionally it may happen that in the axil of the leaf that originates in the first node a lateral branch grows out but this early branch usually remains degenerate. At the beginning of bloom (phases 3I.2.I-3I.4.I) the cuticle on the surface of the third internode is relatively thick but epidermis cells still have narrow walls, with open stomata among them (Fig. 61), which are usually frequent above the chlorenchyma. Behind stomata there is a great substomatal cavity. Chlorenchyma cells are palisade in nature and parallel with the longitudinal axis (Fig. 62). In the very young stem the chlorenchyma dominates. Later its proportion decreases as a result of the appearance of secondary and tertiary vascular bundles. This is connected with the proportional increase in the area of epithelial cells and

oil ducts embedded in the parenchyma cell group developed above these bundles. In the centripetal direction the chlorenchyma is followed by a layer that consists of parenchyma cells with thin walls and of different diameters (Fig. 63). There is a row of small cells, dense in cytoplasm, associated with parenchyma cells, namely the (functioning) interfascicular cambium. Horizontal walls of young, large parenchyma cells are straight (Figs 64, 65) in the beginning and are modified to the letter V or a reversed V as a result of the lengthening of cells in a tangential direction. Cell walls become ingrowth in their tangential walls (Figs 64, 65). Their structure leads us to the conclusion that they are transfer cells whose function is to transfer nutrients in short lateral ways (Gunning and Pate 1969). In the first internode the transfer cell group may be made up of four, or sometimes five, rows of cells (Fig. 66).

These transfer cells are followed by the fibre parenchyma cells as dense as cytoplasm, with somewhat thickened walls and huge lanceolate, perhaps endopolyloid nucleus (Figs 65, 66).



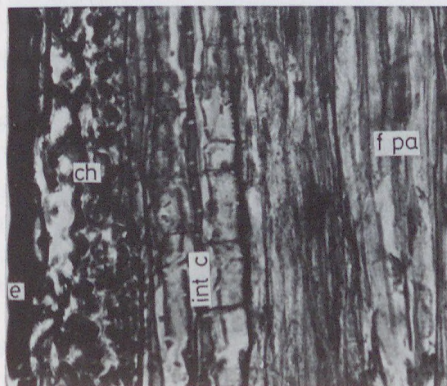
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Fig. 61. Stoma (sto) in the epidermis of the 3rd internode (SEM $\times 3000$, photo: E. Gondár, cu = cuticle, gc = guard cell)

Fig. 62. Oil channel (o) associated to phloem (ph) in the 3rd internode ($\times 350$, photo: E.B. Szikszai, c = collenchyma, ch = chlorenchyma, e = epidermis, ep = epithel, fc = fascicular cambium, x = xylem)



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Fig. 63. Tangential longitudinal section of the 3rd internode ($\times 350$, photo: E.B. Szikszai, ch = chlorenchyma, e = epidermis, int c = interfascicular cambium, f pa = fibre parenchyma)

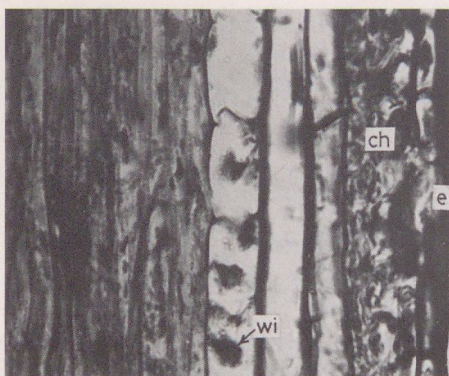
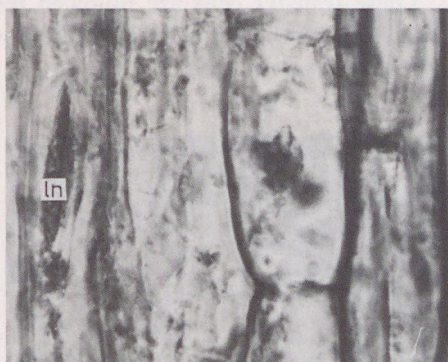


Fig. 64. Wall ingrowth (wi) in cork parenchyma cells (tangential longitudinal section) ($\times 350$, photo: E.B. Szikszai, e = epidermis, ch = chlorenchyma)

Figs 65, 66. Fibre parenchyma cells (some of them with two nuclei) in the 3rd internode ($\times 880$, photo: E.B. Szikszai, ln = large nucleus, wi = wall ingrowth)



The lumen of fibre parenchyma cells increases toward the direction of the pith parenchyma. In addition to the fibre parenchyma, the pith parenchyma touches the xylem parenchyma and fibre elements of vascular bundles as well as the oil ducts located in the pith parenchyma (Fig. 67). Walls of polygonal pith parenchyma cells (Fig. 68) are wrinkled with protuberances (Fig. 69), or perforated (Fig. 68). Between the cells there are triangular intercellular spaces (Figs 67, 68, 69).

In the same developmental phases, the third internode is also characterized by the development of collaterally opened primary, secondary and tertiary vascular bundles. Between the primary vascular bundles and the epidermis there is a parenchyma layer of several cell rows. These cells soon turn into angular collenchyma cells of tight lumen, as a result of a laminar thickening of cell walls. Around oil duct and epithelial cells, parenchyma cells remain narrow-walled or new cells are produced due to the activity of the interfascicular cambium. At primary vascular bundles phloem develops outwards relative to the cambium and xylems inwards.

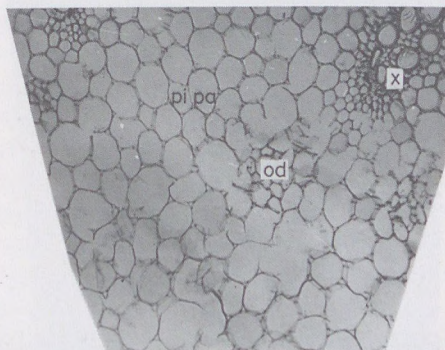
Secondary and tertiary bundles also develop due to the activity of the interfascicular cambium. Phloem, sieve tube, parenchyma and fibre cells touch the

xylem parenchyma. The xylem parenchyma surrounds the tracheae, which form small groups (Fig. 62), contrary to the first internode, where xylem elements that appeared later are radially ordered and linked to the primary xylem elements that penetrate deeply into the pith parenchyma. This makes the old tissue of the first internode similar to that of the root.

Cell walls of water transporting elements are characterized by spiral or bordered-pitted thickenings. Above the parenchyma cells around the oil duct 1–2 rows of chlorenchyma cells still remain for a short time. Then they turn into thick-walled and collenchymatous cells.

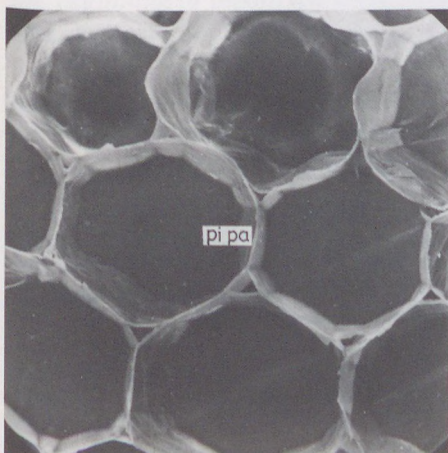
The epidermis of the uppermost internode, which bears the main umbel, that is, the peduncle, consists of smooth and papillate cells with wavy cuticle on their surface. Walls of its collenchyma cells are uniformly thickened (Fig. 70). This internode at the beginning of the bloom (phase 31.3.1) has a much more juvenile structure than the third internode though tertiary and quaternary bundles have already developed here also (Fig. 71). In the first internode a secondary bundle

Fig. 67. Small oil channels in the pith parenchyma (pi pa) ($\times 150$, photo: E.B. Szikszai, od = oil duct, x = xylem)

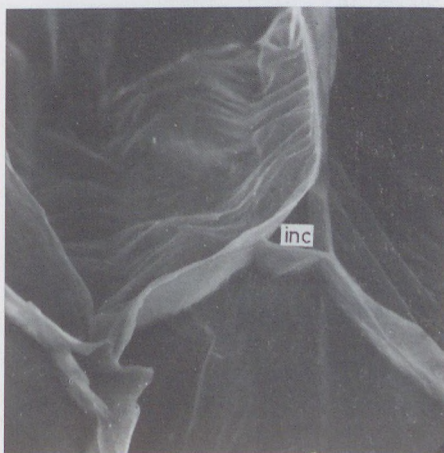


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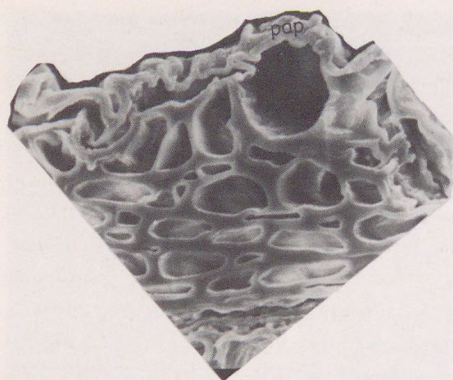
Figs 68, 69. Pith structure (SEM, Fig. 68: $\times 1000$, Fig. 69: $\times 3000$, photo: E. Gondár, inc = intercellular, pi pa = pith parenchyma)



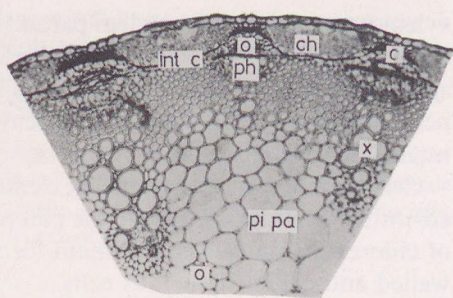
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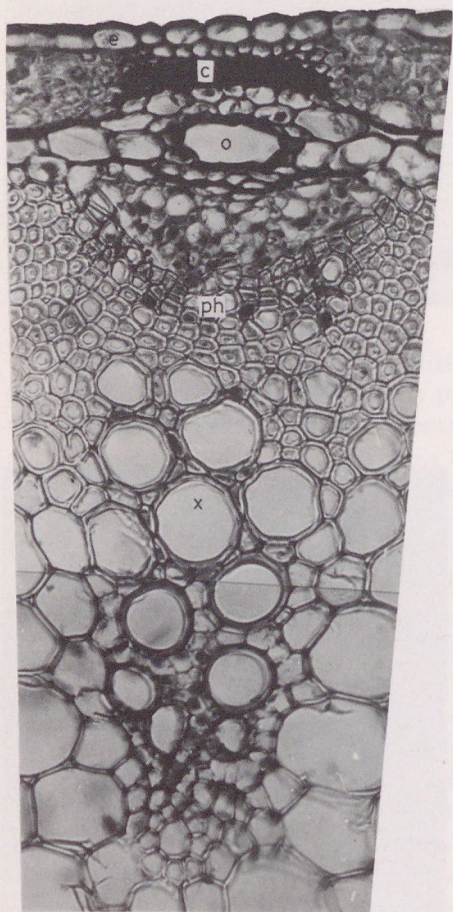
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Fig. 70. Cross-section of the papillate epidermal cells in the uppermost internode (SEM $\times 1500$, photo: E. Gondár, pap = papillae)

Fig. 71. Cross-section of the uppermost internode ($\times 150$, photo: E.B. Szikszai, c = collenchyma, ch = chlorenchyma, int c = inter fascicular cambium, o = oil duct, ph = phloem, pi pa = pith parenchyma, x = xylem)

Fig. 72. Primary vascular bundle with oil duct (o) in the uppermost internode ($\times 350$, photo: E.B. Szikszai, c = collenchyma, e = epidermis, ph = phloem, x = xylem)

never, or only seldom, exists between the two primary bundles, and the proportion of collenchyma to chlorenchyma is one to one. Later the collenchyma tends to become dominant. In the third internode, however, between the two primary bundles the area of chlorenchyma is about twice as much as that of collenchyma. By the beginning of bloom new vascular bundles develop resulting in a change of collenchyma to chlorenchyma producing a one to one ratio. In the uppermost internode the proportion of collenchyma to chlorenchyma is 6 to 1, which decreases to about 1.5 to 1 as a result of the permanent development of new vascular bundles (Fig. 71). All in all, the proportion of assimilating tissues to transporting tissues tends to change to the advantage of transporting tissues.

There is no pith parenchyma at the basal part of the first internode and it occupies a small area at the middle of the internode. Hence, about up to the half of the internode supporting and transporting tissues are dominant. In the third internode the layer of fibre, parenchyma and fibre-parenchyma cells between two vascular bundles consists of 16–17 rows. While the same layer at the same point of time in the uppermost internode consists of only 8–9 cell rows (Fig. 71). Topologically, with the aid of cross-sections taken from the stem at distinct levels of height, that is, from distinct internodes, one can demonstrate the process that had taken place much earlier in the first internode than in the third internode.

Later the sclerenchyma layer in the uppermost internode also changes so that it consists of several cell rows (Fig. 72) with highly thickened cell walls (Fig. 73). It is in this internode that the activity of the interfascicular cambium is most characteristic. The interfascicular cambium consists of a single cell layer between the two vascular bundles, at the boundary between chlorenchyma and transfer cells, then it bifurcates the parenchyma cell group that surrounds the oil duct, and finally, on the other side, it consists of a single cell row again. So it presents itself as a wavy and as a cyclic line at the same time (Fig. 71).

Contrary to the earlier developed internodes, in the uppermost internode at the beginning of bloom the interfascicular cambium as well as the fascicular (or vascular) cambium still functions.

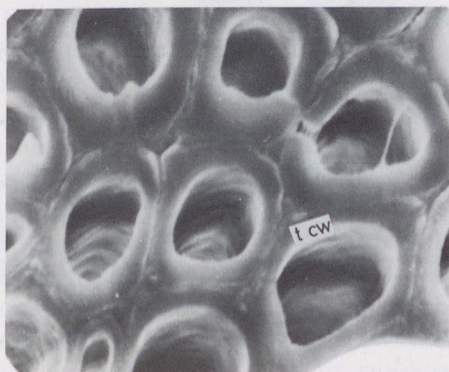


Fig. 73. Secondary thickened cells in the uppermost internode (SEM $\times 6000$, photo: E. Gondár, t cw = cell wall)

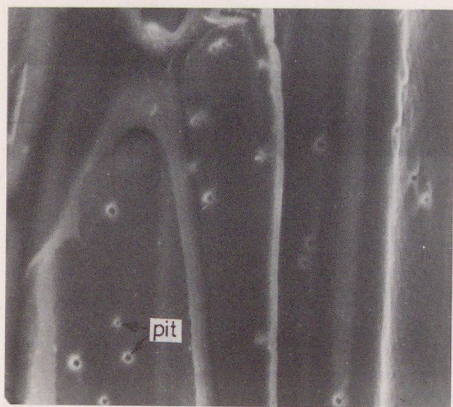


Fig. 74. Pitted (pit) cell wall in fibres (SEM $\times 1000$, photo: E. Gondár)

In the stem of coriander the presence of interfascicular cambium in the cork parenchyma makes the cork parenchyma different from that of the dill (Boros and Szujkó-Lacza 1970) or the anise (*Pimpinella anisum*) (Szujkó-Lacza 1976). In coriander the xylem increases in both directions, toward the phloem and toward the pith parenchyma (Fig. 71). In this plant the tracheae are (may be) surrounded by a parenchyma ring of several cell rows. Cell walls of the strengthening layers are characterized by wall ingrowths and perforateness (Fig. 74).

Thus, in the 31.3.1-31.4.1 developmental phases, the inner structure of the uppermost internode points to an intensive nutrient transport through this structure.

LEAF

LEAF SHEATH

Leaves that originate at the first node have long sheaths, petioles and laminae, which tend to become even longer and longer. The leaf sheath enfolds the node almost up to its two-third. Its epidermis has a wavy surface and stomata with large substomatal cavities are frequent among the epidermal cells. On the abaxial side under the epidermis there is an assimilative layer with an extremely long first and a very short second palisade parenchyma cell layer.

A group of collenchyma cells with thick cell walls substitutes for the palisade parenchyma above the five largest vascular bundles. In the petiole sclerenchymatous and assimilative tissues alternate with each other, which is a family-specific feature (Napp-Zinn 1974). Lassányi and Lörincz (1967, 1970) observed subepidermal hypoderm in coriandrum petiole.

The phloem of the seven vascular bundles forms a half circle, below the xylem, contrary to stem bundles. Oil ducts form not only above but also below the

bundles. The latter are small in diameter. On the adaxial side the epidermis is followed by a hypoderm that consists of a single cell row, under the vascular bundles (Lassányi and Lőrincz (1967, 1970)). Between the assimilative tissue on the abaxial side and the epidermis on the adaxial part there are huge parenchyma cells with wall ingrowths, whose structure implies that they function as transfer cells. Their structure makes an intensive short-distance metabolite transport possible. A high proportion of phloem area in the bundles implies an intensive vertical metabolite transport (Fig. 75). The interfascicular cambium in the 31.3.1-31.4.1 phases is still active and at the same time cell divisions can be observed in phloem and xylem parenchyma cells of the vascular bundle.

The leaf that corresponds to the uppermost internode has a short petiole and its blade touches the leaf sheath. At the sheath base between the vascular bundles a narrowing parenchyma layer develops. Between the bundles the thick-walled cells appear to be strung down (Fig. 75), and the leaf lamina becomes pinnate.

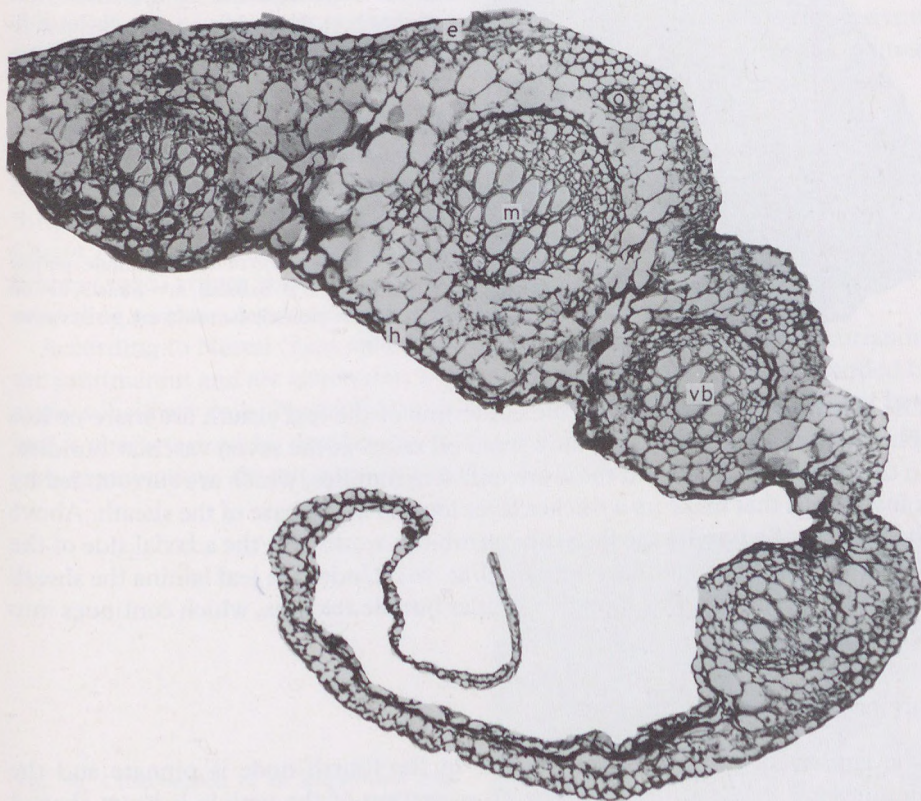
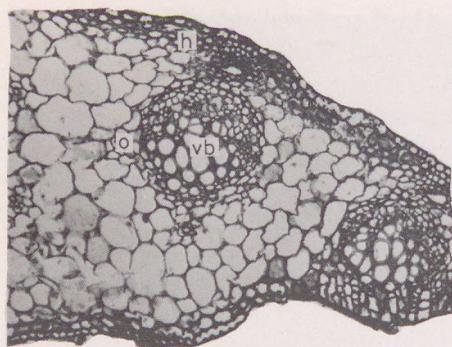


Fig. 75. Cross-section of the uppermost stem leaf sheath at the base ($\times 150$, photo: E.B. Szikszai, e = epidermis, h = hypodermis, m = midrib, o = oil duct, vb = vascular bundle)

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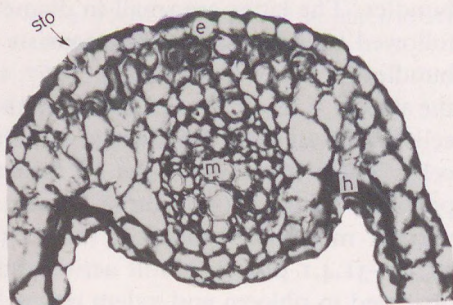


Fig. 76. Cross-section of the uppermost stem leaf sheath at the middle ($\times 150$, photo: E.B. Szikszai, h = hypodermis, o = oil duct, vb = vascular bundle)

Fig. 77. Cross-section of the uppermost stem leaf sheath at the leaf blade (phenophase 31.4.1) ($\times 150$, photo: E.B. Szikszai, e = epidermis, h = hypodermis, m = midrib, sto = stomata)

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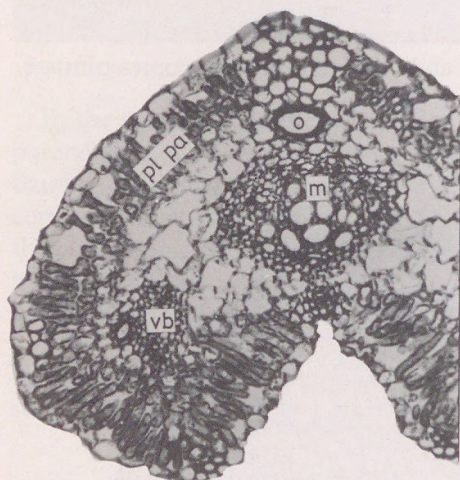


Fig. 78. Cross-section of leaflet (pinnule) petiole ($\times 150$, photo: E.B. Szikszai, m = midrib, o = oil duct, pl pa = palisade parenchyma, vb = vascular bundle)

The chlorenchyma cells under the epidermis of the leaf sheath are more or less sphere-shaped and there are many small oil ducts at the seven vascular bundles. In the middle of the sheath there are only five bundles, which are surrounded by transfer cells that make up a thicker layer located at the base of the sheath. Above the phloem of a bundle the fascicular cambium works. On the adaxial side of the sheath the hypoderm is characteristic (Fig. 76). Under the leaf lamina the sheath becomes narrow and only a single vascular bundle remains, which continues into the lamina (Fig. 77).

PETIOLE

The lamina of the leaf that grows out in the fourth node is pinnate and the pinnules are thin and narrow. The cross-section of the petiole is heart-shaped (Fig. 78). Its epidermis consists of papillate cells, among which there often occur stomata with large substomatal cavities accompanying the extremely huge pali-

sade cells. Some of the palisade cells, not uniform in size, are arranged in two rows, with shorter cells in the second row of cells. The number of vascular bundles of the amphivazale type is three, with the largest located in the middle (Fig. 79). Under and above the bundle there are collenchymatous cell groups (Fig. 78). The two lateral bundles are associated with collenchymatous cell groups, which consist of only a few cell rows. In the transfer cells occasionally plastids, perhaps amyloplasts, occur.

It is worth mentioning for comparison that bundles in the stem are collaterally open whereas types of petiole bundles range from types where the phloem is dominant to an amphivazale arrangement.

LEAF LAMINA

The first information concerning the anatomy of coriander leaf are due to Meyer (1937). According to this author, the lamina bears a striped cuticle, thick palisade layer and a papillate leaf apex. Leaf stomata are $38\text{ }\mu\text{m}$ long and $26\text{ }\mu\text{m}$ wide, surrounded by 3–5 subsidiary cells. According to Ostroumova (1990) stomata of coriander are of anomocytic type with navy anticlinal cell walls after their development.

The first base leaf with an entire lamina is crenate-serrated and covered by a wrinkled cuticle (Fig. 80), which reflects cell shapes in the whole leaf surface, demonstrating cell wall thickness and fitting. Stomata are somewhat sunken and the guard cells have strongly thickened, bridge-like longitudinal walls (Fig. 81). Guyot (1966) examined stomata types in species of the Umbelliferae family. Gupta (1970) argues that *Coriandrum* stomata belong to the syndetocheilic type according to their development but may vary by other organs.

According to Nestel (1905, in Napp-Zinn 1974), leaf stomata of the coriander are protuberant and are covered by a thick cuticle layer. They are surrounded by many subsidiary cells. Nestel (1905, in Napp-Zinn 1974) states that the first base leaf is characterized by protuberant stomata of a xeromorphous nature, but my own examinations do not corroborate this description.

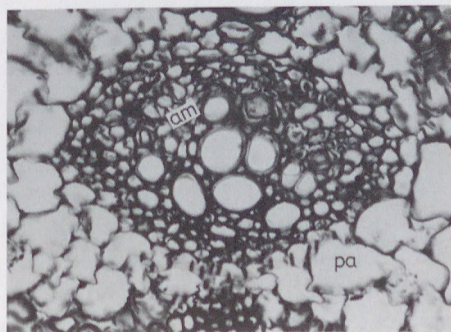


Fig. 79. Cross-section of an amphivascular type midrib in the petiole ($\times 300$, photo: E.B. Szikszai, am = amphivascular midrib, pa = parenchyma)

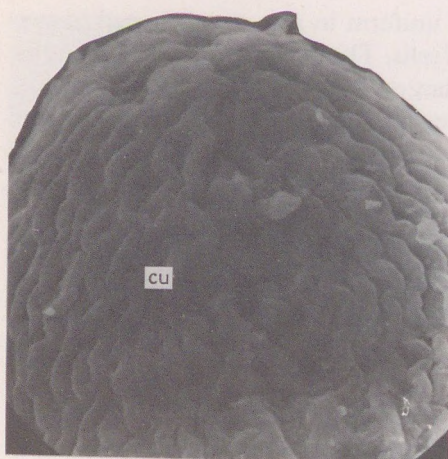


Fig. 80. Thick cuticle (cu) covered leaf tooth in the first rosetting leaf (SEM $\times 800$, photo: E. Gondár)

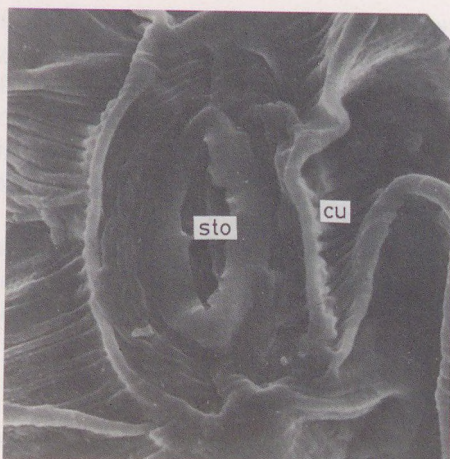


Fig. 81. Stomata in the first rosetting leaf (SEM $\times 4000$, photo: E. Gondár, cu = cuticle, sto = stomata)

In the mesophyll of the leaf the palisade layer contains one cell layer while the spongy mesophyll consists of three cell layers. The middle layer is remarkably well-developed and this cell row closely sticks to sheath parenchyma cells of the bundle. Bundles are branched, and the xylem is made up of elements with annular, helical and scalariform thickenings. Oil ducts associated with bundles are also branched. Their epithelial cells are first like short bricks and later like lengthened bricks, with large nuclei. According to Lassányi and Lörincz (1967), oil ducts in leaves will have developed by the time the protoxylem elements are lignified. My observations lead to the conclusion that oil ducts come into existence simultaneously with bundle differentiation. They are rather associated with the development of the phloem.

The leaf that originates in the third node is solitary. Its lamina consists of five segments, which are split and divided. The cells in the epidermis of leaflets have wavy walls and are rich in stomata on both sides (Fig. 82). The wrinkled cuticle that covers the surface implies an intensive movement of the epidermal cells, which is prominently likely in the case of subsidiary cells of stomata. Epidermal papillae may have various shapes (Figs 83, 84) and they occur at various locations not only in leaf apices.

The palisade parenchyma consists of a single cell row but the height of palisade cells equals that of the spongy mesophyll layer, which consists of three cell rows. The proportion of thickness of the two layers is one to one (Fig. 82). In the marginal parts of leaflets palisade cells are dominant, and even the reverse side is characterized by a slight dominance of palisade cells (Fig. 85). Substomatal cavities extend into both parenchyma layers and are extremely large (Figs 85, 86).

Guard cells and subsidiary cells of stomata that are near to vascular bundles are also large (Fig. 87) while those near to serrated tips are smaller by about one-third (Fig. 88). Cells in apices of serrated tips show a wide variety in length (Fig. 89) and their cuticle wrinkled and heavily patterned (Fig. 90).

Midribs and greater subsidiary veins in leaflets fill the mesophyll from upper epidermis to lower epidermis while small traces, whose number equals the

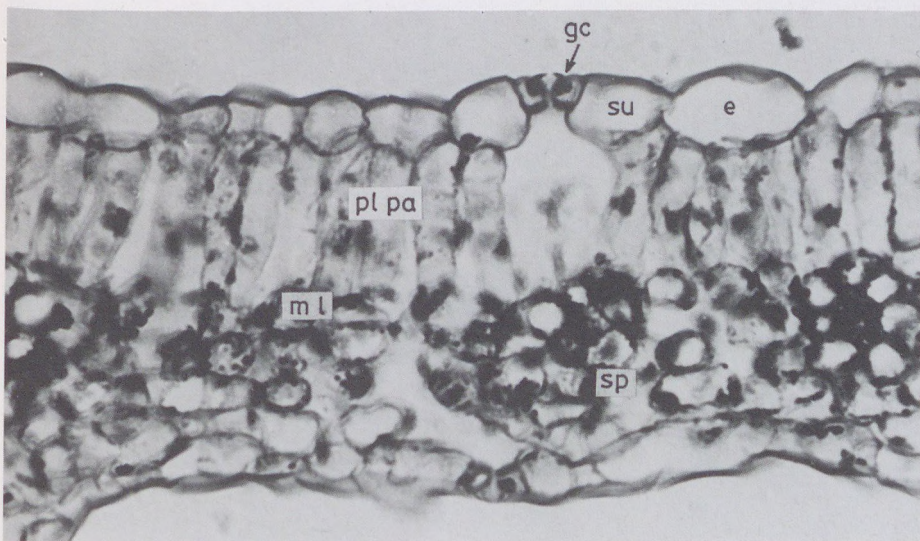


Fig. 82. Cross-section of the 3rd stem leaf ($\times 350$, photo: E.B. Szikszai, e = epidermis, gc = guard cell, ml = middle layer, pl pa = palisade parenchyma, sp = spongy parenchyma, su = subsidiary cell)

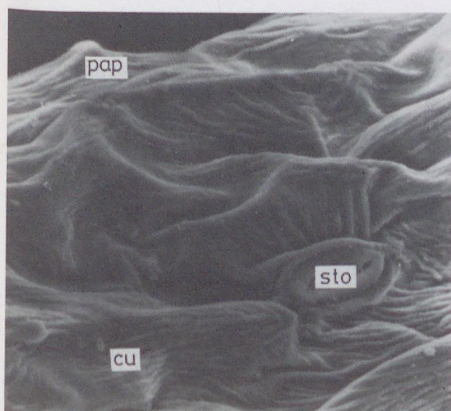


Fig. 83. Leaf surface at the margin (SEM $\times 1000$, photo: E. Gondár, cu = cuticle, pap = papillae, sto = stomata)

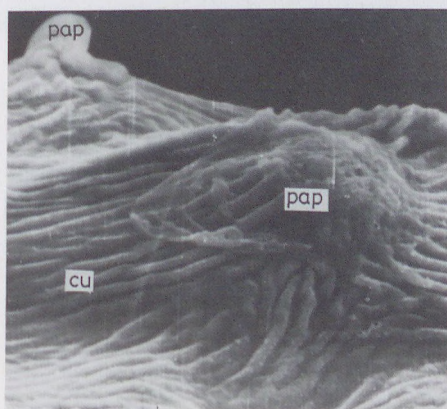
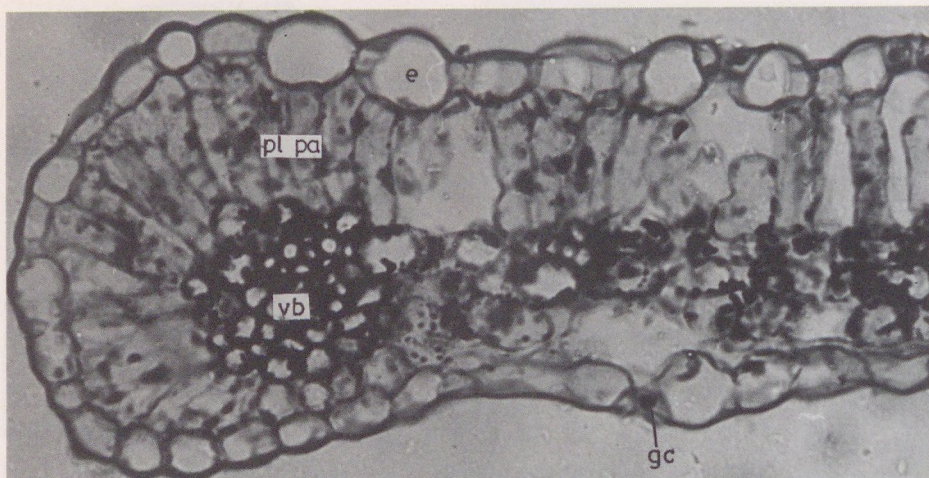
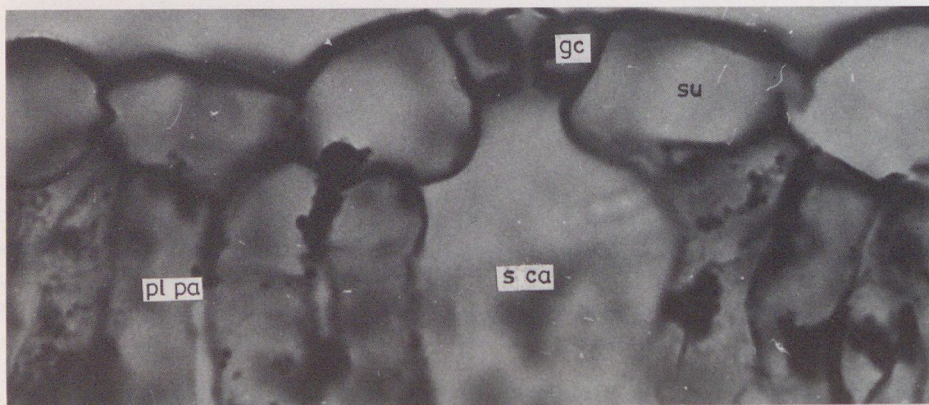


Fig. 84. Pattern of papillate leaf surface (SEM $\times 4000$, photo: E. Gondár, cu = cuticle, pap = papillae)

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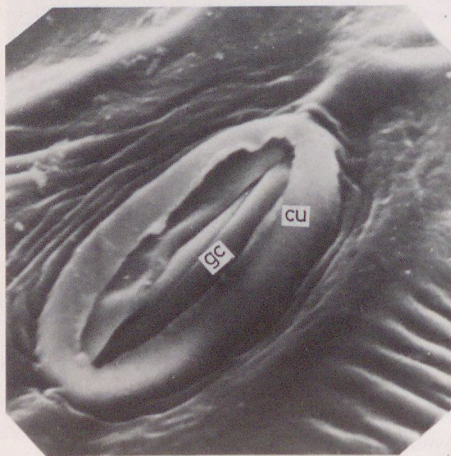


Fig. 85. Cross-section of the leaf margin ($\times 150$, photo: E.B. Szikszai, e = epidermis, gc = guard cell, pl pa = palisade parenchyma, vb = vascular bundle)

Fig. 86. Extremely large substomatal cavity among palisade cells (pl pa) ($\times 880$, photo: E.B. Szikszai, gc = guard cell, s ca = substomatal cavity, su = subsidiary cell)

Fig. 87. Perivascular stoma (SEM $\times 6000$, photo: E. Gondár, cu = cuticle, gc = guard cell)

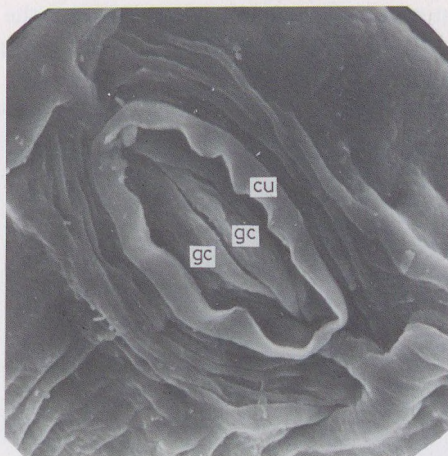
Fig. 88. Stoma in leaf tooth (SEM $\times 6000$, photo: E. Gondár, cu = cuticle, gc = guard cell)

Fig. 89. Unequally long cells in leaflet tooth at the 3rd stem leaf (SEM $\times 400$, photo: E. Gondár)

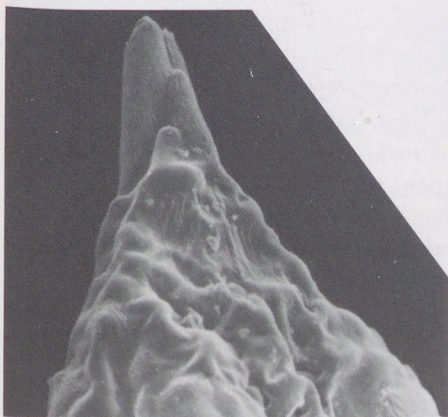
Fig. 90. Wavy cuticle in the leaf tooth (SEM $\times 1000$, photo: E. Gondár)

Fig. 91. Cross-section of phloem (SEM $\times 2000$, photo: E. Gondár, co = companion cell, si = sieve tube)

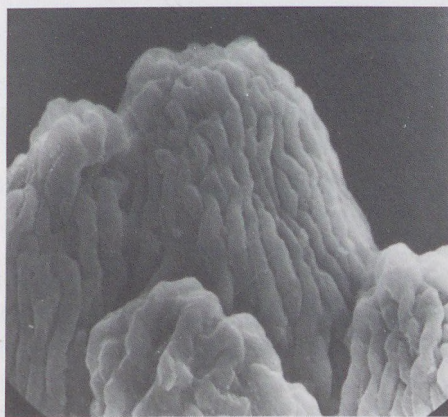
Fig. 92. Wall thickening in phloem parenchyma (ph pa) and fibre (fi) in the leaflet (SEM $\times 8000$, photo: E. Gondár)



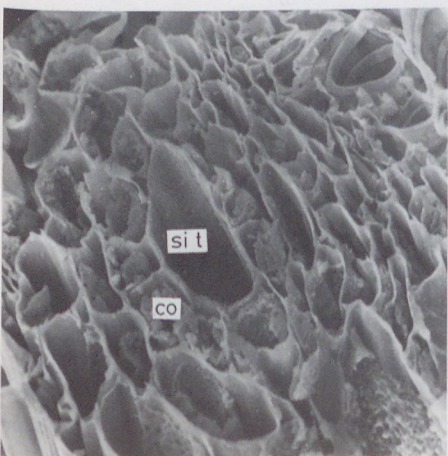
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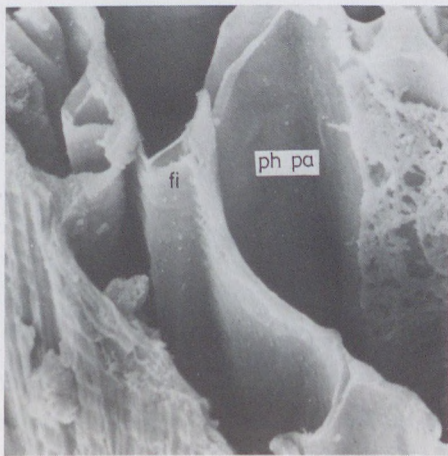
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number of serrated apices, occupy the area between the spongy layer and the palisade. The sieve tube of the phloem in the midrib is situated in the centre (Fig. 91) and its companion and parenchyma cells are closely associated with the sieve tubes (Fig. 92). Primary tracheary elements are characterized by annular thickenings while water transporting elements, developed later, are characterized by scalariform thickenings with xylem parenchyma and xylem fibre cells among them. Vascular bundles are surrounded by bundle sheath parenchyma (Figs 93, 94). Oil ducts situated above the phloem, and their epithelial cells, also surrounded by parenchyma cell groups, touch the bundle sheath parenchyma. In the leaf lamina, however, the phloem as well as the oil ducts can be found on the abaxial side of the leaf (Fig. 94).

The leaf located on the uppermost node is short and its lamina is divided into leaflets. Its epidermis has a wavy surface everywhere and is papillate and rich in stomata. The palisade parenchyma consists of a single cell row. The proportion of the palisade parenchyma to the spongy parenchyma is 1.2:0.7. The proportion of the palisade parenchyma is greater in comparison with that in the lower leaves and the entire mesophyll structure typically reflects a 'light leaf' nature (Fekete and Szujkó-Lacza 1973). Structural changes in the leaves across plant levels, on succeeding internodes were first described by Zalensky. Such changes were quantified by Szujkó-Lacza (1974) in *Pimpinella anisum*, a species that belongs to the Umbelliferae. A change in environment around a given plant is reflected in the inner structure of organs (leaves) that have developed in different points of time and places (leaf levels), that is, under different circumstances.

In respect to the mesophyll cells of the leaf located on the uppermost node, the palisade parenchyma is remarkably rich in cells with huge nuclei and the bundle sheath parenchyma cells possess double nuclei.

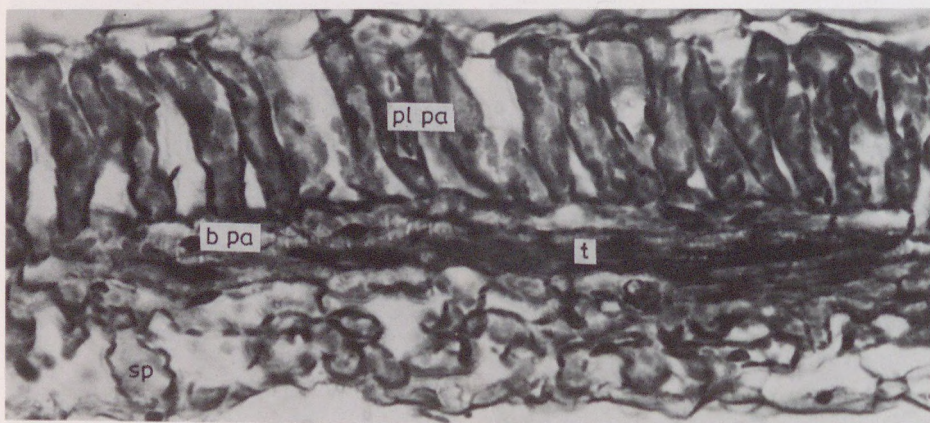


Fig. 93. Bundle sheath parenchyma (b pa) around vascular trace in leaf ($\times 350$, photo: E.B. Szikszai, pl pa = palisade parenchyma, sp = spongy parenchyma, t = trace)

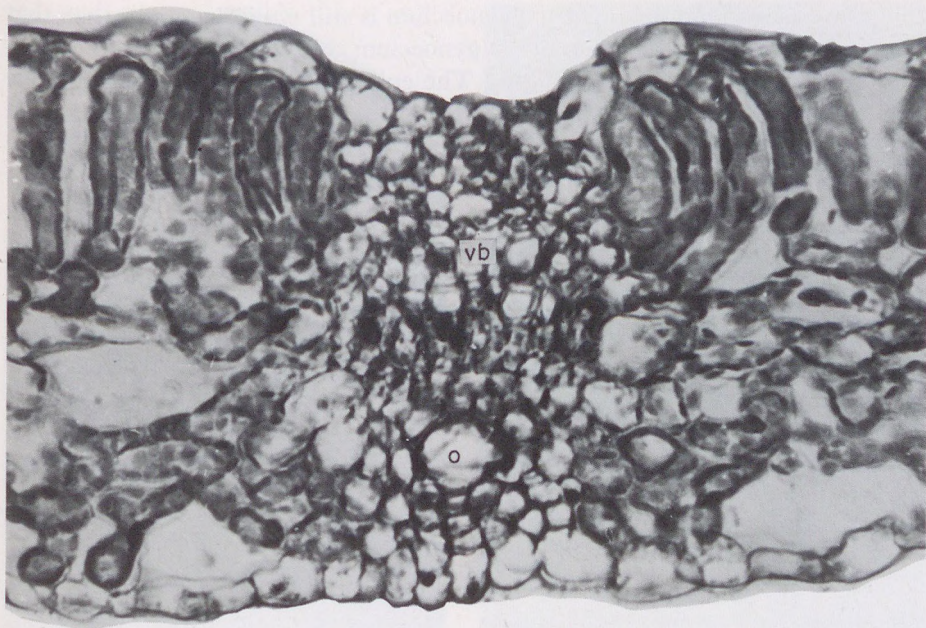


Fig. 94. Bicollateral vascular bundle (vb) at branching point of leaflet ($\times 350$, photo: E.B. Szikszai, o = oil duct)

The structure that is increasingly suitable for intensive assimilation and dissimilation can mainly be observed in the leaflets on upper lateral branches (Fig. 94), where vascular bundles are bicollateral, with several sieve tubes in both parts of the phloem. The lower phloem part is furnished with large oil ducts. On the upper stem leaf and on these lateral branches there is an indication of xeromorphy, the vascular bundles are sunken in mesophyll (Fig. 94).

Ticha (1968) pointed out differences in physiological activity of leaves in *Plectranthus fruticosus*, that also conform to Zalensky's rules.

SCHIZOCARP

The inflorescence is a compound umbel. Outer umbellets are the first to develop and here peripheral flowers appear sooner than those in the centre.

Several phases of gynoecium development in *Coriandrum sativum* are described by Paliwall (1950, 1951), Adatia and Shah (1952), Gupta (1964), and Lassányi and Lörincz (1970).

From the gynoecium primordia, soon organs develop that can be determined well in green, closed buds at the developmental stage 31.1.3 (Figs 5, 95, 96). In

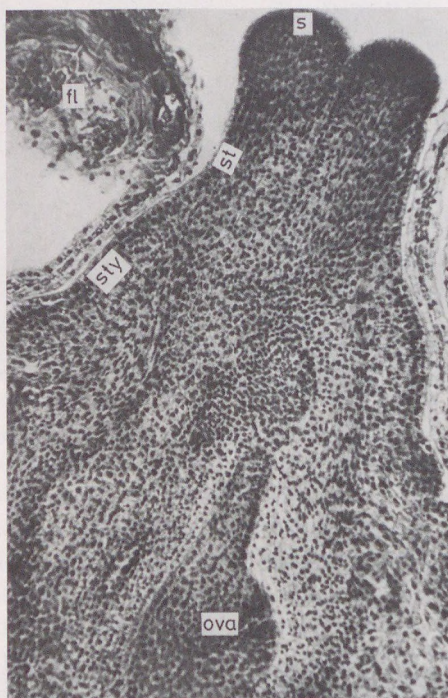
this phase the differentiation of the gynoecium is still typically slower than that of petals and sepals. At the top of the gynoecium the stylopodium soon constitutes a dome-like structure (Fig. 96). The epidermal cells of the stigma have angular shape (Fig. 7). On the adaxial side of the future mericarps, which cells still touch each other, in the middle, there is the shared trace bundle of the carpophore funicle and two oil ducts per mericarp (Fig. 97).



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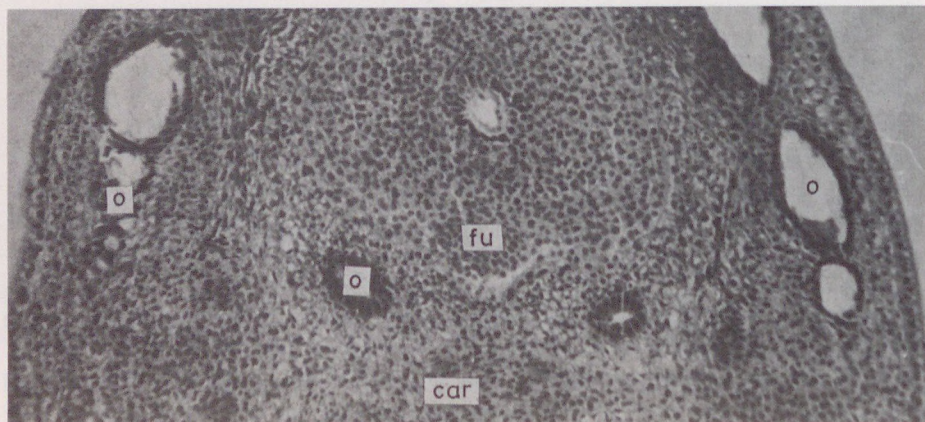
Fig. 95. Bud cross-section in phenophase 31.I.3 ($\times 150$, photo: E.B. Szikszai, a = anther, fl = flower, ova = ovary)

Fig. 96. Longitudinal section of the gynoecium in phenophase 31.I.3 ($\times 150$, photo: E.B. Szikszai, fl = flower, ova = ovary, s = stigma, st = style, sty = stylopodium)



96

Fig. 97. Separated bundles of carpophore (car)-funicle (fu) complex in cross-section of the ovary ($\times 150$, photo: E.B. Szikszai, o = oil duct)



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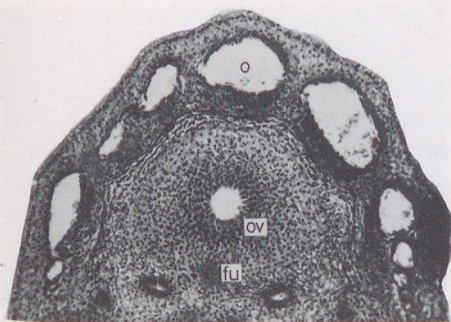
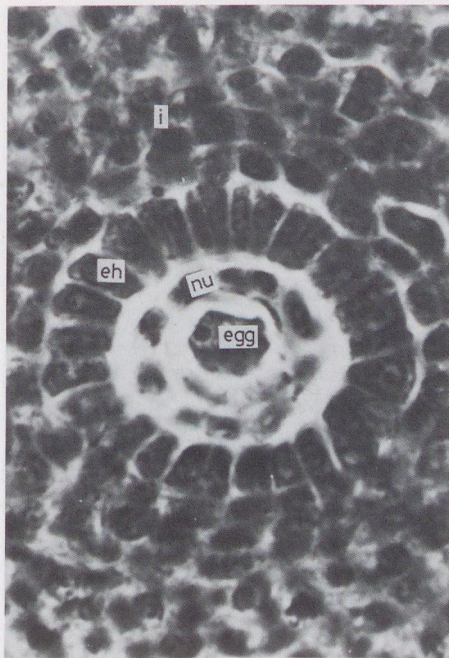


Fig. 98. Schizogamous oil ducts (o) in the ovary in phenophase 32.3.2 ($\times 150$, photo: E.B. Szikszai, fu = funicle, ov = ovule)

Fig. 99. Endothelial tapetum around the nucellus and the embryo sac ($\times 350$, photo: E.B. Szikszai, egg = egg cell, eh = endothel, i = integument, nu = nucellus)



99

The ovary wall under the epidermal cells continues in a huge parenchyma layer, which contains 30 or more oil ducts different in size in phase 32.3.2 (Fig. 98). Furthermore, there develops a row of permanently increasing oil ducts, those near the commissure being very tiny and the last ones on the abaxial side being huge. Oil ducts are schizogenous in nature, and are separated only by epithelial cells.

In a later phase of development in the mesocarp the vascular bundles that consist of protoxylem and phloem elements are situated on the inner side of the large oil ducts and characterized by phloem dominance. The layer that contains the oil ducts and vascular bundles ends in two or three rows of cyclically lengthened, isodiametrical cells. Then there follows a tissue layer of narrow but long cells, in which two scarcely developed oil ducts can be found at both half carpophores (Fig. 98).

This layer is followed by the parenchyma layer of the integument, whose inner epidermis turns into an integumental tapetum, or in other words, an endothelial cell row (Fig. 99). According to Gupta (1964), the radial lengthening of inner epidermis cells of the integument—the integumental tapetum—begins when the embryo sac with two nuclei comes into existence. Håkansson (1923) and Adatia and Shah (1952) regard the development of endothelial cells as a family-specific feature.

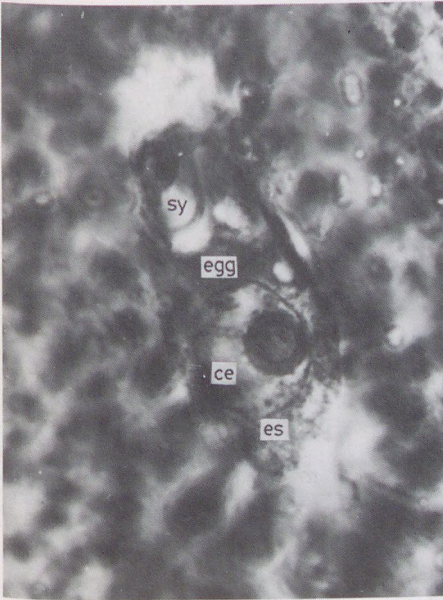
MEGASPOROGENESIS

The anatropous ovule appears in the ovary hole. In the hypodermal layer of the lengthened nucellus the megaspore mother cell is already observable (Fig. 100). According to Gupta (1964), the hypodermal archeospore may consist of 1–4 cells in the *Coriandrum sativum*. One of the archeospore cells immediately serves as megaspore mother cell. In the first phase of meiosis the dyad comes into existence but occasionally the upper cell of the two cells is smaller. According to observations of Paliwall (1950), this smaller upper cell does not divide and hence a triad comes into existence in the second phase of meiosis. Furthermore, the micropylar megaspore may lengthen but the embryo sac develops from the chalazal megaspore. Undergoing three succeeding mitotic cycles of division, the nucleus of the functioning megaspore forms an embryo sac of two, four and eight cells, which belongs to the *Polygonum* type (Johri 1963). Håkansson (1923) is the first to mention embryo sacs with one, two, or occasionally four spores in the Umbelliferae. According to Gupta (1964) the coriander tends to belong to the type where embryo sacs contain two spores.

Chronology of fertilization. First, the polar cells fuse. The resulting diploid central cell is situated immediately under the egg cell and synergids (Fig. 101) before the penetration of the pollen tube into the embryo sac (Gupta 1964), and it retains this position also after the fertilization of the egg cell, in the 32.3.2 phase of development (Fig. 101). The fusion consists of the following steps: first the two cell plates touch each other, then the cytoplasms fuse, and finally the nuclei fuse. Through the fertilization after the fusion the triploid primary endosperm cell comes into existence. From the pollen tube the male nucleus penetrates through the synergid into the egg cell. After the fusion of polar cells, antipodal

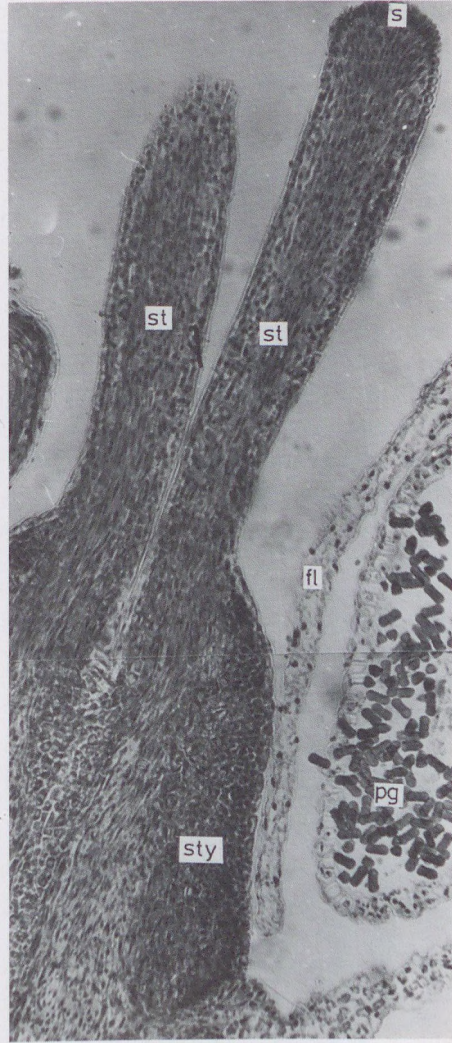


Fig. 100. Hypodermal archeosporial cell in the nucellus (nu) ($\times 880$, photo: E.B. Szikszai, ar = archeospore mother cell)



101

Fig. 101. Egg (egg), synergids (sy) and central cell (ce) in the embryo sac (es) ($\times 880$, photo: E.B. Szikszai)



102

Fig. 102. Styles (st) and stylopodium (sty) in longitudinal section ($\times 150$, photo: E.B. Szikszai, fl = flower, pg = pollen grain, s = stigma)

and hypostase cells remain active for a while following the division of the primary endosperm cell. The material that they secrete might play a role in the formation and development of the central vacuole of the embryo sac. Håkansson (1923) reports antipodal cells to disappear in the *Hydrocotyle* and to remain after double fertilization for a long time in *Astrantia*, *Eryngium* and *Oenanth* species. Integumental tapetum or endothelial cells are large, entire, and completely surround the embryo sac. In other species their partial development or discontinuous appearance was also mentioned by Kapil and Tiwari (1978). In the phase that precedes double fertilization (31.3.1) styles are almost parallel (Fig. 102), epidermal cells

of the stigma are wrinkled or still smooth on surface (Fig. 16), its cells are rich in cytoplasm, they are extremely large (Fig. 103) and lengthened but still not secreting. Glands of the stylopodium form a half circle, their cytoplasm strongly stains and the ovary has lengthened longitudinally (Fig. 104). Fertilization takes place in phase 32.3.1 (Fig. 105). The pollen tube penetrates in the synergid and the male gamete into the egg cell, which is almost angular that time (Fig. 105). After double fertilization the triploid primary endosperm cell, which is close to the zygote, begins to divide. The resulting free endosperm nuclei first gather around the zygote (Fig. 106), and then form a single layer and occupy an area parietally between the embryo sac wall and the central vacuole (Fig. 107). Simultaneously with the beginning of coenocytosis, endothelial cells begin to be dissolved. In the same period of time styles get farther from each other (Fig. 17) and their surfaces become full of wavy wrinkles (Fig. 38). In the embryo sac synergids remain for a long time. According to Jensen's (1965) histochemical examinations concerning the ultrastructure of synergids in cotton, which corroborate Haberman's (1906, in Jensen 1965) opinion that synergids transport metabolites to egg cell, embryo and endosperm, and one of them transports the pollen tube. I think that synergids must contain hormones that control, or hinder zygote differentiation because their life time coincides with that of the zygote. Then begins an intensive vesiculation from the micropylar apex (Fig. 108). Gupta (1964) argues that this vesiculation is characteristic of the stage when there are

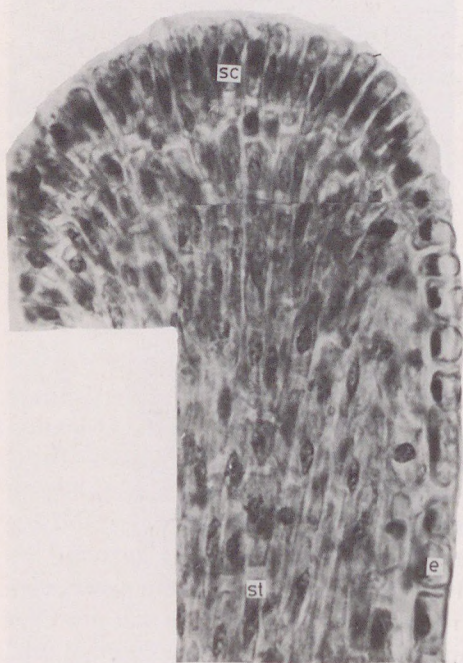


Fig. 103. Papillate stigma above parenchymatous stigma and style part ($\times 880$, photo: E.B. Szikszai, e = epidermis, sc = stigma, st = style)

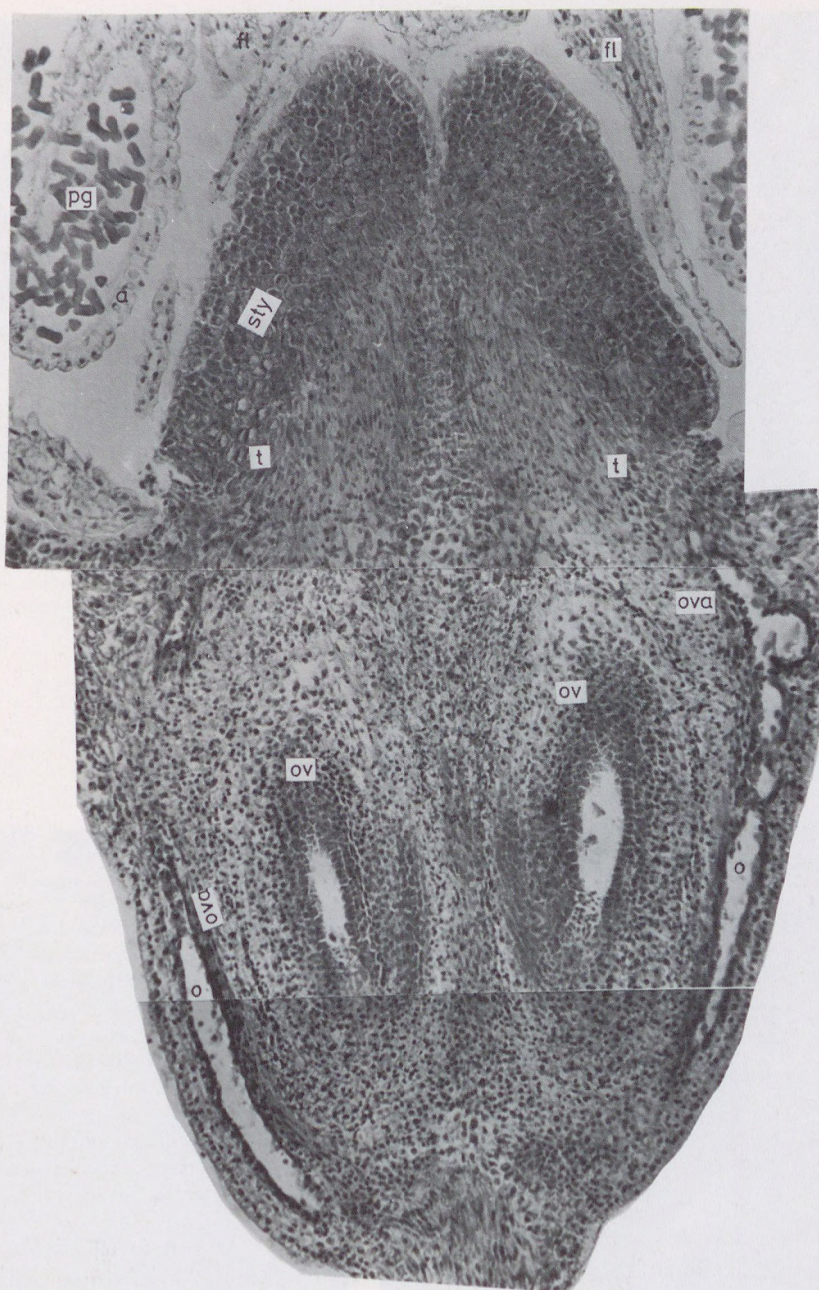
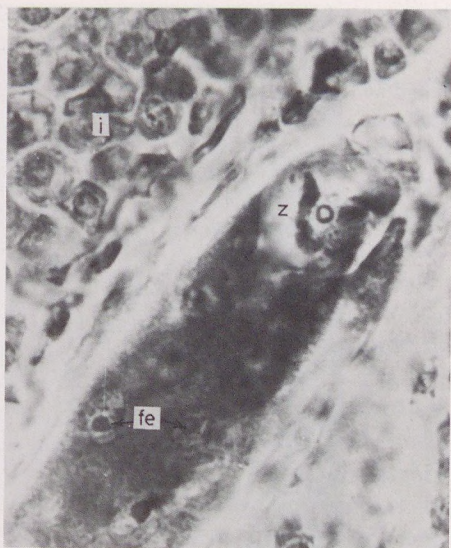


Fig. 104. Longitudinal section of the gynoecium ($\times 150$, photo: E.B. Szikszai, a = anther, fl = flower, o = oil duct, ov = ovule, ova = ovary, pg = pollen grain, sty = stylopodium, t = trace)

105



106



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Fig. 105. Embryo sac of coriander ($\times 880$, photo: E.B. Szikszai, egg = egg cell, es = embryo sac, i = integument, pt = pollen tube, sy = synergid)

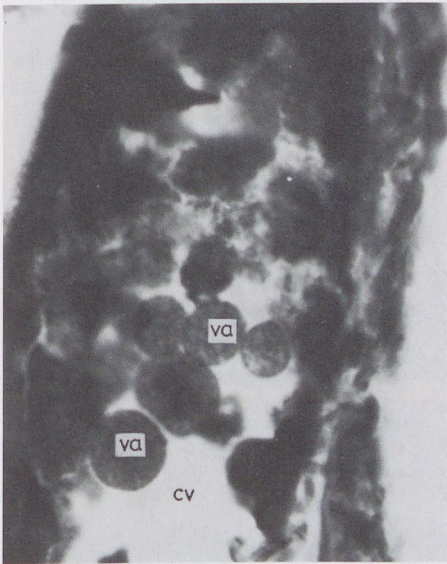
Fig. 106. Elongated zygote (z) and free endosperm nuclei (fe) in the embryo sac ($\times 880$, photo: E.B. Szikszai, i = integument)

Fig. 107. Coenocytic stage around the 'rest' zygote (z) ($\times 880$, photo: E.B. Szikszai, cv = central vacuole, fe = free endosperm nuclei)

128 free endosperm nuclei. The author observed the same vesiculation process in species such as *Anethum graveolens*, *Daucus carota*, *Heracleum sphondylium*, and *Psammogeton biternatum* though the origin and role of pinocytosis could not have been elaborated. The topography of vesicles inside the embryo sac may lead us to the conclusion that their formation has something to do with the formation

of certain secreting cell groups, such as hypostase, antipodal cells and dissolving integumental tapetum cells. As a result of the pinocytosis in these cell groups the content of the central vacuole is increased. Vesicle membranes are incorporated into the tonoplast of the vacuole. Soon pinocytosis comes to an end, when the whole volume of the central vacuole, a onefold coenocytic state, has been formed by a parietal arrangement of free endosperm nuclei (Fig. 107).

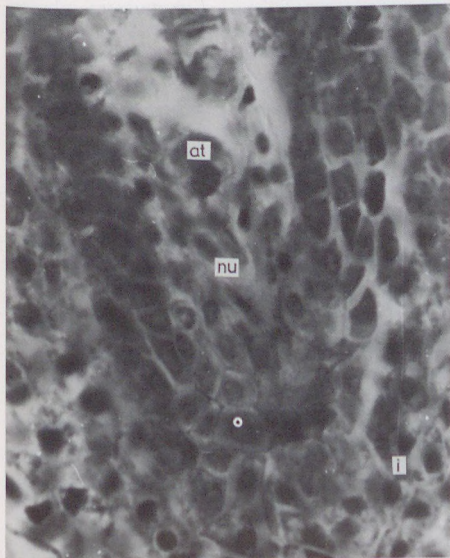
Fig. 108. Vacuoles (va) of pinocytic origin in the embryo sac ($\times 880$, photo: E.B. Szikszai, cv = central vacuole)



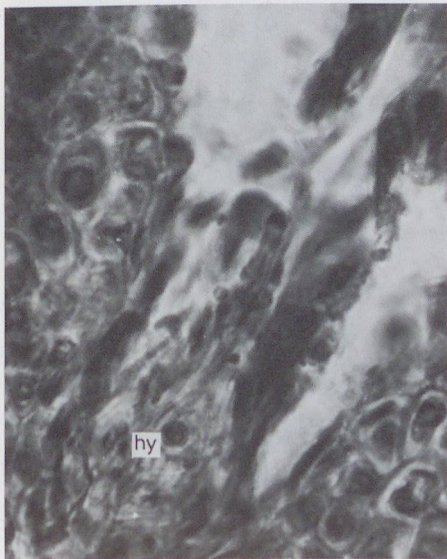
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Fig. 109. Hypostase under antipodal cells (at) in the embryo sac in phenophase 31.3.1 ($\times 880$, photo: E.B. Szikszai, i = integument, nu = nucleolus)

Fig. 110. Elongated hypostase (hy) cells in phenophase 32.3.3.1 ($\times 880$, photo: E.B. Szikszai)



109



110

The hypostase in phase 31.2.2 of development surrounds the chalazal apex of the embryo sac and consists of 12–13 large cells (Fig. 109). Above the lower cell row, in a radial position, additional large cells with large nuclei touch the embryo sac, to about the level of polar cells. According to Adatia and Shah (1952) and Gupta (1964), these cells make up the hypostase in coriander. In phase 32.3.3.1 cells of the hypostase are lengthened (Fig. 110), and among them a pit develops. Adatia and Shah (1952) and Gupta (1964) argue that the hypostase is a secretory cell group of nucellar origin in coriander and it functions only for a short time. In *Anethum graveolens*, however, the hypostase cells surrounding the pit under the embryo sac show an opposite behaviour. They function until the coenocytic state has been reached (Szujkó-Lacza 1978).

In the embryo sac of the coriander, nuclei in the coenocytic state are almost sphere-shaped near the zygote (Fig. 106), further from it are lengthened and appear almost pointed (Figs 111, 112).

The zygote with a double cell wall will not undergo cell division in the course of the coenocytic process but its shape will significantly change. Before fertilization egg is almost square then it takes on the shape of a drop (Fig. 107) and later its apex will become pointed (Fig. 106). The nutrition of the zygote is continuous from the direction of synergids and integument (Figs 106, 107). The micropyle above the zygote remains open until the end of coenocytosis (Fig. 112) and obturator, transmitting cells also retain their normal shape.

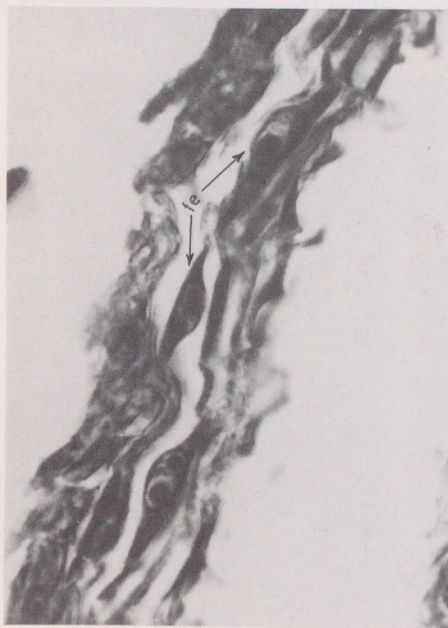


Fig. 111. Taper form endosperm nuclei at the side of the embryo sac ($\times 880$, photo: E.B. Szikszai, fe = free endosperm nuclei)

112

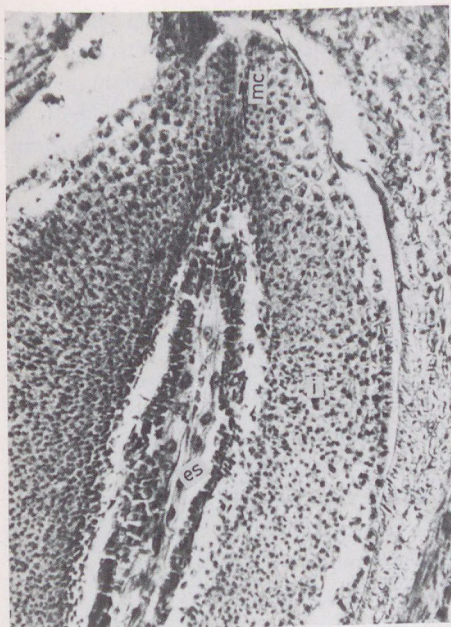


Fig. 112. Open micropyle (mc) in the coenocytic stage ($\times 150$, photo: E.B. Szikszai, es = embryo sac, i = integument)

113

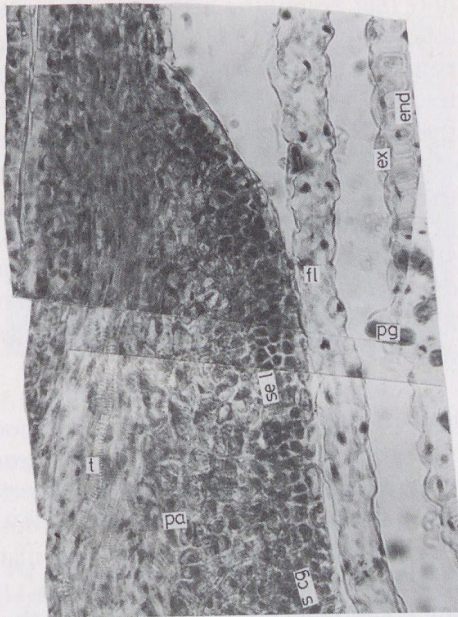
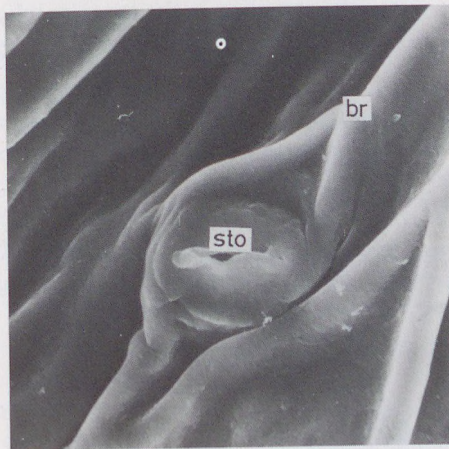


Fig. 113. Structure of the stylopodium in phenophase 3I.3.I ($\times 150$, photo: E.B. Szikszai, end = endothecium, ex = exothecium, fl = flower, pa = parenchyma, pg = pollen grain, scg = secretory cell group, sl = secretory layer, t = trace)

Fig. 114. Stomata (sto) in the stylopodium (SEM $\times 4000$, photo: E. Gondár, br = bridge)



114

In phase 3I.3.I the stylopodium consists of small cells that stain strongly. There are parenchymatous secretory tissues under and between stomatal pores whose function has modified. Those below the stomatal pores form hemispheres and those between the pores form columns of 3-4 cell rows. This layer is followed by a zone of somewhat larger cells, which is rich in cytoplasm. In the third zone, cells are positioned in the vertical direction and among them bundle elements can be seen (Fig. 113), some of which continue in the style. It may be interesting to

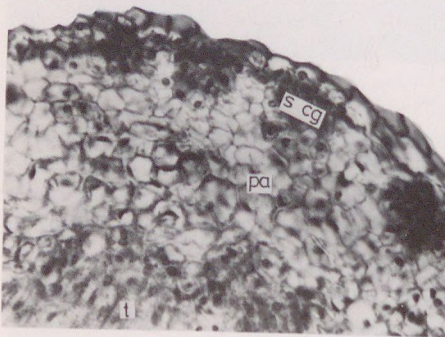
note that examining nectary in *Acer platanoides*, Vassilyev (1969) was led to the following conclusion: 'It is assumed that the sap exuded by the phloem does not penetrate into the protoplasm of nectary cells, but mostly trickles through the free space within the cell walls. Apparently, the function of the nectary cells is the enzymatic conversion of sugars transported from the phloem and the control of the content accumulating non-sugary compounds by means of their active transport in the opposite direction, i.e., to the phloem.' Stylopodium structure in coriander refers to an active transport of sugars and dissolved material. Stomata developed on the stylopodium are small (Fig. 114), and according to Gupta (1970), stomata in the Umbelliferae belong to the anomocytic or anisocytic types depending on whether they can be found on stylopodium or in pistil wall, respectively.

In phases 32.3.1–32.3.4 the embryo sac is in the coenocytic state, and by this time the majority of cells of the stylopodium have already been vacuolized (Fig. 115) with the exception of the cell groups under the stomata that form hemispheres (Fig. 116). In this phase of development styles have got farther from each other and on stigma surface nectar drops have appeared (Figs 37, 39). The cuticle is wrinkled and sunken over the papillate epidermal cells (Fig. 42) and there are germinating pollen grains on it (Figs 117, 118). Sphere-shaped nuclei of secreting epidermal cells can be found at the cell base (Figs 117, 118).

This phenomenon is the same as what was observed by Owens et al. (1984) in species that belong to the Commelinaceae family. Presumably, the subepidermal

Fig. 115. Stylopodium in secretory stage (phenophases 32.3.3–32.3.4) ($\times 150$, photo: E.B. Szikszai, pa = parenchyma, s cg = secretory cell group (gland), t = trace)

Fig. 116. Distribution of glands in the stylopodium ($\times 350$, photo: E.B. Szikszai, pa = parenchyma, se l = secretory layer, t = trace)



115



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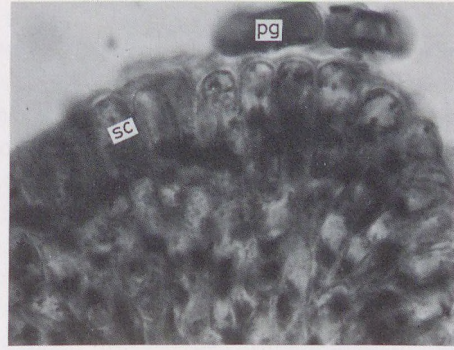
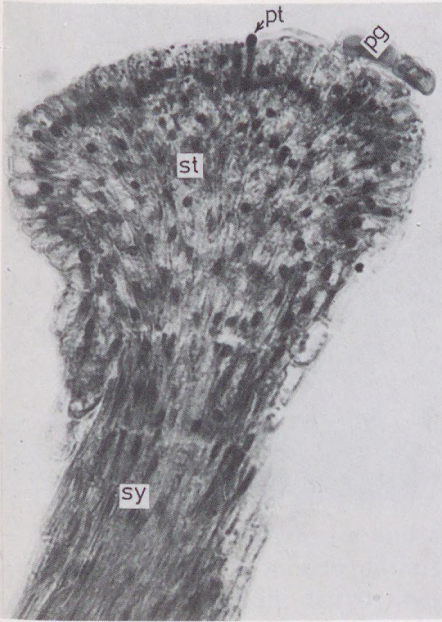


Fig. 117. Longitudinal section of the receptive stigma (st) ($\times 150$, photo: E.B. Szikszai, pg = pollen grain, pt = pollen tube, sy = style)

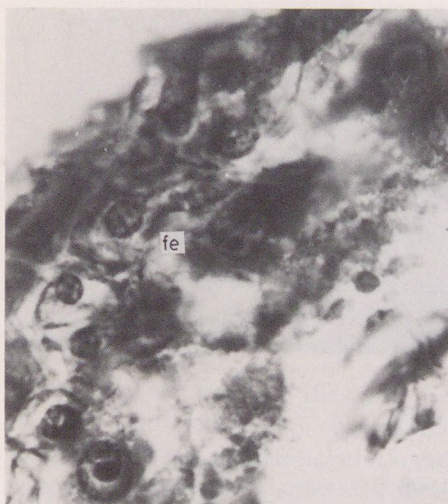
Fig. 118. Germinating pollen grains (pg) on the stigma surface ($\times 880$, photo: E.B. Szikszai, sc = stigma cells)

layer takes part in the production of secreted material that comes to surfaces of epidermal cells. In this approach the stigma structure of the coriander differs from what was described by Kandasamy and Kristen (1987) but coincides with the general 'wet stigma' structure of Dumas et al. (1974). They characterized the stigma as a secretory organ associated with the 'sexual sphere' in the reproduction. Coriander stigma cells that form spheres (Figs 117, 118) gradually turn into a cylindrical style parenchyma layer. In the style there are one or two vascular bundles associated with their oil ducts and surrounded by a parenchyma layer. The style structure is solid.

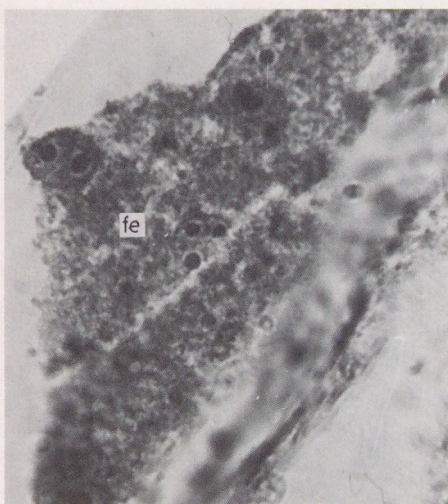
In coriander germinating pollen grains on stigma surface can be observed in the final phase of coenocytosis.

After the 256 free endosperm nuclei have come into existence, the following step of the process is the fusion of nuclei and nucleoli (Figs 119, 120). There is no consensus in the literature on the question as to what kind of process produces the cells of distinct ploidy in the secondary endosperm tissue. The process may involve earlier fusions or endoploidy. The following events can be observed at the end of the coenocytic phase. At first membranes of two or three nuclei touch each other, then the fusion of nucleoli occurs (Fig. 120), which is followed by an extremely intensive vesiculation (Figs 121, 122). From the direction of the integument, wall ingrowth of the embryo sac is an indication that a stream of metabolites, presumably polysaccharides, moves through on it (Szujkó-Lacza et al. in press). A part of the material that constitutes the large central vacuole inside

119



120



121



Figs 119, 120. Fusion of free endosperm nucleus (fe) and nucleoli ($\times 880$, photo: E.B. Szikszai)

Fig. 121. Vesiculation process in different parts of the embryo sac ($\times 880$, photo: E.B. Szikszai, es = embryo sac, fe = free endosperm nuclei, i = integument, sy = synergid, v = vesicle, z = zygote)

the embryo sac, may get into the cytoplasm of the endosperm as tiny vesicles, by exocytosis (Fig. 123). As far as I know, it has never been mentioned in the literature that the central vacuole takes part in cell wall biogenesis in higher plants. (In the coenocytic state the fluid that fills the central part of the embryo sac and its tonoplast are usually called the central vacuole.) As the origin of the 'central vacuole' has not been known so far, it may also be assumed that it is in

part an immense sacculus of dictiosomal origin (Popova and Szujkó-Lacza 1990). The nutrient and enzyme content of the central vacuole takes part in cell wall formation. The central vacuole increases as a result of the pinocytosis of the cell population of the integument through the embryo sac wall. (Analogous cases are known in some algal species living in coenocytic state.)

The fact that the function and origin of the central vacuole of the embryo sac has not been elucidated suggests that the vacuoles are different in respect of origin as well as function.

Vesicles of different sizes and vacuoles formed the fusion or incorporation of smaller vesicles. The vesicles seem to be combined by their membranes along wall ingrowths of the embryo sac. This double origin in the process is increased by the participation of the cisternal endoplasmic reticulum (ER) in the production of vacuoles. Presumably, in the first step the cisternal ER and/or the content of vesicles of dictiosomal origin dissolve the cytoplasm among free endosperm nuclei (Fig. 122) and their membranes create and grow the cell plate (Fig. 123), whose conversion into cell wall in the endosperm tissue still requires further steps. In addition to vesicles and smaller or bigger vacuoles the cytoplasm contains leucoplasts, mitochondria that gather near cell plate (Fig. 123), oil drops, and occasionally dictyosomes (Fig. 122). Greater vacuoles sometimes incorporate cell organelles or parts of cell organelles (Figs 122, 123). This

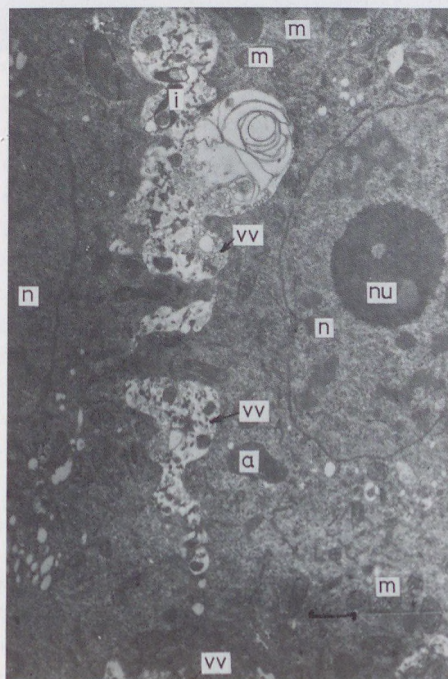
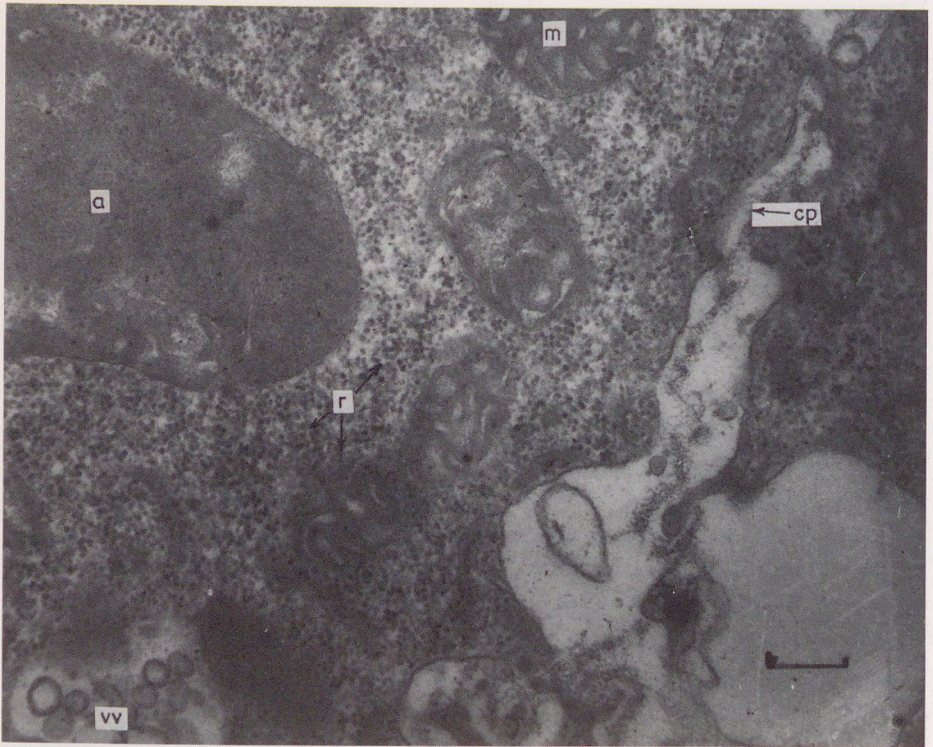
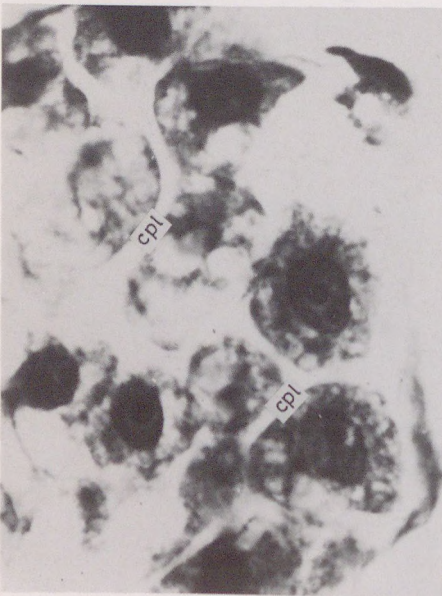


Fig. 122. Convolute chain of vesicles and vacuoles (vv) between the two free endosperm nuclei (scale bar: 200 nm, photo: A.F. Popova, a = amyloplast, i = incorporated organelles, m = mitochondrion, n = nucleus, nu = nucleolus)



123

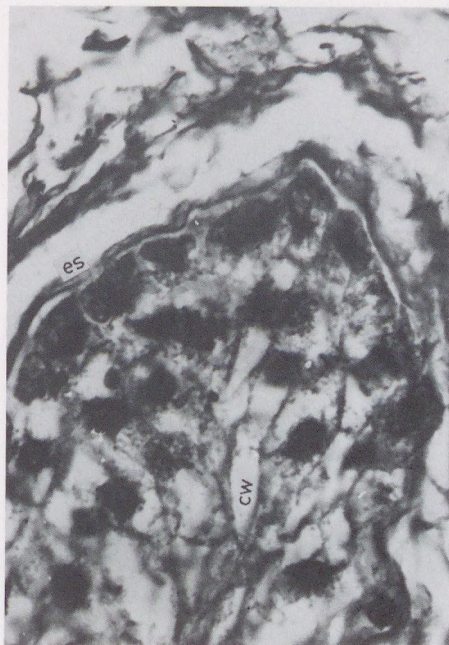


124

Fig. 123. Dissolution of cytoplasm and cell plate (cp) formation (scale bar: 500 nm, photo: A.F. Popova, a = amyloplast, m = mitochondrion, r = ribosomes, vv = vesicles and vacuoles)

Fig. 124. 'Separated' cytoplasm around the free endosperm nucleus ($\times 880$, photo: E.B. Szikszai, cpl = cell plate)

Fig. 125. Primary cell wall in the secondary endosperm tissue ($\times 350$, photo: E.B. Szikszai, cw = cell wall, es = embryo sac)



incorporation in the course of the development of convolute cell plate and cell wall of the endosperm, and the presence of a quite large number of mitochondria implies an intensive cytoplasmic streaming and respiration.

The formation of endosperm cell plate and cell wall is simultaneously controlled by wall ingrowths of the embryo sac from the direction of the integument, the osmotic pressure and the content of the central vacuole inside the embryo sac, and pieces of information coming from nuclei (Szujkó-Lacza et al. in press).

Examining the process with the aid of a light-microscope in coriander, greater areas can be observed (Figs 124, 125). Cell differentiation begins more or less simultaneously in the tissue of the secondary endosperm that bears cell wall and in the zygote. During the period when the embryo is sphere-shaped the endosperm consists of a single layer on the micropylar side and 2–3 cell rows on the chalazal side.

EMBRYO DEVELOPMENT

Gupta (1960, 1964) and Kordyum (1967) examined embryo development in coriander. Gupta (1964) scrutinized the development of the proembryo. According Gupta (1964), first the zygote divides into two cells in transversal direction and then the resulting two cells divide again in the same direction, forming the

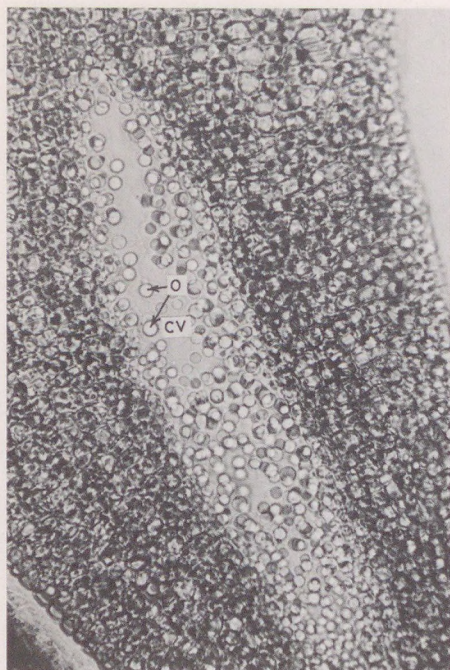


Fig. 126. Oil drops (o) in the secondary endosperm tissue; site of cotyledon touched with remained central vacuole (cv) ($\times 150$, photo: E.B. Szikszai)

four-celled linear proembryo. It is also possible, however, that of the first two cells only the basal one divides again in transversal direction.

The octane (8-celled embryo) develops from the three lower cells of the four-celled proembryo. Cotyledons derive from the apex, while the hypocotyl and the radicle derive from the apical cell. If both cells divide, then the long suspensor that consists of two cell rows derives from the basal cell of the proembryo. According to Pillai and Kumar (1983), the plumule of the embryo at its apex can be flat or concave, with a definite outer cell row. The tunica consists of a group of chromophil cells and the corpus involves as few as 4–6 cell rows. The phenomenon that the tunica consists of a single cell layer is generally characteristic of species that belong to the Umbelliferae family (Rauch and Rappert 1954, in Guttenberg 1960). Initial cells of the stele are wide and are similar to stele found in species of several dicotyledon families (Heydel 1958, in Guttenberg 1960). The pleroma is normal or Cruciferae type.

In the carpel of the coriander, after the cell wall biogenesis and cell differentiation of the secondary endosperm, cells are gradually saturated with nutrient reserve, which consists of aleuron, starch, and oil (Fig. 126). In cells of an embryo of the Solanoid type when it takes on the shape of a horseshoe oil drops appear similar to those with which the secondary endosperm cells are saturated (Fig. 127). Cells of the embryo touch the membrane of the central vacuole (Figs

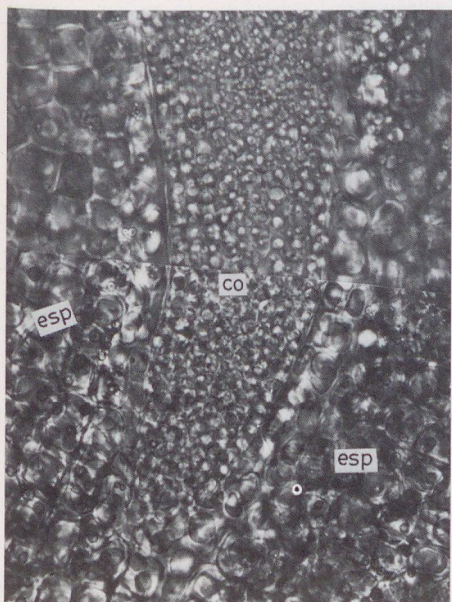


Fig. 127. Endosperm (esp) and cotyledon (co) filled with oil drops and other nutrients ($\times 350$, photo: E.B. Szikszai)

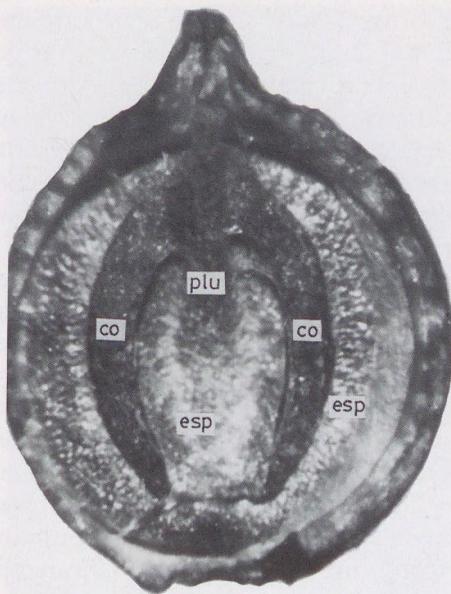


Fig. 128. Longitudinal section of the coriander fruit ($\times 22$, photo: E.B. Szikszai, co = cotyledon, esp = endosperm, plu = plumula)

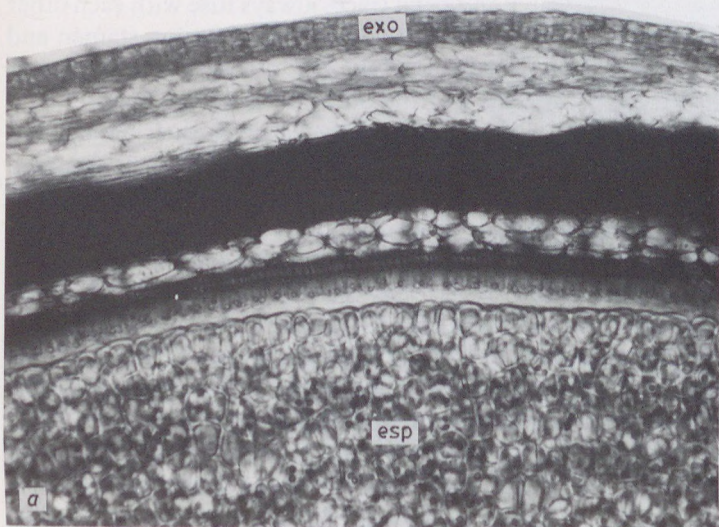


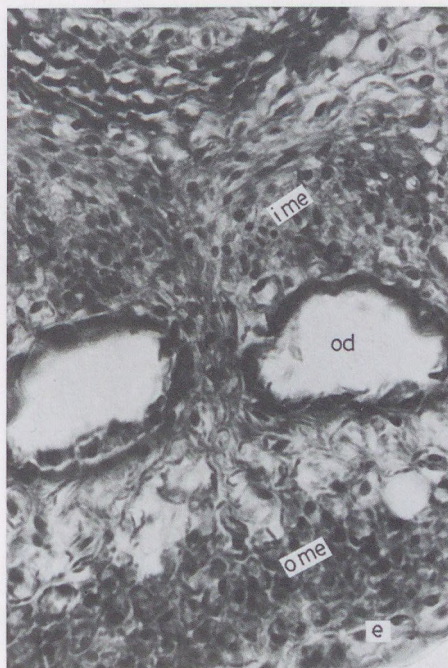
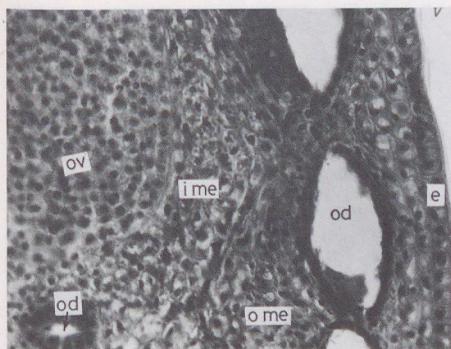
Fig. 129a. Transverse section of pericarp and endosperm (esp) ($\times 150$, photo: E.B. Szikszai, exo = exocarp); b. Detail of slightly thickened parenchymatous wall endocarp (ec) and the remained one-cell row integument ($\times 350$, photo: E.B. Szikszai, me = mesocarp)

126, 127). In the mature schizocarp the radicle is short while the falcate cotyledon is large (Fig. 128). Hence, it is possible that the exocytosis of the central vacuole is continuous also towards the embryonic tissues. The integument in coriander still consists of many cell layers at the time of endospermal cell wall development, but later, parallel with the development of the embryo and the endosperm, its cell rows decrease in number. The most cell rows remain near the carpophore. The only single cell row that remains is the one touching the endothecium (Figs 129a, b). In phase 32.2 the carpellary wall consists of two well-discernible layers, of which, in the inner layer at each carpophore there are only two still undeveloped oil ducts (Figs 97, 98, 130), whereas in the outer layer there are various size oil ducts that are already active and which will turn into schizogenuous ducts later (Figs 130, 131, 132). Between the large oil ducts one may occasionally discern the trace of the fused calyx leaves (Fig. 131). In the carpel wall, too, oil ducts are also associated with vascular bundles. These bundles are rich in phloem, but not in xylem, elements (Figs 131, 132).

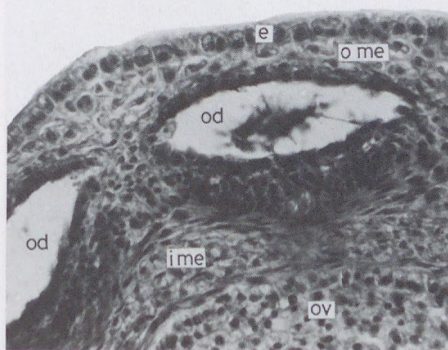
The interpretation of the inferior ovary is closely related to studies concerning bundle and/or pistil development. According to most European authors, the sporogenuous leaf (carpel) is covered by an axial tissue in the inferior ovary of species that belong to the Umbelliferae family. Authors of the other group, the Anglo-Saxon sphere, argue that the inferior ovary is appendicular in origin. They reject the hypothesis that the direction of vascular bundles refer to the fact that axial tissues have grown into the carpel. They claim that the direction of bundles should lead one to the conclusion that sepals, petals, stamens and carpels have perfectly grown together. Calyx and petal traces always fuse with each other and then, at the origin of the filament, they diverge again, forming stamen and calyx traces. The number of vascular traces in the Hydrocotyleideae subfamily is 10, out of which five are petal veins and the other five are sepal veins.

As sepals, petals and stamens being grown into the carpel at their basal parts, their vascular traces lie fused in the same radius, demonstrating their common origin. They originate from the central vascular cylinder, and they branch only later, in the upper part of the carpel, towards different organs (Roth 1977). According to Tseng (1967), however, only five outer traces and the trace of the carpophore belong to each mericarp. In each mericarp of the coriander there are 15-17 oil ducts that differ from each other in size and a corresponding number of independent vascular traces, which show all vascular trace and oil duct complexes of the ancient sepal, without a total fusion of the ancient sepal traces. Hence, the facts in coriander coincide with neither the opinion of the Anglo-Saxon authors nor the conclusions of Tseng which he deducted concerning other species of the family. Calyx leaf traces continue in calyx teeth while traces in alternating petals and stamens diverge towards the corresponding organs in the neck of the stylopodium. Within the Apiodeae subfamily the coriander seems to have evolved in an early period in respect of development and fusion and remained that way. This hypothesis is also supported by the calyx teeth of

130



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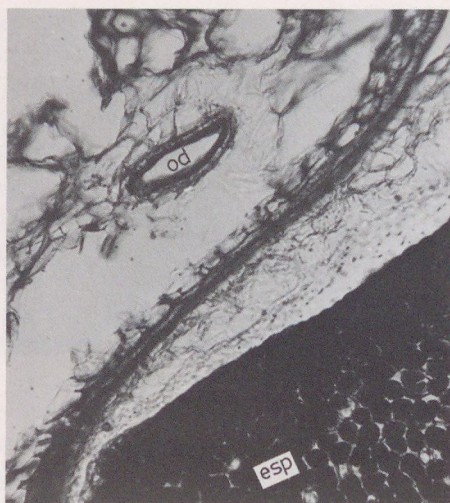
Figs 130, 131, 132. Cross-section of different parts of the ovary in phenophase 32.3.2 ($\times 150$, photo: E.B. Szikszai, e = epidermis, ime = inner mesocarp, od = oil duct, o me = outer mesocarp, ov = ovule)

unequal length and the great number of complexes of traces and oil ducts. Presumably, the dill (*Anethum graveolens*) and the anise (*Pimpinella anisum*) are more developed, that is, more reduced, members of the same subfamily since in these species any trace of the calyx is absent (Szujkó-Lacza 1976). Concerning the origin of coriander ovary (Figs 133, 139), DeCandol's (1827, cf. Puri 1978) opinion seems to have been verified.

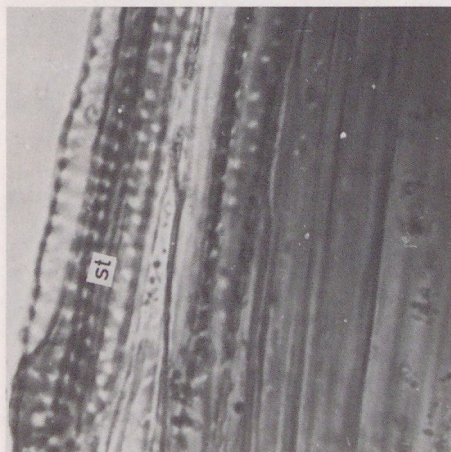
By the time of the development of the cellular secondary endosperm, the oil ducts on the abaxial side of the 'mesocarp' of calyx leaf origin collapsed and ceased to function (Gupta 1964, Lassányi and Lörincz 1970). Furthermore, the



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Fig. 133. Young carpel with carpophore (car) (SEM $\times 400$, photo: E. Gondár, esp = endosperm, exo = exocarp, me = mesocarp)

Fig. 134. Structure of the pericarp beside the carpophore and reserved nutrients in the endosperm (esp) ($\times 150$, photo: E.B. Szikszai, od = oil duct)

Fig. 135. Longitudinal section of the ripened carpophore ($\times 450$, photo: E.B. Szikszai, st = sclerified trace)

previously functional vascular traces became sclerified by this time (Figs 129a, 134). The carpophore, which consists of xylem and fibre elements and which used to contain mainly helical proto- and metaxylem thickenings in its earlier stage already thickened by this time (Fig. 135). The large oil duct at the carpophore (Figs 137, 138) is still active and will retain its activity until the saturation of the endosperm tissue, when its epithelial cells will collapse (Fig. 138). Lassányi and Lőrincz (1970) also observed differences in oil components of abaxial and adaxial oil ducts.

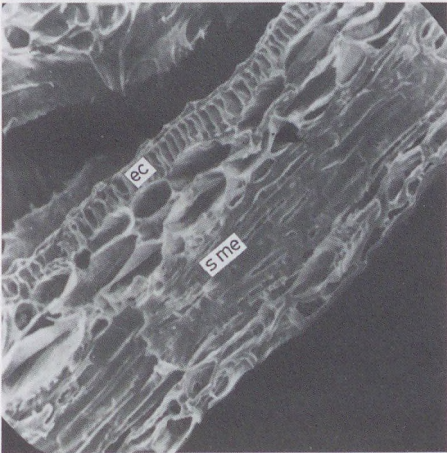
The carpel wall of the coriander is the pericarp. It is composed by several layers in the following order from inside out. First, there is an endocarp of a single cell layer with wavy striped wall thickenings, whose cells are positioned

as parquet staves and take on the hemisphere shape of the fruit (Roth 1977) (Figs 129a, 136, 139). Then comes the layer of the sclerified vascular bundles. The vascular bundles are followed by a less solid parenchyma layer. Finally comes the exocarp, which is of epidermal origin. Cell arrangement in the exocarp is almost radial around the previous stoma meristem initials (Fig. 140).

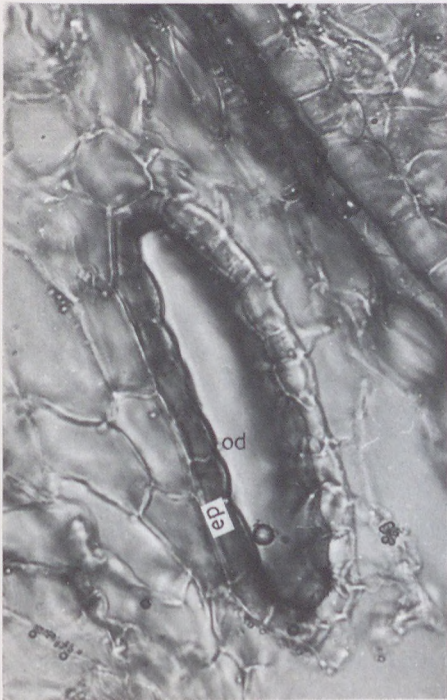
Fig. 136. Pericarp structure with sclerified mesocarp (s me) ($\times 3000$, photo: E. Gondár, ec = endocarp)

Fig. 137. Oil duct with active epithelial cells (ep) beside the carpophore ($\times 350$, photo: E.B. Szikszai, od = oil duct)

Fig. 138. Oil duct with inactive epithelial cells (c ep) beside the carpophore ($\times 350$, photo: E.B. Szikszai, c ep = collapsed epithelial cell, od = oil duct)



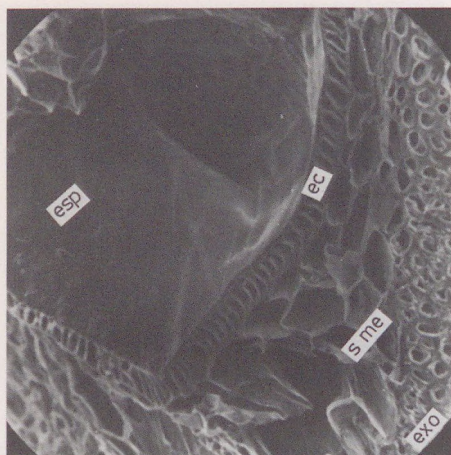
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Fig. 139. Pericarp structure at the chalazal end (SEM $\times 3000$, photo: E. Gondár, ec = endocarp, esp = endosperm, exo = exocarp, s me = sclerified mesocarp)



140

Fig. 140. Epidermis of the pericarp ($\times 14$, photo: E.B. Szikszai, sto = stoma)

The mericarp in dill and anise is characterized by outer ribs and furrows, which also shows the distribution of vascular bundles and oil ducts in the mericarp. The coriander, however, is characterized by another kind of outer appearance and inner structure.

According to Roth (1977), the pericarp usually consists of three layers: there is an outer exocarp of a single cell row, which corresponds to the epidermis, then there comes a mesocarp, often parenchyma-like, and finally there is a parenchymatous or prosenchymatous endocarp. As a result of metamorphoses, the mesocarp can be divided into an outer part and an inner part. The inner part often bears lignified cell walls. The testa has grown into the pericarp. Where there is a sclerenchymatous layer in the pericarp, the testa is less developed. Contrary to this, where there is no sclerenchyma, the testa becomes thicker, and may range up to 6 mm in diameter in *Conium* and *Carum*. In *Hydrocotyle* and *Coriandrum*, the testa together with a hard layer in the pericarp are only 2.5 μm in diameter and consist of 1–2 cell layers.

According to Roth (1977), the inner epidermis (endocarp) of the *Coriandrum sativum* is one-layered. Its elements often have thin walls and parquet-like (V-shaped) patterns, which latter come into existence as a consequence of a parallel cell division of mother cells. These epidermal cells are often lengthened tangentially or become prosenchymatous.

Tseng (1967) makes the following general remarks on volatile oil ducts of mesocarp in Umbelliferae: The secreting part is of schizogenous origin, or it is a continuous oil duct. If it is a continuous duct it links to the vascular bundle as a companion canal or, more often, serves as an oil-storing hole, whose end can be found under the peduncle.

CALYX TOOTH

The epidermis of the calyx tooth is rich in stomata, which are small in size. Its surface is covered by a slightly waved cuticle (Figs 141, 142). Diverging calyx teeth on the green fruit are somewhat reclinate, hence the epidermis on the abaxial side is strongly crumpled. Under the calyx teeth epidermis there are tiny circle-shaped mesophyll cells. The following layer consists of a few larger parenchyma cells with chloroplast content. The branching vascular traces with their oil ducts are embedded in this layer.

The trace is surrounded by bundle sheath parenchyma. On the adaxial side there develops a regularly lengthened palisade parenchyma (Figs 143, 144), which may even consist of two cell rows in the case of larger calyx teeth. The



Fig. 141. Papillate calyx tooth surface (SEM $\times 2000$, photo: E. Gondár, cu = cuticle, sto = stoma)

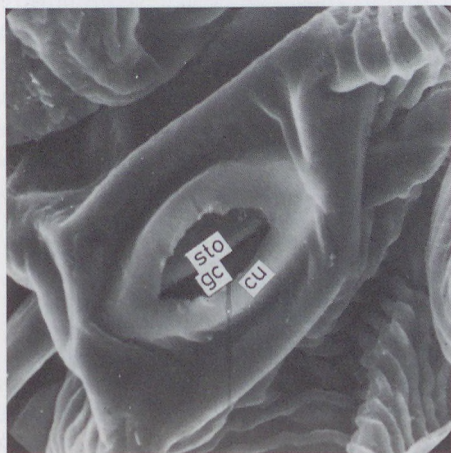
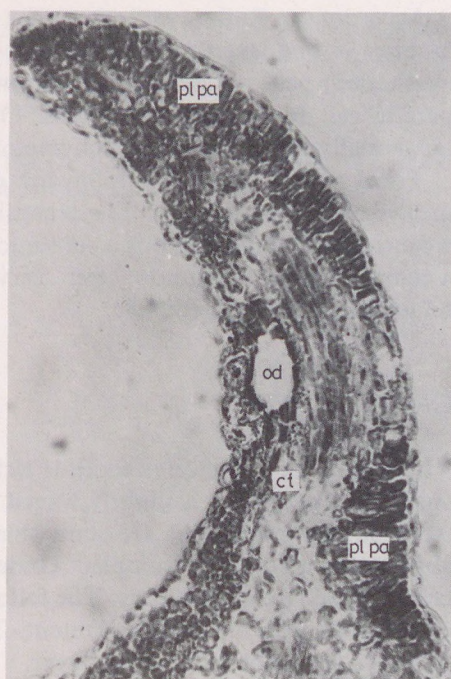


Fig. 142. Small stomata (sto) in the calyx epidermis (SEM $\times 6000$, photo: E. gondár, cu = cuticle, gc = guard cell)



143



144

Figs 143, 144. Longitudinal section of a long and a short calyx tooth (ct) ($\times 150$, photo: E.B. Szikszai, a = anther, e = epidermis, od = oil duct, pe = petal, pl pa = palisade parenchyma)

unequal length of calyx teeth might refer to the fact that during the course of flower development these teeth must have been 'leaves' originating at different levels, which, by the reduction of internodes, have grown together with the sporogenous leaves above them, forming the flower. Now, only their apices have remained, serving as calyx teeth. It is more likely, however, that a schizocarp has grown together with fringes of the uppermost two leaf blades under it, apices of pinnules serving as calyx teeth. Umbellet rays in the umbel show a similar asymmetry.

CARPOPHORE

In coriander the carpophore originates from two traces of bundles. These traces are divergent. The funicle of the ovule develops from one branch and the carpophore develops from the other one (Figs 97, 98). The carpophore trace in the young pericarp is still only a tiny independent trace bundle, which mostly consists of proto- and metaxylem elements. The xylem elements are short, branching, and later they become strongly sclerified (Fig. 135). The traces that

still stand far from each other in the ovary and in the young carpel gradually turn into a column that is wider at its basal part and becomes narrower at its upper part: this is the carpophore (Figs 133, 145). According to Jackson (1933), carpophore bundles are to be derived from fused adaxial traces of the carpel. The author argues that in an earlier phase of evolution the adaxial vascular bundle used to be the first and sixth bundle of the sporophyll. These bundles located next to each other as a result of the modification of the sporophyll and grown together. The central vascular bundle of the carpophore has developed in a similar way in other species such as *Aegopodium podagraria*, *Daucus carota* and *Pastinaca sativa*. In coriander the two mericarps remain together even when they are mature. They will separate from the carpophore only after drying (Fig. 145).

According to Jackson (1933) and Gupta (1964), the carpophore is of receptacle or axial origin in its basal part, while it is of appendicular origin in its upper part. Puri (1951) states the carpellar origin of the carpophore. The carpophore image of the coriander (Figs 133, 145) supports Puri's opinion. According to Tseng (1967), between the mericarp and the carpophore there is a parenchymatous, separative, tissue. This mechanical tissue ranges from the outer epidermis to the middle of the fruit, forming a cuneate shape along the separating line. In coriander this parenchyma does not function as a separative tissue but its look coincides with that Tseng (1967) has described (Fig. 146).



Fig. 145. Ripened mericarp with carpophore (car) ($\times 14$, photo: E.B. Szikszai, co = cotyledon, esp = endosperm, perc = pericarp, st = style)



Fig. 146. Cross-section of separation tissue containing carpophore (car) ($\times 150$, photo: E.B. Szikszai, cv = central vacuole, se t = separation tissue)

PETALS

Petals originate in the neck of the stylopodium (Szujkó-Lacza 1976) and alternate with the filaments. The two halves of each reclinate petal cover neighbouring halves of two anthers. The other halves of the anthers are covered by other half petals (Figs 6, 13, 14, 18, 147). In phase 31.1.2 petal epidermis cells are scarcely wavy or have a perfectly smooth surface. The mesophyll is meristematic (Fig. 95), the oil duct associated with the central vascular bundle consists of cells with large nuclei and cross-walls that are still entire.

Between phases 31.1 and 31.2.1 outer flowers of the umbel are asymmetric. Out of the five petals one has lengthened so that it resembles a propeller. These are the ray flowers (Figs 5, 147). The lengthened petals are reclinate and up to their shoulders they contain large epidermal cells, among which stomata can be found. Parenchyma cells of petals stand loosely, oil ducts are already cisternal or tube-shaped, and their epithelial cells are rich in cytoplasm. Lofty apices of these same petals, however, still consist of meristematic tissues (Fig. 147). Tissue differentiation in middle flowers of the umbel is similar to those of ray flowers.

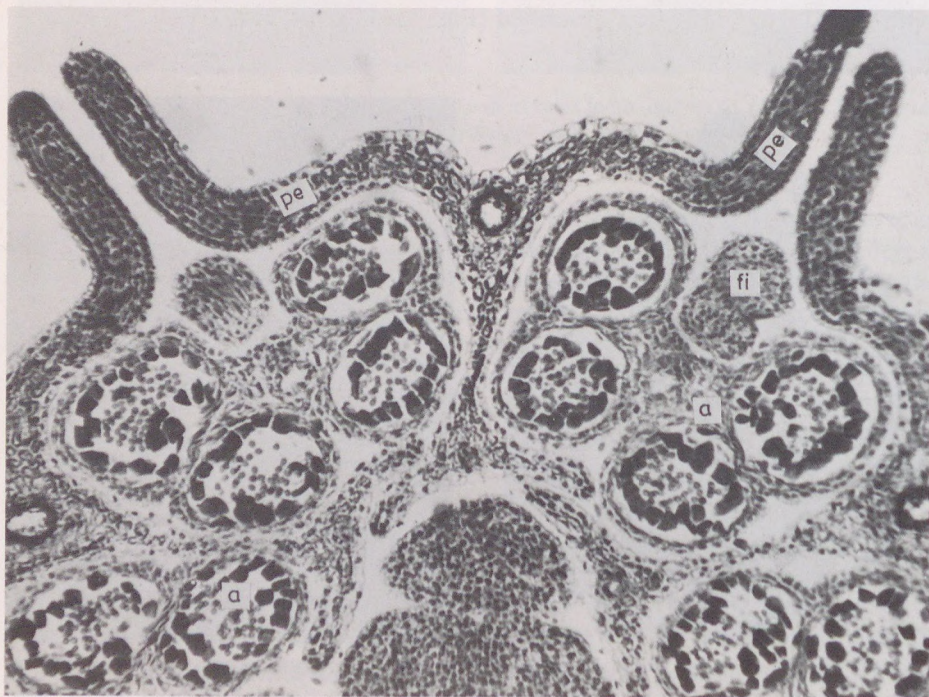


Fig. 147. Cross-section of flower bud with petals (pe) and anthers (a) ($\times 150$, photo: E.B. Szikszai, fi = filament)

148



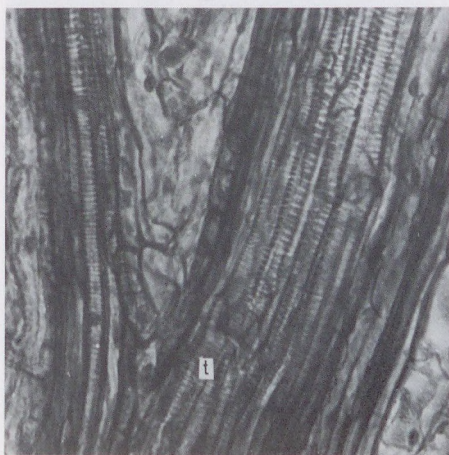
Fig. 148. Transverse section of petal (pe) and anther (a) wall ($\times 350$, photo: E.B. Szikszai, od = oil duct, pap = papillae, pg = pollen grain)

Fig. 149. Stomata (sto) in the petal epidermis (SEM $\times 6000$, photo: E. Gondár, cu = cuticle)



149

Fig. 150. Branched vascular trace (t) in the petal ($\times 150$, photo: E.B. Szikszai)

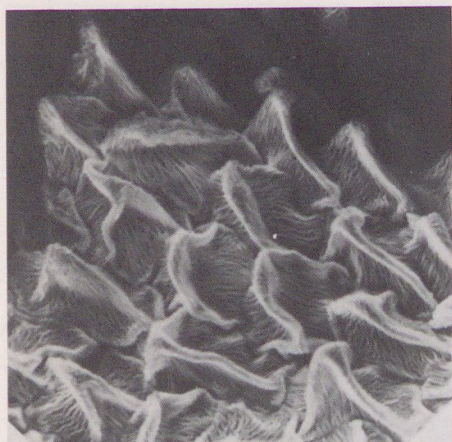


150

The development of petals in the middle flowers is also similar to the ray flowers but they are entirely reclinate. Microsporogenesis in anthers under these petals has still reached only the tetrad stage.

In phase 31.2.2 in the outer flowers both the mesophyll and the epidermis of petals have undergone a remarkable change. Mesophyll cells have large nuclei and they are rich in cytoplasm. Epidermal cells have turned into large papillae (Fig. 148). In anthers, which are still protected by petals, the tapetum cells and the middle layer have been dissolved. The exothecium, which has a wavy surface, and the endothecium, which is slowly becoming fibrillate, have both developed.

Mesophyll cells of the entirely developed petal have become much larger. Among them there are large intercellular spaces. Its epidermis depends on petal topography. It is irregularly wavy along the midrib of the open outer flower, with



151



152



153

Figs 151, 152, 153. Pattern of papillose cells in different particles of the petal (SEM, Figs 151, 152: $\times 2000$, Fig. 153: $\times 6000$, photo: E. Gondár)

tiny stomata (Fig. 149). In the mesophyll, vascular traces associated with oil ducts are branching and surrounded by bundle sheath parenchyma. They are characterized by the dominance of xylem elements (Fig. 150). The adaxial side of ray petals of the flower, which side used to touch the anther, is typically papillate now. Shapes of papillae show a wide variety in various parts of petal (Figs 151, 152, 153). From among the entirely developed petals, the stamens bend out and the anthers are still closed (Fig. 19).

Parallel with the differentiation of its tissue, the function of the petal also undergoes a change. In the partially open flower the inflected half petals, which still partially or totally consist of meristematic tissues, tightly cover anthers so as to 'guard' them. By the time the flower fully opens differentiation results in a significant change in structure and then the main function of petals appears to be volatile oil production.

MICROSPOROGENESIS

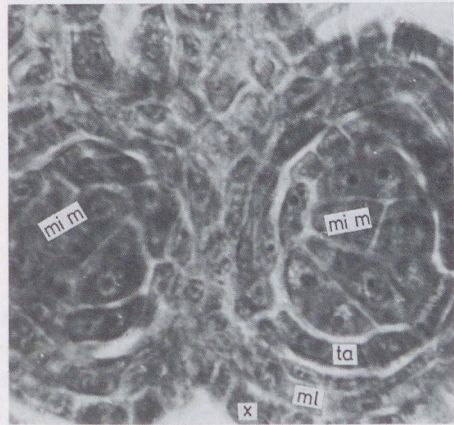
The one-layered archesporium undergoes a hypodermal differentiation in every microsporangium. The primary parietal layer divides periclinally (Fig. 154), resulting in the middle layer, and the tapetum. The middle layer could be partially two layered. Out of these three layers it is the tapetum that immediately surrounds the microspore mother cells (Fig. 155). The sporogenous tissue becomes multi-layered by radial and anticlinal division. According to Gupta (1964) the sporogenous layer produces 60–80 microspore mother cells per microsporangium.

In pollen mother cells chromatin content and nucleus can be found in a solid state in the leptotene stage (Bennet 1975). A more intensive change in nucleus structure is characteristic of the zygotene stage, and following stages, which are:

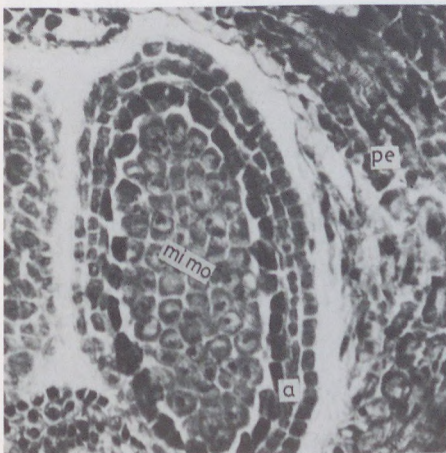
Fig. 154. Cross-section of the anther ($\times 880$, photo: E.B. Szikszai, mi m = micro archeospore mother cell, ml = middle layer, ta = tapetum, x = xylem)

Fig. 155. Longitudinal section of the anther (a) and petal (pe) ($\times 350$, photo: E.B. Szikszai, mi mo = microspore mother cell)

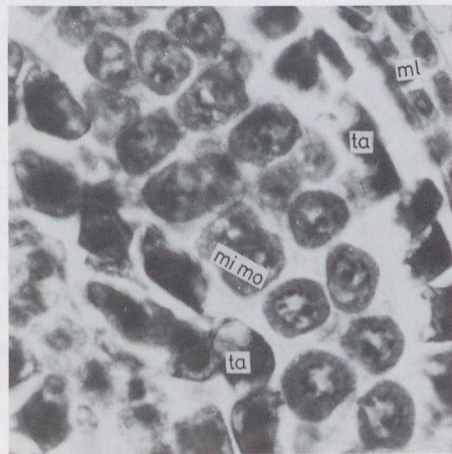
Fig. 156. Microspore mother cells (mi mo) in the interphase ($\times 880$, photo: E.B. Szikszai, ml = middle layer, ta = tapetum)



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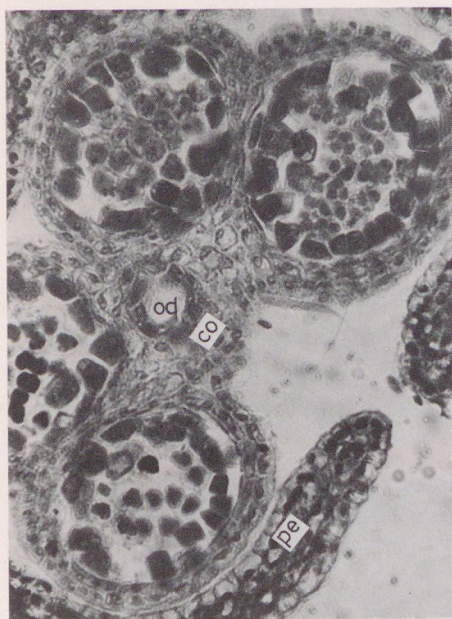


Fig. 157. Anther cross-section with four locules ($\times 350$, photo: E.B. Szikszai, co = connective, od = oil duct, pe = petal)

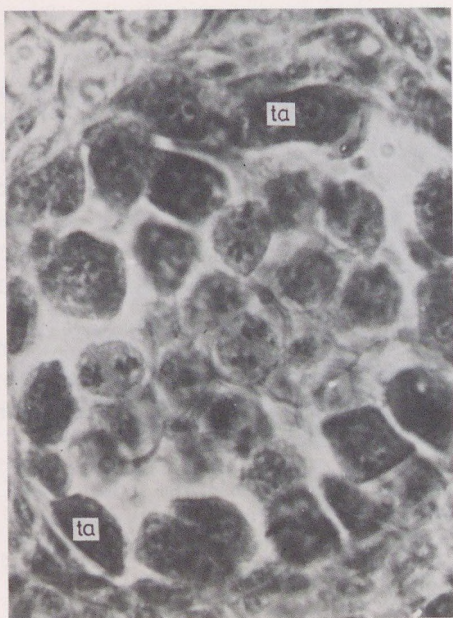


Fig. 158. Microspores in the anaphase and telophase I ($\times 880$, photo: E.B. Szikszai, ta = tapetum)

pachytene, diplotene, diakinesis. These stages can occur simultaneously in one and the same microsporangium in the interphase (Fig. 156). Various stages of microspore development can be observed in the four microsporangia of an anther of a single closed flower in phase 31.1 (Fig. 157).

In microsporangium *a* the majority of pollen mother cells are in anaphase I and telophase (Fig. 158), in *b* the tetrad stage is the most frequent (Fig. 159), while in *c* the tetrads are inside the callose integument but separate from each other (Fig. 160). The asynchronous nature of meiosis had already been mentioned by Gupta (1964).

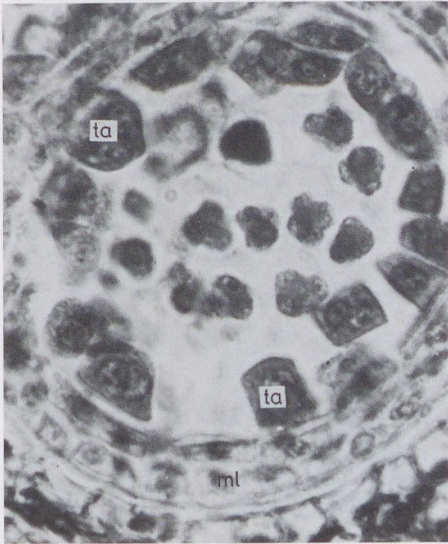
A simultaneous observation of tapetum and sporogenous tissue in coriander is a customary practice (Gates and Rees 1921, Maheshwari 1950, Mascré and Thomas 1930, Carniel 1954, Turala 1958, Dickinson and Bell 1976, Turala et al. 1964). Such observations provided detailed information. The tapetum consists of a single cell layer in the microsporangia of the coriander. As a result of a simultaneous presence of zygotene and leptotene stages, microspore mother cells are in interphase. Few tapetum cells have a single nucleus, the majority have two nuclei developed by endomitosis (Fig. 159), and occasionally tapetum cells may have three nuclei. Tapetum cells have dense cytoplasm. Pollen mother cells are in anaphase I and telophase (Fig. 158). Certain tapetum cells show mitosis but

the majority already have two or more nuclei. Differences between tapetum cells in size and nucleus number remain through tetrads stage inside the callose integument (Fig. 160). In this stage the vacuolization of tapetum cells is already easy to detect also with the aid of a light microscope. After the dissolution of the callose integument, microspores are oval-shaped and tapetum cells with several nuclei have been vacuolized to various extents (Fig. 161). The autolysis of

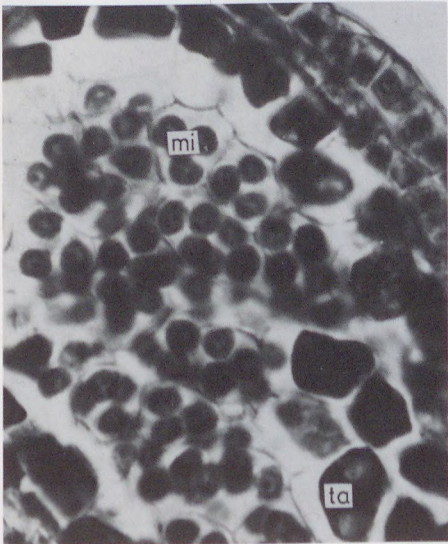
Fig. 159. Tetrads and tapetal cells (ta) in the locule ($\times 880$, photo: E.B. Szikszai, ml = middle layer)

Fig. 160. Microspores (mi) in callose envelope ($\times 880$, photo: E.B. Szikszai, ta = tapetum)

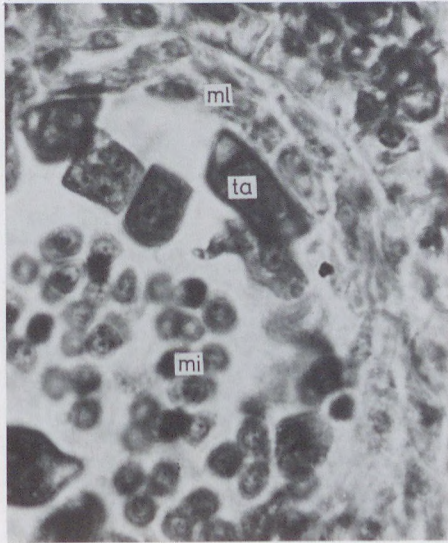
Fig. 161. Tapetal cells with two, three or more nuclei ($\times 880$, photo: E.B. Szikszai, mi = microspore, ml = middle layer, ta = tapetal cells)



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tapetum cells increases, which implies an intensive secretion. In the equatorial plain of pollen grains, which resemble sponge fingers, the cytoplasm sheath has developed around the generative nucleus (Fig. 162).

In the next phase (31.3.1-2: closed flower) the would-be exo- and endothecium of the anther wall have differentiated. Both cell rows consist of vacuolized cells with large nuclei. Cells are rich in cytoplasm. The tapetum cells still retain their

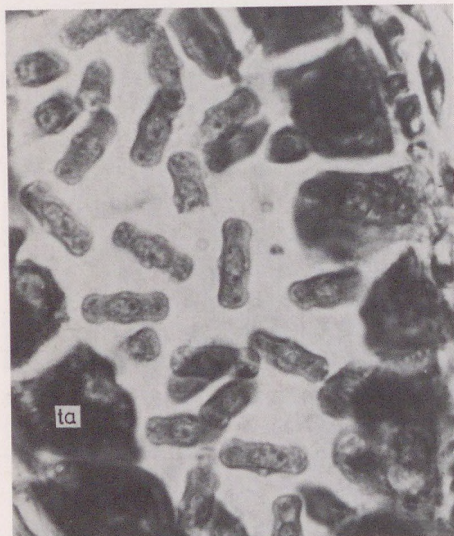
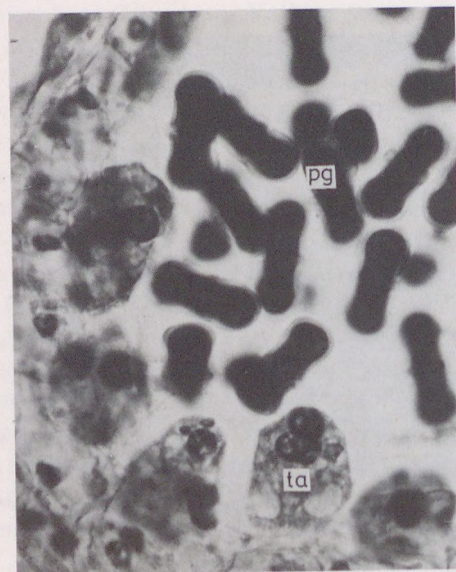
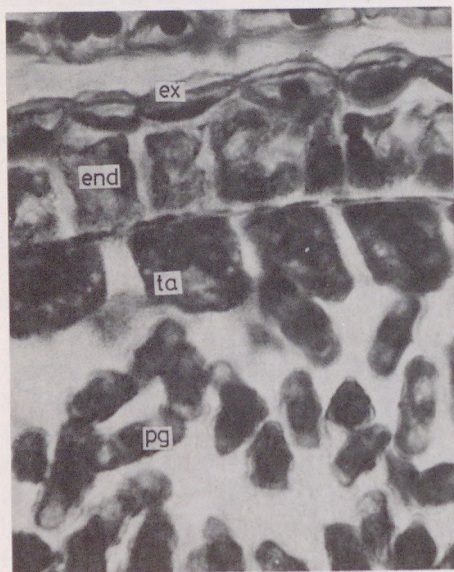


Fig. 162. Male nucleus in the equatorial plane of the pollen grain ($\times 880$, photo: E.B. Szikszai, ta = tapetum)

Fig. 163. Exo- and endothecium (end) cells rich in cytoplasm in the anther wall ($\times 880$, photo: E.B. Szikszai, ex = exothecium, pg = pollen grain, ta = tapetum)

Fig. 164. Secretory tapetal cells (ta) in active phase ($\times 880$, photo: E.B. Szikszai, pg = pollen grain)



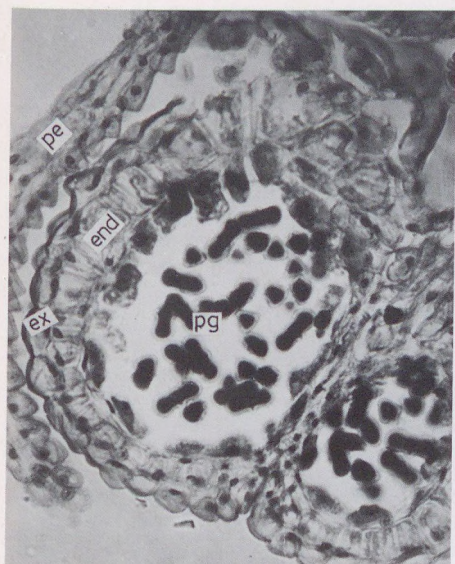


Fig. 165. Wall thickening in endothecium (end) cells ($\times 350$, photo: E.B. Szikszai, ex = exothecium, pe = petal, pg = pollen grain)

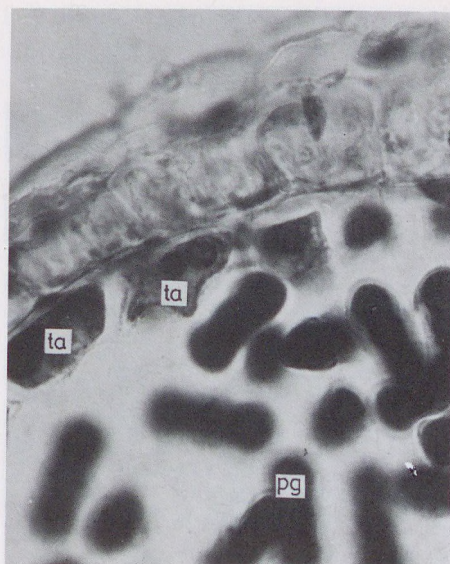


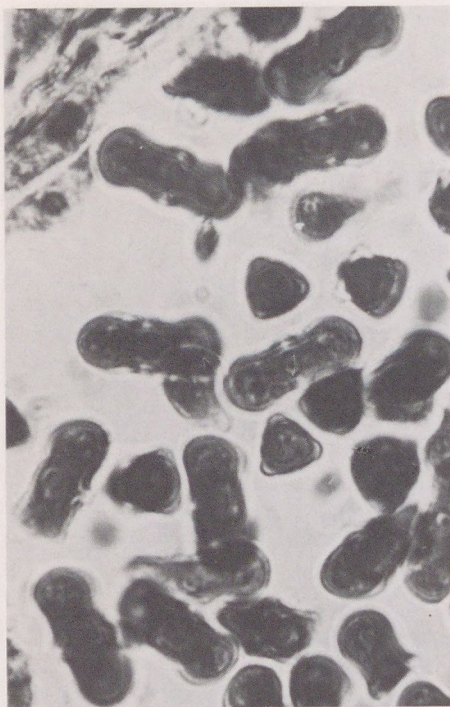
Fig. 166. Secretion process results in dissolution of tapetal cells (ta) ($\times 880$, photo: E.B. Szikszai, pg = pollen grain)

shape. Pollen grains usually contain two vacuoles, and the nucleus is situated in the equatorial plain (Fig. 163). Gupta (1964) described cell differentiation in coriander microspores. The nucleus moves to a pole of the microspore and here divides into a small generative nucleus and a large tubular nucleus. Around the generative nucleus a cytoplasm sheath develops while the generative nucleus moves into the equatorial plain (Fig. 162), where it produces male germs by a new division. These germs move back to the pole but it may also occur that they remain in the equatorial plain and the tubiform nucleus is located between them at the aperture.

In this phase several tapetum cells are still large on the connective side (Fig. 164). On the opposite side of the theca endothecium cells have begun to undergo fibrous cell wall thickening. The middle layer is very thin. The autolysis of tapetum cells already concerns the nuclei, the cells take on an amoeboid shape (Figs 165, 166). The microspores consist of two cells (Fig. 167).

Secretion of tapetum cells first affects the cytoplasm and later the nuclei. This chronology suggests that secretion is controlled by nuclei or the membranes of nuclei are more resistant to dissolution.

In this phase petals still entirely embrace (guard) anthers, in which even the stomium has already developed (Fig. 168). The formation of exo- and endothecium, and microspores is a process that is simultaneous with the lysis of tapetum



167

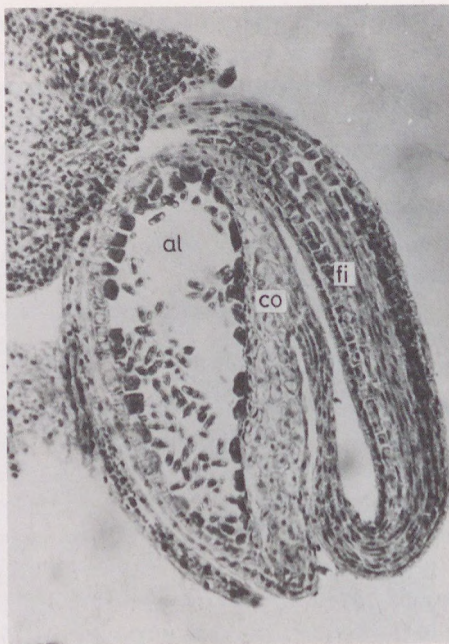
Fig. 167. Two-celled pollen grains ($\times 880$, photo: E.B. Szikszai)

Fig. 168. Longitudinal section of anther surrounded by half part of the petal (pe) ($\times 150$, photo: E.B. Szikszai, pg = pollen grain)

Fig. 169. Transverse section of the anther, the connective (co) and the filament (fi) ($\times 150$, photo: E.B. Szikszai, al = anther locule)



168



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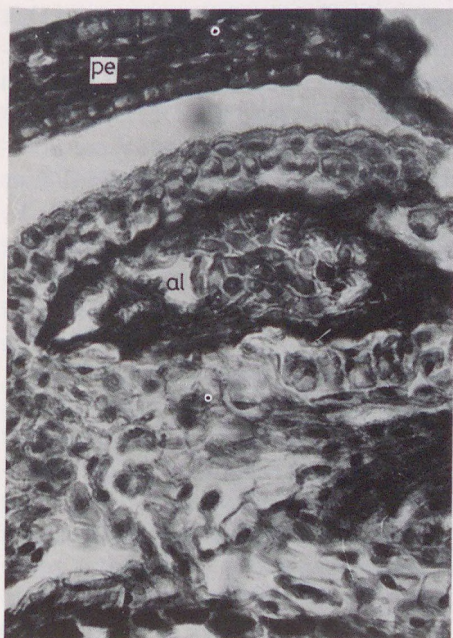


Fig. 170. Melted tapetal cells in the anther ($\times 350$, photo: E.B. Szikszai, al = anther locule, pe = petal)

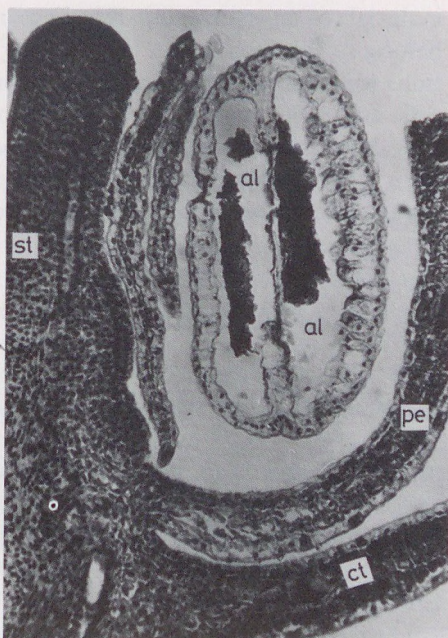


Fig. 171. Connective and endocarp dissolved by tapetal cells ($\times 150$, photo: E.B. Szikszai, al = anther locule, ct = calyx teeth, pe = petal, st = style)

cells. In the microspore the two generative nuclei are near to each other, or farther from the equatorial plain in the neighbourhood of poles.

The filament has a simple structure (Fig. 169). Under the epidermis that is covered by a wrinkled cuticle a vascular trace and a large oil duct next to each other have developed in the parenchyma layer.

Zenkter (1962) observed the disorganization of pollen grains in the microsporangium of *Daucus carota*. A similar phenomenon can be observed also in coriander. Around microspores tapetum cells have merged into each other forming a layer (Fig. 170) but the differentiation of exothecium and endothecium is not disturbed. Elsewhere these also undergo damage and malformation (Fig. 171). According to Zenkter this phenomenon must have something to do with the overfunctioning—early disintegration—of tapetum cells.

The structure of pollen grain wall is well known in numerous species (Esau 1977, Rudall 1987). Juel (1915) was the first to assume that the role that tapetum cells play in spore wall construction is metabolite transport. Takats (1962) marked cells with ^3H -thymidin and detected their content in tapetum cells in microspore walls of *Lilium longiflorum*. Heslop-Harrison (1976) pointed out

materials of tapetum origin among exine columns of pollen grains in species that belong to the Cruciferae, Compositae and Malvaceae families. These examinations together with further observations refer to a connection between tapetum cells and pollen grain wall construction also in coriander.

A thorough classification of microsporogenesis (Batygina et al. 1963) considered a large number of species. They concluded that within the Umbelliferae family microsporangium wall development is uniformly similar.

SUMMARY

OUTER STRUCTURE

11.0 Dormant seeds.

21.1-33.1 From the seed there develops a dicotyledonous plant of Th (thero-phytonous) life-form with rosetting leaves. The coriander belongs to the Th life-form plants. According to Raunkiaer (1904) such plants survive the unfavourable seasons in seed stage and need relatively short time for their full development.

21.4.2 The rosetting leaves number is 3-5 with difference in length. That leaves form rosettes as a consequence of the reduction of the internodes that used to be among them.

22.1-24.0 The succeeding internode lengths are distinct and length distribution can be characterized by a slightly asymmetric normal curve (Fig. 3). The length of an internode shows a close topological correlation to the length and shape of the stem leaf that grows out in the same node (Figs 1a, b). The reduction of the petiole is parallel with the relative increase of the rachis between leaf segments, or in upper parts, pinnules. The length of the petiole sheath and the number of vascular bundles reduce from the first leaf up to the uppermost leaf. Contrary to this, the length of pinnules increases. This makes it likely that both the bracts and/or bracteoles are of leaf lamina origin. This conclusion is opposite to the opinion of Cerceau-Larrival (1962), who argues for the derivation of bracts and bracteoles from the rachis in the Umbelliferae family.

The appearance of the lateral branch that bears the fertile umbel is simultaneous with the process of the leaf lamina becoming pinnate. The shape of leaves of lateral branches is not perfect copy of shape of leaves of the main branch. Their first leaf of a lateral branch has the same structure as that of the leaves growing out in the node in which the lateral branch originates or that of those growing out from the next node located higher on the stem (Krenke 1940).

INFLORESCENCE-FLOWER

24.0-31.1 The umbel has relatively few rays. These rays, that is, flower architecture, refer to reduced elements of an ancient helical structure. The spatiotemporal development of the umbel requires at least the partial development of the vegetative shoot section.

Of sepals only the calyx teeth are free. The 'calyx leaves' make up the outer part of the pericarp, about up to the half of the thickness of the mesocarp, which is partially sclerified. The lack of ridges and furrows on the fruit may be connected with the pericarp's composition of calyx leaves and carpels. Such pericarp structure results in the mature mericarps remaining together for a long time in

spite of the development of separative tissues and carpophore between them (Figs 145, 146).

Petals of outer flowers are asymmetric; they have ray petals, short petals and half petals that bend inwards (Fig. 8). Petals of flowers situated in the centre are short and reclinate, and more or less the same. Two halves of a distinct petal surround (guard) anthers of each of stamens, which alternate with petals to the time the filament lengthens (Fig. 18). Until the development of the entire architecture the plant undergoes the following stages: anabiotic (seed), juvenile, adult including generative stage, and senile phase (41.1). Individual stages are related to each other, they require the preceding phases and present themselves in the form of different phenophases. The dependence is not uniform. The anabiotic stage requires a whole preceding ontogenetic cycle, and the adult and anabiotic stages require an earlier realization of the juvenile stage. Generally, the initial condition for every stage is the total or partial realization of at least one earlier stage. Unfavourable environmental circumstances may result in omitting of certain stages and ending with incomplete ontogeny.

INNER STRUCTURE

As in the case of every vascular plant, metabolite transporting elements, which are partly supporting elements as well, that transport from soil to top have differentiated separately from those that transport in the opposite direction. In coriander the nutrient transporting elements differ in vascular bundle type. In the leaf the bundle sheath parenchyma around bundles (Figs 77, 79, 93), and in the shoot axis the cork and pith parenchyma cells (Figs 63, 64, 65, 67, 68, 69) have been specialized for lateral metabolite transport by developing transfer cells (Gunning and Pate 1969). Intercellular spaces among parenchyma cells, which are usually large, make it possible for cells to fit together flexibly (Figs 68, 69) and for tissues to retain their gas content (CO_2 , O_2) periodically and diffuse it if necessary.

Topologically, with the aid of cross-sections taken from the stem at distinct levels of height (first, third, and uppermost internodes), one may demonstrate a simultaneous process in the course of development. Functional complexes of assimilation, respiration, nutrient transport and those which support respiration and nutrient transport gradually become dominant. The metabolite transport system is increased in time and space by the developing vascular bundles and parenchyma cell groups that are continuously being produced by the interfascicular and intrafascicular cambia.

The insertion-dependent change in leaf structure was described by Zalensky at the beginning of this century. Szujkó-Lacza (1974) provided a generalized quantification of this change in the Umbelliferae family.

The ontogenetic difference between organs whose place is fixed in the plant gradually develops as the shoot grows. Phytohormones that undergo a permanent

change during the course of growth, and the habitat simultaneously affect the inner structure of organs (leaves) that develop in different points of time, hence, under different physiological, architectural and environmental conditions. The number and quantity of phytohormones and relevant effects of the habitat are increasingly more important up to the development of the embryo. For regulating growth sexual hormones may combine with other hormones depending on the age of the plant (Chailakhyan and Khrianan 1987). As a result of hormonal and habitat regulation the time of blossoming is the period when maximal morphological and histological diversity are detectable (Figs 1a, b, 4, 5, 8). The most diverse phase of dependence on habitat in a plant is undoubtedly the phase of fertilization. In addition to internal factors, such as metabolites, energy and gaseous materials necessary to assimilation, in this phase the indirect interaction with insects that carry out biological pollination is also necessary.

SECRETORY SYSTEM OF THE PLANT

From root to fruit the whole plant is characterized by the presence of epithelial cells producing volatile oil, which are associated with phloems of the vascular bundles. These groups of secretory cells, which surround oil ducts, work until their cells collapse as a consequence of the development of the collenchyma in the stem, the hypoderma in the petiole and the sclerenchyma in the pericarp, and they work in stamens and petals until these organs dry out.

New epithelial cells develop due to the paracambium of the root and the fascicular and interfascicular cambia of the stem. In the pericarp, epithelial cells on the abaxial side cease to work sooner but those next to the carpophore (Figs 130, 137, 138) appear later and remain active until the saturation of the endosperm and the embryo.

If secretory cell populations are regarded as a subsystem, the stylopodium and the transmitting glands, function as autonomous compartments. Their secretion is needed for pollen grain germination, pollen tube development, pollen tube growth, and perhaps nutrient transport. At the top of the epigynous ovary the stylopodium takes on a dome shape. Here it is not disc-shaped, and its glandular tissue is differentiated in both vertical and horizontal directions (Figs 102, 104, 113, 115). The secretion of the glandular tissue of stylopodium surfaces through modified stomata (Figs 114, 115). Its functioning strongly depends on the supply of water and temperature.

In addition to the stylopodium, transmitting tissues consist of the secreting stigma (Figs 103, 117) and the funicular epidermis (obturator cells) around the micropyle (Dalmer 1880, Tilton and Horner 1980). In coriander, as well as in every species that belongs to the Apioideae subfamily, all three cell populations (secreting stigma, style and obturator cells) remain active until the development of free endosperm nuclei, or rather, until the coenocytic stage comes to an end.

The integumental tapetum, or endothelial cell row, around the embryo sac (Figs 99, 104) and the hypostase (Figs 109, 110) serve for a short time as glands perhaps specialized for metabolite and sexual hormone transformation and transport in the carpel.

The secretory cell group in the embryo sac consists of synergids and short-lived antipodal cells. In antipodal cells, in addition to hormone secretion, they may play role in the creation, and perhaps the development, of the central vacuole.

One of the synergids is specialized for guiding the pollen tube (Fig. 105). Their life span lasts until the appearance of free endosperm nuclei, and only then comes the zygote differentiation (Fig. 121). Their function might be the hormonal regulation of zygote differentiation.

The one-layered anther tapetum, whose secretion is so intensive that it entirely dissolves the cells by autolysis, plays an important role in microspore development and wall differentiation (Figs 164, 166, 168). The second cell row of the middle layer in the anther (Figs 159, 161) will also be entirely dissolved but there are no data available concerning the transport of the cell content. Its accommodation might lead one to the conclusion that it contributes to the anther wall and pollen grain development simultaneously.

TRANSFER CELLS OF THE REPRODUCTIVE ORGAN

The integument (Figs 99, 104, 112) and the embryo sac (Figs 105, 106, 107, 108) are to be regarded as a special group of transfer cells. Integumental cells carry out not only the lateral transport of metabolites from the pericarp and from the funicle towards embryo sac through the vascular bundles, but they also transport their own cell content to the embryo sac, similarly to the tapetum cells which transport their own cell material to the anther. They make possible the transport of large quantities of nutrients, mainly polysaccharides, along wall ingrowths to the ever increasing embryo sac, to this giant cell, from the time of egg cell fertilization to the time when the endosperm has been saturated with nutrients.

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SUBJECT INDEX

Italicized page numbers indicate main discussion of term

- Acacia baileyana* 9
- Acer platanoides* 66
- adult phase 12
- Aegopodium podagraria* 81
- amitosis 7
- anabiotic phase 12
- Angiospermatophyta 1
- Anethum graveolens* 5-7, 8, 10, 62, 64, 75
- anther 10, 13, 25-26, 28, 82, 83, 90
- antipodal cells 58, 63
- Apiaceae 1
- Apioideae 1, 3, 5, 6, 11, 74
- Araliaceae 11
- Araliales 1
- archeospore 58
- archeosporium 85
- Astrantia* 59
- Bifora* 2
- bract 20
- bracteole 20, 21
- branch 15, 19, 20, 32
- bundle sheath parenchyma 50, 54, 79
- calyx teeth 12, 13, 20, 23, 25, 26, 32, 74, 79, 80
- cambium 42
- Capsella bursa-pastoris* 8
- carpel 3, 76
- carphophore 6, 7, 56, 57, 74, 76, 80, 81
- cell plate 69, 70
- wall 9, 68
- central cell 58, 59
- central vacuole 59, 60, 63, 67, 68, 69, 74
- chlorenchyma 13, 23, 37, 39, 40
- Citrullus lanatus* 5
- coenocytic state 9, 10, 63, 64, 66, 67
- collenchyma 13, 37, 39
- cork parenchyma 37, 39
- cortex 37
- cotyledon 12, 15, 18, 34, 72-74
- Crocus 4
- Cucurbita pepo* 8
- cuticle 5, 18, 26, 27, 43, 51, 79
- Cytinus hypocistis* 9
- Daucus carota* 62, 81
- dictyosome 69
- Dicotyledonopsida 1
- disc or stylopodium 3, 12, 30, 60, 65-66
- egg cell 58, 59, 60
- embryo 8, 9, 11, 71, 72
- sac 10, 58, 60, 62, 66, 67
- endocarp 11, 73, 76
- endodermis 34
- endomitosis 7, 8, 9
- endoplasmic reticulum (ER) 9, 69
- endosperm 8, 9, 10
- endothecium 26, 28, 29, 74, 88
- endothel 3, 10, 11, 57, 60
- epidermis 7, 11, 37, 83
- epigynous flower 3
- epithelial cell 42, 57, 77
- Eryngium* 59
- exocarp 11, 77
- exodermis 34
- exothecium 26, 29, 88
- fascicular cambia 40, 48
- filament 13, 21, 23, 24, 25, 26, 27, 28, 90-91
- Foeniculum vulgare* 10
- free endosperm nuclei 9, 60, 62, 63, 67, 69
- fruit 11, 14, 20, 73
- Fuchsia* 7
- funicle 56, 80
- Galtonia candica* 7
- Golgi apparatus 9
- Grevilla robusta* 8
- Glycine maxima* 6
- gynoecium 13, 24, 26, 55-56, 61

- Haemanthus catherinae* 9
Helianthus annuus 9
Heracleum sphondylium 62
 Hydrocotyloideae 1, 74
 Hydrocotyledoneae 6
 hypocotyl 15, 34, 72
 hypodermis 46
 hypostase 59, 63, 64

 integument 10, 57, 74
 intergumental tapetum 3, 10, 11, 57, 59, 63
 interfascicular cambium 37, 39, 40-41, 42, 45
 internode 12, 13, 15-17, 19-20, 37, 39

 juvenile phase 12

 leaf 12, 17, 18, 19-20, 33, 46
 leaf lamina 12, 49
 — sheath 18, 46, 47
 leaflet 12
Leontodon autumnalis 7
Lilium longiflorum 4, 5, 91
Lycoperson peruvianum 5

Mandhuca indica 5
Medicago sativa 5
 medullary ray 35
 megasporogenesis 58
 megaspore mother cell 58
 mericarp 6-7, 74
 mesocarp 9, 11, 75, 77
 mesophyll 34, 50, 83
 micropyle 64, 65
 microspore mother cell 86
 microsporogenesis 7, 85, 86-87
 middle layer 7, 50, 85
 midrib 15, 47
 mitochondria 69, 71
Morus indica 7

 nectar 3, 4, 5
 nectar drop 60
 nectary cells 66
Nicotiana tabacum 5
 node 12, 15, 18-20
 nucellus 57-58
 nucleus 7, 9, 64, 67

 obturator 3, 5
Oenanthe 59
 oil channel 9, 41
 — duct 11, 37, 39, 42, 50, 57, 74-75, 79
 ontogeny 12, 94
 ontogenetic code 12
Ornithogalum caudatum 5
 ovary 13, 21, 31-32, 56-58, 74-75
 ovule 58

 palisade parenchyma 34, 49-50, 54
 papillae 4, 26, 28, 43, 83-84
 paracambium 35
Pastinaca sativa 81
 pedicel 13
 peduncle 43
 pericambium 34
 pericarp 76, 78
 periderm 35
 petal 3-4, 13, 20-21, 22-23, 24, 26, 31, 82-83
 petiole 12, 18, 46, 48
 phloem 34, 37, 42
Pimpinella anisum 3, 5, 6, 10, 46, 54, 75
 pinnatifid 12
 pinocytosis 62-63, 69
Pisum banksiana 8
 pith 39, 42-43
Plectranthus fruticosa 55
 polar cells 58
 pollen grain 5-7, 13, 26-27, 32, 48, 66-67, 88-89
 — mother cell 8, 10, 86
 — tube 4-6, 58
 primary endosperm 58, 59
Prunus armeniaca 10
Psammogeton biternatum 62

Quercus gambellii 9

 rachis 18
 radicle 12, 15, 34, 72, 74
 ray flower 12, 20-22
 rhizodermis 34
Ribes 7
 root 15, 34
 Rosaceae 4
 rosetting leaf 12, 18-19

- Saniculoideae 1, 3, 6
schizocarp 6-7, 11-14, 32-34, 55, 74
secondary endosperm 9, 67, 71-72
secretory system 95
seedling 15
senescence phase 13
spongy parenchyma 34, 50, 54
stamen 3-4, 13, 26, 31
Stellaria media 9
stem 15, 20, 23, 37-38
stigma 3-6, 13, 21, 24-26, 30-31, 60, 66-67
stoma 3, 40, 49-50, 66
Strelitzia reginae 6
style 4-6, 13, 21, 24-26, 30-32, 59, 66-67
synergid 58-60

tapetum 3, 7-9, 85-86, 89
theca 29
trace 74-75
Trifolium pratense 4-5

transmitting tissue 5-6
Trillitium undulatum 8
Triticum aestivum 9
T. vulgare 9
tuberculate 29-30

umbel 12-13, 20, 22-23, 32
Umbelliferae 1, 3-11, 34, 39, 49, 54, 58, 66,
72, 74, 79, 92
umbellet 13, 20, 22-23, 32

vacuole 69
vesicle 63, 68-69
vesiculation 60, 62, 67

wall ingrowth 42, 67, 69, 71
Wistroenia indica 7

xylem 34, 36, 37, 39, 42

zygote 60, 62, 64, 71





1258, —



We are witnessing a revival of herbs and medicinal plants in practical daily use. This has prompted the author to present the morphological and anatomical elaboration of coriander, as a favourite herb since the Egyptian New Empire (1800 BC) also utilized as a traditional sacrificial offering at the tombs. By making light-microscopic, SEM and TEM studies of the relationships between the architecture, structure and function of the plant, she has cast new light on this important species from the Umbelliferae family. For many people this book will serve as an example in the development of an Umbelliferae plant.

Code numbers were assigned to the development of the inflorescence, flower and pistil thereby revealing the change in the interior structure indicated by exterior changes.

Readership: morphologists, anatomists and cytologists and people interested in coriander because they are working with medicinal plants, spices or vegetables.

