Embryology of Flowering Plants

Terminology and Concepts

Volume 1: Generative Organs of Flower

Edited by
T.B. Batygina

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Contributors:

G.K. Alimova, T.B. Batygina, J. Bednara, N.N. Bhandari, F. Bouman, A.M. Bugara, B. Chaudhry, A.A. Chebotaru, P. Chitralekha, M.F. Danilova, G.El-Ghazaly, O. Erdelská, N.I. Gabarayeva, H.N. Gerassimova-Navashina, I.N. Golubovskaya, G.E. Gvaladze, D.A. Hamilton, O.P. Kamelina, G.A. Komar, V.A. Konnova, I.A. Korchagina, E.L. Kordyum, N.N. Kruglova, J.P. Mascarenhas, A.P. Melikyan, H.L. Mogensen, Z.I. Nikiticheva, V.F. Ogorodnikova, I.N. Orlova, V.P. Pechenitsyn, V.A. Poddubnaya-Arnoldi, O.B. Proskurina, B. Rodkiewicz, I.D. Romanov, S.D. Russell, R. Shah, I.I. Shamrov, S.V. Shevchenko, V.K. Simonenko, E.S. Teryokhin, V.N. Tikhomirov, G.E. Titova, V.E. Vasilyeva, M.R. Vijayaraghavan, M.T.M. Willemse, N.A. Zhinkina, G.Ya. Zhukova

Explain the meanings of words and you will deliver mankind from half its errors.

R. Descartes

This differentiation in terms is not a mere play on words, but is necessary for correct insight into the nature of things.

L. Van der Pijl

Preface

The principal aim of the present publication (in three volumes) is to summarize classical and current concepts of the generative organs of flowers, their structure and development, and seed formation processes. In preparing this publication, extensive use was made of the five-volume book *Comparative Embryology of Flowering Plants* (1981, 1983, 1985, 1987, 1990). The book contains ample material that can be utilized in theoretical generalizations, analyzing the distribution of features (or their uniqueness) and evolutionary transformations of structures. This offers vast possibilities for revising existing classifications and concepts and developing new ones.

While preparing the present publication, the contributors have drawn on the works of prominent botanists and plant embryologists, such as *Anatomie der Angiospermen-Samen* (1926) by F. Netolitzky, *Embryologie der Angiospermen. Archegoniaten* (1929) and *Vergleichende Embryologie der Angiospermen* (1931) by K. Schnarf, *An Introduction to the Embryology of Angiosperms* (1950) by P. Maheshwari, *Foundations of the Evolutionary Morphology of Angiosperms* (1964) by A. Takhtajan, *General Embryology of Angiosperms* (1964) and *Cytoembryology of Angiosperms: Principles and Perspectives* (1976) by V.A. Poddubnaya-Arnoldi, *Systematic Embryology of Angiosperms* (1966) by G.L. Davis, *The Seeds of Dicotyledons* (1976) by E. Corner, and *Embryology of Angiosperms* (1984) by B.M. Johri (ed.). P.A. Baranov's original work *The History of Plant Embryology* (1955) also proved particularly helpful. The author has summarized information on the main stages of development of embryological science and emphasized the outstanding contribution of Russian plant embryologists to world science. Formulations of individual terms and concepts were made with reference to the *Latin-Russian Dictionary for Botanists* (1957) by N.N. Zabinkova and M.E. Kirpichnikov, *Russian-Latin Dictionary of Botanical Terms* (1977) by M.E. Kirpichnikov and N.N. Zabinkova, and other dictionaries and manuals.

The present publication is a unique and unconventional endeavour to combine the terminological dictionary principle with a monographic description of individual structures and processes. Concomitantly, the traditional scope of embryology is expanded. The problems of seed dormancy and germination, ecological aspects of plant reproduction and other issues are also discussed.

The publication comprises three volumes. Volume 1 is divided into three parts: **Flower**, **Anther**, and **Ovule**. Volume 2, titled *The Seed*, comprises the following

principal parts: **Double Fertilization, Endosperm, Perisperm, Embryo, Seed, Seed Dormancy** and **Germination**. Volume 3 is devoted to reproduction systems.

In contrast to the traditional dictionary structure, terminological entries are arranged on according to subject matter rather than in alphabetical order, to give a comprehensive idea of the processes occurring in the generative organs of the flower.

The text consists of a number of general, theoretical and terminological articles dealing with individual structures and processes. In each entry, the definition of the term is given, its semantics and historical background are clarified, and information on the genesis and functions of various embryonal structures and generally recognized classifications of generative structures and their development provided. For example, microsporangium wall development is treated in conformity with the accepted classification of G. Davis (1966); the principles and names in the description of types of embryo sac development follow the classification of I.D. Romanov (1971, 1981).

At the same time, a number of new or modified (refined) classifications and new theoretical concepts are profiled in the book, all of them based on up-to-date information; modern notions about evolutionary transformations of generative structures are also dealt with.

The occurrence and distribution of the structures described are illustrated by examples in flowering plants drawn from the above-mentioned 5-volume book *Comparative Embryology of Flowering Plants*.

Articles contributed by foreign authors appear without much editing. Also included in the book (albeit somewhat summarized) are papers by classical researchers which retain their topicality even today. These are articles by H.N. Gerassimova-Navashina (1951, 1954, 1958) on the evolution of male and female gametophytes, I.D. Romanov (1981) on the principles of embryo sac classification and by V.A. Poddubnaya-Arnoldi (1976) on megaspore tetrads.

The number of references had to be kept to a minimum because of space limitations, the references cited bearing, for the most part, upon the priority of discoveries and terms and the uniqueness of the feature discovered. No reference is made to the author(s) where a popular opinion is expressed or the feature described is widespread. Each article or entry is provided with illustrative material, such as drawings, micrographs (LM, TEM, SEM), or diagrams, collected in Plates at the back of the book.

Z.I. Nikiticheva

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Tatyana Batygina

Introduction

Plant embryology, as a science studying the mechanisms of origin and the pattern of early development of a plant organism, is now in its heyday due to the general progress in natural sciences. Plant embryologists are currently investigating not only the development of embryo and seed as a whole, but also complicated morphogenetic processes involved in asexual reproduction, as well as various abnormalities occurring during sexual reproduction. Instead of remaining a purely morphological branch of science, embryology is nowadays acquiring the features of morphophysiological and ecomorphological science. Morphogenetic and morphophysiological correlations determining normal development of the embryo and seedling cannot be established without investigating plant–environment interactions which change during ontogenesis.

The objective of modern embryology is control of the development of organisms. This aim can only be achieved provided there is a close collaboration between plant embryologists and experts in cytology, physiology, genetics, ecology and plant breeders. **Embryological evidence is becoming increasingly essential for theoretical and experimental studies on plant reproduction.** Exciting discoveries in the twentieth century, such as experimental haploidy, parasexual hybridization, propagation of plants via somatic cell culture etc., are all of great general biological significance. They cannot be used to full advantage, however, without further elaboration of the embryological aspects of these phenomena. Moreover, today plant embryology per se offers a number of fundamental discoveries pertaining to reproduction which are of great practical importance, e.g. cytoplasmic male sterility (CMS), apomixis, etc.

At the junction of embryology, anthecology, carpology, genetics, physiology and plant breeding, a new and rapidly evolving discipline, **reproductive biology,** has emerged. **Elaboration of theoretical foundations of sexual and asexual reproduction** is one of the objectives of reproductive biology. Reproductive biology involves studies of various interrelated stages of ontogenesis: flower organogenesis, anthesis, pollination, fertilization, embryogenesis, seed maturation, dispersal and germination, and propagation by seeds. All of these are in one way or another connected with embryology **in the broad sense.**

The **primary objective** is to tackle the problems of amphimixis and apomixis, to elucidate the mechanisms of embryogenesis, incompatibility and self-incompatibility, as well as the patterns of variation in potential and actual seed productivity and, consequently, in crop yield.

The development of reproductive biology is especially important for the introduction and repatriation of rare and vanishing plants, as well as of plants of

great agricultural importance. Cytoembryological studies concerned with the effect of pollutants on reproductive structures (anthecology). constitute part of the environmental protection programme. Investigations of this kind have become increasingly important in recent years (the age of ecological stresses), because it is the reproductive structures that suffer most from adverse environmental factors.

Of special interest are apomixis phenomena requiring full-scale studies. Parthenogenesis, apospory, diplospory and polyembryony call for further intensive investigations to meet practical needs. Such types of agamospermy as vivipary and adventive embryony, i.e., possible intermediate forms between vegetative reproduction and propagation by seeds, merit special attention from plant embryologists.

Elucidation of evolutionary patterns of ontogenesis in conjunction with the problems of phylogeny and systematics remains a major line of inquiry in modern embryology. Relatively conservative, embryological features can be employed to supplement and refine our present notion of the systematic position of some orders, families, genera and even species. One urgent task is to investigate poorly studied taxa. This is essential for refining the criteria of evolutionary and taxonomic significance of embryological features.

New data accumulated by descriptive and experimental biology, morphology, reproductive and developmental biology should stimulate studies in evolutionary embryology. An important contribution is also forthcoming from some recently published monographs, particularly those concerned with various aspects of **descriptive** and **comparative embryology** (Poddubnaya-Arnoldi, 1976, 1982; Johri (ed.), 1984; Johri *et al.*, 1992; *Comparative Embryology of Flowering Plants*, 1981-1990; and others), as well as from a more comprehensive analysis of works of the founders of plant embryology, namely W. Hofmeister, A.S. Famintzyn, A.T. Bolotov, R. Souèges, K. Schnarf, J. Goroschankin, N. Zheleznov, W.I. Belyaev, S.G. Nawaschin, D.A. Johansen, P. Maheshwari, H.N. Gerassimova-Navashina, V.A. Poddubnaya-Arnoldi, I.D. Romanov, M.S. Yakovlev and others.

In the 5-volume work *Comparative Embryology of Flowering Plants*, families are characterized according to the A. Takhtajan (1980) system. It was compiled by embryologists of the Komarov Botanical Institute (Russian Academy of Sciences, St. Petersburg) and summarizes the results of research in descriptive embryology, from the beginning of the nineteenth century to the present day. The publication represents a wide panorama of development and differentiation of embryonal structures in dicotyledons (Volumes 1 to 4) and monocotyledons (Volume 5) covering a full range of forms found in these plants. The compendium is intended as a manual and guide for continuing work in reproductive biology and contains summarized evidence on sexual and asexual reproduction (including apomixis) in economic, rare and vanishing plants.

While constituting a basis for in-depth studies in various fields of embryology of seed plants, the aforesaid work concomitantly demonstrates the need for refining existing classifications of embryonal structures and processes in flowering plants and for their typification. In recent years, a number of new classifications have been worked out by Russian scientists: that of the modes and types of reproduction in angiosperms; types of embryo sac and embryo development; and anther, tapetum, and apomixis. A unique concept of the reproductive system of flowering plants has

been developed and a new type of asexual reproduction—embryoidogenic—recognized.

As new evidence accumulates, classifications exhibit increasingly higher objectivity and better approximation to actual evolutionary processes. This encourages deeper involvement of embryologists in research on systematics and phylogeny of flowering plants. However, theoretical foundations of classification of embryonal structures have not been sufficiently elaborated. The importance of these classifications for systematics and phylogeny can be increased through progress in our understanding of the evolutionary processes occurring in plants, the forces (ecological, genetic, etc.) behind this evolution, and the patterns of evolutionary changes in plant ontogenesis. This suggests that embryonal structures, as entities most comprehensively embodying the peculiarities of the evolution of ontogeny, deserve special attention, and that all these problems and new classifications need to be discussed at scientific conferences and symposia, with the participation of both embryologists and taxonomists.

Within the comparatively short period of its development, plant embryology has become a ramification of biology.

In evolutionary embryology, a new approach to the study of evolutionary adaptation of plant organisms—**an ecomorphological approach**—has emerged. Studies with parasitic plants have revealed that underlying the evolutionary transformations of their reproductive structures are such general biological phenomena as metamorphosis, neoteny and reduction. It is from this point of view that hypotheses on the possible mechanisms of evolution of the monocotyledonous condition of the embryo have been considered in the context of existing heterochrony and syncotyly hypotheses.

Ecological embryology is the most important line of investigation of early ontogenesis directed towards identifying critical periods in it. Plasticity and tolerance of reproductive systems are also the subject matter of ecological embryology. In this connection it is important to study embryonal structures (ovules, embryos, etc.) with a view to assessing the potentialities and sustainability of biological systems.

This line of inquiry merges with **population embryology** concerned with morphogenetic and phenotypic variability within a population (life cycle variation and reproductive system diversity).

The immunological direction in embryology is expected to play an important role in overcoming the barriers of cross-incompatibility.

Recent trends incorporate **synthesis of embryological and genetic evidence**, i.e., **genetic embryology**. N.K. Koltsov (1935) had already pointed out that 'it is only the integration of the two disciplines [experimental embryology and genetics—T.B.] with one another, as well as with cytology and biochemistry, that will create a single science capable of solving problems of general biology'. All the problems related to morphogenesis—differentiation, specialization, evaluation of characters, definition of such concepts as 'gene and character', 'genotype and phenotype'—are to a greater or lesser extent the concern of embryology and genetics.

Recent years have witnessed a rapid development of **experimental embryology** which, unlike descriptive embryology, provides answers not only to the question of how complex morphological processes of embryonal development evolve, but also why specific processes show this or that particular trend.

As far back as 1950, the outstanding plant embryologist P. Maheshwari predicted that the future of embryology would undoubtedly lie with experimental embryology. The needs of practical breeding (e.g. uncovering the causes of sterility and partially filled ear, with subsequent correction; use of adventive embryos; etc.) have spurred the development of experimental plant embryology.

Plants regenerated from cultured cells, tissues, organs and embryos (embryoculture) have become, especially in recent years, a model for studying mechanisms of differentiation and molecular genetic laws of morphogenesis of embryonal structures. Some interesting results have been obtained on the effects of various abiotic factors on plant morphogenesis and possible means of formation of embryoids and other structures suggested. Success of an embryoculture depends on the correct choice of developmental stage of the generative structure to be used in the in-vitro culture as well as on the state of donor plants. Of vital importance is the **elaboration of a theoretical basis for the in-vitro cultivation** of vegetative and generative structures (ovary, anther, ovule, embryo, endosperm, embryo sac, sperm, etc.). The experimental approach, combined with thorough knowledge of the genesis of reproductive structures, allows one to predict the morphogenetic pathways of regenerants, to determine the optimal developmental stage of the embryo to be used for embryoculture, and so forth. This direction merges with cell engineering and biotechnology.

Embryological evidence becomes increasingly important in designing genetic and breeding programmes and developing effective biotechnology methods since it provides an insight into the processes leading to normal seed formation and uncovers the causes of abnormalities arising during embryogenesis.

A systems approach to generative structures used in the in-vitro culture elaborated by embryologists of the Komarov Botanical Institute has enabled some theoretical assumptions to be made, in particular concerning the autonomy of the embryo, critical periods in the development of generative structures, and so on. These principles are applied in breeding work and have resulted in the production of new plant forms.

It has become increasingly apparent that **applied embryology** holds much promise. Among the problems to be addressed, the following should be mentioned.

Ecological problems: development of special methods for producing normal seeds of rare and economic plants; conservation of plant genetic resources, i.e., establishing a genebank (seeds, embryos, gametes); estimating the degree of plasticity and tolerance of reproductive systems, and the proportions of different modes of reproduction within various taxa of plants exposed to adverse factors.

Biotechnology problems: development of effective methods for mass production (propagation) of new forms and varieties as well as of rare and vanishing plant species. This can be done on the basis of embryoidogenesis (somatic embryogenesis) and gemmorhizogenesis (organogenesis).

Agricultural problems: increasing actual production capacity; development of new forms and varieties via distant and parasexual hybridization; overcoming the barriers of cross-incompatibility; etc.

Progress in embryology is largely dependent on application of modern methods of electron microscopy, autoradiography, tracer labelling, modelling, microsurgery, etc. These methods open up new vistas for research at different levels of organization: molecular, cellular, tissue, organ, organismal, and population.

Unique data on fine structure and functions of generative organs and tissues have been obtained with the aid of such methods as fluorescence (including immunofluorescence), phase-contrast, electron (TEM, SEM), Nomarski-interference microscopy, as well as application of methods of modern cell biology: immunocytochemistry, time-lapse photography, video-image processing, etc. Some other findings are also worthy of mention: sperm dimorphism, feasibility of enzymatic isolation of such structures as generative cell and sperms, embryo sac, as well as of individual cells of the female gametophyte. Utilization of endoenzyme markers has enabled elucidation of specific features of meiosis.

Quantitative mRNA studies of pollen grains and sperms have provided new evidence on their fine structure, mRNA as well as specific genes controlling microsporogenesis were identified in mature anthers.

Major advances in embryology made in recent decades call for a new comprehensive survey, such as that offered by the present book. The system approach was adopted for treating the genesis of particular embryonal structures; reproduction of flowering plants is viewed from a modern perspective.

It is worth mentioning that recent international congresses and symposia dedicated to plant embryology (Italy, 1988; USSR, 1990; USA, 1992; Austria, 1994) have reaffirmed the need for a publication such as this. Not only plant embryologists, but also geneticists, physiologists, cytologists, and biotechnology specialists participated in the symposia. Researchers in various fields of biology are very much in need of generalized embryological data and in particular unified terminology.

All the foregoing prompted preparation of the present 3-volume publication, *Embryology of Flowering Plants: Terminology and Concepts*. Participating in the preparation of volume 1 have been plant embryologists and morphologists of the Komarov Botanical Institute (Russian Academy of Sciences), their colleagues from CIS (the Ukraine and Georgia) and from other countries of the world: the USA, the Netherlands, Poland, Slovakia, India, and Sweden. In this publication, the results of studies, the hypotheses and conceptions advanced by Russian embryologists are presented more comprehensively than in any of the latest monographs of plant embryology (Johri [ed.], 1984; Johri et al., 1992).

It is hardly possible for a large team of authors to maintain uniformity of style. It was the Editor's task, therefore, to impose uniformity and to avoid unnecessary repetition of material in different sections. Individual articles, along with an objective presentation of factual evidence, unavoidably reflect the author's own view of the structures and processes described. This makes some of the articles open to discussion. But disputes are essential for the progress of science. In this respect, the present publication will be useful to research workers, experts in plant embryology, anatomy, taxonomy, genetics, physiology, cytology and ecology; to specialists in molecular biology, biotechnology, plant growing and to plant breeders; as well as to college and university students and lecturers of biology and to all those interested in biology. This 3-volume work on plant embryology should hopefully demonstrate the great role played by modern embryology in solving problems of general biology in this age of ecological stresses. It ought also to further theoretical and experimental studies in plant embryology. Any criticisms and useful suggestions are welcome and will be taken into account in future work.

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OVERVIEW

Flower—the most important reproductive structure of angiosperms (Plate 1). Processes such as micro- and megasporogenesis, pollination and fertilization, embryo development and lastly seed and fruit formation take place in it. The flower is most frequently regarded as a metamorphosed, monaxonic, shortened shoot exhibiting limited growth and performing a reproductive function.

Flowers vary widely in structure, colour and size, ranging from a few millimetres to one metre and more in diameter, as in *Rafflesia*.

The flower crowns the stem, the main or a lateral one. The portion of the stem below the flower, normally leafless, is termed the **pedicel**. Pedicels vary in size in different plants and play an important role in the formation of various types of inflorescences (umbels, corymbs, racemes, etc.). Sometimes, the pedicel is shortened, hardly distinguishable or even lacking; in the latter case, the flowers are said to be sessile.

The pedicel gradually turns into the floral axis, or **floral receptacle**. The receptacle is usually broader than the pedicel and shows poorly distinguishable internodes. The receptacle nodes carry all flower organs, both sterile (**sepals** and **petals**) and fertile (**stamens** and **carpels**). The receptacle may vary in shape—oblong, flattened, convex, etc. In some angiosperms, the receptacle varies greatly in size and coloration during fruit maturation and serves as an attractant for biotic agents assisting in fruit dispersal (as in strawberry, brier, etc.).

Sepals and petals together form the **perianth**. Sepals normally serve to protect the inner flower parts, especially prior to flower opening (i.e., within the flower bud). When green, they also act as accessory photosynthetic organs. Occasionally, sepals become petaliform and function as petals, thus attracting vector organisms effecting cross-pollination (as in *Delphinium*, wolfsbane and trollflower belonging to the Ranunculaceae). Sepals may also serve to protect the developing fruits, be involved in formation of fruit structure and assist in fruit dispersal. As biologically polyfunctional structures, sepals are subject to various changes. They are of leaf origin and appear to have originated from top vegetative leaves. Transitions from top leaves to sepals are prominent in members of some families (e.g. Paeoniaceae, Calycanthaceae, Dilleniaceae, etc.).

Petals forming the **corolla** usually perform a function over and above those of sepals. At early stages of flower development, they also serve to protect the inner floral organs but later, in an open flower, their primary function is to attract pollinators and to ensure successful cross-pollination. The origin of petals is not the same in different groups of flowering plants. In most cases, petals are of staminal origin (Ranunculaceae, Papaveraceae, Nymphaeaceae, Rosaceae, and many others). However, in a number of families, mostly archaic ones, such as Magnoliaceae, Paeoniaceae, Winteraceae and Schisandraceae, petals, like sepals, are of leaf origin. Therefore, it is common practice now to distinguish andropetals (petals originating from stamens) and bracteopetals (those originating from bracts).

The corolla size, shape and coloration vary widely and are associated with the biology of pollination. Petals often fuse at the margins to form a sympetalous corolla. Such a corolla evolves from a choripetalous corolla independently in different

evolutionary lines of angiosperms. When the perianth is differentiated into calyx and corolla, it is called a double one. In cases where petals are either absent or there is no marked difference between sepals and petals, the perianth is termed simple. A simple perianth is said to be corolla-like if its lobes are showy, or calyciform if its coloration is unattractive, exhibiting various shades of green.

From the perianth inwards, stamens are arranged in cycles, and the carpels are located in the centre of the flower. The collection of stamens carried by a flower is referred to as the **androecium** and that of carpels as the **gynoecium**.

Flower organs are initiated on the floral receptacle in the form of meristematic primordia, normally in a strictly specified sequence: from the periphery to the centre (centripetally), i.e., sepal primordia are formed first, then petal, stamen and, lastly carpel primordia. But not infrequently, the sequence is partially altered. Moreover, members of some taxa (including large ones) exhibit a centrifugal sequence of initiation of the androecium parts (when polyandrous), i.e., from the centre to the periphery.

The spiral or acyclic arrangement of flower parts on the receptacle appears to have been the initial one in the evolution of angiosperms. In living angiosperms, circular or cyclic flowers predominate, with flower parts forming distinct cycles, whorls or circles (e.g. 5 petals in one circle, 5 petals in the next one, 10 stamens in two circles, and a pistil composed of 5 carpels). Among the more common types are pentacyclic, tetracyclic (especially where one cycle of stamens is lacking) and tricyclic flowers. However, a reduction or an increase in the cycle number (oligotaxy and pleiotaxy, respectively) may occur. Finally, there are hemicyclic flowers whose outer phyllomes (the entire perianth or the calyx alone) are arranged in cycles, and the inner ones (stamens and pistils) in a spiral (i.e., acyclically).

In cyclic flowers, the rule of cycle alternation is normally observed, i.e., the members of each subsequent cycle alternate with those of the adjacent cycles rather than lying opposite them. Occasionally, this rule is violated. Thus, if a flower has two cycles of stamens (i.e., is diplostemonous), then the outer stamens may lie opposite the petals rather than sepals, a condition termed obdiplostemony.

Flowers may be **unisexual** (with androecium and gynoecium) or **bisexual** (with either androecium or gynoecium alone). Moreover, bisexual flowers may occur on a single plant, as in oak, birch and maize, and the plant then termed monoecious, or occur on different plants, as in poplar, sea buckthorn and hemp, the plant then termed dioecious. When both unisexual and bisexual flowers occur on a single plant, as in many members of Compositae and Cucurbitaceae, the plant is said to be polygamous. It is currently believed that bisexual flowers have evolved from unisexual ones and that dioecy in them is a more recent phenomenon than monoecy.

A very important feature of the flower is its symmetry, primarily determined by the arrangement of perianth segments. If a flower possesses radial symmetry, i.e., can be bisected vertically by any number of planes to form two identical halves, it is termed actinomorphic (regular). Most angiosperms have actinomorphic flowers.

In the course of specialization, associated primarily with the biology of pollination, actinomorphic flowers evolved into zygomorphic (irregular) ones in many angiosperms. Unlike actinomorphic flowers, zygomorphic ones possess only one plane of symmetry, i.e., division into two identical parts (one-half being the mirror-image of the other) can only be made along one longitudinal plane, as in violet or pea. In addition to regular (i.e., actinomorphic) and irregular (zygomorphic) flowers, there

also exist asymmetrical flowers which cannot be bisected along the plane of symmetry to produce two identical (symmetrical) halves, e.g. canna.

To facilitate studies of the flower structure, starting in the middle of the XIXth century, scientists began using special diagrams and formulas. The most precise method of constructing a floral diagram is, for all practical purposes, performing a section of a mature flower together with the cataphyllary leaf and floral bracts, if any, and accurate representation of the resultant picture. The diagram offers a means of determining the number of flower parts, their interrelationships, relative positions (arrangement), type of flower symmetry, etc.

A more concise, but no less illustrative way of providing a general view of the flower structure is by means of a formula (flower formula). Using the accepted conventional symbols and numbers, the flower formula may also incorporate such features as type of symmetry, acyclic or cyclic arrangement of flower parts, number of components, their fusion, increase in number due to separation, position of the ovary, etc.

Emergence during the evolutionary history of plants of a structure such as the flower was an aromorphosis event of great biological significance. In angiosperms the flower provided an opportunity for involving numerous biotic and abiotic agents (vectors) in the cross-pollination process, thereby offering them considerable advantages over other groups of higher plants.

With respect to the origin of the flower, there are several prevailing views. Most commonly, the flower is regarded as a metamorphosed, shortened shoot exhibiting limited growth and adapted to perform specific functions (the euanthous or strobilar theory). In doing so, the flower is assumed to have originated from the strobilus (cone) of a specific group of gymnosperms, in particular the Bennettitaceae and Cycadaceae. However, it is currently believed that both the flower of angiosperms and strobili of gymnosperms share a common origin in the reproductive shoots of the then strobilus-free seed ferns (Pteridospermae). According to other views, the flower evolved from a set of shoots rather than from a simple shoot and hence is more likely to be homologous to the inflorescence ('pseudanthium'), although specific morphological solutions here may vary widely (pseudanthous theory). There is also the telome theory treating the flower as a modification of telomes of the earliest higher plants. Finally, some authors believe that the enormous polymorphism of angiospermous flowers makes it impossible to trace them back to a single, original prototype and, consequently, flowers in different taxa are not necessarily strictly homologous.

Be that as it may, in practice the **flower** is, in most cases, most conveniently likened to a **simple, short shoot** having an **axial part** (floral receptacle or torus) and **leaf-shaped phyllomes**, both **sterile** (perianth) and **fertile** (stamens and pistils).

Of course, estimates of the degree to which morphological features of flowers of angiosperms are primitive or, conversely, evolutionarily advanced depend on the existing views of the origin of this group of plants. Based on prevailing concepts, most workers regard the following features as primitive: a convex or conical receptacle, acyclic arrangement of flower parts, multiplicity and indeterminacy (non-fixiform condition) of its parts, actinomorphic condition, absence of fused segments, phylloid stamens without a well-differentiated filament and usually with a conspicuous supraconnective, apocarpous gynoecium, semiclosed carpels, peripterous stigmas, etc. On the other hand, alternative features—flat or point receptacle, fixed number of

cyclically arranged segments, sympetalous condition, coenocarpy, etc.—are considered evolutionarily advanced features.

Androecium (Greek: *aner*, gen. *andros-man* and *oikos* = home)—a collection of stamens. The term was proposed by De Candolle in 1827.

Stamens in a flower are arranged in a strictly specified fashion. Moreover, in members of comparatively more archaic families, they are spirally arranged and usually numerous, their number indefinite. However, in most angiosperms stamens are arranged in cycles or whorls, their number strictly definite and usually not large.

Stamens may fuse, such that either filaments (as in Leguminosae) or anthers (as in Compositae) become united. Fusion rarely proceeds so far as to obliterate the outlines of anthers (as in some members of Cucurbitaceae). Stamens may also fuse, over a greater or smaller part of their length, to the perianth, especially to the corolla. They also tend to fuse to the style (e.g. gynostemium in Orchidaceae). All types of stamen fusion have evolved due to various modes of pollination and are generally, extremely permanent.

As mentioned earlier, in the course of evolution of angiosperms, the number of stamens in flowers reduced, becoming strictly definite. However, in some evolutionary lines the number of stamens again increased, which is typical for example of Cactaceae and some members of Rosaceae. This increase in number of stamens is associated with the biology of pollination and is normally characteristic of flowers lacking nectar and in which pollen grains serve as an attractant for biotic agents effecting cross-pollination.

Stamen—a generative organ of the flower. It is a microsporophyll that has been transformed in the course of evolution (Plates 2 and 3).

In most flowering plants, the stamen consists of a proximal sterile part, the **filament**, and a distal fertile part, the **anther**. Filaments vary in shape, size and longevity. Typically, this is a provisional organ but occasionally, having become ligneous, stamens attached to the fruit persist (as in *Kingia*). Appendages of various origin performing diverse functions are sometimes formed on the filament. Most commonly, the occurrence of these adaptations is associated with a particular mode of pollination. The stamen of most species of flowering plants has a vascular bundle. Normally, the bundle extends along the whole length of the stamen, terminating in the connective tissue or at the base of the anther. In some plants, the staminal vascular bundle is partially or completely reduced.

The anther is composed of one or several **microsporangia**, in whose locules **pollen** is formed. The **anther connective** is a sterile tissue linking the microsporangia in a structural unity, the anther. The connective may project above the microsporangia, forming appendages varying in shape and size. In most species of flowering plants (95%), the connective has a single vascular bundle; in cereals, bundle sheath cells differentiate round the vascular bundle (Batygina, 1974b). The anther shape is largely determined by the connective shape, size and degree of differentiation.

The filament, the connective and its distal appendages are microsporophyll parts. Therefore, it is not quite correct morphologically to say that the anther is 'attached' to the stamen. Based on the nature of the connection between the anther and the filament, several types of stamens (ingrown, versatile, etc.) have been distinguished which are viewed as taxonomic features.

In some primitive members of Magnoliaceae, Degeneriaceae and others, the microsporangia differentiate and develop inside a lamellar, trinervate microsporophyll. In these species (e.g. *Degeneria vitiensis*), the stamen is not differentiated into filament and anther. In some species (e.g. members of genus *Juglans*), the filament has undergone in the course of evolution, a reduction resulting in sessile stamens. However, sessile stamens may be a result of the effects of a number of other factors.

The number of microsporangia and their position within the microsporophyll are not the same in different taxa. Changes in location of microsporangia are partially traceable to their genesis, but generally these changes are difficult to identify since they are a result of long-term evolutionary transformations (adaptation to different modes of pollen dispersal). Two types of disposition of microsporangia have been distinguished: **abaxial** and **adaxial**. In addition, the disposition of microsporangia within an anther is also determined by the mode of anther dehiscence: **extrorse, introrse, lartrorse** and variations of these. All these features are taken into consideration by taxonomists and are essential for understanding the evolution of microsporangia and microsporophyll in general.

In most flowering plants, the anther is **tetrasporangiate**, i.e., carries four microsporangia arranged in pairs. However, many members of Adoxaceae, Malvaceae, Phyllidraceae and others have **bisporangiate** anthers. There are families (Araceae, Asclepiadaceae, Asteraceae, Moringaceae, etc.) in which both bisporangiate and tetrasporangiate anthers have been found in a single flower. Anthers carrying eight and more microsporangia also exist.

The **anther** or half of it is referred to as the **synangium** (Eames, 1961), and stamens or anthers that have fused to form a single structure, as the **synandrium** (Takhtajan, 1980b).

The chamber in which pollen is formed is described by various terms: microsporangium, anther locule, pollen sac, pollen chamber, and theca. Morphologically, most of these terms are inaccurate, because they fail to describe the structure adequately. In some species, in the course of maturation of both tetra- and bisporangiate anthers, the number of microsporangia 'decreases', as it were, to a single one because they 'fuse' as a result of degeneration of walls (septa) between the adjacent microsporangia. Such a reduction in the microsporangium number may be due to other factors, including abortion. Regrettably, Davis (1966) attaches diagnostic value to these secondary modifications and erroneously regards tetrasporangiate anthers with disrupted septa as bilocular, and bisporangiate ones as unilocular. Therefore, the term 'unilocular anther', for example, may have quite different morphological meanings. In view of this, the term 'anther locule' loosely equated by many workers to the term 'microsporangium' should not be used. The same applies to the term 'theca' which, Eames (1961) believes, should be avoided for the same reason. Suffice it to say that in some members of Cucurbitaceae and in genus *Callitriche*, all four microsporangia are united in a single 'theca'.

In mature lartrorse anthers of some plant species, microsporangia fail to unite since they occur in isolated positions in the sporophyll corners, such that the 'theca' represents a single sporangium and the anther is a 'tetrathecal' one (Eames, 1961). The term 'theca' is common in Russian literature and is used to denote two lateral microsporangia (dorsal and ventral) of a pair within a tetrasporangiate anther.

In some members of Nymphaeaceae, Calycanthaceae and Magnoliaceae, a proportion of stamens become sterile and are then termed **staminodia** (Latin *stamen*

and Greek *oidos* = kind). Staminodia vary in shape and size, often representing intermediate forms between the stamen and the petal.

Reduced stamens, occasionally found in pistillate flowers, are also referred to as staminodia. In some plant species they function as nectaries (as in *Coptis*). Staminodia have a vascular supply characteristic of stamens, but in the case of reduced stamens (as in some members of Scrophulariaceae), the vascular bundle is either completely lacking in the stamens or no more than its vestiges are present in the floral receptacle.

In the course of evolution of certain groups of plants, some parts of the stamen—filament, connective—as well as the number of microsporangia, number of microsporangium wall layers and number of pollen grains have undergone varying degrees of reduction. Thus, for instance, in lamellar sporophylls the connective tissue is usually massive whereas in such a specialized family as Poaceae it is represented by no more than a group of cells. A simultaneous reduction may occur in both the number of microsporangia and the distal appendage of the connective; in the parasitic plant *Arceuthobium* (Viscaceae), a single kidney-shaped microsporangium persists in the anther.

Gynoecium (Latin *gyne* = woman and Greek *oikos* = house, abode)—a combination of carpels carried by an angiospermous flower (Plate 4). The flower can possess one or more carpels which may be free, i.e., not fused (**apocarpous gynoecium**; Greek *apo* = one and *karpos* = fruit), or united in a structural unity (**syncarpous gynoecium**; Greek *syn* = together).

With respect to the gynoecium, the term '**pistil**', strongly engrained in the literature, has also been applied. It refers either to each carpel in an apocarpous gynoecium (simple pistil) or to the entire syncarpous gynoecium (compound pistil). Some botanists (e.g. Eames, 1961) suggest that the term 'pistil' be abandoned; however, the term, as defined above, continues to be useful even today.

Carpel—a generative organ of the flower (Plate 4). It is considered by many authors to be homologous to the megasporophyll. The carpel is a phylloid structure which, in an **apocarpous gynoecium**, is conduplicate, i.e., folded along the midrib such that its adaxial surface occurs inside the chamber and its margins come more or less closer to each other, draw together or fuse. The mode of carpel folding is regarded as a taxonomic feature (Eames, 1961). In many taxa, during pistil formation the straight, non-involute margins of the carpels are folded to form a marginal zone. This zone seems to have undergone reduction in width. In another type of apocarpous gynoecium, the carpel margins first become involute and only later do they fold and fuse by their abaxial surfaces, such that the marginal vascular bundles of carpels are inverted. At maturity, the carpel with a reduced marginal zone is often hard to distinguish from a carpel with involute margins.

The fusion of carpels in a **syncarpous gynoecium** occurs in one of three ways: adjacent carpels, closed or united after the first pattern (with non-involute margins) or the second one (with involute margins) fuse by their flattened, abaxial sides with one another. Occasionally they additionally fuse to the styliform carpophore, resulting in a **coenocarpous** (Greek *koinos* = common) bilocular or multilocular gynoecium. Where the partitioning septa disintegrate, a unilocular gynoecium composed of two to several carpels, the so-called **lysicarpous gynoecium** (Latin *lysis* = disintegration, dissolution; Greek *lysos* = dissolution, degradation) is formed. In a syncarpous

gynoecium of the third type, initially or subsequently, non-conduplicate carpels, completely or partially unfolded, fuse with one another at their margins, resulting in a unilocular, so-called **paracarpous gynoecium** (Latin *parallelicus* = parallel). These principal methods of fusion of carpels may vary due to secondary modifications. An example of such a modification is to be found in members of Brassicaceae, Boraginaceae and Lamiaceae where the locules of the gynoecium composed of two fused carpels are divided in two by a pseudoseptum formed by placental outgrowths at the margins of carpels.

In evolutionally more advanced taxa, the carpel of an apocarpous gynoecium differentiates into a lower, broadened fertile portion, the **ovary**, in whose chamber (locule) ovules are formed, and an upper, tapered, sterile portion, the **stylodium**. In the most primitive taxa, stylodia are lacking. Formation of a syncarpous gynoecium primarily involves fusion of fertile parts of carpels (ovaries) as well as of stylodia to form a **style**.

Along the carpel margins in the more primitive taxa and on stylodia or the style in more advanced ones, a kind of secretory tissue differentiates which secretes mucilage and sugary fluid that serve to entrap pollen and aid in its subsequent germination. These carpel parts are termed **stigmata**. Depending on shape and position, the following types of stigma are distinguished: sutural ('stigmatic crest'), peripterous, apical (capitate, globular, oval, spherical, concave, cylindrical, plumose, lobate, penicillate, etc.). In some primitive taxa, a so-called 'inner stigma' is formed which sometimes completely lines the ovary chamber (Eames, 1961). When the style or stylodium beneath an apical stigma is reduced, the stigma is termed **sessile**.

Placenta (Greek *placus* = cake, scone)—the **site of ovule initiation on the carpel**. It may be a rather large outgrowth which occasionally almost completely fills the ovary lumen (Plate 4).

According to a number of authors, the most primitive type of placentation is the laminar (diffuse or surface) one which results in the ovules being scattered over the entire inner surface of the carpel, as in Butomaceae and Limnocharitaceae. Most flowering plants have submarginal or sutural placentae. In cases like these, each carpel carries two placentae running close to its margins. Sometimes a placenta is said to be sutural, marginal, but there is no general agreement among authors regarding this (Eames, 1961; Takhtajan, 1964).

The type and position of the placenta depend on the method of carpel fusion and type of gynoecium (Puri, 1951). Placentation is most commonly **submarginal** and **sutural** (subsutural) in an apocarpous gynoecium, **central-angular** (or central-sutural) in a coenocarpous, **columnar** (or central) in a lysicarpous, and **parietal** in a paracarpous gynoecium. In a unilocular ovary, the placenta may be located at the very base of the ovary, in which case placentation is termed **basal**. In other taxa, placental and chalazal tissues are linked in a structural unity, the so-called **placentochalaza** (for details, see Part III: Funiculus).

PART TWO—ANTHER

OVERVIEW

Anther (Latin *anthera*, from Greek *anthos* for flower)—the fertile part of the stamen where, in microsporangia, microsporogenesis occurs and pollen grain formation and maturation proceeds (Plate 5). The term was introduced by Linnaeus. The first morphological description of anther and pollen dates back to the late seventeenth century (Grew, 1672; Camerarius, 1694). In the early eighteenth century, Linnaeus defined all the parts of the stamen and anther. The terminology proposed by him has been universally accepted.

In anther development, three periods are distinguished: premeiotic, meiotic, and postmeiotic (Kamelina, 1981a). The premeiotic period is marked by an enhanced mitotic activity resulting in the formation of an anther wall and sporogenous tissue, that is, microsporangia are formed. It is completed with cessation of divisions in the sporogenous tissue and by transformation of sporogenous cells into microsporocytes. During the meiotic period, microsporangium wall layers differentiate and meiosis proceeds in microsporocytes, resulting in tetrads of haploid microspores. In the postmeiotic period, pollen grains develop and mature concurrent with the associated changes in the microsporangium wall structure.

In a mature anther, locular fluid is lacking, with only those wall layers persisting which are involved in anther dehiscence. Anther dehiscence is most commonly longitudinal, occasionally valvular (Berberidaceae), by pores (Ericaceae), or by other means. In many species, anther dehiscence is preceded by disruption of septum separating microsporangia within a theca, such that locules of two microsporangia unite and then open by a single pore. At the site of the thecal opening, some plant species (e.g. members of Liliaceae, Bignoniaceae and others) develop ridges of enlarged epidermal and endothecial cells (stomium) which are closed by a few small cells. These latter cells are ruptured to effect dehiscence. However, anthers without a stomium carrying small closing epidermal and endothecial cells are more common, with the cells forming no fibrous thickenings. In some species, microsporangia remain separated within the anther right up to the time of dehiscence (Dipsacaceae, Morinaceae, Valerianaceae and others).

Evolution of the anther of flowering plants was towards reduction in size of the anther connective and a lower number of vascular bundles, number of layers in the microsporangium wall as well as altered positions of microsporangia and changes in other features.

Microsporangium (Greek *micros* = small, *sporá* = seed, spore, and *angeion* = conceptacle, reservoir)—the sporogenous portion of the anther where the development of microspores and subsequently of pollen grains occurs. Alternative terms: anther locule, pollen sac (Plate 5).

In a typical case, at early stages of anther development, the anther primordium is represented by a meristem enclosed in the epidermis. Later, four protuberances become conspicuous. In each of these, one or several subepidermal cells develop into archesporial cells. Successive periclinal divisions of an archesporial cell and its derivatives result in the formation of a microsporangium wall and a sporogenous tissue. On the anther connective side, the inner portion of the tapetum and, in some

species, also the other layers identical to the microsporangium wall layers develop from the active meristem adjoining the sporogenous tissue.

Tetrasporangial anthers are characteristic of most flowering plants. In some species, however, the number of microsporangia per anther may be lower, namely one (Diapensiaceae), two (Moringaceae, Marantaceae and some members of Monimiaceae), and three (Daphniphyllaceae, along with four), or higher, i.e., eight (Zannichelliaceae, Cymodoceaceae, along with four) and even as many as fifty (Mimosaceae). Variation in microsporangium number may be due to various factors: reduction in part of the anther or its transformation into a sterile appendage (Cannaceae, Marantaceae), fusion of a pair of microsporangia at an early stage of anther development—a sporadic occurrence (Daphniphyllaceae, Nitrariaceae), stamen splitting (Adoxaceae), or anther primordium fusion at early stages, it may also be due to formation of additional septa within a microsporangium. In some families (Myristicaceae, Aristolochiaceae), the anthers unite to form synandria carrying numerous microsporangia.

The microsporangia carried by a single anther may be equal or different in size, with microsporangia located on the abaxial side of the anther being smaller than those on the adaxial side (Eupomatiaceae, Ceratophyllaceae, Berberidaceae, Nandinaceae). Microsporangia vary in shape from oval, to rounded to horseshoe-shaped (in species with the anther connective outgrowths projecting into the locule, as in Lamiaceae, Bignoniaceae, and some members of Campanulaceae). Microsporangia also vary in size. At early developmental stages, they may exhibit differential numbers of sporogenous tissue layers and different microsporocyte sizes, with the pollen grain number and size varying at later stages.

In microsporangia of a single anther, the processes of microsporogenesis and pollen grain development normally occur synchronously. But occasionally they are asynchronous. Thus in Peganaceae, all meiotic stages—from the interphase of meiosis I (at the base of the anther) to telophase (towards the anther tip)—can be observed to occur successively in one and the same microsporangium (Kapil and Ahluwalia, 1963). Asynchronous development is also observable in different microsporangia of a single anther, as in Bignoniaceae and Zygophyllaceae (Kamelina, 1985e; Kamelina *et al.*, 1990). In many plants, postmeiotic microsporangia are filled with locular fluid surrounding the microspores which disappears in the course of anther maturation and dehydration.

Epidermis (Greek *epi* = on, above, atop and *derma* = skin)—the ground tissue completely enclosing the anther. Synonym: **exothecium** (Plate 6).

At early stages of anther development, the epidermal cells of the microsporangium wall and anther connective are not dissimilar. They look like a meristem, their characteristic feature being that they only divide anticlinally. But as the wall layers become differentiated, these differences are reflected in altered sizes and shapes of cells and nuclei, presence of storage reserves, cytoplasm density and viability of the cells proper.

In the course of development, epidermal cells of the **microsporangium wall** undergo changes in size, shape, condition of organelles, and in other parameters. In most cases, the epidermis persists in a mature anther, but occasionally shrinks or peels off (Nitrariaceae, Tetradiclidaceae). In some plants, most commonly where the anther dehisces by pores or in some other way, rather than longitudinally, the wall of a mature anther is represented by the epidermis alone (Bignoniaceae). In specific cases,

the epidermis develops fine fibrous thickenings (Empetraceae). The microsporangium wall epidermis is covered by a cuticle which varies in thickness (very thick in *Peganum harmala*) and shape (e.g. stellate, spinulate in Coriariaceae, comb-shaped in Morinaceae). In some species, the cuticle on the outer tangential wall arises very early, even prior to meiosis (Elaeagnaceae, Brexiaceae). In early developmental stages, epidermal cells often contain starch (Valerianaceae, Dipsacaceae), certain species accumulate tannins (Brexiaceae, Cyrillaceae, Myristicaceae), with calcium oxalate crystals (genera *Ixerba* and *Malacocarpus*) and chloroplasts (Zannichelliaceae, Ruppiaceae) also being present. In some species, the epidermis develops hairs (Calycanthaceae) and specific structures in the form of acute spicules aiding in the mechanics of anther dehiscence (*Incarvillea*), and trichomes (peltate glandules in *Stachys trinervis*, Lamiaceae). Occasionally, stomata occur in the epidermis (Geraniaceae).

Connective—the sterile part of the anther joining all the microsporangia together. It is essentially an extension of the filament.

Connectives may vary in structure, shape and in the number of tissue layers present in them. In some species, the connective is very massive (Magnoliaceae, Eupomatiaceae, Degeneriaceae, Trapaceae, Brexiaceae), in others (which are many) it is not bulky, being sometimes represented by no more than a few tissue layers (Tetradiclidaceae). In some aquatic plants, air pockets occur between the cells of the connective (Zannichelliaceae). Occasionally, the connective develops multicellular outgrowths—placentoids—which grow into each microsporangium (Eames, 1961), thus giving a horseshoe-like appearance to the connective (Lamiaceae, Verbenaceae, Bignoniaceae, some members of Campanulaceae). These outgrowths may also originate at the septum between the microsporangia (Lamiaceae, Verbenaceae). The anther connective cells accumulate starch (Nandinaceae, Bignoniaceae), tannins (Escalloniaceae, Brexiaceae, Marantaceae), and calcium oxalate crystals (Peganaceae). Within the anther connective of some plants, specific storage cells occur which accumulate various substances: fats (Pittosporaceae), mucilage of polysaccharide nature (Nitrariaceae), etc.

In some species, at later stages of anther development, the layer of the connective cells adjoining the locule undergoes differentiation which follows the pattern seen in the endothecial cells with characteristic fibrous thickenings in the cells (Datiscaceae, Parnassiaceae, Tamaricaceae, Escalloniaceae and others). Fibrous thickenings also occur in subepidermal cells of the connective (Daphniphyllaceae, Magnoliaceae, Cneoraceae, Peganaceae and others), in its placentoids (some members of Campanulaceae) and in the subjacent layers (Brexiaceae, Morinaceae). A vascular bundle(s) runs along the central part of the connective (they are numerous in *Ostrowskia magnifica*, Campanulaceae).

The anther connective is a polyfunctional structure which performs mechanical (joins together the two thecae of an anther) and storage functions and is involved in transport of nutrients from the filament and maternal plant to the microsporangia.

MICROSPORANGIUM WALL

Microsporangium Wall—structure comprising layers of microsporangium cells enclosing the sporogenous tissue (Plate 7). The origin and development of the

microsporangium wall is one of the most knotty questions in plant embryology. Warming (1873) was the first to note the **centrifugal** mode of the microsporangium wall development in angiosperms. Under this mode of development, the **tapetum** (if it originates from the parietal layer) is the **initial product** of the **parietal layer** development. By contrast, under the **centripetal** mode of the microsporangium wall development, the **tapetum** is an end product of the **parietal layer** differentiation (Carniel, 1961). In speaking of the centrifugal and centripetal modes of the parietal layer development, we mean a vector running from the centre of a microsporangium to its margin or, conversely, from the margin to its centre. Due to complex morphogenetic transformations in the anther, the microsporangium wall of most taxa exhibits a variety of modes of development (Teryokhin *et al.*, 1993). A distinction needs to be drawn between the **formed wall** of a microsporangium which shows a finite, taxon-specific number of layers, and the **wall of a mature microsporangium** at the moment of dehiscence. In the course of anther maturation, further differentiation and specialization of cells of all the microsporangium wall layers occurs, usually concurrent with meiosis and pollen formation. In most angiosperms, the formed microsporangium wall is composed of the **epidermis, endothecium, middle layer** and **tapetum**. It is thicker in primitive taxa than in more advanced ones. An increase in the microsporangium wall massiveness normally occurs due either to an increased number of middle layers (Magnoliaceae, Degeneriaceae, Ranunculaceae) or to a higher number of the tapetum layers (Magnoliaceae, Trochodendraceae, Schisandraceae and others). In some members of Rubiaceae, Oleaceae and other families, the tapetum is multilayered only on the connective side of the anther. In members of Magnoliaceae and Schisandraceae, the endothecium is non-uniformly bilayered one while in Scrophulariaceae (*Chelone glabra*) it is represented by two to six layers. However, a multilayered endothecium has also been reported in some primitive families (Bhandari, 1971; see also *Comparative Embryology of Flowering Plants*, 1981-1990). During the evolutionary history of many plant species, reductions have occurred both in number of the microsporangia per se (*Arceuthobium pusilum*) and in number of their different layers. In spite of the impressive progress in our understanding of the genesis of angiosperm microsporangia, there remain some disputable points related to the earlier stages of development and crucial for elucidation of the mechanism of microsporangium formation. As rightly pointed out by Bhandari (1984), the topicality of the problem stems from the scarcity of studies on early stages of microsporangium development. However, evidence summarized in *Comparative Embryology of Flowering Plants* (1981-1990) and findings of some Russian and other (FSU) plant embryologists (Batygina *et al.*, 1963; Sladkov and Grevtsova, 1988; Teryokhin *et al.*, 1993; and others) make it possible to raise and discuss a number of issues concerning the morphogenetic regulation of development of the anther as a plant (flower) organ. One such important issue is the origin of some layers of the microsporangium wall, especially on the anther connective side. The microsporangium wall was long thought to be formed only on the outside of the microsporangium (Warming, 1873; Schnarf, 1929, 1931; and others). That is why in subsequent studies of the microsporangium wall the primary emphasis was also on its formation on the outside of the microsporangium only, i.e., on the side opposite to the connective. Since the early 1960s, attention has been given to the formation of the microsporangium wall both on the outside of the microsporangium and on the connective side. Carniel (1961) was the first to notice that in *Zea mays* the microsporangium wall completely encloses the sporogenous

tissue, **the tapetum is derived from the parietal layer,** but the origin of the latter did not seem to be the principal concern of the author. However, Batygina and co-workers (1963) and Batygina (1974b, 1987a) came to the conclusion that in *Triticum* the tapetum is also a derivative of the parietal layer but has a **dual origin: a portion of it** (on the connective side) is differentiated from cells of the **meristem,** and on the outside, the parietal layer cells **are derived from archesporial cells.** There are at least two ways in which the tapetum can be formed on the connective side of the microsporangium: either **from the anther meristem adjoining the connective,** or **from the meristem which is a component of the microsporangium itself.**

Periasamy and Swamy (1966) suggested a **'dual origin of the tapetum'** in microsporangia of flowering plants. In doing so, they implied that **on the connective side the tapetum is invariably** formed from the **meristem of the connective, and not from the parietal layer.** Some authors even now hold this view (Kamelina, 1981a,b,c,d, 1991). Later, this assumption was corroborated for a number of taxa of flowering plants by studies on the origin of the tapetum (Vijayaraghavan and Ratnaparkhi, 1973; Nikiticheva, 1987; *Comparative Embryology of Flowering Plants,* 1981-1990). Indeed, at least some of the taxa of flowering plants can be noted to exhibit dual origin of certain layers of the microsporangium wall or its initials, although morphogenetic pathways leading to its formation are not the same in members of different taxa. However, an **alternative pathway of tapetum formation,** i.e., **from parietal tissue,** as previously demonstrated for *Zea mays* and *Triticum* (Carniel, 1961; Batygina *et al.,* 1963) and confirmed for *Triticale* (Bhandari and Khosla, 1982) must not be ruled out. The authors have clearly demonstrated the tapetum in microsporangia of the aforesaid cereals to be formed **exclusively from the parietal tissue, such that it envelops the sporogenous tissue in a concentric layer.** For lack of detailed studies on the earliest stages of microsporangium development, the origin of the parietal layer and other microsporangium wall layers is still an open question. It suffices to mention that in specific cases with a multicelled archesporium, the possibility was demonstrated of the parietal layer (in all its parts) being formed from sporogenous tissue (Shreve, 1906; Holmgren, 1913; Batygina *et al.,* 1963). However, the evidence for the tapetum being differentiated from the sporogenous tissue (Maheshwari, 1950; Bhandari, 1971, 1984; Lakshmanan and Poornima, 1988) needs to be verified.

Thus, the problem of microsporangium wall genesis, important as it is for understanding the level, nature and mechanisms of regulation of microsporangium formation, cannot yet be considered completely solved.

Parietal Layer (Latin *paries* = wall)—a microsporangium wall layer originating by periclinal division of archesporial cells and giving rise to other layers. The term was coined by Nägeli (1842) while describing the tissues of a young anther; all the wall layers were termed parietal. Primary and secondary parietal layers are distinguished. The former arises from an archesporial cell(s) and its cells divide periclinally. Depending on the mode of microsporangium wall development, the following may be derived from the primary parietal layer: a tapetum and a secondary parietal layer (in the case of centrifugal type of development), an endothecium and a secondary parietal layer (centripetal type), or two secondary parietal layers (basic type) (Davis, 1966). Periclinal division(s) of cells of the secondary parietal layer(s) results in the formation of an endothecium and a middle layer (centrifugal type), a tapetum and a middle layer (centripetal type), or all the layers of the wall; of an endothecium, two

middle layers and a tapetum (basic type). The cells of parietal layers (parietal cells) exhibit features of the formative tissue (meristem).

Endothecium (Greek *endon* = inside and *theke* = conceptacle, reservoir)—an outer layer of the microsporangium wall located below the epidermis (Plate 8). The term was coined by Purkinje (1830) to refer to all the layers of the wall of a dehiscent anther lying below the epidermis. The endothecium is a derivative of either the primary or secondary parietal layer, resulting in differential timing of its differentiation: earlier in the former case and later in the latter. In a young anther, endothecial cells differ little from epidermal cells or from middle layer cells. Endothecial cells become significantly enlarged during the meiotic period in some plants and, more frequently, during the postmeiotic period in others. Starting at the first mitosis of pollen grains, the so-called **fibrous thickenings** (bands) are formed on anticlinal and inner tangential cell walls of the endothecium. These are mainly oriented at right angles to the epidermal layer. In some instances, no fibrous thickenings are formed, whereas radial and inner tangential walls of the envelope become greatly thickened (Nandinaceae), or all the envelopes with sieve pores become thickened (some members of Magnoliaceae). In individual cases, the endothecial cell envelopes do not become thickened, nor are fibrous bands formed in them (Empetraceae, Epacridaceae). This is also the case in some aquatic plants (Zannichelliaceae, Cabombaceae, Ceratophyllaceae) and cleistogamous ones.

At early developmental stages, endothecial cells show the presence of starch; occasionally they accumulate tannins (Elaeagnaceae, Ebenaceae, Brexiaceae). In most plants, the endothecium persists in the wall of a mature anther and is involved in anther dehiscence. In some cases (*Incarvillea*), an endothecium with fibrous thickenings persists only in the vicinity of the stomium.

Typically, the anther wall endothecium may be monolayered, occasionally irregularly bilayered (*Maranta*), or multilayered.

Middle Layer (takes its name from the fact that it is located between the tapetum and the endothecium; Coulter, 1898)—a derivative of the primary and/or secondary parietal layer. The number of middle layers within a microsporangium wall varies between one (in rare instances, entirely absent) and 5-7 (Nandinaceae, Marantaceae) (Plate 9). Middle layers increase in number due to additional periclinal divisions (often irregular ones) occurring in one or two middle layers already formed. At early stages, middle layer cells are not dissimilar to epidermal and endothecial cells and often show the presence of starch. During the meiotic period, flattening of middle layer cells and nuclei occurs followed by their degradation and lysis in the postmeiotic period or by partial enlargement and expansion of the cells after tapetum disintegration. In many cases wherein the middle layer is represented by a single layer, it is transitory and, with commencement of meiosis, gradually degenerates and disintegrates prior to the onset of lysis of the tapetum (Dipsacaceae, Valerianaceae). In other instances, it remains functional following tapetum lysis, up to the time of pollen grain maturity (Poaceae). Where numerous, middle layers persist for a long time, gradually disintegrating centripetally (Daphniphyllaceae, Nandinaceae). Where there are two to three middle layers in an anther, they occasionally show differential developmental patterns. The middle layer(s) adjoining the tapetum disintegrates, and that adjacent to the endothecium persists in the mature anther. Moreover, the surviving

cells of the middle layer develop fibrous bands (thickenings) which, more often, differ in shape from those formed in the endothecium (Daphniphyllaceae, Datiscaceae, Morinaceae and others) but occasionally are similar to them (Escalloniaceae, Winteraceae). In some instances, the middle layer is retained in the wall of a mature anther but its envelopes show no fibrous thickenings (Actinidiaceae, Davidiaceae, Peganaceae). The two middle layers in anthers of *Beta vulgaris* differ in cell ultrastructure: the outer layer cells exhibit a more developed plastid apparatus (plastidome) and those of the inner layer a more developed endoplasmic reticulum (ER) as well as a higher ribosome density and a lower degree of vacuolation (Golubeva, 1989). The cells of the persisting middle layers sometimes accumulate tannins (Brexiaceae, Myrsinaceae). In Araceae, the middle layer adjoining the tapetum is involved in the formation of a periplasmodium (Pacini and Juniper, 1983). The numerous middle layers found in anthers of Marantaceae secrete a mucilage of polysaccharide nature into the locule (Kamelina, 1990a,b). Carotene and lipid bodies have been reported to occur within middle layers (Liliaceae) (Reznickova, 1984).

Thus the middle layer has multiple functions: storage (deposition of starch and other nutrients), transport of assimilates, secretion (including involvement in pollenkitt formation) and mechanical, concerned with opening of anther wall.

Fibrous Thickenings—specific bulges of cell walls of various anther tissues (Plate 8). They occur in the endothecium (in most plants), in persisting middle layers of a mature anther (Datiscaceae, Morinaceae, Zygophyllaceae), in the anther connective subepidermis (Daphniphyllaceae, Magnoliaceae), in the connective outgrowths (placentoids) (*Ostrowskia*), and, very rarely, in the anther epidermis (Empetraceae). Fibrous thickenings are formed in differentiated cells, generally prior to or during mitosis I in pollen grains. Upon their formation, the inner tangential wall of the cell becomes considerably thickened (which is particularly the case with the endothecium), with fibrous bands extending outwards to radial walls and terminating near the outer tangential wall or, occasionally, spanning it. Fibrous thickenings exhibit the following chemical composition: alpha-cellulose (De Fossard, 1969), pectin and lignin. They have been observed to produce intense phosphorescence in polarized light.

Fibrous thickenings vary in band thickness, disposition and shape. Although Eames (1961) has recorded a multitude of structural variants, there is no comprehensive classification of fibrous thickening types. For some families, such as Araceae (French, 1985a,b, 1986), Asteraceae (Dormer, 1962; Vincent and Getliffe, 1988), Poaceae and Restionaceae (Manning and Linder, 1990) and Orchidaceae (Feudenstein, 1991), more detailed classifications have been proposed of the endothecial fibrous thickenings as they are thought to be an important taxonomic feature.

The primary function of fibrous thickenings is that of aiding in the mechanics of anther dehiscence. Upon cell dehydration, they (endothecial and middle layer bands) act as a spring forcing the walls of the anther thecae apart. Obviously, the fibrous bands of the anther connective and placentoid tissues function during anther dehiscence as a mechanism assisting in the expulsion of pollen grains from the anther.

Tapetum (Greek *tapes* = lining, carpet)—a polyfunctional tissue immediately adjacent to the sporogenous tissue of the anther and ensuring effective meiosis, normal development of microspores and pollen grain maturation. Alternative term: lining (Plate 10).

The tapetum may be homomorphic or heteromorphic when its inner portion is multilayered or is represented by large papillate cells (Lamiaceae, Bignoniaceae and others). In some instances, the tapetum develops transient auxiliary partitions (septa or trabecules) between sporogenous cells (Gentianaceae, Balsaminaceae). Tapetal cells may be mono-, bi- and multinucleate.

Tapetum and Orbicules (Ubisch Bodies)

The tapetal cells form a well-defined layer which surrounds the microsporogenous tissue in the anther. They show the following characteristics: (1) they are distinctly enlarged and always ephemeral; (2) the cytoplasm is rich in ribosomes and active organelles; (3) tapetal cells may be multinucleate or polyploid; (4) various irregular mitotic divisions and nuclear fusions take place in the tapetal cells; (5) their rapid and intense activity ends in degeneration of the cytoplasm (Plate 11).

Two main types of tapetum tissue are distinguished:

1. **Glandular (secretory) type**, in which the cells remain in their original position and disintegrate later.
2. **Amoeboid type (invasive** or **periplasmodial)**, in which the protoplasts of the cells penetrate between the pollen mother cells and the developing pollen grains where they fuse with one another to form a tapetal periplasmodium.

In some cases, the tapetal cells repeatedly enter into periods of hypersecretory activity until near maturity of pollen grains. For example, in *Nymphaea* (Rowley *et al.*, 1990) there are two distinct intervals during which tapetal cells protrude into anther locules. Following each interval of locular invasion, then retract and become arranged as a palisade around the loculus.

As information accumulates, the border between types of tapetum tissue becomes less clear. Variations in tapetum morphology may be an adaptation to pollen grain size, shape, mode of dispersal, pollenkitt and probably other factors (Pacini, 1990).

Functions of the tapetum. The main function of tapetum tissue is that of supplying nutrients to the developing microspores. In addition, the tapetal cells may take part in the following activities:

1. Secretion of the enzyme callase to dissolve the callosic wall of the tetrad (Stieglitz, 1977) and release the microspores.
2. Secretion of polysaccharides into the loculus during free microspore stage and their subsequent absorption by the developing microspores (Pacini and Franchi, 1983).
3. Formation of exine precursors which, according to recent results of degradation experiments (Schulze Osthoff and Wiermann, 1987), could be phenols or p-coumaric acid (Wehling *et al.*, 1989). The male gametophyte, along with the tapetal cells, contributes to formation of the exine.
4. Tapetal cells may have other activities resulting in the formation of various structures characteristic of some families. For example, in Onagraceae tapetal cells play a role in the formation of fine flexible threads known as viscin threads, which are an extension of the outer layer of the exine (Hesse, 1984). In family Compositae (Asteraceae), the tapetum forms an acetolysis-resistant membrane outside the sporogenous tissue (Heslop-Harrison, 1969). This membrane is known as the culture sac or peritapetal membrane (Shivanna and Johri, 1985).
5. Formation of orbicules (Ubisch bodies).

6. Formation of pollenkitt, a hydrophobic layer composed mainly of lipids and carotenoids (Pacini and Casadoro, 1981; Rowley and El-Ghazaly, 1992). Pollenkitt is generally deposited on the exine surface and helps to bind pollen grains together, probably for efficient insect pollination.
7. Formation of tryphine, a mixture of hydrophobic and hydrophilic substances. Tryphine is usually deposited on the pollen surface and possibly helps in protection of pollen grains and in insect pollination (Dickinson and Lewis, 1973).

Orbicules. Orbicules were first observed by Rosanoff (1865) to occur in close association with the tapetum and to have a composition similar to the exine of pollen grains. Useful light microscopical observations were published later by Schnarf (1923) and Ubisch (1927). Schnarf (1923) was apparently the first to describe such exine-like bodies in *Lilium martagon*. Kosmath (1927) suggested that these bodies should be called 'Ubisch granules', because of the contribution Ubisch made towards their characterization. Heslop-Harrison (1962) used the term 'plaques' to describe such bodies, and Erdtman *et al.* (1961) proposed the term 'orbicules'. These structures were too small to be investigated solely by light microscopy; with the advent of the electron microscope they were easily reidentified and it became possible to consider their morphology and ontogeny.

Orbicules are generally spheroidal structures found in the anthers of many genera of angiosperms, both monocotyledons and dicotyledons, and many gymnosperms. Orbicular shape varies in different species. It may be rod-like, doughnut-shaped, oval or rounded triangular or plate-like with undulating or jagged margin, etc. Orbicules frequently fuse into large compound aggregates, as in *Oxalis pes-caprae*. The morphological variation of orbicules might be of taxonomic importance (Raj and El-Ghazaly, 1987; El-Ghazaly, 1989).

The wall of orbicules apparently consists of sporopollenin, a material of conspicuous durability. The surface pattern of orbicules and exine can be remarkably similar (El-Ghazaly and Jensen, 1986a).

Concerning the function of orbicules, many definitive functions have been attributed by various investigators. These include, for example, a transport mechanism for conveyance of sporopollenin, or providing a non-wettable layer lining the anther locule from which pollen grains are readily detached, or they may be associated with pollen dispersal (for a detailed review, see Echlin, 1971a, b; Pacini *et al.*, 1985).

Development of orbicules. This begins in the cytoplasm of tapetal cells on small globular bodies (pro-orbicules) with a diameter of about 0.1 μm. The origin of the pro-orbicules seems to be associated with the endoplasmic reticulum of the tapetal cells. At the sporogenous stage, numerous membrane-bound pro-orbicules appear in the tapetal cytoplasm. The membrane coat of the pro-orbicules fuses with the plasma membrane of the tapetal cell and young orbicules pass through the plasma membrane and arrange themselves on its surface; sporopollenin starts to accumulate on the surface of the pro-orbicules until their wall is developed. The orbicules apparently remain attached to the plasma membrane of the tapetal cells and are located in the outer and inner tangential layers and the radial sides of these cells (El-Ghazaly and Jensen, 1986a; Hesse, 1986; Rowley and Walles, 1987).

Tapetal Membrane—structure completely enclosing each cell of a secretory tapetum (Plate 12). The term was coined by Banerjee (1967) to describe an acetolysis-resistant

membrane which is formed on the surface of tapetal cell walls on the anther locule side. Synonyms: **tapetal pellicle** (Romanov, 1970c), **orbicular wall** (Christensen *et al.*, 1972), **pellicle** (Cousin, 1979).

In addition to the tapetal membrane enveloping each tapetal cell (Ogorodnikova, 1976a, b, 1986, 1990; Golubeva, 1983), an acetolysis-resistant membrane was discovered which binds all the tapetal cells on the middle layer side. It is variously called the extratapetal membrane (Heslop-Harrison, 1969), peritapetal membrane (Dickinson, 1970) or peritapetal pellicle (Reznickova, 1984). Tapetal and extratapetal membranes are formed during post-tetrad stages, concurrently with the formation of the pollen grain exine. The structure of these membranes, as viewed from the surface side and in cross-sections of anthers acetolysed in concentrated sulphuric acid, was examined under an electron microscope. The extratapetal membrane structure, as viewed from the surface, appears as an electron-light layer with sporopollenin globules, and in cross-sections, as an electron-dense line which extends up to and onto the radial walls of the two neighbouring cells and forms a V-shaped lamella (Walles and Rowley, 1979). The tapetal membrane structure has been found to vary according to the membrane topography. This prompted the introduction of specific terms for particular tapetal cell walls: the inner tangential wall, the outer tangential wall and radial walls. The inner tangential wall is a cell wall facing the cavity of the anther locule, the outer tangential wall is a cell wall presented to the middle layer cells, while radial walls face the neighbouring tapetal cells. In plants with secretory tapetum, four types of the tapetal membrane structure can arbitrarily be recognized.

I. **Pinaceae**-type. The membrane structure of all cell walls is fairly uniform. It is represented by fibrillar material with orbicules embedded in it on the inner tangential wall. This type of membrane structure occurs in members of Pinaceae, Schisandraceae, Simmondsiaceae, Moraceae, Chenopodiaceae, Alliaceae and Ruscaceae.

II. **Rosaceae**-type. This type of tapetal membrane differs from the previous one by lack of orbicules in fibrillar material and is found in members of such families as Rosaceae, Fabaceae, Linaceae and Polygonaceae.

III. **Solanaceae**-type. The tapetal membrane structure is represented by a network of strands completely enclosing each cell. Orbicules are attached to the membrane on the inner tangential wall. A structure like this occurs in members of the Solanaceae family.

IV. **Poaceae**-type. The membrane structure varies with membrane position. The tapetal membrane of the inner tangential wall comprises three components: a perforated layer, a network of strands and orbicules. Structurally, the tapetal membrane of the radial walls generally resembles that on the inner tangential wall, differing in that orbicules occur over approximately one-third the surface of the radial walls, closer to the anther locule. The tapetal membrane of radial walls partially overlaps the outer tangential wall while rounding the exterior corners of the cell. The membrane of the outer tangential wall is made up of fibrillar material. This composite and unique structure of the tapetal membrane is characteristic of the Poaceae family.

To date, the tapetal membrane structure has been studied by light- and electron microscopic techniques in members of 30 families with the secretory tapetum.

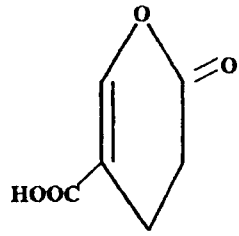
In plants with the **amoeboid type of tapetum** (Asteraceae, Caprifoliaceae and others), no membrane is formed other than the extratapetal one, which appears as an electron-light layer with sporopollenin globules (Heslop-Harrison, 1969).

The chemical composition analysis of the extratapetal and tapetal membranes, like that of the pollen grain exine, shows them to be made up of an acetolysis-resistant substance belonging to the sporopollenins. The functional significance of the extratapetal membrane is still unclear. It is assumed to form a *culture sac* for retention of pollen grains (Heslop-Harrison and Dickinson, 1969). In grasses, the tapetal membrane on inner tangential walls presumably ensures a single-layer arrangement of pollen grains in the anther locule owing to the exine bacula 'adhering' to the spinules of orbicules (Romanov, 1970c). It is believed that orbicules aid in the shedding of mature pollen from the anther, since ripe pollen grains are readily detached from their non-wettable surface (Heslop-Harrison and Dickinson, 1969). The structure of the tapetal membrane components, like that of the pollen grain exine, exhibits stability and constitutes an important taxonomic feature. Orbicules vary in shape, size and number according to the genus.

Sporopollenin—a biopolymer contained in the exine of pollen grains, in the exosporium of spores, as well as in the cells of some fungi and algae at certain stages of their life cycle. The term was coined by Zetzsche (Zetzsche *et al.*, 1937).

Sporopollenin is a highly resistant (both physically and chemically) polymer and is only slightly soluble in 2-ethanolamine and chromic acid. The chemical composition of sporopollenin has not been elucidated, nor have its precursors and their sites of synthesis been clearly identified (Southworth, 1990a, b). The first report suggested sporopollenin to be an oxidized hydrocarbon with a chemical composition between $C_{90}H_{134}O_{20}$ and $C_{90}H_{150}O_{33}$ (Zetzsche *et al.*, 1937). Brooks and Shaw (1968, 1978) believed sporopollenin to be formed via oxidation copolymerization of carotenoids and carotenoid esters. The authors observed a hundredfold increase in carotenoid content during zygospore formation in the fungus *Mucor mucedo*, as well as incorporation of ^{3}H beta-carotene in sporopollenin of some fungi and of ^{14}C carotenoids in the pollen of *Lilium* and *Cucurbita*. More recently, however, formation of the sporopollenin wall of *Cucurbita pepo* pollen was found to be only slightly affected by carotenoid synthesis inhibition (Prahl *et al.*, 1985). Spectroscopic analysis of the chemically resistant material of the outer cell wall of the alga *Botryococcus braunii* showed this substance to be distinctly of non-carotenoid nature (Berkaloff *et al.*, 1983; Largeau *et al.*, 1984). Moreover, in the sporopollenin fraction of the developing microspores of tulip, phenylalanine was detected (Prahl *et al.*, 1986) which, the authors presume, is involved in sporopollenin biosynthesis as a direct precursor of phenols. It is not inconceivable that terpenoid metabolism is implicated in sporopollenin biosynthesis. Sporopollenin samples isolated from pollen of plants belonging to different taxonomic categories were also analyzed by ^{13}C nuclear magnetic resonance spectroscopy (Guilford *et al.*, 1988). Sporopollenin has been found to be not a unique substance, but rather a combination of related biopolymers (Hemsley *et al.*, 1992) derived from saturated precursors such as fatty acids. Electron cytochemical studies of developing microspores of *Liriodendron chinensis* employing enzymes prior and subsequent to fixation provided evidence supporting the assumption of lipoproteins conceivably being precursors of sporopollenin (Gabarayeva, 1990; 1991a). Following isolation of sporopollenin from pollen of *Pinus mugo* and its examination by mass spectrometry, the resultant spectrum was found to be dominated by peaks characteristic

of p-coumaric acid (Wehling *et al.*, 1989). Chemical degradation of sporopollenin using AlJ_3 also showed p-coumaric acid to be a major product of its degradation, suggesting that p-coumaric acid is a genuine structural unit of the sporopollenin skeleton (Fig. 1) (Wehling *et al.*, 1989; Wiermann and Gubatz, 1992).



p-Coumaric acid

Fig. 1: Sporopollenin

Southworth *et al.* (1988) developed a technique for exine and cytoplasm purification with a view to producing sporopollenin antibodies. Preliminary results indicated that any chemical extractions removing non-sporopollenin components of pollen grains reduced the frequency of binding of antibodies to pollen grains, suggesting that a proportion of antibodies had previously bound to protein or other components of exines (Southworth *et al.*, 1988). On the other hand, the findings of Rowley and coworkers (Rowley and Prijanto, 1977; Rowley *et al.*, 1981b; Rowley, 1990) on exine structure showing the exine to be composed of glycocalyx components 'embedded' in sporopollenin, inspire little hope for the possibility of producing pure (uncontaminated) sporopollenin. As for the intention of identifying the site of sporopollenin synthesis through the use of antibodies, this task appears quite hopeless since its precursors in the cytoplasm exhibit a distinctly different chemical composition, and the antibodies are not expected to interact with them. It is known that no traces of intracellular sporopollenin have been found, the cell secreting nothing more than a substance which is a precursor of sporopollenin and which is not polymerized until it lands on the surface of microspores. It is considered to be a fairly well-established fact that in most plants sporopollenin precursors are synthesized by the microspore itself during the tetrad period and predominantly by the tapetum in the post-tetrad one. Opinions differ as to their sites of synthesis in various cellular organelles, with preference increasingly given in recent years to endoplasmic reticulum (ER) cisternae. It has been suggested that synthesis of sporopollenin precursors is accomplished by short tubular cisternae of the smooth endoplasmic reticulum (SER) of microspores (Dunbar, 1973; Gabara, 1974; Dickinson, 1976; Gabarayeva, 1991b). Interestingly, in terpenoidogenic cells of many plant (and animal) species, SER was demonstrated to be involved in the synthesis and transport of lipids terpenes and steroids (Vassilyev, 1977), i.e., substances belonging in the same groups in which presumably sporopollenin