Peter Leins • Claudia Erbar

Flower and Fruit

Morphology, Ontogeny, Phylogeny,
Function and Ecology

Schweizerbart
Science Publishers

Flower and Fruit

Morphology, Ontogeny, Phylogeny, Function and Ecology

By
Peter Leins and Claudia Erbar

with 258 f gures and 3 tables

Dedicated to the great French f ower morphologist
Jean-Baptiste Payer 1818–1860

Jean-Baptiste PAYER
1818-1860

Preface

Studying structure on the basis of development, combined with function, ecology and phylogeny, is plant science of its best. In particular flowers and fruits are fascinating objects to contribute to the understanding of the mechanisms of evolution. The authors of this book turned their attention to these exciting pivotal players of the evolution of flowering plants in their German text book "Blüte und Frucht" (first edition 2000, second edition 2008).

By request of several colleagues we have dared a translation of the second edition of our text book into the English language. Our former student, Holger O'Malley, had taken over the proof reading, and we are much indebted to him for his useful help. Since we have not adopted all his suggestions, any mistake is on our responsibility.

Many thanks are also due to the publishers, Dr. Andreas Nägele and Dr. Walter Obermiller, for their competent advice and their efforts to carry out all our wishes. We are also much grateful to Hilke Bornholdt from E. Schweizerbart'sche Verlagsbuchhandlung (Nägele und Obermiller) Stuttgart, for her excellent layout.

In comparison with the second edition of our German issue we have actualized the text in our English issue, especially the systematic appendix, which now follows APG III (2009). Our special thanks we want to address to our colleagues Mark Chase (Kew) and Peter Stevens (St. Louis) for their help in actualizing the phylogenetic tree of the flowering plants by sending us the APG III paper before publication. New in our English issue is a glossary at the end of the text. For a better readability we also have in the English issue not worked literature citations into the running text. Selected literature the reader can find at the end of each main chapter.

This book not only addresses to students but also to teachers and amateurs interested in botany and biodiversity. Our aim is to introduce to a living science and to animate the readers to make own observations, e.g. during their walks. Those amateurs which may have difficulties with chapters that acquire some specific expert knowledge, we advice simply to turn over and to pick up the threads later.

We now wish all, who love flowers and fruits, that they may find enjoyment in reading the diverse chapters of this book. Please don't hesitate giving constructive criticism to us.

Heidelberg, November 2009   Peter Leins and Claudia Erbar

Contents

Beforehand some thoughts on the origin and the important role of the flowers in the life cycle of plants

To understand the importance of the flower in the life cycle of plants, it is necessary to cover some basics. Flowering plants (angiosperms) have originated from gymnospermous ancestors possibly even before the Cretaceous. Gymnosperms for their part arise, roughly speaking, from primitive ferns, which originated together with moss plants from green algae. The groups of land plants mentioned share some important, very conservative features with green algae. These include the assimilation pigments (chlorophyll a and b, β-carotene), the assimilation product (starch), the cell wall composition (cellulose), the type of flagellation of flagellate cells, e.g. of the gametes (isokont, that is usually two flagella are of same length and shape) and the structure of the plastids. Land plants (mosses, ferns, seed plants = gymnosperms + angiosperms) are characterized without exception by a **heteromorphic**, **heterophasic alternation of generations**. In a heterophasic life cycle, as it is often also found in green algae, two generations that differ in their nuclear phase alternate regularly. A haploid generation generates gametes by mitosis (mitogametes). The zygote resulting from the fusion of two gametes grows up into a diploid generation in which meiosis takes place. The haploid cells arising from meiosis are called meiospores. From a meiospore the next haploid organism develops. The haploid, gametes-producing generation is called **gametophyte**, whereas the diploid, meiospores-producing generation is called **sporophyte**. Within green algae, gametophyte and sporophyte can be of the same shape. In this case the life cycle is called isomorphic (➜ Fig. 1, top left). A life cycle is heteromorphic if both generations differ from each other in their shape. A heteromorphic life cycle – as common in all land plants – is already found occasionally in green algae. In mosses (➜ Fig. 1, bottom left), the haploid generation dominates. It represents in fact the moss plant itself,[1] whereas the sporophyte itself has a relatively simple structure and is dependent on the gametophyte. To a great extent it even subsists on the latter. In contrast, a progressive reduction of the gametophyte occurs within the ferns (➜ Fig. 1, top right) and seed plants (➜ Fig. 1, bottom right); finally, namely in the seed plants, the gametophyte is nutritionally dependent on the sporophyte. Another feature of the alternation of generations in the seed plants is **heterospory**, which also evolved independently within some fern lineages, e.g. in the spikemosses *Selaginella*. Heterospory means that the sporophyte produces two kinds of spores, **megaspores** (= macrospores) and microspores. The containers in which the megaspores or microspores are generated are called **megasporangia** or **microsporangia**. Heterospory is correlated with sexual dimorphism of the gametophytes. The megaspores generate larger female gametophytes, whereas the microspores generate smaller male gametophytes. In seed plants a further "complication" exists concerning the development of the seeds that are typical of them. These develop from specific (enveloped) megasporangia, which are also called ovules. Not only does meiosis occur in the ovule, but also the development of the female

---

1   The young moss plants develop on an algae-like protonema, which for its part results from meiospore germination.
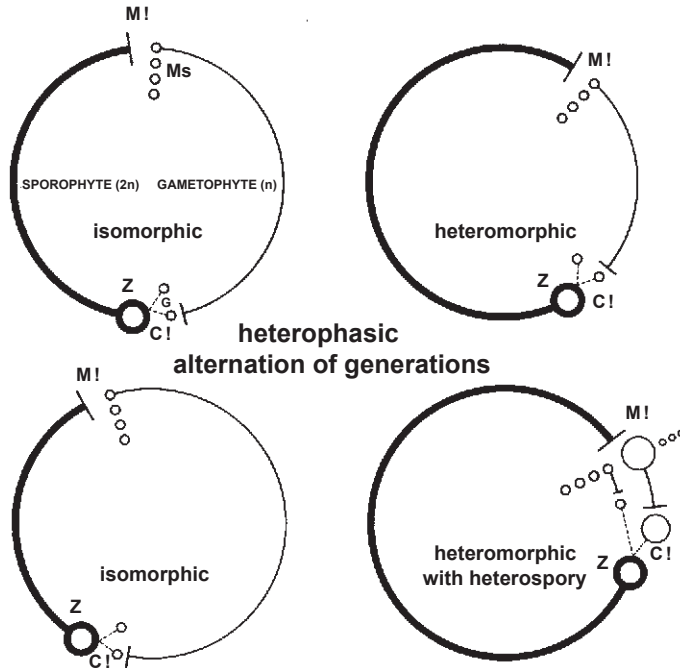
Fig. 1. The heterophasic alternation of generations in plants. In the four life cycles, the diploid phase (2n) is drawn with a thic k line, the haploid phase (n) with a thin line (C! = copulation of the gametes   , M! = meiosis, Ms = meiospores, Z = zygote). Top left: life cycle, e.g. of the sea lettuce (*Ulva lactuca*), a green alga occurring in the sea, bottom left: life cycle of a moss, top right: life cycle of a f ern, bottom right: life cycle of a seed plant.

gametophyte. The latter develops from one of the four haploid cells that result from meiosis, whereas, in general, three disintegrate. Furthermore, fertilization takes place within the ovule, and, ultimately – still within the ovule ! – the young sporophyte, the embryo, develops from the zygote. The development of the seeds is finalized when the embryo enters into dormancy and a more or less firm seed coat (testa) has differentiated from the special additional envelope around the megasporangium.[2] It is not until now that the seeds detach from the sporophyte as dispersal units.

Turning towards the life cycle of the flowering plants (angiosperms) in particular, we refer to the diagram in ➡ Fig. 2. We start with the diploid plant, the sporophyte. In general, the sporophyte's vegetative part is organized in three basic organs – root, stem, leaf. These basic organs have a certain position with respect to each other. Lateral shoots and flowers (unless they terminate the main axis) are borne in the axil of leaves (axillary ramification). The sporangia-bearing organs are aggregated within the flower, all arising from a floral axis of determinate growth and mostly surrounded by a perianth (sterile envelope). Very often and presumably originally, the flowers of the angiosperms are bisexual (hermaphrodite) which means that they have microsporangia-bearing (outward) as well as megasporangia-bearing

---

2   The envelope is known as integument(s). One or two integuments arise in each case from a ringwall at the base of the megasporangium or ovule. According to their development, they leave a little opening at the apex, which is called the micropyle (see chapter "The ovules").
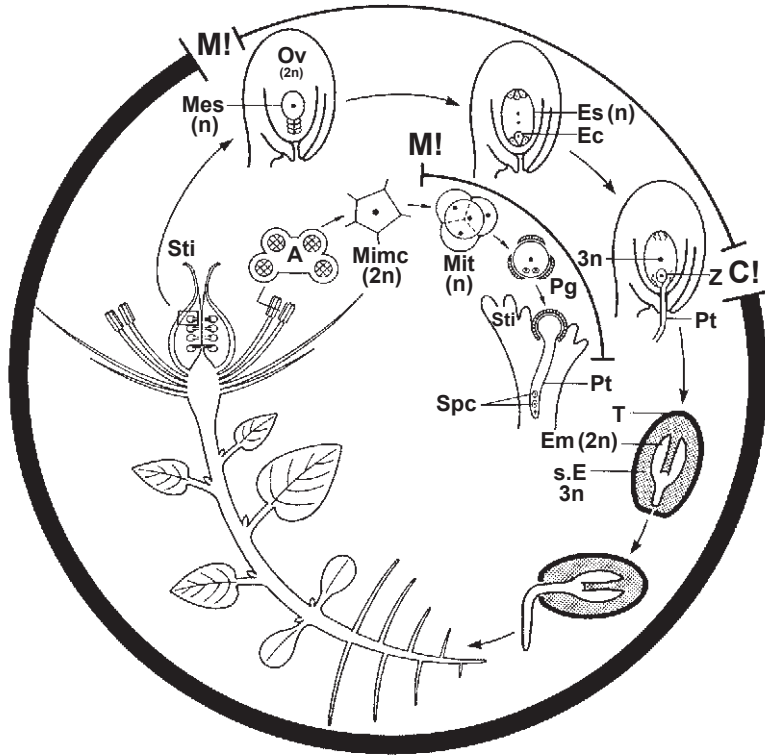
Fig. 2. Life cycle of a f owering plant, short version. A = anther, C! = copulation of gametes, Ec = egg cell, Em = embryo, Es = embr yo sac (= female gametophyte), M! = meiosis, Mes = megaspore, Mit = micro-spores tetrad, Mimc = microspore mother cell (pollen mother cell), n = haploid, 3n = tr iploid, Pg = pollen grain, Pt = pollen tube, Ov = ovule, s.E = secondary endosperm, Spc = sperm cells, Sti = stigma, T = testa, Z = zygote; the diploid phase (2n) is drawn with a thick, the haploid phase (n) with a thin line.

organs (inward). Within the angiosperms the microsporangia-bearing organs are called sta-mens and the megasporangia-bearing organs are called carpels. A stamen normally bears four confluent (synangial) microsporangia (pollen sacs). The carpels generate the megasporangia (ovules) at their margins; this is possibly the original behaviour. Originally, every carpel forms an ovary, in which the ovules are enclosed by folding of the carpel. In the majority of taxa the carpels of a flower form a common pistil with ovary, style and stigma. The common ovarium shelters all the ovules.[3]

The ovules – the megasporangia provided with a special envelope (integuments) – are mostly curved towards their place of insertion at the carpel margin (anatropous ovules). In the tissue of the actual megasporangium (nucellus) a megaspore mother cell differentiates. It becomes recognizable by its large size. The cell, which of course is diploid, now undergoes meiosis. Meiosis in most cases yields four haploid cells, the megaspores, three of which are distinctly smaller and perish. The fourth remaining megaspore, surrounded by the nucellus, undergoes three mitotic divisions to produce the female gametophyte, also called the embryo

_____

3   The ovules are not always situated at a carpel. They may also arise directly from the floral apex, i.e. floral axis. In this case carpels only serve to envelope the ovules.

sac. The latter typically is composed of seven cells: A relatively large, oval cell with initially two nuclei (the polar nuclei) is the central cell of the embryo sac. At its micropylic end the female gamete, the egg cell, clusters with two cells by its side, named auxiliary cells or synergids. Three further cells are located at the opposite side (away from the micropyle). These cells are called antipodes.

The development of the male gametophytes begins as soon as the meiospores have developed in the microsporangia (pollen sacs). The meiospores arise from numerous microspore mother cells via meiosis. The latter are initially arranged in tetrads. Still within the microsporangia the haploid microspores divide unequally, each resulting in a larger, so-called vegetative and a smaller, so-called generative cell. There is only one more cell division to come, and then the male gametophyte is completed as regards cell number: The generative cell divides into two sperm cells. This can either happen when the male gametophytes are still within the microsporangia (pollen sacs) or only later, when the vegetative cell develops into the so-called pollen tube. The young two- or three-celled gametophytes, which are covered by two wall layers, are released as so-called pollen grains by opening of the microsporangia, the pollen sacs. Now the pollen grains have to be transferred either by animals or by wind to the receptive tissue (stigma) on top of the carpels (preferably in flowers of another individual of the same plant species). This process is referred to as **pollination**. On a suitable stigma the pollen grain germinates as the vegetative cell produces a pollen tube. The pollen tube grows through the style down to an ovule, usually entering the ovule through the micropyle. The pollen tube's function is to deliver the two sperm cells into the female gametophyte. This happens as the tip of the pollen tube opens under destruction of one of the two synergids and releases both sperm cells. One sperm cell fuses with the egg cell, whereas the other sperm cell reaches the large central binucleate (or diploid)[4] cell of the embryo sac. The fusion of the latter nuclei results in the formation of a triploid nucleus. The phenomenon of **double fertilization** in this manner is unique to flowering plants.[5] A nutritive tissue develops from the triploid cell. This tissue is the so-called secondary endosperm, which surrounds the young sporophyte, the embryo, in the ripe seed. However, the storage of nutrients may be taken over later on by the cotyledons of the embryo. In the ripe seed (stop of embryo growth, firm seed coat resulting from the integuments), the nucellus (the wall of the megasporangium) is hardly recognizable any more. It has been displaced to a great extent by the developing endosperm and the embryo, respectively. The mature seeds separate from the mother plant and germinate into an independent plant through consumption of the stored nutrients. This new plant (the sporophyte) will later on generate spores itself. Seed germination mostly happens only after a resting period (dormant period). The phytohormone abscisic acid plays an essential role in seed dormancy.

When comparing flowering plants with modern-day gymnospermous plants, the former do not only differ in the phenomenon of double fertilization and the fact, that the carpels enclose the ovules (angiospermy), but also in the very frequent appearance of **bisexual** (hermaphrodite) **flowers**. These are absent in the gymnosperms that exist today. Hermaphrodite flowers, however, appeared in the fossil gymnospermous class Bennettitatae. Originating in the Upper

---

4   Both nuclei of the large central cell of the embryo sac may fuse to a diploid, so-called secondary embryo-sac nucleus already before the fertilization.

5   The double fertilization observed in the genera *Ephedra* and *Gnetum* within the gymnosperms results in two diploid cells. In contrast to the (mostly) seven-celled/eight-nucleate female gametophyte of the angiosperms, in basal angiosperms, namely in the waterlily *Nymphaea*, the star-anise *Illicium*, the Trimeniaceae and Austrobaileyaceae, a four-celled/four-nucleate female gametophyte and a double fertilization yielding a diploid endosperm as well as the diploid zygote are reported. In the basalmost recent angiosperm family, the Amborellaceae (see chapter "Early angiosperm flowers"), an eight-celled/nine-nucleate female gametophyte is found (an additional fourth cell in the region of the egg cell and both synergids exists).
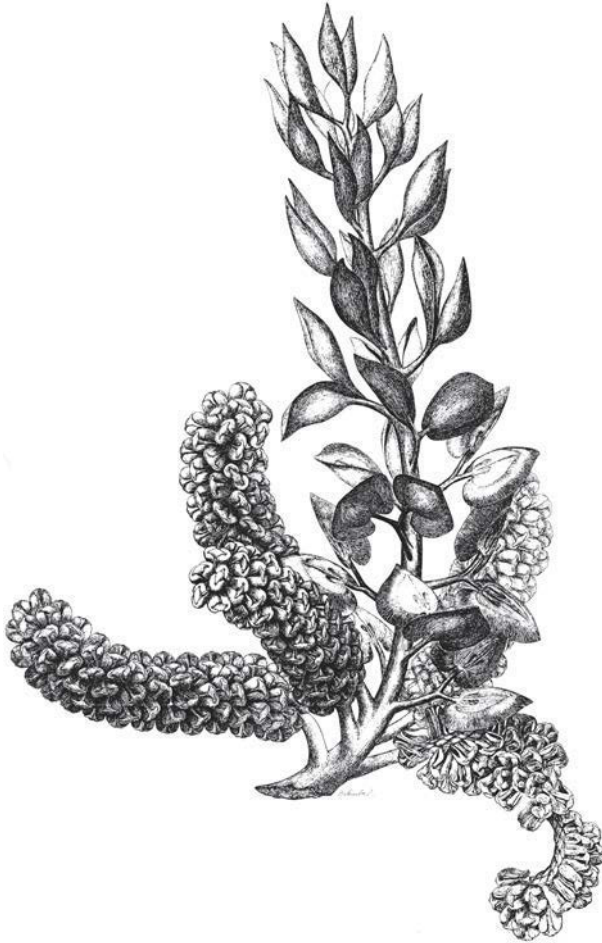
Fig. 3. A reconstruction of the hermaphrodite f ower of *Irania hermaphroditica* from the Upper Triassic of Northern Persia; about double of natural size. From Schweitzer 1977.

Triassic, about 190 million years ago, they already became extinct in the Lower Cretaceous, having, so to say, surrendered to the competition of the flowering plants.

An interesting hermaphrodite flower from the Upper Triassic needs to be mentioned in this context. It was found as a fossil in the Rhaet of Northern Persia (approximately 200 million years old) and was described by its discoverer as *Irania hermaphroditica* Schweitzer. In this fossil of a bisexual flower the complex microsporangia-bearing organs are remarkable (see reconstruction ➡ Fig. 3). Each of these consists of an axis on which subunits of two microsporangia are closely arranged. However, it is difficult to interpret the seed-bearing part of the hermaphrodite flower. It is unclear whether the seeds are already enclosed by an (valvate?) envelope or are still standing exposed. At any rate, *Irania* does not seem to be a direct ancestor of modern angiosperms; it appears to be one of several "attempts" to organize a bisexual flower.

The origin of bisexual flowers stands in close relation to the "use" of insects as a new agent to transfer pollen grains. Originally the pollination of the gymnosperms was provided by the

wind. As existent in present-day gymnospermous conifers, the pollen-producing organs are more or less remote from the ovule-bearing organs. Probably pollen-eating insects, possibly beetles, exerted a selection pressure on the gymnospermous seed plants at the end of the Triassic, about 200 million years ago. The one-sided parasitic relation between pollen-eating insects and plants was changed into a mutualistic relation by a simple "trick", namely by aggregating the pollen-producing and the ovule-bearing organs into that what we call a hermaphrodite flower. Now the insects are virtually invited for food by the creation of optical and olfactory signals through coloured perianths and emission of floral fragrances. Pollen grains from other flowers, which are transported by insects on their bodies, can now be directed close to the ovules and onto the stigma, respectively, with much higher probability than it usually is the case in wind pollination. The loss of pollen grains by feeding can easily be accepted.[6] Moreover, the pollen as the original "lure" was substituted – probably early in the evolution of the flowering plants – by abundantly available "sugar water", the nectar. Insects with licking-sucking and sucking mouthparts suitable for nectar intake developed (bees, butterflies etc.) in coevolution. It is self-evident that typical nectar-flowers often only have few stamens. Later, other animal groups joined the insects as pollinators.

   In the different flower forms that developed during evolution, insects (and other pollinating animals) come into contact with the pollen grains or microsporangia with different parts of their body. The parts of the body on which the pollen grains become attached and thus carried away are often of limited size and dependent on the respective floral architecture. Given that the pollinating insects (or other animals) show the same behaviour in other flowers of the same plant species, it is required that the stigma onto which the transported pollen needs to be deposited has the same position as the microsporangia. However, this would inevitably lead to self-pollination or self-fertilization,[7] had not mechanisms to counteract this problem developed at the very beginning of the angiosperm evolution. Without these mechanisms the great diversity of the angiosperms would hardly be conceivable. A separate chapter will deal with the mechanisms preventing or reducing self-fertilization (or promoting cross-fertilization) in detail. It will be demonstrated that these mechanisms could only evolve in correlation with the enclosure of the ovules in a container. This phenomenon is called **angiospermy**. Angiospermy is one of the concepts for success of the flowering plants.

■ Early angiosperm flowers – the fossil *Archaefructus*

Fossil records provide the only basis to attempt to answer the question of the origin of the angiosperms (flowering plants). As well as using dating for the interpretation and classification of the fossils, it is useful to consider the early phylogeny (reconstruction of the phylogenetic tree) of extant flowering plants based on DNA-sequence analyses. However, the problem is whether we are actually dealing with the most archaic flowering plants when looking at the oldest fossil records. It remains uncertain whether even older angiosperm fossils are hidden in older sediments or rock formations.

   According to present knowledge in paleobotany the oldest records of angiospermous reproductive structures have been found in the Lower Cretaceous with a minimum age of 125 million years (pollen records of presumed angiospermous plants are dated to be about 140–130

---

6   Examples of primary "pollen flowers" can be found in the magnolia family (Magnoliaceae), waterlilies (Nymphaeaceae), and star-anise family (Illiciaceae).
7   Self-fertilization following self-pollination is as a rule disadvantageous due to the decreased genetic recombination rate.

million years old). Predominantly, the flowers are small (< 5mm), often unisexual and consist of only a few floral organs. This seems to align well with the floral state of the basalmost extant angiosperm family, namely the Amborellaceae. This family is native to New Caledonia and consists of the single species *Amborella trichopoda*. The flowers are rather small (< 5mm), unisexual and dioeciously distributed. Male flowers consist of 5–11 perianth organs and 10–21 stamens. The floral organs are arranged in a spiral sequence. Female flowers possess a few sterile stamens (staminodes) between the perianth and some (mostly 5–8) free carpels. With regard to today's flowering plants, Amborellaceae are followed by the waterlily family (Nymphaeaceae), generally characterized by quite large bisexual flowers with an indefinite number of organs.

Recently, a fossil found in north-eastern China caused a stir: **Archaefructus** (with two species *A. liaoningensis* and *A. sinensis*). Originally, the fossil was dated as Late Jurassic. Newer datings provide strong evidence, though, that it is Early Cretaceous (approximately 125 million years old), hence close to the age of the well-known reproductive structures of old angiosperms that were discovered elsewhere.

In *Archaefructus* (→ Fig. 4), long reproductive axes bear numerous carpel-like, plicated (conduplicate) structures at their distal end, enclosing either a few (*A. liaoningensis*) or many (*A. sinensis*) ovules or seeds, respectively. A zone with numerous microsporangiate organs, which may be similar to typical stamens of recent flowering plants, lies beneath the carpel-like organs. Owing to the sometimes poor preservation, it is not entirely clear whether the microspores- or pollen-producing organs consist of four microsporangia (pollen sacs) with a pair of them separated by a connective (see under "stamen" in the chapter "The androecium"). Sometimes microsporangiate organs are not present, i.e. the axis only bears "carpels". Closer

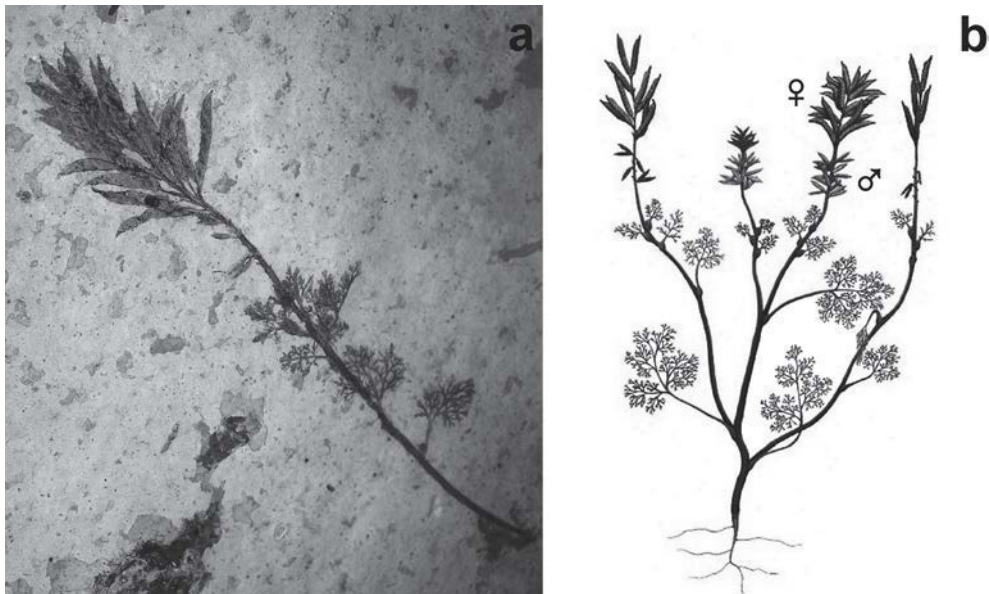

Fig. 4. The oldest known fossil of an angiosperm: *Archaefructus sinensis* from the Early Cretaceous. – a, Fossilization (in Senckenberg-Museum Frankfurt). – b, Reconstruction (Original by K. Simons & D. Dilcher in Sun et al. 2002). Pollen-producing (♀) organs (microsporangia) are located beneath the many-seeded, plicate carpels (♂).

analysis reveals that at least in some areas the pollen-producing organs are not borne directly by the axis. Rather, they are grouped in pairs or in small clusters on short common stalks, which arise from the axis. Also the pedicellate "carpel structures" sometimes seem to be grouped in pairs. This raises the question: bisexual flower or bisexual inflorescence? Assuming that the flower of a recent angiosperm is a **uniaxial** system of determinate growth (in spite of the fact that the organs arising from the axis can either be of more "axis-like" character, e.g. stamens, or of more "leaf-like" character, e.g. perianth members), the previously discussed reproductive unit of *Archaefructus* is, as it is multiaxial, formally an inflorescence.

Developing this as a theoretical model, the multiaxial reproductive structure can easily be changed into a uniaxial one, namely by reduction and condensation. Then, simply a "flower"-envelope has to be added (*Archaefructus* lacks perianth parts) and we have a hermaphrodite flower (of the pollen type). This phylogenetically based speculation is only "playing with a model" because there is high probability that *Archaefructus* was already a more specialized early flowering plant and was not a precursor of such angiospermous plants with large bisexual flowers and relatively high and unfixed organ number. *Archaefructus* was – as can be judged from the good preservation of vegetative parts connected with the reproductive structures – presumably a submerged water plant. Similar to many recent submerged aquatic plants (e.g. water-milfoil *Myriophyllum*, hornwort *Ceratophyllum*), the leaves are dissected, thus producing an enlarged surface. This can be interpreted as an adaptation to the low O_2–content in the water.

Although we do not know what the flowers of the first angiosperms looked like, we can judge from our current state of knowledge in paleobotany that there was a high plasticity in the flower structures already during the Lower Cretaceous. This especially concerns the number and arrangement patterns of the floral organs. In addition, we may assume that the borderline between flowers (uniaxial) and inflorescences (multiaxial) was a lot more flexible during the Lower Cretaceous than it is today.

Selected references and further reading

Bateman et al. 2006, Crane et al. 2004, Crepet & Friis 1987, Crepet et al. 1991, Endress 2001, Endress & Igersheim 2000a, Friedman 2006, Friis & Endress 1990, Friis et al. 2000, 2003, 2005, Labandeira 1997, Hofmeister 1851, Schweitzer 1977, Stuessy 2004, Sun et al. 1998, 2002, Tobe et al. 2000, Wettstein 1924, Williams & Friedman 2002, 2004

Short description of an angiosperm flower – some basic terms

The flower, which is the object of our consideration, cannot be defined all-embracingly. The flowers of the angiosperms are too diverse and our knowledge of their phylogenetic origin is too limited. Thus, it only makes sense to name the different parts that make up a flower. If a model like the one shown in ➜ Fig. 5 is used, we need to keep in mind that it neither exists in reality nor at all implies an "ancestral flower" ("Urblüte") in a phylogenetic sense. The model is no more than a didactic construct, which (for the present) comprises all essential parts and serves well for the definition of some basic terms.

A complete angiosperm flower is composed of **perianth** (envelope, often differentiated in sepals and petals), **androecium** (area of pollen-producing organs = microsporangia-bearing organs = stamens) and **gynoecium** (area of the ovules or megasporangia-bearing and/or megasporangia-enclosing organs = carpels; these very often form a common pistil with ovarium, style and stigma). The floral organs are arranged from outside to inside (according to the sequence mentioned above) on the **receptacle** (floral axis). The floral axis is determinate in growth, i.e. its top is occupied by the carpels and is being integrated in their development. It becomes obvious that ➜ Fig. 5 only represents a model of a flower because a deviation in the androecium is shown (on the left side) as the stamens may be fascicled, i.e. are connected with the floral axis via a common base (fascicled or "complex" androecia).
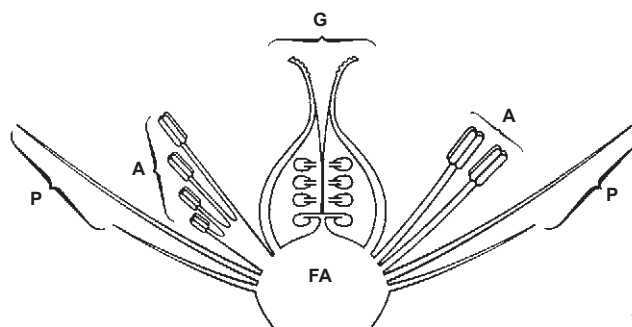

Fig. 5. Model of an angiosperm fl ower. A = androecium (on the left:stamen fascicle, on the right: individual stamens), FA = fl oral axis, G = gynoecium (of car pels), P = perianth (perigone or differentiation in calyx and corolla).

The genetic approach to the floral organ determination – from the A-B-C model to the A-B-C-D-E model

Molecular-based genetic research is preferably carried out in *Arabidopsis thaliana* (thale cress, Brassicaceae). The advantage of this model organism lies on the one hand in its rapid life cycle – it takes only one month from seed germination to ripe fruit – and on the other hand in its small genome and a relatively high mutation rate. *Arabidopsis thaliana* has the smallest known genome of the higher plants (in fact, it was the first plant genome to be sequenced, in the year 2000). Thus, *Arabidopsis* can be compared to the genetic experimental animal *Drosophila*. Similar to other Brassicaceae, *Arabidopsis* has four sepals, four petals, two outer shorter and four inner longer stamens as well as a pistil composed of two carpels (as it is typical of the family; diagram ➜ Fig. 6a). Genetic studies on the flowers of *Arabidopsis* have shown that the determination of these four organ categories is controlled by so-called homeotic genes[8] belonging to three classes of genes named A, B and C. The activities of these three classes of genes alone or in coordination specify the different floral organs. Expression of class A genes specifies sepal formation. The combination of class A and B genes specifies the formation of petals. Class B and C genes specify stamen formation, whereas expression of class C genes alone determines the formation of carpels (➜ Fig. 6b). Transitional forms between different organ categories may also be explained using the A-B-C model. These forms can either be of teratological nature or they occur permanently between perianth and androecium members, as it is the case in the flowers of *Nymphaea*. Applying the A-B-C model, these transitions may be interpreted as weaker or stronger expression of genes overlapping in their expression (see also chapter "Nectary organs").

In *Arabidopsis*, there are mutations that affect the identity of organs in the different whorls, but the position and number of organs in the whole is maintained (➜ Fig. 7). For instance, in the mutant "apetala 2–1" the four petals are replaced by four additional stamens. In the mutant "apetala 3–1" ("pistillata-2") the stamen positions are occupied by six additional free fertile carpels. Thus, we can conclude that organ position on the one hand and organ identity on the other hand are regulated at different genetic levels.[9]

Corresponding molecular genetic analyses on the floral development of the snapdragon (*Antirrhinum majus*) followed soon after. The results are equivalent to those in *Arabidopsis thaliana*. Since even within these rather unrelated angiospermous taxa – the snapdragon belongs to the scrophulariaceous alliance (Plantaginaceae-"Scrophulariaceae") – the organ identity genes are interchangeable and yet retain their function, an ubiquity of the gene classes within

---

8   This term is derived from "homeosis". It refers to the incorrect position of a floral organ: A floral organ is found in a place where organs of another type are normally found (e.g. the formation of carpels instead of stamens; see above in the following paragraph).

9   Perhaps glutaredoxins (= oxidoreductases) as well as others are candidates to play a role in this scenario. Known as a key component of plant antioxidant defence, they recently came to attention as they seem to be involved in different processes of floral development due to their capability to posttranslationally modify protein activity.
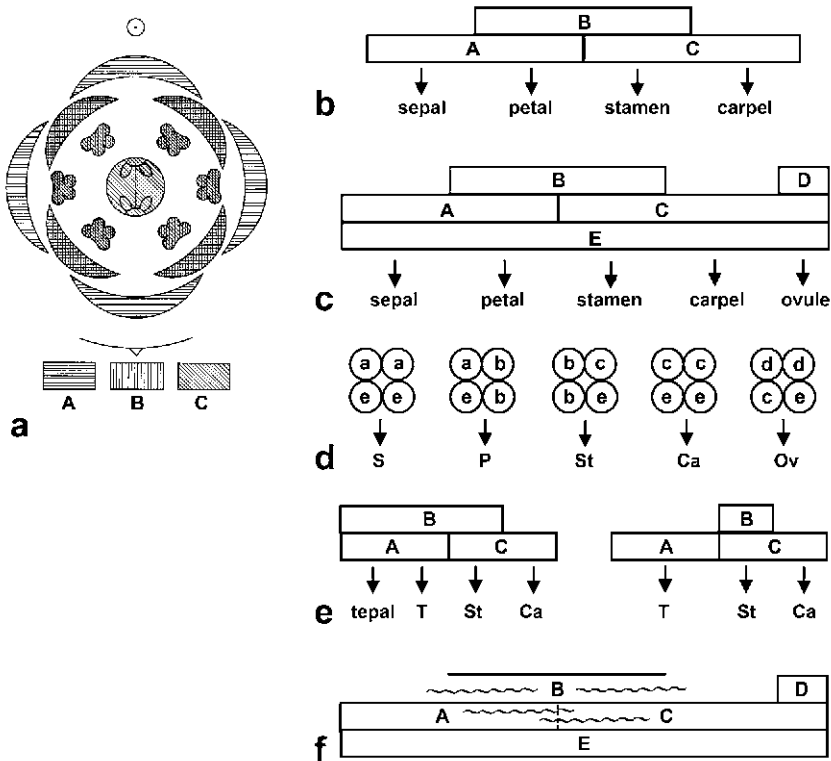
Fig. 6. Genetic model of organ identity. – a, Floral diagram of *Arabidopsis* (Brassicaceae). The morphoge-
netic area of activity of the genes A (horizontal hatching), B (vertical hatching) and C (diagonal hatching):
The four organ regions of a fower are the domains of action of three classes of homeotic genesFollowing
Coen & Meyerowitz 1991. – b, Classical A-B-C model in a block diagram (see a). – c, A-B-C-D-E model of
f oral organ identity in core eudicots (see cladog ram Fig. 258 in appendix; modif ed after Theissen 2001,
Zahn et al. 2005a). – d, "Floral quartet" model of organ specif cation (in *Arabidopsis*). This model directly
links f oral organ identity to the presumed action of f ve different tetrameric transcription factor complexes
of MADS-box proteins (modif ed after Theissen & Saedler 2001, Zahn et al. 2005a). – e, Modif cations
of the A-B-C model (on the left: *Tulipa*, on the right: *Rumex*): "sliding-boundary-model". D+E-function not
considered for means of simplicity. – f, A-B-C-D-E model for basal angiosperms: "fading-borders-model".
e + f constructed after Kanno et al. 2004, Buzgo et al. 2005, Kim et al. 2005. – A, B, C, D, E: domains of
action of the f oral homeotic genes; a, b, c, d, e: interaction of the proteins (tr anscription factors), Ca =
carpel, Ov = ovule, P = petalum, S = sepalum, St = stamen.

the angiosperms was inferred, which was confirmed by studies in some further angiosperm
species.

On the basis of studies first carried out in *Petunia* (Solanaceae) and later also in other species,
the ovules have to be regarded as fifth organ category which is determined by expression of
an additional gene class, namely D genes. Thus the classical A-B-C model could be extended
to an A-B-C-D model.

However, the A-B-C-D genes alone are not sufficient for the determination of the organ
identity. For that function another class of homeotic genes is required, named class E. Thus the
classical A-B-C model as proposed in 1991 was extended in 2001 to the A-B-C-D-E model,
in which the E function is required to determine the organ identity of all five organ categories
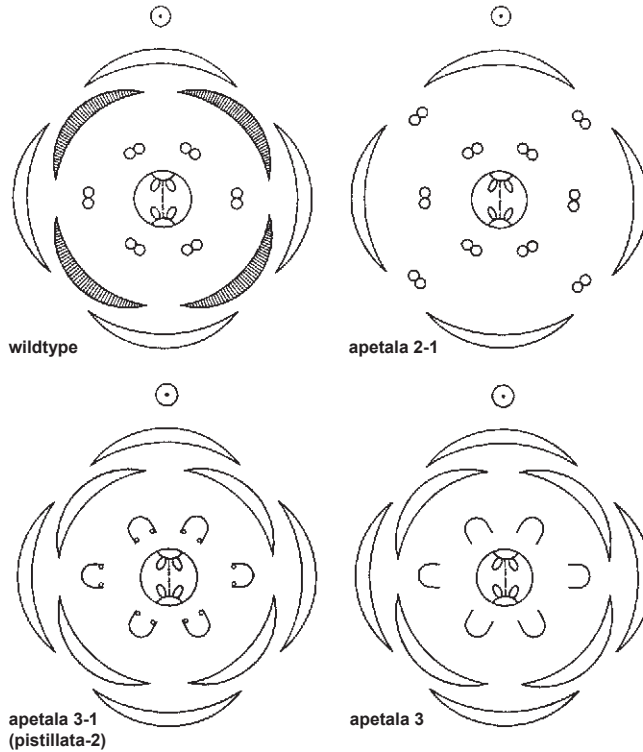(➜ Fig. 6c).

Fig. 7. Floral diagrams of the wild-type and of homeotic m utants of *Arabidopsis thaliana* (Brassicaceae; mutants drawn after Meyerowitz et al. 1989, 1991).

The question remains by which mechanisms the homeotic genes of these five different classes interact. The genes A, B, C, D and E encode transcription factors, i.e. proteins, which recognize specific DNA motifs of other genes and influence their transcription. Most A, B, C, D and E genes are members of a transcription factor family that has a characteristic conserved DNA binding domain structure, termed the MADS box.[10] This sequence encodes for the DNA-binding site of the corresponding transcription factor. The resulting A-B-C-D-E proteins bind to the target gene, whose transcription they control in complexes larger than a dimer. Thus the "quartet model" of floral organ specification postulates that five different tetrameric transcription factor complexes composed of MADS proteins specify floral organ identities (➡ Fig. 6d).

Since homologues of the A, B, C, D, and E genes are present in all investigated angiosperms, it can be assumed that the determination of the organ identity is generally conserved. The A-B-C-D-E model proposed so far refers to flowers that can be found in most **eudicots** (= Rosatae; ➡ Fig. 258 in the appendix). Nearly 74% of all angiosperms belong to this large

---

10 MADS is an acronym derived from the founding four members of this transcription factor family: MCM1 from yeast, AGAMOUS from Arabidopsis, DEFICIENS from *Antirrhinum* and SRF from human. Function A is carried out partially by members of the APETALA2 transcription factor family.

group in which the floral organs are arranged in five or four whorls[11] with a fixed number of organs in each whorl. In contrast to the well-differentiated sepal and petal whorls of eudicots, the two outer floral whorls in many members of the **monocots** (= Liliatae), which comprise approximately 22% of angiosperm species, are identical in morphology. In the monocots, the floral organs are typically arranged in five trimerous whorls. How does the A-B-C-D-E model have to be modified? In *Tulipa* (Liliaceae) – and presumably likewise in many mono-cots – class B genes are expressed in both tepal whorls (as well as in the stamens). Compared to the model of the eudicots, the B function is extended towards the periphery of the flower (➜ Fig. 6e left). Another possibility is found in the (dicotyledonous) common sorrel (*Rumex acetosa*, Polygonaceae), where the perigone is realized without the B function (➜ Fig. 6e right). The modifications mentioned in tulip and sorrel can be described by the "sliding-boundary" model of the B domain, since the perigone is achieved either by outward shift (expansion) or by inward shift (contraction) of the outer boundary of the B gene function.

The remaining approximately 4% of angiosperm species belong to the **basal angiosperms** (= Magnoliatae) which comprise *Amborella*, the waterlily family (Nymphaeaceae), the Aus-trobaileyales (with the star-anise *Illicium*) and the large "magnolia alliance". Despite the small number of species, the Magnoliatae exhibit a great diversity in floral form and structure. The flowers vary in size, number of floral parts, and arrangement of the floral organs (spirals or whorls). Genes of the B class are expressed both in spiral and in whorled perianths as well as in stamens (and, if existing, in staminodes). However, the expression patterns are neither uniform nor constant during the perianth development (in the eudicots, B expression is constant throughout all stages of petal and stamen development). Likewise, A and C genes are being expressed across a larger area of the floral apex. These results are taken into account by the "fading borders" model (➜ Fig. 6f), which posits that organ identities in basal angiosperms are regulated by broad and overlapping expression of floral genes although with weaker ex-pression at the boundaries of their expression.

The A-B-C-D-E model with fixed borders of gene expression (➜ Fig. 6c) is only applicable to the core eudicots and seems to be the end point of an evolutionary series with transitional and overlapping gene domains (➜ Fig. 6f). In other words, the broad pattern of gene expression of the homologous A, B and C genes represents the ancestral condition, whereas the A-B-C-D-E model with fixed borders of gene expression is the derived condition.

The B genes in basal angiosperms, monocots as well as basal eudicots (e.g. in Ranunculales, which are sister to all other eudicots; ➜ Fig. 258 in the appendix) belong to the so-called "paleo-lineages" of the different homologous B genes. As already mentioned, these exhibit a spatial and temporal expression pattern that implies more complex functions and interactions than those underlying the more fixed and (presumably) uniform A-B-C-D-E model of the core eudicots. The paleo-lineages result from a gene duplication event that occurred after the splitting of gymnosperms and angiosperms well before the further diversification. Another major event of gene duplication is supposed to have occurred just prior to the diversification of the core eudicots. This may have contributed to the canalization of the core eudicot flower structure and the petal-specific function of the B genes.

Homologues of the floral homeotic genes of classes B, C and D are present in diverse gymnosperms. Since B homologues are expressed in male reproductive organs only, it can be assumed that the ancestral function of B genes was to distinguish male (B gene expression "on") and female (B gene expression "off") reproductive organs. Thus, the "A-B-C-D-E system" of floral organ identity can be derived from an older, but functionally related "B-C/D system". The absence of class A genes from gymnosperms and the ancestral function of B genes in sex-determination in gymnosperms fit well into the assumption that the first angiospermous flowers

---

11 In morphological terminology an androecium is defined as consisting of two whorls if an outer and an inner whorl of stamens are formed alternating and sequentially. In the genetic approaches the term "whorl" unfortunately is used in a "broad" sense covering the domain of action of the homeotic genes so that this operational definition is quite different from the morphological one. It is much better to use the term "organ category" instead of "whorl" in the genetic models.

were perianth-less (see fossil *Archaefructus* ➜ Fig. 4; however, as already stated, the reproductive system of *Archaefructus* may also be interpreted as a bisexual inflorescence).

During the angiosperm evolution, the B function must have undergone substantial changes: Having originally only controlled sex-determination, the B genes acquired a new, additional role in specifying distinct petals (perhaps mediated by tepals that were already coloured). Class A as well as class E genes seem to have originated later than the B, C and D genes. Since especially the class E genes are required for the identities of all floral organs and consequently are flower-specific, these E genes seem to have a key function in the origin of bisexual flowers.

Selected references and further reading

Albert et al. 1998, Buzgo et al. 2005, Coen & Carpenter 1992, Coen & Meyerowitz 1991, Colombo et al. 1995, Cui et al. 2006, Endress 1992a, Erbar 2007, 2010, Erbar & Leins 1997a, Greyson 1994, Jack 2004, Jordan 1993, Kanno et al. 2003, Kim et al. 2004, 2005, Kramer & Hall 2005, Kramer & Irish 1999, Kramer & Zimmer 2006, Leins & Erbar 1997, Meyerowitz et al. 1989, 1991, Park et al. 2004, Smyth et al. 1990, Theißen 2001, 2005, Theißen & Saedler 2001, Theißen et al. 2002, Xing et al. 2006, Zahn et al. 2005a, b

Differential growth and organ delimination

The protrusion of the floral apex can be considered as the first developmental process of the flower. Flowers are mostly borne in the axil of a leaf which, in contrast to the foliage leaf, is usually a reduced bract. The floral apex is, similar to the vegetative apex, composed of meristematic tissue (growth or division tissue). After expansion, a typical histological differentiation can often be observed in mostly two, rarely three or more outer layers whose cells are plasma-rich and only divide anticlinally: New cell walls arise during cell division perpendicular to the surface of the apex (➜ Fig. 8a). Plasma-rich growth or division tissue is referred to as **embryonal meristem**. The embryonal meristem coat of the apex surrounds a core of cells that are also capable of dividing. The embryonal character of these cells, however, disappears as smaller or larger vacuoles are formed. Nevertheless, in doing so, the mitotic activity of this so-called **vacuolized meristem** may last for a long time. Of course, the vacuolization of the cells is accompanied by cell enlargement.

As soon as the floral apex has reached a distinct size, the floral meristem generates organ primordia; the primordia, as a rule, appear from bottom to top or from periphery to centre (in an acropetal or centripetal sequence) on the floral apex. The small bulges are generated by periclinal cell divisions in the second and/or third outer layer: After anticlinal cell elongation and subsequent mitosis new cell walls arise parallel to the surface of the apex (➜ Fig. 8b-c). The outer layer follows the expansion of the surface solely by anticlinal cell divisions. The outermost layer remains one-layered during further development. In this developmental stage it is termed dermatogen; in later stages it is called epidermis. The small bulges of the young organ primordia are often hemispherical and initially consist solely of embryonal division tissue. As a rule, stronger growth soon occurs in the outer side of the organ primordia, which is also referred to as dorsal side. This is caused not only by cell divisions, but also by cell elongation, the latter accompanied by vacuolization. As a result, the primordia bend towards the floral centre (hyponasty, acrovergence, ➜ Fig. 8d). During further organ differentiation, higher or lower division activity may occur at different sites. Depending on the position of the meristem in the organ we can distinguish between **apical**, **flank** and **marginal meristem**. A so-called **intercalary meristem** is active within or beneath the organs (e.g. in the receptacle). Apical and marginal meristems are often of the embryonal type. However, this does not infer that mitotic activity is higher in this area than in neighbouring more vacuolized tissue (for example during the increase of the surface of a petal, mitoses are regularly distributed in the different developmental phases; ➜ Fig. 9). An intercalary meristem can be characterized by two different patterns of cell divisions; correspondingly, it is either called **initial meristem** (with an initial zone in which mitosis occurs more frequently; ➜ Fig. 10) or **diffuse meristem** (with regularly distributed cell divisions and an expansion of the division tissue to the same extent as the corresponding organ part; ➜ Fig. 101). Meristems can also be described by their origin. A **primary meristem** derives directly from the floral (or vegetative) apex whereas a **secondary meristem** arises anew (de novo meristem). Among the latter we can rank areas
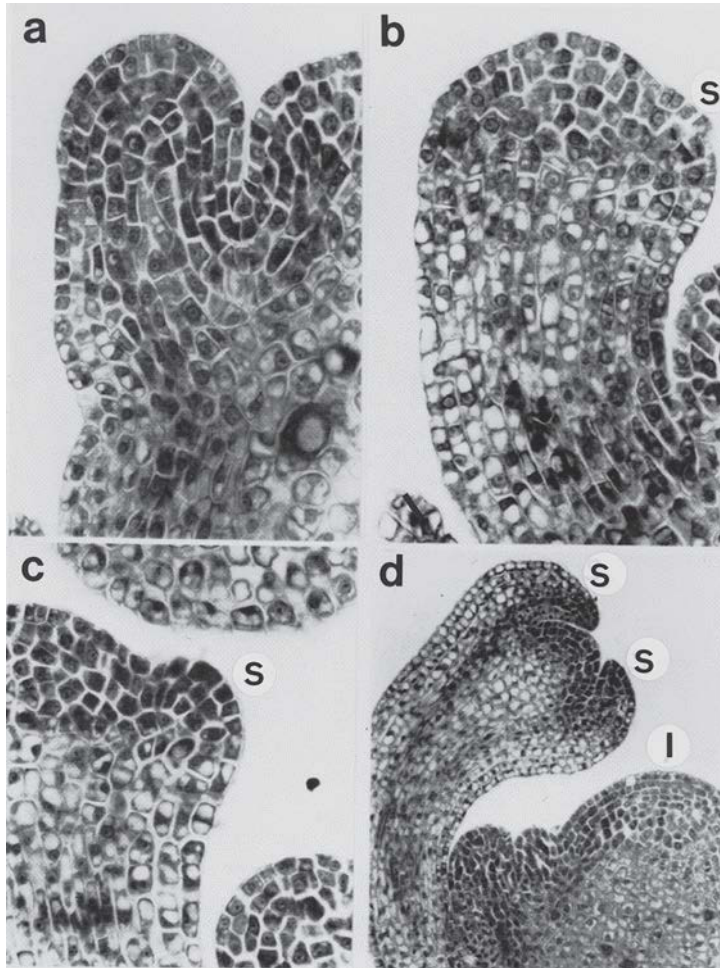
Fig. 8. *Sisymbrium strictissimum* (hedgemustard, Brassicaceae). – a, Longitudinal section through a foral primordium with foral apex still void of organs. – b, Floral primordium with one sepal primordium just formed. – c, Somewhat older sepal primordium. – d, Longitudinal section through an older foral primordium with two sepal primordia. – I = top of the inforescence apex, S = sepalum. From Merxmüller & Leins 1967.

with higher activity and definite direction of cell division within an already existing meristem with lower activity of cell divisions.

In summary, development implies differential growth, which is ultimately based on differential gene activation. Initially, growth by division, later more and more growth by cell elongation is promoted. All different floral organs exhibit exogenous formation at the floral apex. The floral apex itself develops into the receptacle (floral axis). Of course, there is a spatial continuum between floral axis and each floral organ. Thus, every borderline is arbitrary. In practice, we want to determine delimitation by the insertion area of the floral organ, being aware that our artificial boundary area runs right through cells.
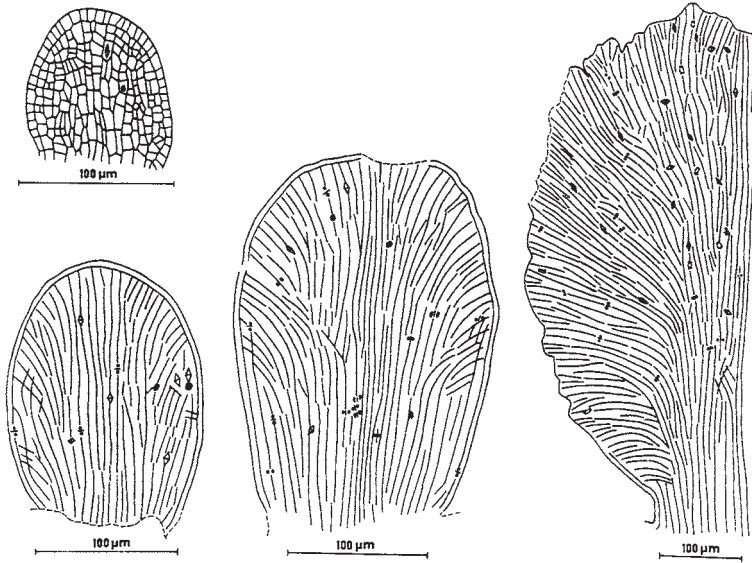
Fig. 9. Surface sections through (inner) petal primordia of different ages of *Hypecoum imberbe* (sicklefruit hypecoum, Papaveraceae-Fumarioideae); phases of mitosis just obser vable. In the three lo wer pictures cell rows are drawn with simple lines. Original by R. Lehminger.
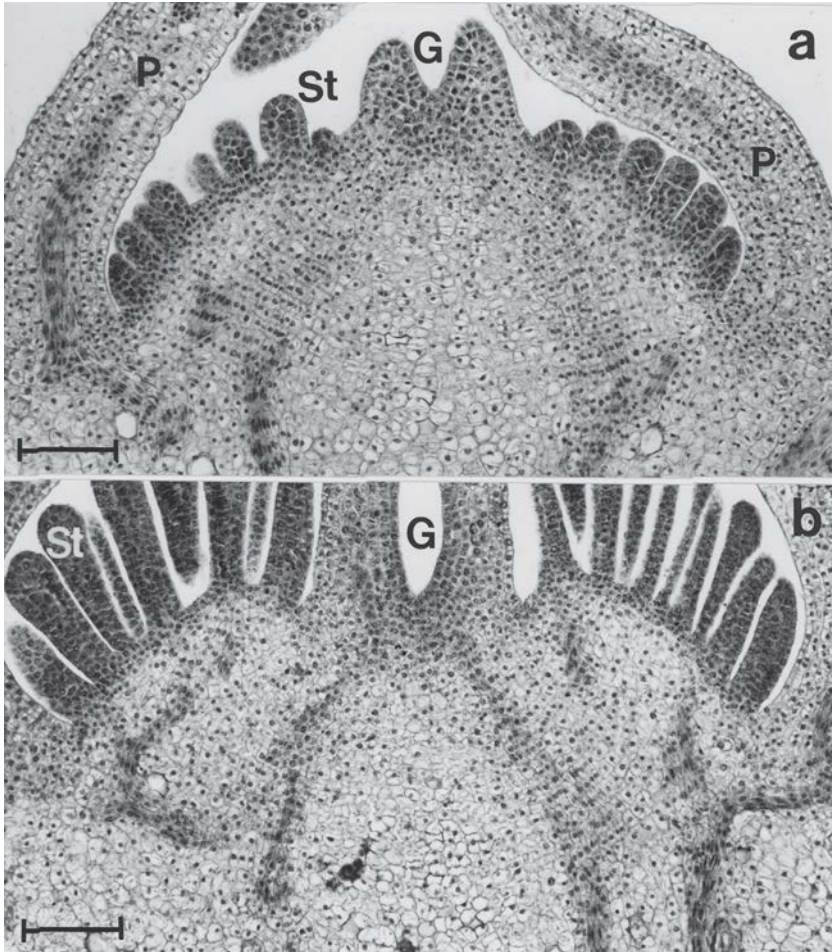
Fig. 10. Intercalary meristem ring in the f oral axis in a member of the custard-apple f amily (*Monodora crispata*, Annonaceae). – a, Young stage in longitudinal section. – b, Older stage. – G = gynoecium, P = petalum, St = stamen; the bar corresponds to 100 μm. From Leins & Erbar 1980.

Selected references and further reading

Guttenberg 1960, Leins 1983, Schüepp 1926

Number and arrangement of floral organs in the flowers

A great diversity as regards number and arrangement of floral organs can be found in the angiosperms. At the one extreme, the flower has a high and variable number of organs in some or all categories (perianth, androecium, and gynoecium; e.g. *Magnolia* species, Magnoliaceae; androecium in *Annona montana*, Annonaceae, about 2000 stamens; gynoecium in *Annona muricata*, about 500 carpels). At the other extreme, a flower exists only of a single stamen (e.g. in *Euphorbia*, Euphorbiaceae, ➜ Fig. 122) or a single carpel (e.g. in *Ascarina*, Chloranthaceae).

■ Spiral flowers with high and indefinite organ number

Flowers with high (but also with smaller) and indefinite organ number often show a spiral (helical) pattern during the initiation of their organs. In the star-anise (*Illicium*, Illiciaceae, ➜ Fig. 11), for instance, all floral organs originate on the floral apex strictly from the outside towards the centre (acropetally or centripetally, respectively) in a spiral with a fairly regular angle between subsequent organs (➜ Fig. 12). This angle is called **divergence angle**. In the star-anise and some other species with polymerous flowers (e.g. in *Magnolia* species), its average value lies between 137 and 138 angular degrees. Individual divergence angles may

Fig. 11. Flower of the Florida anise or star-anise *Illicium floridanum* (Illiciaceae).