

# Goethe's Metamorphosis of Plants and modern Plant Genetics

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## Introduction

Goethe is often quoted in the scientific literature concerning molecular developmental genetics. I have found agreement to Goethe's intentions for example by Enrico S. Coen and Rosemary Carpenter (7). In their article with the expressive title "The Metamorphosis of Flowers" they refer to Goethe's assumption, that the flower is a transformed vegetative plant. "All flowers, which are developing from the buds, are to be looked at as if they were growing on the mother plant, in the way the mother plant is growing on the earth." (9, §95.)

But not only Coen and Carpenter mention Goethe, there are more, well known authors, who quote Goethe (4, 17, 31, and 35). A special passage from the introduction of Goethe's "Die Metamorphose der Pflanzen" is often quoted where Goethe explains, how the regular metamorphosis can be better understood by studying the phenomena of the irregular metamorphosis. Examples of an irregular metamorphoses are flowers converted to vegetative growth (in spite of the carpels a new shoot is build), or filled flowers, which are often found in the gardens. "By the experiences we make with this (irregular) metamorphosis, can we unveil what is hidden by the regular metamorphosis, here we can see clearly, what we only could imagine there, and on this way we hope that we securely reach our intentions." (9, §7.) Molecular genetics is specialised in inducing and describing irregularities, and the analysis of the found abnormalities on the molecular level. The very source of molecular genetics is the irregularity of metamorphosis. A small unpretending herb, *Arabidopsis thaliana*, is often used for genetic analysis. This small crucifer is experimental object of about 3000 scientists all over the world. For molecular biology a golden age has started.

The receipt for the success of modern Biology is simple. "Isolate a mutation that affects the process or structure of interest, clone the gene, find out where, and when it is expressed, where the gene product is located, what it does, and what it interacts with, directly or indirectly." (19).

One can easily find out, that Goethe is not unknown among scientists. We will see how deep the understanding of him has been developed. Goethe, in his days, was very interested in chemistry; both chemistry and morphology were at the beginning of their developments. Two quotations may prove this statement (10, 11): "With the form in general and with the relation and connection of the parts, in so far they are external visible, works natural history at, in so far they become visible only after dissection of the form, we call this effort the art of dismemberment; she studies not only the form of the parts but also die inner structure, and needs soon a magnifying-glass.

When by this way the organic body more or less is disturbed, the form has been dissolved, and the parts can be regarded as matter, then comes sooner or later the chemistry, and presents us *new* and *beautiful* particulars of a matter.

When we now try to palingenise this dismembered creature from our singular observations, and again study it in its sane form, we call these our physiological endeavours."

[...]

"In this way chemistry has exactly observed the changes of the smallest particles and their composition, and her last important activity and accuracy gives her the right to assert a claim on the uncovering of organic natures.

From all these, and also if one does not regard the things I have omitted, it is easy to see that one has reason to order all our abilities, when we truly want to understand those secrecy's, that we are urged to use all inner and outer tools, and to use all benefits when we venture this always endless work. *Even a certain kind of one-sidedness is for the whole not detrimental*, everyone can hold his way for the best one, presumed he planes, and cleans his way, so that the following people can go this way easily." (10, pp. 138-139)

(Translation and Italics Peer Schilperoord)

Goethe has also studied the significance of the colour of the light for the germination of the plant; today this still is an important theme of molecular genetics. Although Goethe was very interested in chemistry, nowadays the results of molecular genetics are hardly used for reflecting and developing our insight in the metamorphosis of plants. Morphology has got a task, which she has recognised only partially. A wealth of observations exists on irregular metamorphosis, which has to be studied, and classified. I'll try to make first steps in this direction today. I will

value an already classical theory, the ABC model of flowering plants. I will show that the common interpretation of Goethe's metamorphosis as a *leaf* metamorphosis should be extended. Most help for the necessary extension of the tenet of metamorphosis we become astonishingly from Goethe himself. Goethe can give us by his way of thinking important impulses. In his estate one can find fundamental reflections on plant metamorphosis, basic reflections which are hardly noticed.

Molecular Genetics unravels the conditions at the molecular level, which are necessary for the appearance of the plant. She does not explain the plant as a whole but admittedly she contributes very much to our understanding of the plants. It was Goethe's interest to let the manifold forms of the vegetable kingdom by comparison of the forms speak to us. The forms should explain each other mutually. Goethe considers gestalt not as a product but as an expression of strength. The comparison of the different forms discloses the actions of the forces.

Although it is easy to show, that scientists one has paid attention to Goethe, I have to state, that the idea of the metamorphosis itself neither has been questioned nor has it further been developed. In spite of that one can prove that the idea although attractive has lost much of its content and contributes few to scientific discussion. In the Book "Arabidopsis" (19), which reviewed the scientific results until 1994 in systematics, genetics, developmental biology, plant pathology, biochemistry and cell biology is neither the word metamorphosis nor morphology, used. The term "morphological gradient" is used. This is the physiological gradient in the apical meristem, which is needed for the differentiation of the various tissues. Further is the term "heteroblasty" (32) mentioned? Heteroblasty is the English name for the German term "Laubblattmetamorphose" (metamorphosis of the leaves of the stem).

I hope, that I can show on the one hand, that it can be interesting to occupy one self with the results of molecular genetics with regard to the metamorphosis of the plants and on the other hand, that it can be of interest for scientists working in the fields of molecular genetics to occupy one self with the methodological considerations of Goethe. Goethe could have said: "The "atomistic" way of looking on nature can be supplemented by the "dynamic" way of looking, and the dynamic look can be supplemented by the atomistic look."

## THE IDENTITY OF THE FLORAL ORGANS

### *The ABC model of flowering organs*

Bowman, Coen, Meyerowitz and other scientists presented 1991 a model by which the plant could determine the identity of her floral organs (3, 6, and 18). The model was developed on account of mutations, which show changes in form and arrangement of floral organs. In the next part I will first describe those mutant forms. I confine myself to the mutant forms of *Arabidopsis thaliana*. This crucifer played as the most used laboratory

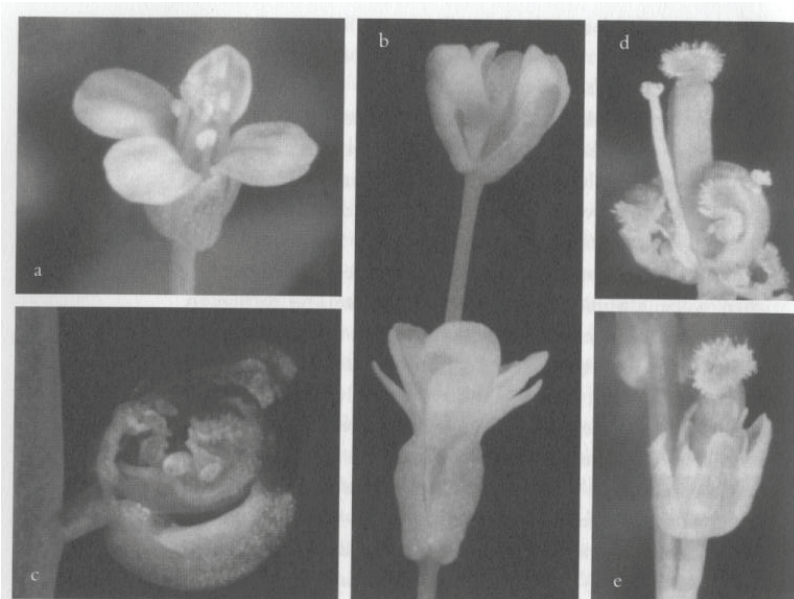


Fig. 1. Phenotypes of wild-type and mutant *Arabidopsis* Flowers. (a) wild type, (b) *agamous-2*, (c) *apetala2-2*, (d) *apetala2-9* and (e) *pistillata-1/pistillata-2*. The plants were grown at 25°C.

plant an important role by the development of the ABC model. *Arabidopsis* shapes a small rosette with a thin taproot, and soon gives she rise to the shoot and the inflorescence. She is 5 to 25 cm tall, and needs by 25 °C only 6 weeks from germination to seed production. The short developmental period and one of the smallest genomes of flowering plants make *Arabidopsis* an ideal object for scientific research. *Arabidopsis* flowers (fig. 1A and 2) consist of four whorls 1, four petals in the second, six stamens in the third and two carpels in the fourth and last whorl. The carpels together form a silique.

One has found three classes of mutants, which affect the organ identity. In class A mutants sepals and petals are missing. In class B mutants are petals and stamens

missing, and in class C mutants are stamens and carpels missing. The model was developed on the basis of the following mutants: *apetala 2* (*ap2*) class A, *apetala 3* (*ap3*) class B, *pistillata* (*pi*) class B and *agamous* (*ag*) class C. The name *apetala* confirms to the phenotype of this mutation, the loss of petals is a striking characteristic of



Fig. 2. Vertical view of the primary inflorescence apex of a 24-day-old plant in which the oldest flower (top) has reached stage 14. The sepals and petals of the stage 14 flower have spread during preparation. Bar = 500  $\mu$ m (0.5 mm).



Fig. 3. Post-dehiscence *ap2-1/ap2-2* trans-heterozygote flower with a phenotype intermediate between *ap2-1* and *ap2-2* homozygotes. In this case, the medial first-whorl organs are solitary carpels (c), the lateral first-whorl organs are leaf-like (l), no second-whorl organs have formed, and the third and fourth whorls are largely normal. All tested *ap2* trans-heterozygotes exhibit phenotypes intermediate between the two respective



Fig. 4. Cross-section of an *agamous-1* flower. *ag-1* flowers are characterised by a large number of whorls of sepals and petals in the pattern: (sepals, petals, petals)<sub>n</sub>, produced by an indeterminate floral meristem

this phenotype. The name *pistillata* confirms to extra carpels, which arise in this phenotype, and the name *agamous* confirms to the loss of all of the carpels. The phenotypes of the mutant plants were thoroughly studied, also the appearance and distribution of the gene products of the intact genes in the developing flowers. The words *apetala*, *pistillata* or *agamous* can be written with capital or small letters. Are small letters used, so is referred to the mutant plant. Are capital letters used, for example *PISTILLATA*, so is referred to a plant with intact genes.

### *The mutants*

Among the mutant plants, scientists discern between single mutants, those plants have only one damaged gene, double mutants; those plants have two damaged genes, and finally triple mutant plants. The phenotypes of single, double and triple mutants are now described.

#### *Single mutant flowers*

A class mutant plants (Fig. 1C, 1D and 3) have lost the original identity of the floral organs in whorl 1 and 2. The identity of the organs in whorl 3 (stamens) and 4 (carpels) is generally not changed. Strong *ap2* mutant forms, like *ap2-2*, form flowers with carpels or carpelloid leaves in the first whorl. No organs are found in the second whorl, but stamens and carpels are formed in the third and fourth whorl respectively. Weak *ap2* mutants, like *ap2-1* form in the first whorl foliage leaves, occasionally with carpelloid characteristics and staminoïdal petals or stamens in the second whorl and normal stamens and carpels in whorl 3 and 4. Other *ap2* alleles show phenotypes intermediate between *ap2-1* and *ap2-2*. *In generally speaking one can say, that the plant in the case of ap2 mutants sepals replaces by carpels and petals by stamens.*

B class mutant plants. A second class of genes is necessary for the identity of the floral organs in whorl 2 and 3. Mutants of this class show normally formed sepals and carpels (Fig. 1E). Two B class genes have been described: *APETALA3* and *PISTILLATA*. *Plants, which are homozygous for strong mutant alleles like ap3-3 and pi-1, develop flowers without petals and stamens. Sepals replace the petals; the stamens are replaced by carpels.*

C class mutant plants (Fig. 1B and 4) with changes in the *AGAMOUS* gene show divergences in whorl 3 and 4. *The organs in the first and second whorl develop normally. In the third whorl petals replace stamens and in the fourth whorl the carpels are replaced by the first three whorls in a reiterative matter, until the apical*

meristem is exhausted.

Among the single mutants three gene classes has been found, called A, B and C, each gene class affects the organ identity in two adjacent floral whorls. A class mutant plants change organ identity in the sepal and petal whorl, B class mutant plants change the status in the petal and stamen whorl, and finally C class mutant plants alter organ identity in the stamen and carpel whorl.

#### Double mutant flowers

Double mutants have been selected after cross-pollination of the single mutant lines. The double mutant plant *ap2 ag*, which has only the intact B class genes disposable, forms in the first whorl foliage leaves or carpel like

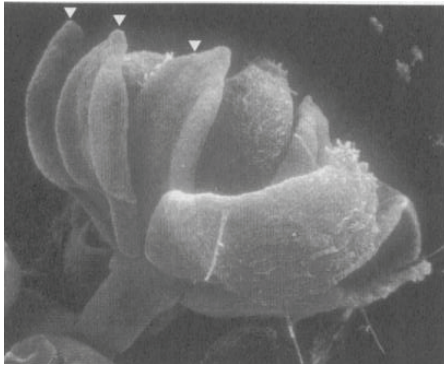


Fig. 5. Double mutant. Mature *ap2-ag-1* flower with carpelloid leaves in the first whorl (l), and petaloid stamens in the second and third whorls (arrowheads).



Fig. 6. Double mutant. Mature *ap2-2 pi-1* flower comprised of four fused carpels.

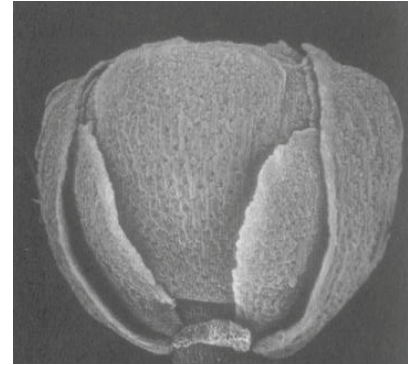


Fig. 7. Double mutant. Mature *ag-1 pi-1* flower, with a lot of sepals.

leaves. She forms in the second and third whorl hybrids of petals and stamens and in the fourth whorl in spite of carpels are the first three whorls reiteratively repeated (Fig. 5).

The double mutant *ap2 pi* with the intact C class gene *AGAMOUS* has flowers with carpels in all whorls. The two lateral leaves of the first whorl form occasionally foliage leaves (Fig. 6).

The activity of A alone, for example in the *ag ap3-1* double mutant (Fig. 7) gives rise to a flower with only sepals. The number of sepals is not fixed.

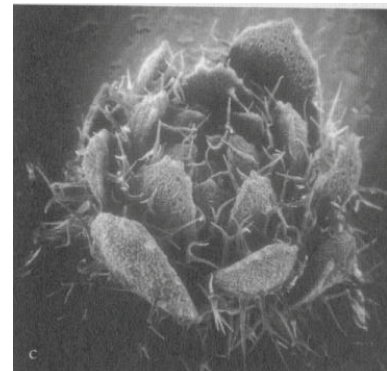
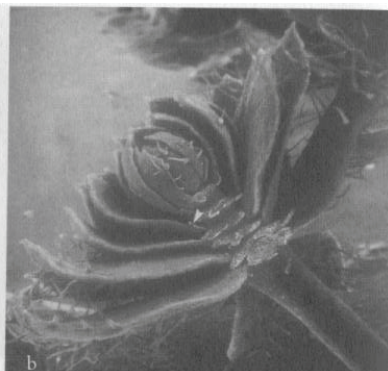
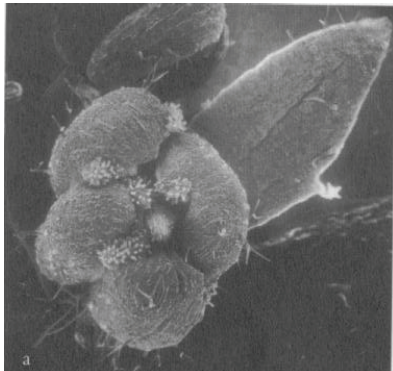


Fig. 8. Triple mutants. (a) Mature *ap2-2 ag-1 pi-1* flower with all organs except the lateral first-whorl leaf-like organ (l) differentiating into carpelloid leaves. Note stigmatic tissue and fusion of the organs, both characteristics of carpels, as well as stellate trichomes, a feature of leaves.

(b) Cross-section of a mature *ap2-1 ag-1 pi-1* flower. All organs are leaf like as evidenced by basal stipules (arrowheads) and numerous stellate trichomes.

(c) Mature *ap2-1 ag-1 ap3-1* flower in which all organs are leaf-like, with numerous stellate trichomes.

#### Triple mutant flowers

When all gene classes are mutated, for example in *ap2 pi ag* or in *apa2 ap3 ag*, we find flowers that can only form whorls of foliage leaves. These leaves bear occasionally stigmatic tissue at the borders. There are also mutant forms without the stigmatic tissue, which only develop foliage leaves (Fig. 8 and 9).

Considering those observations, and on account of the analysis of the allocation of the gene products in normally developed plants, the ABC model was proposed (Fig. 10).

A first and preliminary interpretation of this model could have the following conclusions:

1. The ground state organ (5) of all the flower organs is the foliage leaf. When the three gene classes, which are necessary for floral identity, cannot function normally, and no differentiation of the identity can take place, foliage leaves are developed. The number of the foliage leaves is unlimited, contrasting the limited number of floral organs.
2. For the development of *four* floral organ types the plant needs only *three* gene classes.
3. Petals and stamens arise from a common hybrid type, which has characteristics of petals and stamens. Under the influence of the A class gene is the leafy form emphasised, we find petals. Under the influence of the C class gene is the generative form accentuated; stamens are formed. (The tight relationship between petals and stamens, which has been proposed by many scientists, for example in the case of the water lily and of the filled flowers, is here confirmed.)
4. The development of one of the gene class organs (sepal, petal/stamen and carpel) is independent of the development of another gene class organ. No gene class organ presumes the development of another gene class organ.
5. The model does not explain the limited numbers of the floral organs.

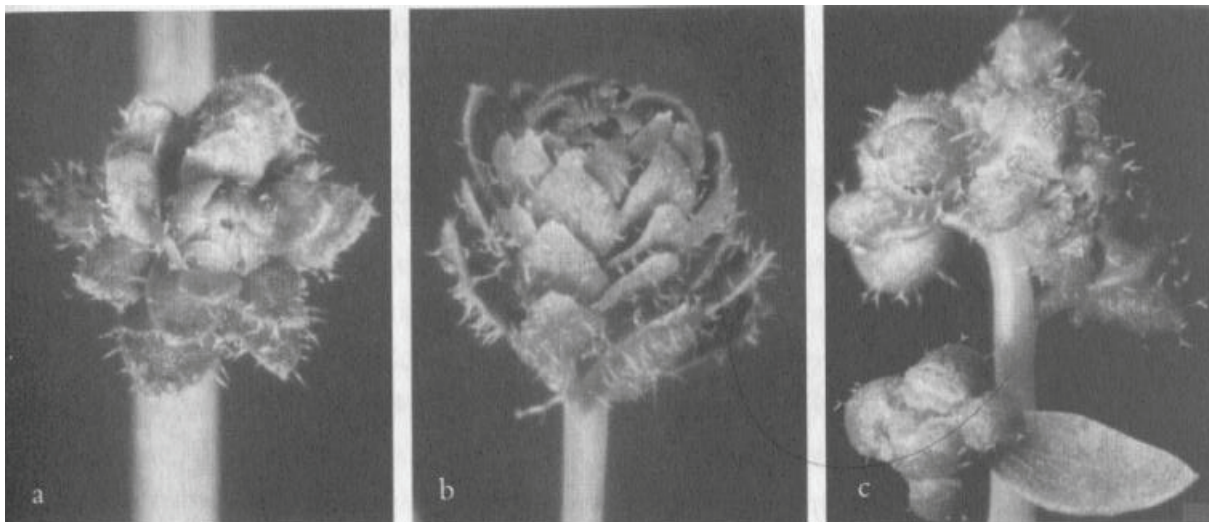


Fig. 9. Phenotypes of triply mutant flowers. (a) *apetala2-1 agamous-1 apetala3-1* (b) *apetala2-1 agamous-1 pistillata-1* (c) *apetala2-2 agamous-1 pistillata-1*. All plants grown at 25°C.

Contradicts the ABC model Goethe's model of plant metamorphosis? What is the rule according to which floral organs develop from foliage leaves? Can floral organs be really derived from foliage leaves alone? Of what kind are the morphological relationships between the different organs? I will trace now these questions.

#### A CRITIC OF THE IDEA OF METAMORPHOSIS

At first I describe, what in general is meant with metamorphosis. Afterwards I have to widen the idea of metamorphosis. Goethe (9) distinguishes three kinds of metamorphosis. He distinguishes between the *regular* or *progressive* metamorphosis, "which makes it self always step by step conspicuous from the seminal leaves up to the last development of the fruit..." this metamorphosis differs from the *irregular* or *retrogressive* metamorphosis. An example of the retrogressive metamorphosis is the filled flower, in which the stamens are replaced by petals und carpels are missing. Finally distinguishes Goethe the accidental metamorphosis, which is induced from outside, for example by insects. To the third kind Goethe did not pay further attention. The regular metamorphosis is often presented in the popular form of the law of the threefold extension and contraction. The first extension and contraction takes place from the seminal leaves over the foliage leaves and bracts up to the sepals. The second one takes place from the sepals over the petals and stamens up to and including the carpels. And the last extension and contraction is performed by the carpel itself. The hypothesis, that metamorphosis is linearly continued from the vegetative plant with its foliage leaves into the generative plant with its floral organs, is disproved. We find already by Goethe starting points which do not agree with this linear view, and I will try to sho better points of view, but at first should the hypothesis of linear development of metamorphosis be falsified.

One scientist, who rejects the thesis of linear metamorphosis, is Bowman (4). He describes in the book "Arabidopsis an Atlas of Morphology and Development" two different hypothesis concerning the development of the flowering organs. The first presumes that communication takes place between two adjacent floral whorls,

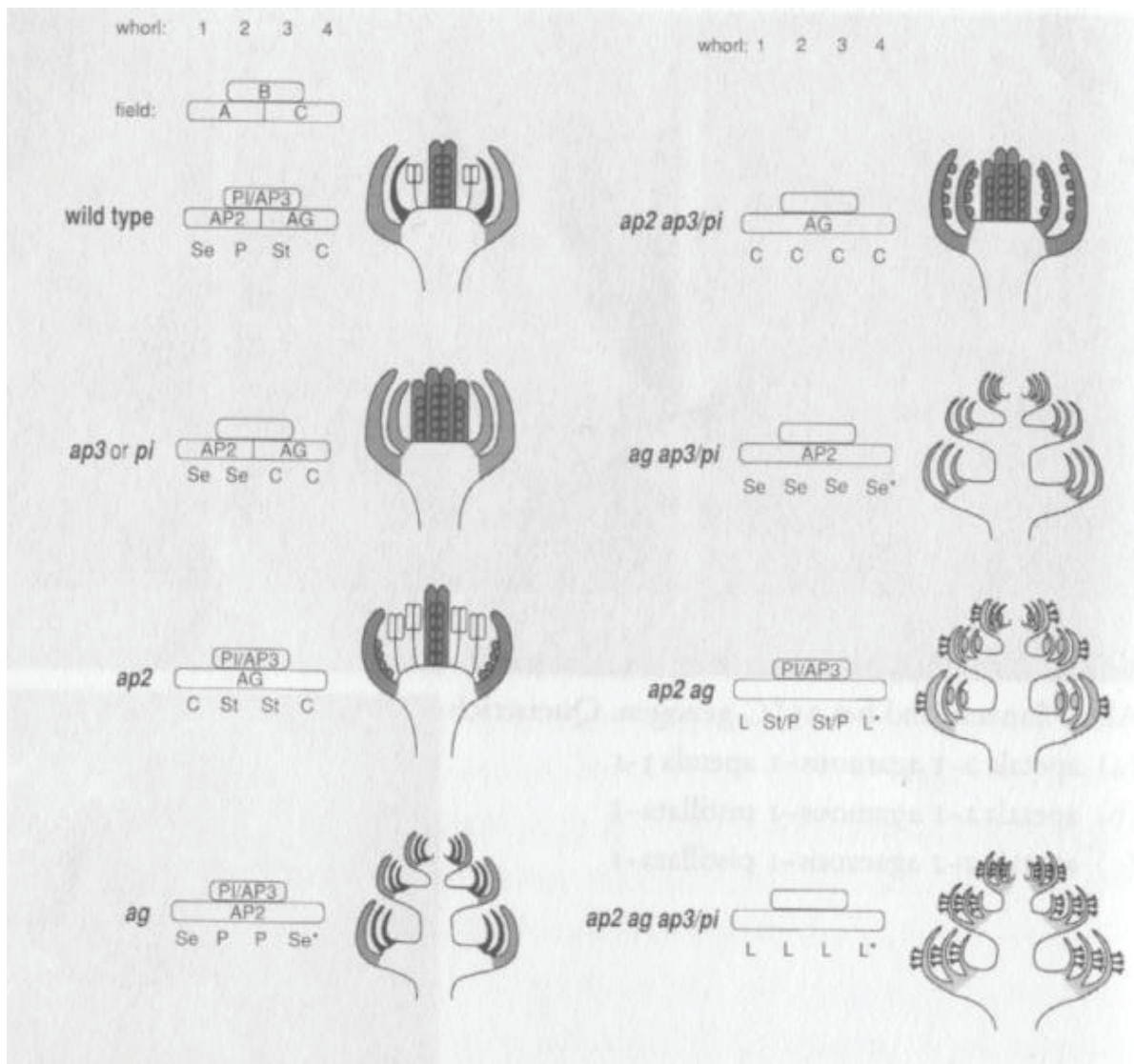


Fig. 10. Schematic representation of the model depicting how three classes of floral homeotic genes could specify the identity of each of the four whorls of floral organs. The numbers 1 to 4 represent the different organ whorls. The boxes represent a cross-section of half a flower. Every box represents a field, where the plant activates a gene class. The mutated genes are written in the column on the left, in the boxes are the intact genes specified. The phenotype is specified beneath the boxes. Se = sepal, P = petal, St = stamen, C = carpel, St/P = stamen like petals and L = foliage leaf. The \* tells, that the ag-genotypes have an indeterminate apical growth. A schematic figure, a longitudinal section, is shown in the column on the right.

which has the consequence that floral whorls develop in a fixed sequence. So would the developing sepals for example omit a signal, either a biochemical or biophysical signal, to the next developing meristem, and let this primordial tissue give rise to petals, and so on. Goethe's hypothesis of the refinement of the plant sap (§§ 29, 30 and 41, (9)) is an example of a linear understanding of the processing of metamorphosis. In § 41 he scribes "The petals are normally larger as the sepals are, and it can be noticed, that the way the organs are contracted into the sepals, these organs can expand again, for the sepals have refined the sap, and let arise us new and very different organs." On account of the shown phenotypes of the different mutant flowers, which show for example the sepals whorls once before and once after the petal whorls or shows carpels at first, it is obvious, that the differentiation of a floral whorl is independent of the adjacent whorl.

The second hypothesis supposes that every floral meristem is subdivided in concentric embryonic fields. Every field becomes its positional information with the help of genes, which the plant needs for determination organ identity. But also in this case, there must take place a kind of biochemical or biophysical communication between cells. Normille (20) and Sieburth et al. (28) have showed that this communication takes place. The difference to the first hypothesis is the relative autonomy of the whorls.

The concept of metamorphosis is not or only seldom used because metamorphosis is generally understood as a *gradual* change in form and gradual changes are not found among the mutant forms. Of course one can find a lot of intermediate forms, forms which were considered as transitional forms (2), but if one can find both mosaic forms of carpels with foliage leaves, as with sepals or even stamens, then are the clues for a regular, gradual, transition between the organs missing. On the other hands show the foliage leaves this gradual change of form clearly. In flowers, this art of change is not existent between all floral organs. The word metamorphosis has been replaced in the english speaking part of the world by the word *homöosis*. Bateson (1) has introduced the idea of homöosis, and defined as: “the assumption by one member of a meristic series, of the form or character proper to other members of the series...” “One speaks of homöosis when an organ develops on a place where in normally developing organisms another organ would arise. The *conversion of one organ into another one* is not been looked at, therefore one speaks of the *replacement of one organ by another one*. The borders between the organ whorls are in Arabidopsis sharply drawn. This herb doesn't show beautifully gliding transitional forms. There are a lot of forms, for example mosaics of sepals and petals, mosaic forms of carpels and sepals, of foliage leaves and petals, of petals and stamens (Fig. 4) and of stamens and carpels<sup>1</sup>. As soon as organ primordial tissues are not separated well, mosaics arise, independently of the nature of the primordial tissues. Do relations between mutant forms exist, which give a hint on a possible metamorphosis in flowers? Put it in another way, do morphological interrelations exist between floral organs, which tell us, that there is a lawful relationship among floral organs? To answer this question an other point of view is necessary. Metamorphosis can never be restricted to a metamorphosis purely of leaves. Important abilities of the plant are branching, which I consider here as a kind of vegetative propagation, and further of cause the generative propagation. By formulating the ABC model, the APETALA1 gene, which is like AP2 also necessary for the normal development of the sepal- and petal-whorl, was not considered. A plant with a strong mutation in AP1 let new flowers arise from the leafaxils of the organs in the first floral whorl. Those organs are not sepals as expected, the sepals are stunted or alike foliage leaves (Fig. 11). The additional flowers do also force additional flowers from the axils of their presumed sepals, and so on. Together with the CAULIFLOWER mutation the Arabidopsis plant develops a cauliflower-like phenotype (Fig. 12). The floral axis is normally not branched. When sepals arise, no lateral buds are established, we find the same inhibition of lateral buds in the axils of bud scales. The APETALA1 gene is expressed both in the sepal and the petal whorl. The plant needs this gene for the correct development of the petals. The petals emphasise, as we have seen, the leafy character of the hybrid type of the petal-stamen-organs. The vegetative propagation by branching as well as the generative propagation by pollen is repressed. At the moment that no more AP1 products can be found in the third whorl, the ability of vegetative reproduction is transformed in to the ability of generative reproduction, pollen are formed. The cauliflower shows excellently what happens, when generative reproductive forces cannot be completely evolved, and the inhibition of axial branching has been suspended. On the one hand one sees an enormous branching within flowers, on the other hand the floral buds stay underdeveloped, only a few complete flowers are found (for the necessary propagation).

The relation between molecular genetics and Goethes idea of metamorphosis is conflicting. The insight Goethes that a metamorphosis takes place within flowers has been denied, but his point of view that floral organs are modified foliage leaves has been confirmed. „The ABC model left at least one complication, though: What happens in the absence of all organ identity activity? Goethe had proposed that floral organs represent modified leaves, suggesting that a vegetative leaf is the ground state of floral organs. This has been confirmed by double and triple mutants. “(35). One could be pleased that Goethe is acknowledged to after 200 years. 1997 Reto Kohler was full of approval for Goethe, when he wrote about “Das Alphabet des Erblühens” in the swiss journal “Neue Zürcher Zeitung” (14). If one tries to imagine how this transformation could take place, one realises soon that it cannot be a “simple” metamorphosis of the leaf. The pollen in the stamens and the ovules in the carpels cannot be understood as a modification of the leaf. One could object now that that the gliding transitions between petals and stamens are obvious examples of such transitions but both organs arise from the same “hybrid” ground state. The relations between sepals, carpels and the organ pair petal/stamen are unclear in the case of Arabidopsis. We now have arrived the point where we will try, with the help of Goethes points of view, with the help of Wilhelm Hofmeister (1824-1877), and last but not least with the help of the results of the research on the mutations of Arabidopsis, to widen the idea of metamorphosis. The next part deals with the ideas of polarity, ground organ and metamer.

## POLARITY

I quote less known text passages from the estimate of Goethe. Here formulates Goethe a central phenomenon of plant development.

<<Organic disunion.

Before, we looked at the plant as a unity. We can see the empirical unity with our eyes. It arises by the association of many different parts of the greatest variety as an apparent individual. A one year old completed plant torn out. Ideal unity: When these different parts are thought to have arisen from an ideal body, and have

developed sequentially. From the very beginning we have to consider this ideal body as simple as possible, and to look at it as disunited, for without the process of disuniting of an entity, a third one cannot develop.

[...]

Germ of the root and the leaf. Both are originally unified with each other, yes one cannot be thought without the other. They are each other opposite from the beginning.>>

(10 p. 133)

At this point one can very well experience Goethe's effort to understand not only the formation, the product, but also the process of formation of the product. Especially the sentence "From the very beginning we have to consider this ideal body as simple as possible, and to look at it as disunited, for without the process of disuniting of an entity, a third one cannot develop." has impressed me. This is completed by a quotation of notes found in his estate (11):

"The small distance between a and b [between the apical meristem of the root and the shoot P.S.] is noticeably elongated, and forms a small stem, that according to its nature is irresistibly directed into the height, so that both poles form one line and both stand oppositely like zenith and nadir. One has to think a line the one end striving to the centre of the earth, the other end striving to the atmosphere."

Like an antithesis to this note, one can read in Strasburger "Lehrbuch der Botanik": "The cormus as a rooted shoot is build by the *three basic organs* axis, leaf and root. The basic organs are not homologous and they perform different basic functions." (29), Fig. 13.

The basic organs are not morphologically related to each other, they are marked off on account of their different functions. The question how these organs can be connected with each other in a morphological way is not made. Further more, the statement that the organs can be marked off on account of different functions is partially false. Both stem axis and root have the function of interchange, the function of interceding between the parts above and the parts beneath earth level. Further more stem axis and root axis are connected with each other by a gliding transformation of the location of the vascular strands. The basic organ theory is not well founded, it is an atomistic model, three parts are hold by the hand, missing is unfortunately the spiritual band.

It was Goethe's very interest to go from the whole to the parts, without losing the whole out of sight. That means, that the parts should be compared to each other in a way that they could appear as parts of a whole.

Reminding the above quotations, we return to the results of molecular genetics, and look what the plant is saying. The first stages of embryo development are in fig. 14 (13) schematically shown.

The plant assesses just with the first division of the zygote an axial polarity. The division is asymmetrically, the upper apical cell is smaller compared with the basal cell. The shoot pole arises from the apical cell, the root pole from the basal cell. What happens, when this first division is not asymmetrically but symmetrically? The mutant called *gnome* develops no apical – basal polarity, the first division is symmetrically. Strong mutants form a spherical cell mass. At the surface an epidermis is formed, then follows mesoderm and in the centre vascular tissue is developed. In weak mutants an embryo arises with a well formed hypocotyl, but without root- and shoot meristems (26). The plant confirms with her first cell division her inner polarity, a polarity which is in harmony with the polarity of heaven and earth. The unity has become a duality<sup>2</sup>.

After three cell divisions, eight cells have been arisen from the apical cell and the further development of these cells has at this stage already been fixed. The seminal leaves and the apical meristem arise from the upper layer of four cells. The hypocotyl and the procambium, arise from the lower layer of four cells. The procambium gives rise to the vascular strands, one part is connected with the apical shoot meristem, the other part gives rise to the root initial cells, and subsequently to the central cylinder and the vascular strands of the root.

The basal cell gives after further cell divisions rise to the suspensor, a kind of haustorium, which takes nourishment up for the developing embryo and also functions as an anchor. Proximally to the suspensor is a cell called *hypophyse* arisen from the basal cell. The descendants of the *hypophyse* form the central root cap and its initials as well as the central cells proximally to the root cap which give rise to the lateral root cap, to the rhizoderm with the root hairs, and to the root cortex and endoderm [Dolan in (4)].<sup>3</sup> Fig. 15 gives a schematic recapitulation of embryogenesis.

#### THE THEORY OF THE GROUND ORGANS AND HER DISPROOF

On account of the outline of embryogenesis, one can try to classify the structure of the seedling. The first arrangement of the zygote, gives rise to a polarised form. A second arrangement after a couple of cell divisions shows a globular form, arisen from the upper cell. At the basal site is the *hypophyse* with the suspensor located, in the middle a part which gives rise to the hypocotyl and the procambium, and at last the upper part. One part of the procambium is part of the apical meristem; one part is part of the root apical meristem. The most important part, which arises from the middle layer, is an axis, in the root the root axis, in the shoot the shoot axis. The axis mediates between the top and the bottom, elongational growth prevails. The upper part of the



globular embryo gives rise to the seminal leaves and a part of the apical meristem.

The shoot appears to be bipartite (dual): the members are the stem and the leaf. But also the root appears to be bipartite: root cap, rhizoderm, root cortex and endoderm all together constitute one member and the root axis the other member. According to the development of the embryo one has to consider the seedling as *quadripartite*, as consisting of four parts.

The quadripartite state is reached in two steps. I have to stress, that the idea of the quadripartite state of the embryo is a hypothesis. This hypothesis is thus far the result of my considerations based on several scientific articles. The hypothesis should be furthermore tested. Nothing the less my basic considerations be can a stimulation for a profound reconsideration of the usually used concept of the seedling as constituted by three different parts which cannot be related to each other in a morphological way.

We have arrived a point, where we have to widen the concept of plantmetamorphosis. It is obvious, that Sitte (29) and also Troll (33) take only one way in consideration to relate the organs of the seedling to each other. "The corm as a rooted shoot is build by the three basic organs axis, leaf and root. The basic organs cannot be homologised with each other and they exercise basic functions." With homologising is meant the process of transforming one organ step by step into another organ. This way of connecting forms with each other is purely quantitatively. It is the merit of Rudolf Steiner (30) who has shown that there are more ways to relate organs to each other, and that there are more kinds of metamorphosis. The organic disunion of Goethe is such a metamorphosis which becomes visible in embryogenesis. Organic disunion is not a quantitative but a qualitative kind of metamorphosis. "From the very beginning we have to consider this ideal body as simple as possible, and to look at it as disunited, for without the process of disuniting of an entity, a third one cannot develop." The plant reveals the ability, the potency, to give rise to a body with to poles starting with a simple uniform body.

Those organs which are completely polar organised to each other are the leaf on the one side and, what I have called in a former paper (27), the root organ. The root organ consists of root cap, root hair zone, root cortex and endoderm<sup>4</sup>. The less polarised shoot and root axis mediate between both poles. The idea of polarity is used by morphologists in the sense of a spatial phenomenon. Here is not only the spatial aspect considered but also *forms* are considered to be polar. It is difficult for morphologists to use the idea of polarity to *characterise* forms. As long as characterisation is thought to be an unscientifically approach, an important part of the plant remains neglected. Troll, one of the greatest morphologists of the pas century, considered himself as a successor of Goethe. He tried in his work to look at the plant in an holistic way. In spite of that is his hypothesis of the ground organs not an holistic approach, it is an atomistic way of looking at the plant organs, morphological relations between those parts are apriori not existent.<sup>5</sup>

#### GOUND ORGANS AND PHYTOMERS

I comment another quotation of Goethe. It can be found in his estate "Gesetze der Pflanzenbildung" (rules of plant formation):

"The whole cycle of the plant is from node to node essentially fulfilled, she only needs, as in the seed a root point or a root node, a cotyledonal node a next node and so is she again a complete plant, which can live along and work along according to her nature. I continue and say all other changes of the plant merely look like changes; they can all be explicated by the rule of the continuation of the nodes and the generation of the same without visible influence of both sexes. Yes both sexes will be at last become explicable by this first way of the simplest art of propagation." (10, p. 57)

"Every known thing, which we call alive in the broadest sense, has the power to generate his equals. Even so, we can say, we call living which shows our senses the power to generate his alike.

When we become aware of this power of being divided we call it the both sexes.

When we study the bodies we call plants we become aware of a twofold power to generate his alike once without a visible action of the sexes and once by their visible action." (10, p. 56).

We have now arrived the point, where Goethe is trying to formulate the morphological relationships between the vegetative and the generative plant. He compares in his metamorphosis chapter 13 §93 seeds to buds and concludes:

"... we are allowed to conclude, that seeds, which are different from buds by their enclosed nature and by the visible cause of their formation and separation of the gemmas, nevertheless are closely related to both. "

He also deals with the problem how one can imagine the metamorphosis of foliar leaves into carpels:

"The simplest plants, which show transitional stages (up to the calyx P.S.) very clearly have here been shown (especially members of the Mangnoliidae and Ranunculidae show such stages P.S.). One arrives easily to the calyx. The difficulty to go further is easily overcome, the transition from the calyx into the petals and

from the petals into the stamens can be seen by eyes and seized by hands. [...]

To explain how the female part arises, a new and very hard and dangerous path has to be gone, one could be almost driven to despair whether one is able to communicate a clear idea." (10, p. 52). Goethe develops two hypothesis. The first one, which is for us here not of interest, is concerned with pollination; the second one is of special interest for us:

"to specify the second hypothesis, and show the leaf in its most transcendent sense, that it as such not only hides one germ in its bosom, but countless number in all of its parts, where they according to the constitution of the building can show themselves internally now in rows now in compartments, and externally now in circles and bunches. The ferns could well assist us here, especially *Osmunda*, also could give us *Arum* occasion to special considerations, although one would still being wandering in the field of the incomprehensible and inexpressible, I am still feeling sure, that in and between both hypothesis the whole secret of propagation lies, which cannot become known on another way."

We have to consider, that the alternation of generations was not known at that time. I think, Goethe would have a great pleasure with Wilhelm Hofmeisters discovery. 1851 published Hofmeister the book "Vergleichende Untersuchungen der Keimung, Entfaltung und Fruchtbildung höherer Kryptogamen und der Samenbildung der Coniferen"(12). Hofmeister had discovered the alternation of generations in mosses, ferns and higher plants. The prothallien of the ferns, which arise from the spores of the leaves and which are haploid, have to be compared with the haploid pollen grain and the haploid embryo sac of the flowering plants. The difference to the ferns is, that the spores of the flowering plants already germinate on the spore producing plant (the sporophyte), grow to maturity and that still on the sporophyte fertilization, embryogenesis and fructification take place.

Goethe's separation of the sexes, the generative propagation gives rise to the production of pollen grains (microgametophytes) in the stamens and to the production of embryo sacs (megagametophytes) in the ovules of the carpels; both types of gametophytes continue the development of the plant. When Goethe tries to understand the carpel with the ovules as arising in a transcendent way from the leaf and the buds, so should we, when we consequently pursue this idea, also put the stamen with the pollen grains in relation to the vegetative plant. One can neither look at the carpel as the result of a leaf metamorphosis nor at the stamen as the result of such a metamorphosis. The leafy nature of both organs is obvious, but she cannot fully explain the metamorphosis. This critic is not new at all. In 1882 Julius Sachs (23) has criticised in his introduction to his "Vorlesungen über Pflanzenphysiologie" the accentuation of the leafy nature of carpels and stamens and he explicitly referred to Hofmeister. According to Sachs was the theory of metamorphosis out of date. I try here, following Goethe's methodical starting points, to further develop his point of view. For that reason, we have to study now the development of the vegetative into the generative plant in details.

It is typical for the vegetative plant, that she repeats equal parts. Goethe describes this fact in § 113: "When we study growth, we see that the plant succeeds from node to node, from leaf to leaf, and that also by sprouting a kind of propagation happens, which is different from the reproduction by the flower and the fruit, for she takes place successively, she shows itself as a series of single developmental steps." This basic unit of the vegetative plant, is often called phytom, phytomer or metamer. I here use the definition of James White (37); a phytomer includes leaf, leaf node, the internode beneath the node, root buds and shoot buds. One could look at the seedling, when I correct interpret the results of McConnell and Barton (16), as a fusion of two phytomers. They have the root and the hypocotyl in common, the leaves remain separate and the eyes of the cotyledons are fused and constitute the apical shoot meristem.

Vegetative propagation takes place by the growth of both main axes, the root axis and the shoot axis, and by the development of lateral roots and shoots. We have already seen, that the seedling is constituted by four ground organs, vegetative reproduction takes place by growth and augmentation of the root and shoot meristems.

During generative reproduction arise the so completely different and polar organised organs pollen grains and embryo sacs. Stamens and carpels arise from the meeting of forces of vegetative reproduction with forces of generative reproduction. The assumption lies near, that the vegetative reproduction forces of the shoot are related and prolonged in the generative reproduction forces of the female gametophytes, Goethe's reflection points in this direction. Goethe often compares the development of seeds with the development of buds and the forces which underlie the formation of the carpels with the forces which underlie by ferns the formation of the spore bearing leaves. When we now in a consequent way continue Goethe's point of view, we have to ask us, what's the matter with the stamens? Do stamens show us, that the vegetative reproduction forces of the root are related and prolonged in the generative reproduction forces of the male gametophytes? Do results of molecular genetics give us essential points for both hypotheses?

## ROOT AND STAMEN SHOOT AND CARPEL

As far as I know there has been found at least one gene, called TIP1, which is both expressed in the root as in the flower (Schiefelbein et al. (26)). The root hairs, which arise at the apical end of the root hair cells, can be hampered in their growth after a mutation in the TIP1 gene, those impeded root hairs are shorter and occasionally branched off at their basis. The same mutation hampers the growth of the pollen tube. It is known, that both for the determination of the growth direction of pollen tubes as for root hairs there is an intracellular gradient of Calcium ions necessary (Ridge (22)). The current used terms "germination" of pollen grains, and "germination tube" point at characteristics, those has the root pole in common with the male pole of the flower.

The root organ is discerned from the leaf by continuous formation and disintegration, by the permanent conic-cylindrical shape, the absence of chlorophyll, and by the each other following processes of arise and decay of the different tissues (columella, rhizoderm, at last rests only the hypoderm which constitutes the border of the root to the surrounding earth). The lateral organs of the roots arise endogenously, inside the central cylinder; the lateral organs of the shoots arise exogenously. The stamen is discerned from the carpel by his short lifetime, the pollen grains arise surrounded by stamen tissue (endogenously), the ovules arise on the adaxial site of the carpel (Exogenously). The plant releases the pollen grains by tearing up the pollen sacs.

New results are important for the understanding of the relationship between carpel and vegetative shoot, those results indicate, that the relationship between vegetative bud and leaf is stronger, as presumed. Jane McConnell and Kathryn Barton (16) have described a gene called PHABULOSA; the plant needs this gene, for the formation of the abaxial site of the leaf. A mutant form of PHABULOSA (phb-1d) has leaves that cannot form the leaf underside. They cannot form a leaf blade and have a radial shape. When the mutation is a weak one, the leaf form is trumpet like with adaxial leaf tissue on the outside and abaxial tissue on the inside. Sepal and petal form is also changed. The sepals are changed in filament or trumpet like structures, and the petals are filamentous, the epidermal cells are of the adaxial type.

Stamens are concerned too, the adaxial and abaxial parts are equally developed, the aperture of the pollen sacs is moved from the adaxial to the lateral side. The biggest changes occur with the carpels. The ovules, which arise normally on the adaxial side of the carpel, arise outside at the base of the carpel.

The buds of Arabidopsis arise normally at the adaxial base of the Leaf (31). The ongoing developmental Processes conceal this early relationship. It is as if the lateral shoot arises from the shoot axis. We have seen, that the formation of the adaxial part of the leaf blade is essential to the development of buds. When the formation of the adaxial leaf blade is blocked, which is the case in PHANTASTICA mutant forms (34), no buds can arise. In the case of the PHABULOSA mutant forms, buds arise in a ring surrounding the leaf base.

Coming to the end I summarise the changes which occur during the metamorphosis of the green, vegetative plant into the generative, flowering plant:

1. The length of the internodes is strongly reduced, the phytomers move together.
2. The process of drawing nearer goes so far, that the spiral formation of the leaves is turned in a cyclic formation.
3. The vegetative reproduction, the formation of lateral shoots and roots is ceased.
4. The unlimited growth of the apical meristem ceases.

Two hypotheses are following yet, which I did not discuss here:

5. The leaf blade provides the basis for the carpel (27).
6. The leaf base provides the basis for the stamen (27).

Further:

7. The way the shoots reproduces it self, is found in a metamorphosed way in the ovules and in the structure of the carpel.
8. The way the root reproduces it self, is found in a metamorphosed way in the pollen grains and in the structure of the stamens.
9. Fertilisation gives rise to something new, a new Unity as the result of organic disunion.

I allow me a remark, which will surely not be appreciated by many morphologists. Goethe has often pointed at the ferns, while ringing to understand the carpels. Ferns showed him the potential forces of leaves, forces he found back in a changed way in carpels. I would say, when one is ringing to understand the stamens, one can point at the horsetails. What ferns are for carpels are horsetails for stamens.

The results of molecular genetics are very important for the further development of Goethe's Metamorphosis. Goethe's method can even so be fruitful for the molecular geneticist modelling the plant. When we really understand Goethe's point of view, this could stop the tendency to chop the plant to pieces in the modelling of the plant.

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<sup>1</sup> Arabidopsis, an Atlas of Morphology and Development, (Bowman, 1994). For example mosaics of sepal and petal, as well as of carpels and sepals (p. 216), mosaics of foliage leaf and petal, petal and stamen (p. 230), mosaics of stamen and carpel (p. 240).

<sup>2</sup> „The first indication of polarity is seen in the unfertilised egg cell, which is present in an asymmetrically organized embryosac and ovule. In many plants the nucleus and much of the cytoplasm are confined to the chalazal pole, while a large vacuole is present at the micropylar end. Die Chalaza forms the basal part of the ovule, where the integuments arise. The micropyle is the opening at the top of the integuments, the pollen tube grows through the micropyle. (...)Embryonic polarity may be established during embryosac development. (...) the plane of division may be less important than the polar organisation of the zygote.” (36).

<sup>3</sup> West und Harada (36) confirm this point of view, they write: „An early compartmentation step appears to involve the creation of three spatial domains along the longitudinal axis of the embryo [...]. The apical domain is composed of the cotyledons, shoot apex, and upper hypocotyl; the central domain includes the majority of the hypocotyl; and the basal domain consists primarily of the root.“ A part of the middle layer gives, as we have seen, rise to a part of the basal part.

<sup>4</sup> In spite of the endoderm, the hypoderm could be also the border.

<sup>5</sup> The ground organ theory has been criticised also by Sattler (24) and Sattler / Rutishauser (25). These authors discuss the problem, that the three ground organs cannot always be clearly recognised. The leaf can for example be compound and at the end a bud can arise. They demand a loosening of the concept of the ground organs and point at the possibilities of shaping which can be realised independent of the substrate (ground organ), and so can one ground organ accept the characters of another organ. Froebe (8) discerns the ground organs at first according to their position in the construction (frame) of the plant. Organ shape can be helpful to determine the status of an organ, but this is not necessary. I try here to point at relationships between organs, which are believed, according to the theory of the ground organs, that they cannot be related to each other.