THE CONCEPT OF MORPHOLOGICAL POLARITY AND ITS IMPLICATION ON THE CONCEPT OF THE ESSENTIAL ORGANS* AND ON THE CONCEPT OF THE ORGANISATION TYPE OF THE DICOTYLEDONOUSPLANT

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ABSTRACT

Dicotyledons are polarly organised in several ways. In plant morphology polarity, a principle, allowing comparison of different plant structures has until yet not been studied. A division**.of the plant in shoot and root as polar structures leads to the distinction of four instead of three basic organs: leaf, shoot axis, root axis and root cap together with the root hairs. The flower is a1so polarly organised, its poles are formed by the carpels and the stamens. The foliage leaves are also polarly organised which is reflected by the morphological relationship of foliage leaf, stamen and carpel. The stamen uses the hypophyll*** as base of construction and the carpel uses the epiphyll**** as base of construction. Hypophyll and epiphyll are the two poles of the foliage leaf. Root and shoot, the polar entities of the vegetative plant and stamen and carpel, the polar entities of the generative plant are, morphologically correlated. Stamen and carpel can be understood as a combination of the basic organs of vegetative and generative parts of the plant. The basic organs of the generative plant are pollen grain and embryo sack with their gametophytes. The quantitative comparison of variable proportions is supplemented by a qualitative comparison of polarities. The result is that the organisation type of the Dicotyledons can yet be understood as constituted of morphological related parts.

* in german Grundorgane
** in german: Gliederung
*** in german: Unterblatt
**** in german: Oberblatt

1. INTRODUCTI0N

Type and essential or basic organ are two fundamental concepts in plant morphology. In every introduction to plant morphology these two terms are mentioned and explained (Troll, 1954; Strasburger, 1993). Until now there was no need to question these concepts. If there are features, which do not fit into these concepts, it is time to reconsider their content thoroughly. The discussion of the basic concepts is subject of the present paper.
The method of plant morphology is comparing forms. The result is, for example, the estab1ishing of basic organs, organisation types, construction types, homology and analogy. Two fields for comparing are generally used in plant morphology: 1. The comparison of structures, which have the same re1ative position in the overall configuration of the p1ants (determination of homologous structures). 2. The comparison of structures, which have the same function, i.e. belong to the same construction type (determination of analogous structures) (Froebe & Classen-Bockboff, 1994).

The morphologist distinguishes in the vegetative plant a shoot and a root. The plant appears in the first analysis as a bipolar entity. The shoot is divided in stem and fo1iage leaf. The three organs: root, shoot axis and leaf are the so-called basic organs. Sitte (1993, p.170) defines these as follows: "die Grundorgane sind nicht miteinander homologisierbar, und sie üben verschiedene Basisfunktionen aus", ("the basic organs are not homologous and they perform different basic functions"). The ground organs are distinguished by this definition.
In the present paper I examine in the dicots first the po1arity of root and shoot. Could polarity not on1y be used in a positional, but also in a morphological sense? A concept of morphological polarity in comparative morphology is until yet missing. A third field for comparing is proposed to deepen our insight in plant morphology.
The consideration of root and shoot as polar structures leads to the characterization of four, instead of three, basic organs: foliage leaf, shoot axis, root axis and root cap with the root hairs. With these four basic organs it is possible to describe the vegetative plant. This distinction is only limitedly app1icable to the generative plant. The basic organs of the generative p1ant are the two sporangiums with their contents and the two gametangiums. The form of the flower is the result of the cooperation of three pairs of polarly organised organs (root and shoot, both sporangiums and the male and female gametangium). This cooperation is shown: 1. by the differentiation of the fo1iage leaf in hypo- and epiphyll as basis for the growth of stamen and carpel. The stamen is partially homologous with the hypophyll, the carpel with the epiphyll. Another morphological relationship between the organs is: 2. the consequence of a qualitative metamorphosis of the lateral vegetative organs (of the lateral roots and shoots), which do not appear in the flower, and the basic organs for generative propagation. From a quantitative metamorphosis bymeasuring the variabi1ity of proportions, it is not possible to derive relationships between the vegetative and the generative way of propagation. Without qua1itative metamorphosis it is impossible to relate vegetative and generative propagation.
The present-day type of the dicot plant is viewed as an organism, composed of several well demarcated parts. This concept contradicts the tendency in morphology to stress the interrelationship of the parts.
Methods: It is important to realise the direction of the cognitive process. One can descend from a bigger level to a subordinate level, one can ascend from a lower to a higher level of organisation, or one compares structures of the same level.
Starting with the morphological analysis of the vegetative plant, the first subordinated level is the level of polarity. Sitte (1993,170): "Through the development of shoot and root pole (in the embryo), a bipolarity is given, which designates further development.[1] The step after the distinction of the plant in shoot and root is the description of the articulation Z in the different organs, for example in axis and foliage leaf. The analysis has to answer the question of what kind of morphological relationships of the distinguished structures gives rise to the unity of the plant, in process; the synthesis of the distinguished structures giving 6 rise to the unity of the plant. In the case of the concept of the three essential organs the analysis is incomplete, the morphological interrelationship of the organs is not recognized (in contrast to the physiological interrelationship) and so a synthesis is not possible.

2. THE VEGETATIVE DICOTYLEDONOUS HERHACEOUS PLANT

[1] In the german language: "Durch die Ausbildung von Spross und Wurzelpol ist eine Bipolarität vorgegeben, die für die weitere Entwicklung der Pflanze bestimmend bleibt."

2.1 Organic Disunion and Polarity

With organic disunion is indicated the process by which from an original unit a dual entity (or two units) arises. In the course of embryogenesis differentiation of polar structures comes into existence. I define polar structures as structures, that have complementarous opposite sites and imply each other.
What does the polarity look like in the vegetative plant?

2.2 Root

I use the term axis similarly for the shoot and the root. So one can distinguish two root organs: 1. the root axis and 2. the root cap with the root hair zone. The lateral roots repeat the same construction. Lateral organs originate endogenously, the root apex cannot branch. Axis, cap and root hair zone arise from the primary meristem of the root apex. The border between root hair zone and root axis is the hypodermis (also called exodermis). After the disappearance of the rhizodermis the soil borders the hypodermis of the root axis. By elongational growth of the axis new areas of the soil can be disclosed. The penetration of the root apex into the soil is facilitated by the continuous formation of the root cap and its decay. The unicellular root hair is ultimately close connected with the surrounding soil particles. The root hair zone follows the root apex continuously, continually arising, continually decaying.

2.3 Shoot

It is well known, that one can distinguish two kinds of shoot organs: axis and foliage leaves. Shoot axis and leaves arise from the primary meristem of the shoot apex. The lateral shoots repeat this construction; they arise exogenously, in other words, from the outer parts of the tissue. The shoot apex does not branch. The elder leaf primordia envelop the apex. The growing leaves open gradually. They are bordered by the epidermis.

2.4 Polarity of Root and Shoot

Considering the plant as consisting of polar structures leads to the following order. First root and shoot divided in:

root apex	-shoot apex
root cap	-envelope of the leaf primordiums
root hair zone	-foliage leaves
root axis	-shoot axis
lateral root primordium	-lateral shoot primordium

The polarity becomes clear in the following. characteristics: 1. in root and shoot axis; a Circular configuration of the vascular strands in the centre of the root axis, and a radial configuration of the strands in the periphery of the shoot axis with respectively endogenous and exogenous origin of the lateral organs. 2. in the leaves and in the root organ (root cap, root hairs and rhizodermis): the root organ arises continually, only one organ arises, which is continually decaying and built up. Several leaves arise, they are spatially separated. The root organ has on1y one form. The leaf has many possible forms. The root organ is not clearly detached from the root axis by its cylindrical shape. The leaf is clearly detached from the shoot axis. Tissue layers of the root organ are spatially separated, the root cap becomes slimy, the inner parts of the organ, the root hairs, are exposed. The tissue layers of the leaf constitute a spatial unit, the inner part of the organ is not exposed, the leaf as a whole stays physically intact.

In the same way as one can describe the leaf as apart of the shoot, it is possible to describe a root organ as apart of the root. The latter organ is unique, homologous forms cannot be found. The ways of examining the shoot and the root are identical. The concept of polarity shows the morphological relationship.[2]

2.5 The Hypocotyl as Intermediary

The hypocotyl has neither the ability to produce leaves nor a hypodermis with root hairs. Lateral roots and lateral shoots can arise from the hypocotyl, like they both can arise from the root axis and the shoot axis. The transitional configuration between the vascular bundles of the root axis and the shoot axis is localised in the hypocotyl. The hypocotyl reveals how at this site in the plant two different organs are connected. Both organs are essential organs, and neither homologous nor analogous. Nevertheless it is possible to transform theoretical1y one organ into the other, by gradual1y changing the configuration of the vascular system. The hypocotyl is the intermediate stage. The relativity of the distinction of the essential organs becomes obvious, when considering that the root axis and the shoot axis become alike by secondary thickening. To speak of different organs is then itself cannot become a root in the course of its further development. The same is true for the root. One bas to distinguish between two kinds of metamorphosis: 1. metamorphosis as a process of differentiation and 2. metamorphosis as a process of transformation. The existing theory of the basic organs considers on1y the second type of metamorphosis.

2.6 Root and Shoot, Their Morphological Relationship

The polar vegetative plant is a unit. The meristem of root and shoot arise from one zygote. The relationship between both meristems is continuous in time. The root and shoot axis connect both meristems. The relationship between foliage leaf and root organ is spatially discontinuous. There is no gradual metamorphosis between root organ and foliage leaf. By comparing different types of foliage leaves, one uses the principle of the variability of proportions. According to this principle one can theoretically change one form of foliage leaf into another by gradually changing the different proportions of the leaf. With this principle it is impossible, to describe the morphological relationship between root organ and foliage leaf. If on I y this principle is admitted as a criterium to establish morphological relationships, then the relationships between root organ and foliage leaf must be denied.
In "Vorarbeiten zu einer Physiologie der Pflanzen" Goethe (1975,98-99) has introduced the concept of "*organische Entzweiung*" (*organic disunion*)[3]3. This concept leads to the concept of polarity, with this concept is the unveiling of the morphological relationship of root organ and foliage leaf possible. In the third chapter "organische Einheit" of his draft he outlines the concept of organic unity and then in the fourth chapter "organische Entzweiung" he outlines his concept of 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.[4]

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[2] The distinction of the root organ is based on the idea of linkage of two parts in the entire vegetative plant. Histological1y, there is no need to distinguish root axis and root organ.
[3] Goethe has not published himself the text "Vorarbeiten..." in contrast to his "Versuch die Metamorphose der Pflanzen zu erklären". The text "Vorarbeiten..." is not a scientific publication, it is a preparatory work.
[4] The german text: "Vorher ward die Pflanze als Einheit betrachtet. Die empirische Einheit können wir mit den Augen sehen. Sie entsteht aus der Verbindung vieler verschiednen Teile von der grössten Mannigfaltigkeit zu einem scheinbaren Individuum. Eine einjährige vollendete Pflanze ausgerauft.

3. FOLIAGE LEAF, STAMEN AND CARPEL

In the previous chapter we dealt with the morphological polarity of root and shoot. In this chapter the morphological relationships between foliage leaf, stamen and carpel are examined. The morphological structures of stamen and carpel can be understood as polar structures.

3.1 The Limits of Determining Homologies I

The present-day preferred interpretation considers foliage leaf, stamen and carpel, on account of their relative position in the configuration of the plant, as homologous organs[5] The criterion of the similar position of foliage leaf, stamen and carpel (homotopy) describes only a partial homology between the mentioned structures. The stamens release pollen grains, the embryo sacks arise on the carpels, comparable structures are not found on foliage leaves. Although the position of stamens and carpels is similar with the position of the foliage leaves, the qualitative differences between these organs are enormous. The criterion of topography has only a limited value. Sachs (1882, 15) distinguishes in his "Vorlesungen über Pflanzenphysiologie" three categories of organs: 1) the vegetative organs: root and shoot. Among the reproductive organs: 2) the asexual sporangiums with spores and 3) the sexual archegonia and antheridia. According to him are the resting types of organs rudimentary or partially developed organs of these categories. Stamen and carpel are on one hand shoot organs; on the other hand they are sexual organs. The foliage leaf belongs to one categorie of organs. Stamen and carpel are partially homologous with the foliage leaf. It happens, that it is impossible to determine the morphological status of an organ. Then the auxiliar criterion, the formation of a sequence of gradual metamorphoses, can give arguments for a decision, e.g. to establish the relationship between foliage leaf and stamen, we can also use this criterium. It is easy to find intermediate forms which show, that the stamen is (partially) homologous with the hypophyll. I refer again to Sitte (1933, 214) who says, that "a comparison of the different leaves in a sequence shows, that more simple forms of leaves like cataphylls, protective scales, floral bracts and floral leaves develop by inhibition of the epiphyll and promotion of the hypophyll, i.e., by reduced growth. The sequence of the leaves is an impressive demonstration of the ability of the metamorphosis of one organ type -in this case the phyllom by shifting proportions.[6] With this quantitative comparison one can show the homology of the hypophyll with the floral leaves, Sitte (1993, 161) gives as an example the well known sequence of leaves of hellebore (Helleborus foetidus) .He gives as an example of intermediate forms of petals and stamens the rose (1993, 161). One can find many intermediate forms between bracts, tepals and stamens in Magnoliidae and Ranunculidae. Intermediate forms of tepals have sometimes more characteristics of the floral bracts sometimes more characteristics of the stamens (Hiepko, 1965). Cronquist (1988) and also Takhtajan (1991) both describe continuous sequences of intermediate forms between bracts

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Ideale Einheit: Wenn diese verschiednen Teile aus einem idealen Urkörper entsprungen und nach und nach in verschiedenen Stufen ausgebildet gedacht werden. Diesen idealen Urkörper, mögen wir ihn in unsern Gedanken so einfach konzipieren als möglich, müssen wir schon in seinem Innern entzweit denken, denn ohne vorher gedachte Entzweiung des einen lässt sich kein drittes Entstehendes denken."

[5] For example Weberling (1981, 16) in his "Morphologie der Blüten und der Blütenstände".
The modified theory of the euanthium (according to Ehrendorfer, 1993, 760) is based too on the premise, that in the course of the evolution stamen and carpel has assumed the characteristic shape of angiosperm leaves and therefore they are homotopic with the foliage leaves.

[6] The original german text: "Ein Vergleich der verschiedenen Blätter in der Blattfolge 7l:,igt, dass einfachere Blattformen wie Niederblätter Tegmente, Hoch- und Blütenblätter durch Hemmung des Oberblattes und Förderung des Unterblattes entstehen, also durch gekürzte Entwicklung. Die Blattfolge ist eine eindrucksvolle Demonstration der Wandlungsfähigkeit eines Organtyps - hier des Phylloms - durch Verschiebung der Proportionen.“

and stamens. However, they do not find; such a continuous sequence in one family. First, a survey of all the families shows a ~ continuous sequence of intermediates. Each species can show only apart of the total leaf sequence of its genus and in its turn the leaf sequence of a genus is part of the leaf sequence in a higher taxonomic unit. In spite of the clear relationship between the hypophyll of the foliage leaf and the stamen, no author considers the hypophyll homologous with the stamen.
The abundance of intermediate forms, which exists between stamens and foliage leaves, doesn't exist between carpel and foliage leaf. Nevertheless, the relationship between foliage leaf and carpel are easily recognizable, as Goethe in 1790 already found out (1975 § 78). He denoted the carpel as a fo1iage leaf with a folded lamina of which the borders were fused. This description fits for the epiphyllous part of the fo1iage leaf. Hagemann (1984, ~~ 339) came to the same conclusion: "Because the carpel has lost its vegetative functions, it no longer needs to be exposed, and hence, the leaf base and leaf petiole may be extremely reduced. As a result, the leaf blade comes into close contact with the shoot apical meristem". It is possible to derive the carpel by varying the proportions of the leaf blade, if one does not take into consideration the existence of the ovules. One could say that the carpel is homologous with the epiphyll, but it is better, what is already mentioned, to speak of a partial homology. Stamen and carpel comprise more than the hypo- and epiphyll of the foliage leaf. The disunion of the sexes ("die Trennung der Geschlechter" according to Goethe), in stamen and carpel, is related with the articulation of the foliage leaf in hypo- and epiphyll.[7] Stamen and carpel are polar structures, which are related with the articulation of the foliage leaf. There are no gradual and regularly ordered sequences of intermediate forms between stamens and carpels. There are many forms, but in some cases the pollen sacs are situated above the ovules, and in other cases below the ovules. An intermediate stable form between stamen and carpel has not been estab1ished in the course of evolution. The contrasts cannot be over bridged. Thus polarity of stamen and carpel is real.
The above presented relationship of foliage leaf, stamen and carpel is based on the articulation of the foliage leaf in hypo- and epiphyll. This articulation is in many cases not clear, for example in the case of the Dipsacaceae or in the case of the Compositae. Such types of leaves, where the distinction between hypo- and epiphyll is not clear, are derived types. If one would only consider these types of leaves, it would not be possible to detect the mentioned relationships, they are hidden. The more simple dicots show these relationships in a clear way. Hagemann (1970, 382-390) bas shown that full grown fo1iage leaves, which show no articulation, show in their ontogenesis an articulation in hypo- and epiphyll. Hagemann demonstrated in his article the polarity of hypo- and epiphyll in a morphogenetic sense.
The conclusion, that foliage leaf, stamen and carpel are homotopic organs, is reached by studying serial leaf sequences. The comparison of the different organs, with on1y the purpose to determine the relative position of these organs, does not take into consideration, with what part of the leaf the organs are compared. The fo1iage leaf with his blade, stalk and base is an entity, which has the potential to let each of the parts grow independently, e.g., the blade is directly inserted on the axis when the petiole and the leaf base are completely reduced.

3.2 The Polar Structure of Stamen and Carpel

To compare stamen and carpel, I have made the following 1ist of paired characteristics, most of them are not morphological:

stamen	carpel
solid	-with internal cavity

[7] Goethe (1975, § IX) did not compare the complete structure of the carpel with the stamen, be considered on1y style and stigma as the female parts.

dissimilating -assimilating
short-lived -long-lived
dying away -further growing, developing
dismissing -receiving
The pol1en grains arise in the pol1en sacks, they arise “endogenously”. The pol1en sacks rupture when they ripen and the pol1en is set free. The embryo sacks arise on the leaf blade, i.e., “exogenously”. They appear to be enveloped by the integuments 1ike the apical meristem of the shoot is enclosed bud1ike in young leaves.
The poles of stamen and carpel are founded on the one side on hypo- and epiphyl1, on the male and female gametophytes. Pol1en grain and embryo sack are basic organs, as Sachs (1882, 15) already concluded. The polarity of the vegetative plant is linear, that of the f1ower radial, within the centre the carpel pole and in the periphery the stamen pole.

3.3 Criterions of Polarity

The comparison of root and shoot gave the fol1owing results:
1. These structures are parts of a superimposed entity, they arise by the process of organic disunion and imply each other.
2. Their positions are expressions of spatial polarity. 3. They have opposite structures and qua1ities.
4. They cannot be related by a sequence of intermediate forms.
If one app1ies a similar comparison to the f1ower, then it is correct to speak of a polarity in the structures of the f1ower:
1. The nature of the leaf of stamen and carpel is founded on the organic disunion of the fo1iage leaf in hypo- and epiphyll. The formation of the gametophytes is based on the meiotic cel1 division (criterion of disunion and its imp1ication).
2. The stamens surround the carpels, which are inserted in the middle of the receptacle (spatial criterion).
3. The third criterion (opposite structures and qua1ities) and the fourth criterion (the absence of intermediates) are also fulfil1ed.

3.4 Different Kinds of Propagation

The question what the relation is between the pol1en grain and the embryo sack on the one hand and the vegetative plant on the other remains. The vegetative plant can reproduce by lateral organs (1ateral shoots and lateral roots). The f1ower does not have this abi1ity. In spite of that, propagation in the f1ower is obviously possible by the growth of the gametophytes and then as germ.[8] Following the descriptions of the vegetative plant and the flower, the relationships between the root pole and the stamen pole and the shoot pole and the carpel pole are obvious.

4. REFORMULATION OF THE CONCEPT OF THE ESSENTIAL ORGANS AND OF THE TYPE OF THE PLANT

[8] The first step is of course that the haploid spores arise. The spores of the spermatophytes germinate already in the stamen and in the carpel, the gametophyte of the pollen grain and the embryo sack are the result of the growing and ripening of these spores.

4.1 The Vegetative Plant

The significance of the theory of the basic or essential organs is that it leads to the knowledge that root, (shoot) axis .and foliage leaf are different organs. The comparison. of morphological equivalent organs is founded by this concept. The type of the vegetative plant is a model, which shows the kind of articulation of the different organs, which have ~ a non interchangeable position in the configuration of the plant. It is possible to determine to which type of ground organ a specific organ belongs on account of his relative topography (main criterion) or, when the relative position is concealed, on account of a sequence of gradual metamorphoses (auxiliar criterion) (Froebe, 1981): The determination of homologies and remains for the science of plant morphology an Important method.

The weakness of this theory is, that the morphological relationships between the ground organs are negatively defined. According to Sitte (1993: 170) the basic organs cannot be 1 homologous and they perform different basic functions. The basic organs are conceptually separated from each other in spite of being related to each other .

I propose to widen the number of possibilities to compare organs to determine the morphological relationship of the basic organs. The first articulation of the plant is the division of root and shoot poles. The process of understanding morphological structures and sampling morphological knowledge should therefore start by the comparison of polar structures. The second step is a further articulation of the polar structures. According to this consequent process of cognition, i.e., awareness of the quality of every next step in distinguishing structures, it becomes obvious, that one should distinguish between four ground organs: shoot axis and root axis on the one side and foliage leaf and root organs ((root cap and rhizoderm with root hairs[9] on the other side. Both axes connect the leaves with the root organ. This implies for the organisation type of the vegetative plant, that it should be understood at first as a bipolar organism, every pole being articulated too. Both axis connect the morphological polarities of leaf and root organ.

4.2 The Generative Plant

With the proposed four ground organs it is possible to describe the vegetative type of the plant. The extension of this concept on the flower is only partly possible. Neither Troll (1973) nor Sitte (1993) call attention to this problem by their discussion of the theory of the (three) ground organs. The well known and slightly modified scheme of Sachs (1882, 48), which Sitte and Troll present as type of the dicotyledonous plant, is not sufficient at all. Troll (1967,53, first annotation) refers to Goethe, when he claims, that Goethe in regard of the "Urpflanze"[10] had spoken of a vegetative type. If one reads the text in Troll's edition of Goethe's morphological work (Troll, 1926, l19)[11], than it is clear that Goethe on1y writes about the vegetative type. The "Urpflanze" is not mentioned[12] at all. The concept of a vegetative type makes on1y sense, when also a generative type is distinguished.[13]

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[9] According to Hansen (1907, 8) Hofmeister, Nägeli and Sachs (1881) have distinguished four ground organs in the vegetative plant. They distinguished between root, shoot axis, foliage leaf and trichoms. Hansen himself interpreted only shoot and root as ground organs.

[10] Troll (1967, 177) understands Goethe's concept of the "Urpflanze" as a concept of the type of the spermatophytes.

[11] Troll refers to the before last passage of Goethe's "Die Absicht eingeleitet", Jena, 1807 (Goethe, 1975, 11).

[12] Troll's annotation (1967,53) is also Hansen mentioned. Hansen (1907,275-285) refers in the context of the "Urpflanze " also to the scheme of Sachs as a visualisation of the idealistic concept of Goethe's "Urpflanze" (Hansen, 1907,281 and plate XVI). The same scheme is used by Troll and Sitte.

[13] A more suitable scheme of the type of the dicots is a scheme of the development of the plant, in which is referred to the alternation of generations

The concept of the generative type includes both pollen grain and embryo sack with their gametophytes. The type of the dicot spermatophyte is articulated in a vegetative and ~ a generative type with their specific ground organs.

4.3 Consequences for the Determination of Homologies

The concept to determine whether structures are homologous or not, which is based on the main criterion of the relative topography and the auxiliar criterion of a sequence of gradual metamorphoses, is in this form only partially suitable for the comparison of floral organs with organs of the vegetative shoot. In combination with the concept of the essential organs of the vegetative and generative plant the concept of homology becomes its necessary framework.

5. METHODOLOGICAL ASPECTS

5.1 The Direction of the Cognitive Process

It is possible to connect different levels of plant structures. The question is how we do this. According to Rutishauser & Sattler (1985) it is not possible, to find cytological and histological. characteristics which have a diagnostic value to distinguish, for example between axis and foliage leaf. The leaf can be axis-like, the axis can be leaf-like The axis concept and the leaf concept cannot be defined on a cytological or histological level of organisation. Starting from the superimposed organisation level of the shoot we analyze the shoot, we observe the shoot as an articulated entity, and so we come to the subordinate level of organisation, on which we distinguish between axis and leaf, consequently when, the axis is leaf-like and conversely.

5.2 The Phytomer or Metamer Concept.

The essential organs of the vegetative plant are specifically interrelated. To understand the change from the vegetative parts of the plant into the generative parts of the plant, it is necessary to regard these interrelationships for these are changed too. The phytomer or metamer concept provides a useful tool to understand these morphological changes. In his metamorphosis Goethe describes the development of the plants. He starts with the seedling and proceeds with the description of the sprouting, flowering and fruiting plant. He considers both shoot axis, foliage leaf and bud. He describes in § ll3 how the plant "from node to node, from leaf to leaf succeeds itself, that when it sprouts a kind of propagation takes place, which differs from the propagation by the flower and fruit, which happens at once, only in the way of being successive, for its shows itself in a sequence of separated, developing steps. This sprouting manifests its power successively and continuously and is the same, with the one which at once develops a considerable propagation.[14] Goethe describes in his text an articulation of the plant in subunits. Such a subunit is also called phyton. Here in this context, I define phyton as that subunit of the plant which includes fo1iage leaf, node, the internode below the insertion of the leaf and the buds of the lateral root(s) and shoot(s).
The first phyton is the seedling, the following parts, which arise from the apical meristem, metamorphose this first phyton. It is not possible to find anatomical boundaries between the succeeding phytons. The phyton is not a basic organ. The phyton is a subunit of the plant,

[14] In german: "... von Knoten zu Knoten, von Blatt zu Blatt fortsetzt, indem sie sprosst, gleichfalls eine Fortpflanzung geschehe, die sich von der Fortpflanzung durch die Blüte und Frucht, welche auf einmal geschieht, darin unterscheidet, dass sie sukzessiv ist, dass sie sich in einer Folge einzelner Entwicklungen zeigt. Diese sprossende, nach und nach sich äussernde Kraft ist mit jener, welche auf einmal eine grosse Fortpflanzung entwickelt, auf das genauste verwandt".

which encloses all the essential organs. It is a general cognitive concept above the level of the distinction of essential organs. One could agree to Troll, when he cites Eichler: "One could imagine at last, (that the shoot is a sympodium of parts of the shoot: nodes, internodes, and leaves PS), I still do not know, how this concept enriches our understanding of the plant[15] and Troll himself: “Then it is not the aim of morphology to dissect a structure (Gestalt), which is always a wholeness, in artificial parts and then to
build up schematically the previous entity out of these parts; …”[16] (Troll, 1937, 172 ff.). The concept of the phyton is here restricted to the vegetative plant. If one extends this concept onto the flower, the case becomes interesting.[17] How can the transition from the vegetative phyton to the phytons of the flower be characterised and the transitions between the different phytons (whorls) in the flower? Following Goethe’s interpretation of the close relationship between the vegetative and the generative propagation, it is clear, that we should not restrict the concept of the phyton to the level of the vegetative plant. In the foregoing chapters I have tried to show the different relations.

5.3 Spatial Discontinuity of the Metamorphosis

If one tries to look at the serial sequence of the leaf organs from the cotyledon up to the carpel as a continuing metamorphosis of one and the same organ, one gets problems at the transition from stamen to carpel. The spatial, linear sequence of the leaves is not identical with the sequence of leaf metamorphosis. In the metamorphosis of the leaves there is, after the foliage leaf, a bifurcation. For the stamen is partially homologous with the hypophyll of the foliage leaf, the carpel is partially homologous with the epiphyll of the foliage leaf.

5.4 Quantitative and Qualitative Metamorphosis

The phyton looses its ability to give rise to lateral organs after the transition from the vegetative to the generative plant. The phyton looses its force of propagation. This ability of propagation must be found in a changed way in the flower. In the flower the force of propagation is disunited. In the stamen (microsporophyll) the pollen grains mature, in the carpel (macrosporophyll) the embryo sacks mature. The phyton of the vegetative plant represents the whole vegetative plant, on the one hand there is the ability to give rise to lateral roots, on the other hand to give rise to the lateral shoots. The vegetative way of propagation is also divided into two parts. Is it possible to compare both the vegetative and the generative way of propagation.

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[15] In german: "Wenn es sich ja schliesslich auch vorstellen lässt, (dass der Stengel ein Sympodium von Sprossgliedern ist PS), so weiss ich doch nicht, was mit dieser Vorstellung eigentlich gewonnen wäre."
[16] In german: “Denn es kommt ja in der Morphologie nicht darauf an, eine Gestalt, die ja immer ein Ganzes ist, durch künstliche Einschnitte zu zerlegen um sodann dieses Ganze aus den Teilen in schematischer Weise wieder zu erbauen;…“.
[17] Nowadays the concept of the phyton plays a very important role in plant morphology, although this is not always recognized. The investigations to reveal the morphogenetic processes are based on a metameric concept (phytonistic concept) of the sprouting and flowering plant (see Meyerowitz et al, 1991; Talbert et al. 1995).

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