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Herzoglich Sachsen-Weimarischen Geheimenraths

Versuch die Metamorphose der Pflanzen zu erklären.

Gotha,

bey Carl Wilhelm Ettinger.

1790.

An ATTEMPT *to* INTERPRET *the* METAMORPHOSIS *of* PLANTS

by

J. W. von GOETHE

1790

Proliferous Rose (*Metamorphosis of Plants*)

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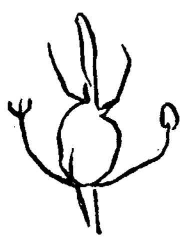

I am indeed not unaware that this path is obscured by clouds, which will pass over from time to time. Yet these clouds will easily be dispersed when it is possible to make the fullest use of the light of experience. For Nature always resembles herself, although she often seems to us, on account of the inevitable deficiency of our observations, to disagree with herself. (Linnaeus, Anticipation in Plants, Diss.[120]).

INTRODUCTION

§ 1

Anyone who pays a little attention to the growth of plants will readily observe that certain of their external members are sometimes transformed, so that they assume — either wholly or in some lesser degree — the form of the members nearest in the series.

§ 2

Thus, for example, the usual process by which a single flower becomes double, is that, instead of filaments and anthers, petals are developed; these either show a complete resemblance in form and colour to the other leaves of the corolla, or they still carry some visible traces of their origin.

§ 3

If we note that it is in this way possible for the plant to take a step backwards and thus to reverse the order of growth, we shall obtain so much the more insight into Nature's regular procedure; and we shall make the acquaintance of the laws of transmutation, according to which she produces one part from another, and sets before us the most varied forms through modification of a single organ.

§ 4

The underlying kinship of the various external members of the plant, such as the leaves, calyx, corolla, and stamens, which develop after one another, and, as it were, from one another, has long been recognised by naturalists in a general way; it has indeed received special attention, and the process, by which one and the same organ presents itself to our eyes under protean forms, has been called the *Metamorphosis of Plants.*

§ 5

This metamorphosis displays itself in three modes: *normal, abnormal,* and *fortuitous.*

§ 6

Normal metamorphosis may also be called *progressive*: for it is that which may be perceived always working step by step from the first seed-leaves to the final development of the fruit. Through the change of one form into another, it passes by an ascent — ladder-like in the mind's eye —

120. This is the translation of the citation as given by Goethe; the full reference is Ullmark, H. (1764): *Prolepsis plantarum. In* Linnaeus, C., *Amoenitates Academicae,* Lugduni Batavorum. Vol. 6, No. cxviii, p. 341. (A.A.).

to that goal of Nature, sexual reproduction. It is this progression which I have studied attentively for a number of years, and which I shall attempt to elucidate in the present essay. This being our standpoint, we will consider the plant, in the following demonstration, only in so far as it is an annual, and passes by continuous progression from the seed up to the fructification.

§ 7

We may give the name of *retrograde* metamorphosis to that which is *abnormal.* As in the normal course, Nature hastens forward to her great end, so in the abnormal, she takes one or more steps backwards. As she there, with irresistible impulse and the full exertion of her might, fashions the flowers and prepares them for the works of love; so here she slackens, as it were, and leaves her creation before it reaches its goal, in an undetermined and powerless condition. Though in this state it is often agreeable to our eyes, in its true inwardness it is feeble and ineffectual. From our acquaintance with this abnormal metamorphosis, we are enabled to unveil the secrets that normal metamorphosis conceals from us, and to see distinctly what, from the regular course of development, we can only infer. And it is by this procedure that we hope to achieve most surely the end which we have in view.

§ 8

We will, on the other hand, avert our eyes from the third kind of metamorphosis, which comes about *contingently,* as a result of external causes, especially through the action of insects; for this phenomenon might frustrate our purpose by diverting us from the direct path which we ought to follow. Perhaps there will be an opportunity to speak elsewhere of these excrescences, which, though monstrous, are still subject to definite limitations.

§ 9

I have ventured to draw up the present work without giving illustrative plates, which however in many respects might seem necessary. I propose to reserve them for the sequel, which can be done the more easily, since enough material is left over for the elucidation and further development of the present short and merely preliminary essay. It will not then be necessary to produce so formal a treatise as this one. I shall have the opportunity of bringing forward much cognate matter; and passages extracted from authors of a like way of thinking will then find their natural place. Especially I will not fail to make use of any suggestions from the experts who today are the glory of this noble science. It is to them that I commit and dedicate these pages.

I. CONCERNING THE SEED-LEAVES

§ 10

Since we have undertaken to observe the sequence of stages of plant growth, let us turn our attention forthwith to the plant at the moment when it germinates. At this stage we may easily and exactly recognise the parts which directly belong to it. It leaves its husks more or less completely in the earth; these we will not now investigate. In many cases, when the root has anchored itself in the soil, the plant brings forth into the light the first organs of its upper growth, which were already present, hidden within the seed-coat.

§ 11

These first organs are known under the name of *Cotyledons.* They have also been called seed-valves, kernel-pieces, seed-lobes, and seed-leaves; these names are an attempt to denote the various forms which the cotyledons assume.

§ 12

They often appear shapeless, crammed, as it were, with crude matter, and as much extended in thickness as in breadth[121]; their vessels are unrecognisable, and scarcely to be distinguished from the mass as a whole. These cotyledons bear scarcely any resemblance to a leaf, and we may be misled into taking them for organs belonging to some special category.

§ 13

Nevertheless in many plants they approach leaf form; they increase in area and become thinner; when exposed to light and air they assume a deeper green; the vessels which they contain become more recognisable, and more similar to the veins of a leaf.

§ 14

Finally they appear before us as true leaves, the vessels of which are capable of the finest development. Their resemblance to the succeeding leaves prevents our taking them for special organs; we recognise them, rather, as the first leaves of the stem.

§ 15

But since we cannot think of a leaf without a node, or of a node without a bud, we may be allowed to conclude that the point where the cotyledons are attached is the veritable first nodal point of the plant. Confirmation of this view is afforded by those plants which put forth young buds immediately at the base of the cotyledonary wings, and produce complete shoots from the first nodes, as the horse-bean (*Vicia Faba* L.) is wont to do.

§ 16

The cotyledons are generally twinned, and this leads us to make an observation, the significance of which will be more fully appreciated at a later point. This is that the leaves of this first node are often *paired* when the succeeding leaves of the stem stand *alternately;* there is here an approach and association of parts which Nature, later in the sequence, disjoins and separates from one another. This is still more noticeable when the cotyledons take the form of numerous small leaves assembled round a common axis, while the stem, developing gradually from their midst, bears the succeeding leaves singly, round about itself. This can be observed to perfection in the growth of conifers. Here the wreath of needles forms, as it were, a calyx. We shall have to recall these cases in connexion with similar phenomena which we shall meet later.

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121. Soret ed., p. 9, translates this incorrectly as "aussi épais que longs". (A.A.)

§ 17

We will not now occupy ourselves with the single cotyledons of indefinite form belonging to those plants which germinate with one leaf.

§ 18

We will, however, notice that even the most leaf-like cotyledons themselves are always relatively undeveloped as compared with the later leaves of the shoot. Their outline, especially, is extremely simple, and bears as little trace of indentations as their surfaces do of hairs or other vessels (Gefässe)[122] characteristic of the mature leaf.

II. DEVELOPMENT OF THE STEM-LEAVES FROM NODE TO NODE

§ 19

We are able now to study accurately the successive formation of the leaves, since the progressive operations of Nature all take place, step by step, under our eyes. A variable number of the succeeding leaves are often already present within the seed, and lie enclosed between the cotyledons; while still in their folded condition they are known under the name of the plumule. The relation of their form to that of the cotyledons and of the following leaves differs in different plants, but they generally diverge from the cotyledons in being expanded and thin in texture; on the whole fashioned as typical leaves; fully green in colour; and attached to an obvious node. Their relationship to the later stem-leaves is indubitable, but they are commonly inferior to them in the fact that their periphery or margin has not reached its full elaboration.

§ 20

The leaf shows a continuous development from node to node, as the midrib elongates, and the lateral veins arising from it stretch out more or less on either hand. The various characters of the nervation are the principal cause of the multifarious forms met with in leaves. Leaves may be indented, deeply incised, or formed of many leaflets; in the last case they prefigure complete small shoots. The date palm affords a striking example of such graded diversification of the simplest leaf form. In a sequence of several leaves, the midrib is carried progressively further into the lamina; the fan-like simple leaf becomes torn and divided; and the end result is a highly complex leaf, vying with a branch.

§ 21

As the leaf itself arrives at the perfection of its form, so the leaf-stalk also develops correspondingly; it may either make a continuous whole with its leaf, or it may form a distinct stalklet, easily detachable at a later stage.

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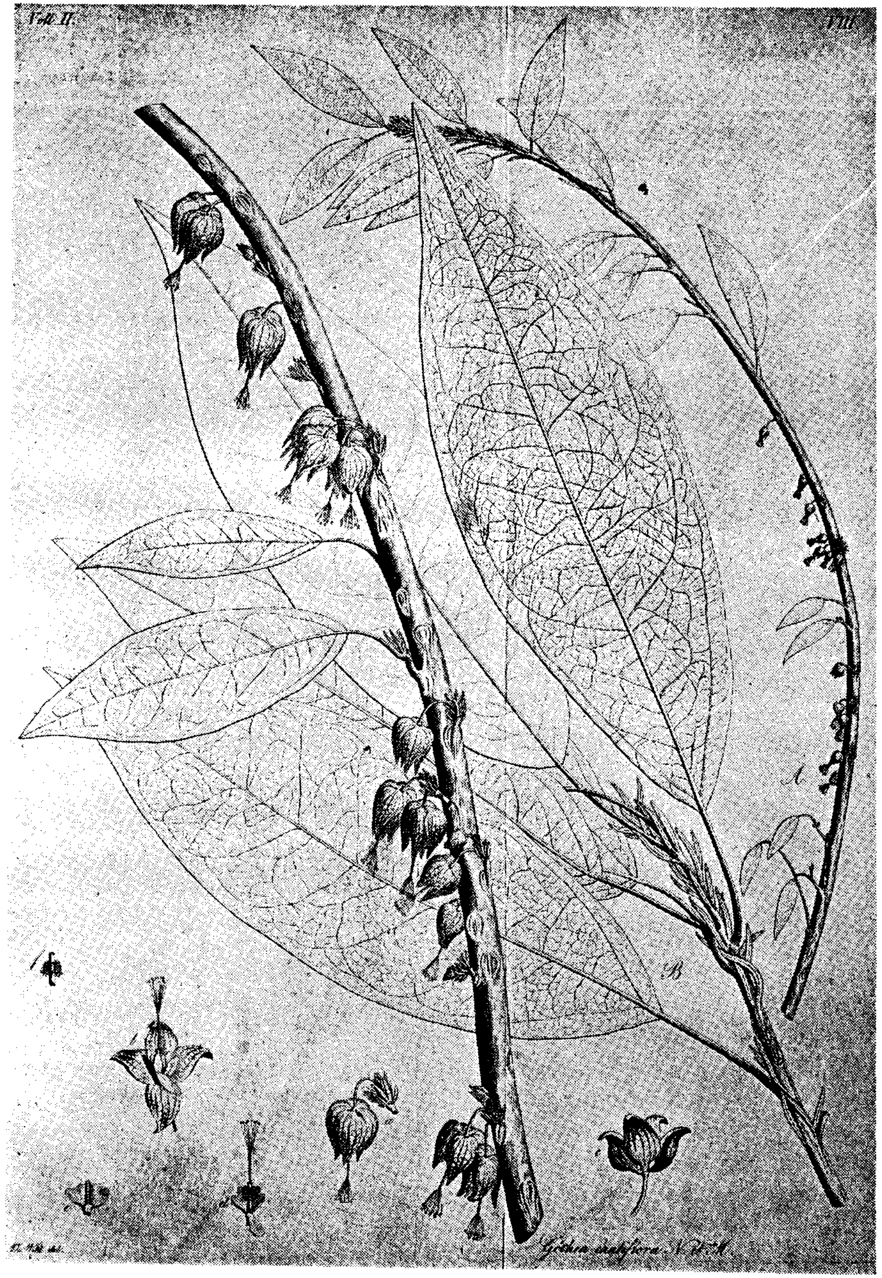
122. Goethe uses *Gefässe* as a vague general term for anatomical elements forming the leaf (*cf.* also § 25). *See* Sachs, J. von (1890): *History of Botany.* Trans. by Garnsey, H. E. F. and Balfour, I. B., Oxford, p. 254, for the indefinite use of the word vessel in the eighteenth century. (A.A.)

Abnormal, funnel-shaped, spirally contorted shoot of Valeriana officinalis L., from Taf. 5 (cf. p. 72) of Schuster, J. (1924): l.c., after Stark's drawing from a sketch by Goethe. (See p. 79 of text.)



GOETHEA CAULIFLORA H. ET M., TYPE SPECIES OF THE GENUS GOETHEA, AFTER JH. WILD'S DRAWING IN NOVA ACTA, VOL. 2, PL. VIII.

§ 22

We see in various plants, for example the orange tribe[123], that this independent leaf-stalk may also have a tendency to transform itself into a leaf-like form. The organisation of such leaf-stalks will in the sequel suggest some considerations to us, which we will put aside for the present.

§ 23

Neither can we now enter upon a special investigation of stipules; we only remark in passing that, especially when they form part of the leaf-stalk, they also become remarkably transformed in the course of its further change.

§ 24

Now as the leaves owe their first nourishment principally to the more or less modified watery fluid which they draw from the stem, so they are indebted to the air and the light for their main development and elaboration. As we find the cotyledons, produced within the closed seed coat, charged as it were with a crude sap only, and organised and developed scarcely at all, or merely in a rough fashion; so the leaves of plants which grow under water are of less perfect organisation than those exposed to the open air. Again, the same plant species develops smoother and less highly perfected leaves when it grows in low and damp places; if on the contrary it is transferred to a higher situation, it produces leaves which are rough, hairy, and more elaborately formed.

§ 25

The vessels[124] which form the skin of the leaf, and which arise from the ribs and feel their way towards one another by their tips, are similarly influenced; their anastomosis, if not altogether caused, is at least much promoted by the more subtle kinds of gas. We are inclined to ascribe to lack of complete anastomosis the fact that the leaves of many plants which grow under water are thread-like or antler-like. The mode of growth of the water buttercup (*Ranunculus aquatilis* L.)[125] affords us clear evidence on this point, since its leaves produced under water have thread-like ribs, while those developed above the water surface are formed with fully anastomosed and entire blades. Indeed the transition can be accurately traced in leaves of this plant which are partly anastomosed and partly thread-like.

§ 26

It has been learnt experimentally that the leaves of plants absorb different gases and combine them with their internal moisture; nor does any doubt remain that they return these refined saps to the stem, and thus greatly promote the growth of the neighbouring buds. The kinds of gas developed from the leaves of many plants, and also from the cavities of reeds[126], have been investigated with convincing results.

123. In a letter to SORET, July 14, 1828 (UHDE, H. (1877): *l.c.*, p. 51) GOETHE says that he used *Agrumen* (the word employed in § 22.) for "die ganze Sippschaft der Citronen, Pommeranzen u.s.w." (A.A.)
124. *See* note to §18. (A.A.)
125. GOETHE uses the name *Ranunculus aquaticus.* (A.A.)
126. The expression "Hölungen der Rohre" used here is translated "cavités des joncs" by SORET; "vaisseaux" by GINGINS-LASSARAZ and MARTINS; and "hollow stems" by COX. (A.A.)

§ 27

We observe in various plants that one node springs from another. In stems which are closed at the nodes[127], as in cereals, grasses, and reeds, this is obvious to the eye; but it is less conspicuous in other plants which have a hollow centre throughout, and appear to be filled with a pith or rather a cellular tissue. The rank, among the other anatomical regions of the plant, formerly held by the so-called pith is now however disputed[128], and, as it seems to us, on excellent grounds. Its apparently predominant influence in growth is denied, while all impetus and developmental force is, on the other hand, ascribed unhesitatingly to the inner face of the second cortex — the so-called *liber*. It thus becomes more convincing that an upper node — since it arises from the one below, and receives the sap by its mediation in a finer and more filtered state, improved by the action of the preceding leaves — must develop more perfectly and convey more delicate juices to its own leaves and buds.

§ 28

Since now the cruder saps are continually drained in this manner, and give rise to purer — the plant meanwhile perfecting itself step by step — the period prescribed by Nature is finally reached. At last we see the leaves in their greatest expansion and development, and soon afterwards we become aware of a new aspect which warns us that the epoch which hitherto we have been studying is past, and a second is approaching — the epoch of the *Flower*.

III. TRANSITION TO THE FLOWERING PHASE[129]

§ 29

We see the transition to anthesis come to pass either *relatively rapidly* or *relatively gradually*. In the latter case we commonly notice that the stem-leaves begin to draw in, as it were, from the periphery, and especially to lose their diverse marginal divisions, while, on the other hand, they show some expansion in their basal regions, where they are connected with the stem. At the same time we see that, even if the stem interval from node to node does not elongate markedly, nevertheless it is much more delicately and slenderly formed than in its earlier state.

§ 30

It has been observed that copious nourishment hinders the production of the inflorescence of a plant, while a moderate or indeed scanty supply of food hastens it. The action of the stem-leaves, considered above, shows itself here still more clearly. So long as cruder saps are still to be carried away, so long must there be production of those organs which are capable of fulfilling this need. If excessive nourishment is forced upon the plant, this operation must be continually repeated, and flowering is thus rendered well-nigh impossible. If, on the other hand, the plant is deprived of food,

127. GOETHE's expression is "von Knoten zu Knoten geschlossen," but the examples he gives suggest that he actually meant "closed at the nodes". (A.A.)
128. HEDWIG, Leipziger Magazin, Part III. (For full reference *see* p. 71 (A.A.))
129. The word which I have translated "flowering phase" is "Blüthenstand"; GOETHE uses this term indifferently for inflorescence and for flower. (A.A.)

this natural process is facilitated and shortened; the foliar organs are refined, the operation of the unadulterated saps becomes purer and stronger, and the transformation of the parts is rendered possible and makes unimpeded progress.

IV. FORMATION OF THE CALYX

§ 31

We often see the change to the flowering phase occur *rapidly*, and in this case the stem, above the node of the uppermost leaf, suddenly becomes tall and slender, while several leaves are gathered together at its apex, grouped around a centre.

§ 32

It may, it seems to us, be proved most clearly that the leaves of the calyx are the same organs as those which up to the present have developed as stem-leaves, but are now, often in very different guise, collected round a common centre.

§ 33

We have already among cotyledons noticed a similar operation of Nature, and have seen several leaves, and thus clearly several nodes, collected round a point and approximated. The conifers, when they develop from the seed, show a radiating wreath of unmistakable needles, which, unlike the generality of other cotyledons, are already highly developed. We thus see, in the first infancy of this plant, an indication, as it were, of that power of Nature through which, at a greater age, inflorescence and infructescence will be produced.

§ 34

Further we see in various flowers unaltered stem-leaves collected into a kind of calyx immediately beneath the corolla. Since their form is completely characteristic, we need only, in proof of their being leaves, appeal to ocular evidence and to botanical terminology, which has distinguished them by the name of floral leaves, *Folia floria*.

§ 35

We have to observe with greater attention the case already mentioned, in which the transition to the inflorescence occurs *gradually*. Here the stem-leaves approach one another little by little, become transformed, and by degrees, as it were, pass into the calyx, as may easily be observed in the calyx[130] of the composites, especially the sunflowers and the marigolds.

§ 36

This faculty of Nature, which assembles a number of leaves round a centre, may be observed to bring about an even more intimate union, thus making these collected and modified leaves still less recognisable; for it unites them between themselves — sometimes completely, but often only partially — inducing concrescence of their lateral margins. The leaves — so closely crowded and pressed against one another — are most intimately

130. This, which GOETHE calls "Kelch," is now described as an involucre of bracts. (A.A.)

in contact in their embryonic condition; they anastomose through the influence of the extremely pure sap present by this time in the plant, and appear before us as the bell-shaped or so-called one-leaved (monosepalous) calyx, which reveals its compound origin by the fact that its upper margin is more or less toothed or incised. We can find ocular evidence of this if we compare a number of deeply cut calyces with those that are many-leaved, especially when the calyces of various composites are exactly considered. We shall see, for example, that the calyx of the marigold, which in systematic descriptions is called *simple* and *much divided,* consists, in reality of many concrescent and superposed leaves, into which, as we have already mentioned, the contracted stem-leaves pass, as it were, almost insensibly.

§ 37

In many plants there is constancy in the number and form in which the sepals, whether free or fused, and the succeeding members are arranged round the stalk as an axis. On this constancy depends, in great part, the progress, the trustworthiness, and the repute of botanical science, which we of late have seen increasing more and more. In other plants the number and structure of these members is not equally constant, but even this inconstancy has been unable to baffle the delicate powers of discrimination of the master workers in this science; their endeavour has been by exact diagnosis to limit these anomalies of Nature, as it were, to a narrower sphere.

§ 38

In this way, then Nature formed the calyx: she *connected together* round a centre several leaves and consequently several nodes, generally according to a certain definite number and plan; these leaves and nodes she would otherwise have produced *successively and at some distance from one another*. If the flowering had been inhibited by the intrusion of superfluous nourishment, these leaves would have been spaced out, and would have appeared in their earlier form. Thus in the calyx Nature produces no new organ, but she unites and modifies only the organs already known to us, and in this way achieves a step towards the goal.

V. FORMATION OF THE COROLLA

§ 39

We have seen that the calyx owes its origin to elaborated saps, which are engendered by degrees in the plant, and that it is thus in its turn adapted for the production of a future organ of a further refinement. This idea can be confirmed when we interpret the process on purely mechanical grounds. For how extremely delicate, and suited to the finest filtration, those vessels must become, when they, as we have seen above, are in the closest contact and appressed to one another.

§ 40

We may observe the transition from calyx to corolla in more than one case; for although the colour of the calyx is still usually green, and remains similar to the colour of the stem-leaves, yet it often changes in one or other of its regions — at the apices, margins, or back, or over its inner surface — while the outer still remains green; and we always see an increase of delicacy associated with this coloration. In this way ambiguous calyces come into being, which may equally well be taken for corollas.

§ 41

We have now remarked that from the cotyledons onwards there is a great extension and elaboration of the leaf, affecting its periphery in particular. Thence to the calyx there is a contraction of the outline, while, with the development of the corolla, we notice that a phase of expansion again sets in. The petals are generally larger than the sepals, and it is to be observed that the organs which were in a state of contraction in the calyx, at the stage now reached expand themselves as petals through the influence of purer saps, filtered through the calyx and in a high degree refined. They assume the appearance of entirely different organs, and their exquisite texture, their colour, and their scent, would quite obscure their origin for us, if it were not that in various exceptional cases we can spy out Nature's ways.

§ 42

So, for example, within the calyx of a pink, a second calyx is frequently found, which in part is fully green, and belongs to the type of the monophyllous toothed calyx, while in part it is laciniated, and, at its apices and margins, transformed into genuine beginnings of petals — delicate, expanded and coloured. Through such a case we once more clearly recognise the relationship of the corolla to the calyx.

§ 43

The relationship of the corolla to the stem-leaves is demonstrated to us in more than one manner; for in various plants stem-leaves occur which are already more or less tinted, long before they approach the inflorescence, while others, in the neighbourhood of the inflorescence, are completely coloured.

§ 44

It also frequently happens that Nature proceeds direct to the corolla, as it were skipping the calyx. In this case we likewise have the chance of observing that stem-leaves may pass into petals. So, for example, an almost completely developed and coloured petal may often be found on the stem of a tulip. A still more remarkable case is that in which such a leaf is half green, with its green half, which belongs to the stem, remaining attached thereto, while its coloured half is carried up with the corolla, so that the leaf is torn into two parts.

§ 45

It is a very probable idea that the colour and scent of the petals are to be attributed to the presence in them of the male fertilising substance[131]. Probably this substance occurs in them in a state in which it is not yet sufficiently isolated, but mixed and diluted with other juices. The beautiful phenomena of colour lead us to the conception that the material wherewith

131. The *Journal of Botany* version (Cox) translates this as "pollen," which does not render GOETHE's expression, "männlichen Samens" accurately. (A.A.)

the petals are filled, though indeed it has achieved a high degree of purity, yet still has not reached the highest grade, in which it appears to us white and colourless.

VI. FORMATION OF THE ANDROECIUM

§ 46

The theory suggested in the preceding paragraph seems still more probable when we consider the near relationship of petals and androecium. Were the relationship of all the other parts to one another so obvious, so generally observed, and so indubitably settled, the present treatise might be held to be superfluous.

§ 47

Nature in some cases shows us this transition in the normal course of development, *e.g.* in *Canna,* and various plants of this family. A true petal, little changed, contracts in its upper margin, and an anther, in connexion with which the rest of the petal takes the place of a filament, makes its appearance.

§ 48

In flowers which are often double, we can observe this transition in all its stages. In several kinds of rose, within the fully developed and coloured petals, there are others which are contracted, sometimes in the middle and sometimes at the side; this contraction is caused by a little callosity, which appears as a more or less complete anther, while, in a degree corresponding to the degree of contraction, the leaf approaches the simpler form of a stamen. In some double poppies, fully developed anthers are borne upon little-changed petals of the strongly double corolla, while in others, anther-like callosities induce more or less contraction of the petals.

§ 49

If all the stamens are changed into petals, the flowers become sterile; but if in a flower, while it becomes double, staminal development still occurs, fertilisation takes place.

§ 50

And so an androecium arises, when the organs which we have hitherto seen expanded as petals, reappear in a highly contracted and, at the same time, a highly refined condition. The opinion propounded above is thus once more confirmed, and we are made more and more aware of this alternating process of contraction and expansion, whereby Nature ultimately attains her end.

VII. NECTARIES

§ 51

Abrupt as is the transition in many plants from the corolla to the androecium, yet we notice that Nature does not always make the passage in a single stride. On the contrary, she produces intermediate organs, which in form and function sometimes approach one member and sometimes the other. Although the structure of these intermediate organs varies greatly, yet they can generally be brought together under the one conception that they are *gradual transitions between the petals*[132] *and the stamens.*

§ 52

Most of the variously formed organs, which Linnaeus distinguished with the name of Nectaries, may be grouped under this definition; and here we find an additional reason for admiring the keen insight of that extraordinary man, who, without having a quite clear idea of the function of this part, yet trusted to a presentiment, and took the risk of calling by the same name organs which were very diverse in appearance.

§ 53

Various petals show their relationship with the stamens by the fact that, without markedly changing their form, they bear little grooves or glands, which secrete a honey-like sap. That this is a fertilising fluid, though still imperfect and incompletely determinate, may be conjectured from the considerations already advanced, and this conjecture will reach a still higher degree of probability, for reasons which we will bring forward later.

§ 54

The so-called nectaries may also appear as independent members, and then they sometimes approach petals in their structure, and sometimes stamens. For example, the thirteen rays of the nectaries of the grass of Parnassus (*Parnassia*), with their corresponding number of red globules, are closely similar to the stamens. Others show themselves as filaments without anthers, as in *Vallisneria* and *Fevillea.* We find them in *Pentapetes* regularly alternating with the stamens in one whorl, but foliar in form; in systematic descriptions they are called petal-shaped emasculated filaments (*filamenta castrata petaliformia*). Just such forms, oscillating between the categories[133], are seen in *Kiggellaria* and the passion flower.

§ 55

Those peculiar organs — *coronas* — likewise seem to us to deserve the name of nectaries, in the sense defined above. For if the formation of petals is brought about through an expansion, so the corona is formed, on the contrary, through a contraction — that is to say, in the same way as the stamens. Thus we see smaller, restricted coronas succeeding the completer, more extended corollas, as for example in narcissus, oleander (*Nerium*), and agrostemma (*Lychnis coronaria* Desr.).

§ 56

Yet other still more striking and remarkable transformations of petals are to be seen in different genera. We notice in various flowers that their petals, on the inner surface at the base, have a small hollow, which is filled with a honey-like sap. This pit, when it becomes deeper in other genera and species, produces a spur- or horn-like prolongation from the back of the petal, and the form of the rest of the petal is correspondingly more or

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132. Though the word "Kelchblätter" is here used, and is translated "feuilles du calice" by Soret, it seems to be an obvious slip for "Kronenblätter". (A.A.)

133. This translation though rather free, seems to convey the sense of "schwankende Bildungen". (A.A.)

less modified. We may observe this particularly in various species and varieties of the columbine (*Aquilegia*).

§ 57

This organ is found in the highest degree of modification, for example, in monkshood (*Aconitum*), and love-in-a-mist (*Nigella*), in which, however, a little attention reveals its foliar character; in *Nigella,* especially, the nectaries readily grow out again into petals, and the flowers become double through their transformation. In *Aconitum,* on careful inspection, the similarity of the nectaries to the hooded petals which enclose them can be detected.

§ 58

Having propounded the idea that the nectaries are approximations of the petals to the stamens, we may now take the opportunity to make some remarks about irregular flowers. So, for example, the five outer leaves of *Melianthus*[134] may be considered as true petals, but the five inner may be described as a corona, consisting of six nectaries, of which the uppermost approaches most nearly to petal form, while the furthest divergence is shown by the lowermost, which is indeed already called a nectary. In just the same sense, the keel (*carina*) of the papilionaceous flower may be called a nectary, since it is the one amongst the petals which most nearly approaches stamen form, and departs very widely from the leaf shape of the so-called standard (*vexillum*). In this manner we can quite easily explain the brush-like bodies which are found attached to the extremity of the keel in some species of milkwort (*Polygala*), and we can come to a clear idea as to the category to which this keel should be assigned.

§ 59

It is surely unnecessary to make the emphatic reservation that the intention of these remarks is not to introduce confusion into a subject which has been already subdivided and pigeon-holed by the efforts of observers and systematists. The writer wishes only to make the variations of plant form more comprehensible through the considerations here advanced.

VIII. FURTHER NOTES ON THE ANDROECIUM

§ 60

Microscopic observations decide beyond all doubt that the reproductive organs of plants, like their other parts, are produced by means of the spiral vessels. We thence deduce an argument for the inner identity of the various members of the plant, which hitherto have appeared to us in such multifarious forms.

§ 61

Now since the spiral vessels lie in the centre of the sap-vessel-bundles, and are enclosed by them, we may picture the condition of strong contraction somewhat more exactly if we imagine the spiral vessels — which appear to us indeed as elastic springs — in their state of utmost energy; they are then dominant, whereas the expansion of the sap-vessels is subordinated.

134. On this case *see* Troll ed., p. 457. (A.A.)

§ 62

The abbreviated vascular bundles can now extend no more; they can no longer seek out one another, and no longer form a network through anastomosis; the tubular vessels, which otherwise fill up the interstices of the network, can no longer develop. All factors which have caused the expansion of the stem-leaves, sepals, and petals, vanish completely at this point, and a weak and extremely simple filament arises.

§ 63

The delicate membranes of the anther, between which the excessively tender vessels come to an end, are scarcely able to develop. If we now admit that at this stage those very vessels, which would otherwise have elongated, broadened, and again sought one another out, are at present in an extremely contracted condition; if we now see the highly elaborated pollen proceed from them, which compensates through its activity for what the vessels which produce it have lost in expansion; if it is at last set free and seeks out the female organ, which, through a natural correlation, occurs in the neighbourhood of the stamens; if it firmly adheres to this organ and communicates its influence to it: there is nothing then to prevent our calling the union of the two sexes an immaterial anastomosis, and believing that, at least for a moment, we have brought nearer together the concepts of growth and of reproduction.

§ 64

The delicate substance which develops in the anthers appears to us as a powder; but these pollen-grains are only vessels in which an extremely fine sap is stored. Hence we agree with the opinion of those who hold that the sap is imbibed by the pistils to which the pollen-grains adhere, and that thus fertilisation is brought about. This is the more probable since some plants secrete no pollen, but only a mere fluid.

§ 65

We recall to ourselves at this point the honey-like sap of the nectaries, and its probable relationship with the elaborated fluid of the seminal globules. Perhaps the nectaries are organs the function of which is preparation; perhaps their honey-like moisture is absorbed by the stamens, made more specific, and worked up fully — an opinion which is the more likely since after fertilisation this sap is no longer observable.

§ 66

We may just notice in passing that in some cases filaments, and, in others, anthers are concrescent, and offer us the most wonderful examples of the anastomosis and union of plant members which in their origin were truly distinct — a feature to which we have already more than once alluded.

IX. FORMATION OF THE STYLE

§ 67

As up to the present I have endeavoured as far as possible to make clear the inner identity of the various successively developed plant members, despite the very great deviations in their external form; so it will readily be conjectured that my object at this point is to explain the structure of the female organ in the same way.

§ 68

We will first of all consider the style apart from the fruit, as we indeed often find it in nature; and we can do this the more readily since in this form it shows itself distinct from the fruit.

§ 69

We notice, then, that the style remains at that stage of growth which characterises the stamens. We were able in fact to observe that the stamens originated through contraction. The styles are often in the same case, and we find them, if not always of similar dimensions to the stamens, still only to a small extent longer or shorter. In many examples the style is almost like a filament without an anther, and the relationship of their external form is closer than that of the other members. As they are both produced from spiral vessels, we see the more clearly that the female member has as little claim as the male to be regarded as an organ belonging to a special category; and if through this consideration we get a real insight into its exact relationship with the male, so we find the idea that fertilisation is a form of anastomosis the more pertinent and enlightening.

§ 70

We very often find the style produced by the concrescence of several distinct styles, while the members of which it consists can scarcely be distinguished, for not even at the tip are they always separated. This process of concrescence, the operation of which we have often noticed, is here even more possible than elsewhere; indeed it cannot but happen, since the delicate rudiments, before their development is completed, are compressed one against another in the midst of the flower, and may form the most intimate connexions between themselves.

§ 71

Nature shows us more or less clearly in various normal cases, the close relationship of the style with the preceding parts of the flower. So, for example, the pistil[135] of iris with its stigma presents to our eyes the complete form of a petal. The umbrella-shaped stigma of *Sarracenia* does not reveal itself so strikingly as compounded of several leaves, but its green colour does not discredit the idea. And with the help of a lens we find that various stigmas, such as those of crocus and *Zannichellia,* take the form of complete monophyllous or polyphyllous calyces.

§ 72

In retrograde development, Nature often shows us the case of styles and stigmas being again changed into petals; *Ranunculus asiaticus,* for example, becomes double by transformation of the stigmas and pistils of the female organ into veritable petals, while the stamens directly under this corolla are often unchanged. Some other significant instances will be cited below.

§ 73

We may recapitulate here the remarks made above, that styles and filaments represent corresponding phases of growth, and thereby once more illustrate the principle of alternating expansion and contraction. From the seed to the fullest development of the stem-leaves, we first noticed an expansion. After this we saw the calyx arise through a contraction; the petals through an expansion; the sexual organs once more through a contraction; and we shall soon become aware of the extreme of expansion in the fruit, and the extreme of concentration in the seed. In these six steps Nature in unresting sequence completes the eternal work of the bisexual reproduction of plants.

135. GOETHE uses the word "Pistill", but he is probably not including the ovarian region. (A.A.)

X. CONCERNING THE FRUITS

§ 74

We shall now have to observe the fruits, and we shall soon convince ourselves that they have the same origin as the other organs, and are subject to the same laws. We are speaking particularly of those seed-vessels which Nature forms to enclose the so-called covered seeds—or, rather, from the inner surface of which she develops a larger or smaller number of seeds as the result of fertilisation. That these seed-vessels are likewise to be explained from the nature and organisation of the members hitherto considered, can also be shown in a few words.

§ 75

Retrograde metamorphosis, again, brings this law of Nature home to us. So, for example, in the pinks — flowers which are well known and loved for their very degeneracy — it may often be noticed that the seed-capsules change back into calyx-like leaves, and that the styles shorten correspondingly. Indeed pinks occur in which the seed-vessel has changed into a calyx, real and complete, while its apical teeth still bear the delicate remains of the styles and stigmas, and, from the interior of this second calyx, a more or less perfect corolla is produced in place of the seeds.

§ 76

Further, Nature has herself in very diverse ways revealed to us, in forms regularly and constantly recurrent, the fruitfulness which lies concealed in the leaf. So the modified, but still completely recognisable, leaf of the lime tree, produces from its midrib a little stalk bearing a complete flower and fruit. In the butcher's broom (*Ruscus*) the manner in which flowers and fruit are borne on the leaves is still more striking.

§ 77

The direct fertility of the stem-leaves in the ferns strikes one as still more intense, and as almost monstrous. These leaves through an inner impulsion, and perhaps without the definite interaction of two sexes, develop and shed countless seeds, or rather gemmae, capable of growth. Here a leaf vies in fruitfulness with a spreading plant, or with a large and branching tree.

§ 78

Bearing these observations in mind, we cannot fail to recognise the leaf nature of the seed-vessels — notwithstanding their various forms, their special modification, and their relations among themselves. So, for example, the legume would be a simple folded leaf concrescent by its margins, while siliquas would consist of several leaves, superposed and fused. Compound seed-vessels would be explained as consisting of several leaves united round a middle point, their inner faces open towards one another, and their margins united. We may convince ourselves of this by observing the appearance presented when such aggregated capsules spring apart after ripening, since each member then reveals itself as an opened pod or siliqua. Moreover a similar process regularly occurs in different species of one and the same genus; for example, the fruit capsule of *Nigella orientalis* takes the form of partly concrescent legumes grouped round a centre, while in *N. damascena* (love-in-a-mist) they appear fully fused.

§ 79

Nature hides the leafy character from our sight most effectually when she forms sappy and soft, or woody and tough seed-cases; but she will not be able to escape our scrutiny when we know how to follow her carefully in all transitional phases. Here it may be enough to have indicated the general conception involved, and to have referred to some examples showing Nature's accordance with it. The extreme multifariousness of seed-vessels gives us material for further consideration in the future.

§ 80

The relationship of the seed-vessels to the preceding members shows itself also in the stigma, which in many cases is sessile and inseparably bound up with the seed-vessel. We have already indicated the affinity of the stigma with leaf form, and we may here refer to it once again; for in double poppies it may be noticed that the stigmas of the seed-capsule are transformed into delicate little coloured leaves, completely resembling petals.

§ 81

The last and most important expansion which the plant exhibits in its growth, shows itself in the fruit. Both in inner energy and in outer form this expansion is often very great, indeed enormous. Since the enlargement generally occurs after fertilisation, it appears that the seed, having entered upon its definitive development, since it draws upon the juices of the whole plant for its growth, gives them a trend towards the seed-case. With the help of these juices the vessels become nourished, dilated, and often in the highest degree filled and expanded. From the foregoing argument it may be concluded that the purer kinds of gas take a great share in this process; this idea is confirmed by the experimental fact that the distended legumes of *Colutea* (bladder senna) contain pure air.

XI. CONCERNING THE IMMEDIATE ENVELOPES OF THE SEED

§ 82

In contrast to the expansion of the fruit, we find that the seed shows the extreme degree of contraction, while its interior is highly elaborated. It may be noticed in various cases that the seed transforms leaves into its immediate integuments, and that it adjusts them more or less to itself — generally, indeed, by its own energy moulding them closely to itself and quite altering their form. Since we have already seen many seeds developed from a single leaf, and enclosed therein, we need not be surprised that an individual seed-embryo should clothe itself in a leafy integument.

§ 83

In many winged seeds we can detect indications of the leafy seed-coat not being perfectly fitted to the seed — for example in the maple, the elm, the ash, and the birch. A very remarkable example of how the seed-embryo gradually draws together more expanded sheaths and adjusts them to itself, is offered to us by the three differing zones of heterogeneously formed seeds in the marigold. The outermost circle still preserves a shape akin to that of the leaves of the calyx, except that a seed-rudiment, straining the midrib, induces a curvature of the leaf, and the concavity is divided lengthways into two parts by a membrane. The succeeding circle has suffered further change, the wings of the little leaf, and the membrane, having quite disappeared. The form, on the other hand, is somewhat less elongated, and the seed-rudiment at the back shows itself more distinctly, while the little protuberances, which it bears, are more conspicuous. These two series appear to be either not at all, or only imperfectly, fertile. To these succeeds the third series; it has the authentic, strongly curved form, with a completely fitting coat, fully developed in all its variegation of ridges and excrescences. Once more we see here a vigorous contraction of an expanded leaf-like member, induced through the inner activity of the seed, just as we previously saw the petal contracted through the influence of the anther.

XII. RECAPITULATION AND TRANSITION

§ 84

And thus we have followed in the steps of Nature as scrupulously as we may; we have accompanied the outward form of the plant in all its transformations, from its development out of the seed, until the seed arose again; and without pretending to disclose the first springs of Nature's action, we have directed our attention to the manifestation of the forces whereby the plant gradually transforms one and the same organ. In order not to lose hold of the thread which we have once grasped, we have throughout considered the plant only as an annual, and we have noticed only the transformations of the leaves associated with the nodes, and have derived all forms from them. But, in order to give this essay the necessary completeness, we must now speak of the *buds* which lie concealed beneath each leaf, and develop under certain conditions, while, under other circumstances, they apparently disappear entirely.

XIII. CONCERNING THE BUDS AND THEIR DEVELOPMENT

§ 85

Nature bestows on each node the power to produce one or more buds. This happens in the neighbourhood of the leaves investing it, which appear to prepare for the formation and growth of the buds, and to cooperate in these processes.

§ 86

Upon the successive development of one node from another, and the formation of a leaf at each node with a bud in its neighbourhood, depends the first simple, gradually progressive reproduction of vegetables.

§ 87

It is well known that the activity of such a bud has a great similarity to that of the ripe seed; and that often in the bud, still more than in the seed, the whole form of the future plant may be recognised.

§ 88

Although a point from which a root will originate cannot be observed in the bud with equal facility, still it is really present there, as in the seed, and develops rapidly and easily, especially under moist conditions.

§ 89

The bud needs no cotyledons, since it is in connexion with its mother plant, which is already fully organised, and out of which, so long as it is in union with it, it obtains sufficient nourishment. If the bud is separated from its parent, it draws its supplies from the new plant on which it is grafted, or if, as a branch, it is planted in the earth, through the roots which are promptly produced.

§ 90

The bud consists of nodes and leaves, more or less developed, which are able to carry the future growth further. The lateral branches, which spring from the nodes of plants, may be regarded, then, as individual plantlets which take their stand upon the body of the mother, just as the latter is fixed in the earth.

§ 91

The seed and the lateral branch have frequently been compared and contrasted, and especially with so much insight and accuracy not long ago, that we may content ourselves with referring to this work with unconditional assent[136].

§ 92

We will cite only this much: that, in highly organised plants, Nature distinguishes buds and seeds clearly from one another, but, if we descend to the less complex, the distinction between the two seems to vanish, even to the sight of the keenest investigator. There are indubitable seeds and indubitable gemmae; but the point at which the truly fertilised seeds (isolated from the mother-plant by the operation of the two sexes) coincide with the gemmae (which are directly derived from the plant and detach themselves with no obvious cause) may indeed be apprehended by the intellect, but in no way by the senses.

§ 93

This being well pondered, we may venture to infer that the seeds — which are distinguished from the buds by their enclosed condition, and from the gemmae by the evident cause of their formation and detachment — nevertheless are closely related to both.

136. Gaertner, *De fructibus et seminibus plantarum.* Cap. I. [§ 92 also relates to this work by J. Gaertner. On gemmae *see* vol. I, Stuttgart, 1788, *Introductio generalis,* Cap. I, p. xi, etc. (A.A.)]

XIV. FORMATION OF COMPOUND FLOWERS AND FRUITS

§ 94

We have hitherto sought to explain simple flowers, as likewise seeds which are enclosed in seed-vessels, through the transformation of nodal leaves. It will be found on closer investigation that in this case no buds develop — indeed the possibility of such a development is completely annulled. But in order to interpret both compound flowers and collective fruits borne around a single cone, a single spindle, a single disc, and so forth, we must call to our aid the development of buds.

§ 95

We frequently notice that stems, without preparing for some time, and holding themselves in reserve for a single flower, produce their flowers nodally, and often proceed thus continuously to their apex. But the phenomena thus displayed may be explained on the theory proposed above. All the flowers which develop from lateral buds are to be regarded as entire plants, which are set in the mother plant, as the mother plant is set in the earth. Since, under these circumstances, they receive purer saps from the nodes, so even the earliest leaves of the branchlets are indeed much more highly perfected than the first leaves of the mother plant which succeed the cotyledons; so much so that the formation of calyx and flower is often immediately possible.

§ 96

These same flowers, which are developed from lateral buds, would with increased nutrition have become branches, and would have experienced, in like manner, the fate to which the mother-stem, being in the same case, is obliged to submit.

§ 97

As now from node to node flowers of a similar kind develop, so we notice the same changes of the stem-leaves as we observed above in the gradual transition to the calyx. These stem-leaves gradually contract more and more, and finally dwindle almost completely. Since they then diverge more or less from leaf form, they are given the name of bracts. Correspondingly the stem becomes slenderer, the nodes become more closely set, and all appearances noticed above may be again traced here, except that no sharply defined inflorescence follows at the end of the stem, since Nature has exercised her right already from bud to bud.

§ 98

As we have now fully considered a stem adorned with a flower at each node, we shall be able to interpret a *collective inflorescence* quite easily, provided we call to our aid what has been said above about the origin of the calyx.

§ 99

Nature forms a *common calyx* from *many* leaves, which she crowds upon one another and collects round an axis. With the same strong growth impetus she modifies *an elongated stem,* as it were, in such a way that *all its* *buds are produced at once in the guise of flowers, thronged together in the closest possible proximity;* each floret fertilises the seed-vessel already prepared below it. In this monstrous crowding, the nodal leaves do not invariably disappear; in the thistles the bract faithfully accompanies the floret, which develops from its associated bud. To illustrate this paragraph, the structure of the teasle (*Dipsacus laciniatus* L.) should be examined. In many grasses, each flower is accompanied by such a bract, which in this case is called the glume.

§ 100

In this way it will become apparent to us how it is that *the seeds developed by a composite flower are genuine buds, perfected and elaborated through the operation of the two sexes.* If we hold fast to this conception, and consider in this sense the growth and fructification of various plants, personal observation of a comparative kind will best convince us.

§ 101

It will then indeed not be difficult for us to explain the fructification of enclosed or exposed seeds, often collected round an axis, in the middle of a single flower. For it is all the same whether a single flower surrounds a complex fructification — the concrescent pistils absorbing the generative saps from the anthers of the flower and imbuing the seed with them — or whether each seed possesses its own pistil, its anthers, and its own corolla.

§ 102

We are convinced that with some practice there is no difficulty in explaining the multifarious forms of flowers and fruits in this way. It will admittedly be necessary for this purpose to operate with the conceptions of expansion and contraction, of compression and anastomosis, established above, as easily as with algebraic formulae, and to know how to use them in the right places. Now much depends upon the accurate observation and comparison with one another of the various stages which Nature follows, as well in the formation of genera, species, and varieties, as in the growth of a single plant; hence a collection of illustrations, arranged in order for this end, and an application of the botanical terminology of the various plant members, purely from this point of view, would be desirable, and certainly would not be without use. Two examples of proliferated flowers, giving strong support to the theories adduced, will, if demonstrated to the eye, afford crucial instances.

XV. PROLIFERATED ROSE

§ 103

All that we have hitherto sought to comprehend with the power of the imagination and intellect alone, is revealed with the greatest clearness in the example of a proliferated rose. Calyx and corolla are arranged and developed round the axis, but there is no *growth-inhibited*[137] seed receptacle in the centre, with the male and female reproductive organs placed *in orderly sequence* on it and around it; instead of this, the stalk, half *reddish* and half *greenish, elongates* again, while smaller petals develop upon it *in succession.*

137. This expression is used for GOETHE's "zusammengezogen". (A.A.)

These are dark red and folded on themselves, and some of them bear traces of anthers. The stem goes on growing, and prickles are seen on it again. The coloured petals which follow are spaced apart; they become smaller and merge before our eyes into partly red and partly green stem-leaves. A succession of regular nodes is formed, from the buds of which arise little rosebuds, which are, however, imperfect.

§ 104

This example gives us thus a visible proof of the considerations previously advanced; namely that all calyces are floral leaves, only united by their margins. For here the calyx, regularly arranged round the axis, consists of five completely developed compound leaves of three or five leaflets, just like those that are borne by the branches of roses at their nodes.

XVI. PROLIFERATED PINK

§ 105

After we have studied this phenomenon carefully, another, which is to be observed in a proliferated pink, will seem to us almost more remarkable. We see a complete flower, the calyx of which has a double corolla above it, terminating in the midst with a seed-capsule, which is, however, imperfect. From the sides of the corolla, four complete new flowers develop, separated from the mother-flower by means of stems with three or more nodes; like the mother-flower, they have calyces, and are doubled, but not so much by means of individual petals as, either by means of corollas, the claws of which are concrescent, or, more usually, by means of petals, which are united in branchlet form, and clustered round a stalk. Notwithstanding this monstrous development, the filaments and anthers are present in some. The seed-vessels with styles are to be seen, and the placental region[138] has again grown out into leaves. In one of these flowers the seed-envelopes[139] were associated into a complete calyx, containing, in its turn, the rudiment of a complete double flower.

§ 106

We have in the rose a flower, as it were, half perfected, out of the centre of which a stem again shoots forth, bearing on itself new stem-leaves. So we find in this pink that — in addition to a normally formed calyx, a complete corolla, and *a pistil in the very centre — buds develop from the region of the petals,* and display actual branches and flowers. Both cases then show us that Nature, in the ordinary course, carries growth to a conclusion in the flower, and as it were sums it up, so that — in order the more quickly to reach the goal through the formation of seeds — she puts a stop to the possibility of an indefinite and gradual progression.

XVII. LINNAEUS' THEORY OF ANTICIPATION

§ 107

If I have stumbled here and there on this road, which one of my predecessors, who sought it moreover under the guidance of his great teacher,

138. This expression is used as a possible equivalent for GOETHE's "Receptakel der Samen". (A.A.)
139. The word "Samendecken" used here is translated "arilles" by SORET. (A.A.)

describes as full of terrors and perils[140]; if I have not levelled it sufficiently; nor succeeded in sweeping away all obstacles for my successors: I still hope not to have undertaken this labour fruitlessly.

§ 108

It is now time to take into consideration the theory which Linnaeus proposed for the interpretation of these very phenomena. The observations which prompted the present essay could not elude his keen glance. And if we are able to pass beyond the point at which he halted, we owe it to the common efforts of so many observers and thinkers, who have cleared away various impediments and have dissipated many prejudices. An exact comparison of his theory and that set forth above, would delay us too long. Experts will easily make the comparison for themselves, and to render it clear to those who have not previously attended to the subject, would involve too much detail. We will only indicate shortly what it was that prevented Linnaeus from progressing further and reaching the goal.

§ 109

He made his observations especially on trees — those complex and long-lived plants. He noticed that a tree in a large pot, supplied with excessive nourishment, produced branch after branch for several years in succession, while the same tree, cultivated in a smaller pot, rapidly brought forth flowers and fruit. He saw that the successional development in the former, suddenly became telescoped in the latter. Hence he called this process of Nature *Prolepsis,* an *Anticipation,* since the plant seemed to forestall six years in passing through the six steps to which we have alluded above. And so he worked out his theory in relation to the buds of trees, without paying any special regard to annual plants, since he must indeed have observed that to them it was less applicable. For according to his doctrine one needs to suppose that each annual plant must, intrinsically, have been destined by Nature to grow for six years, and that it all at once anticipates this long period of time in reaching the stage of flower and fruit, and thereupon dies.

§ 110

We, on the contrary, have first followed the growth of the annual plant; starting from this point, the application of the argument to perennial plants is easily made, since a bud shooting forth from the oldest tree is to be regarded as an annual plant, even if it develops directly out of a long-existent stem, and may itself be destined to a prolonged life.

§ 111

The second cause which hindered Linnaeus from advancing further, was that he visualised the various concentric zones of the plant body — the outer and the inner cortex[141], the wood, and the pith — too much as parts which acted equally, and were in an equal degree living and essential; and he ascribed the origin of the flower- and fruit-members to these various zones of the stem, since these members, as well as the stem-zones, appear to enclose one another and to develop out of one another; but this was only a superficial observation, which will not endure closer scrutiny. For the outer cortex is not fitted for further development, and in long-lived trees it becomes, towards the outside, an indurated and isolated mass, as the wood becomes hardened towards the centre. In many trees the outer cortex is shed, and in others it may be removed without injuring them in the least. It cannot therefore bring forth either a calyx or any other living part of the plant. It is the second cortex[142] which possesses all the capacity for life and growth. If it is partially destroyed, to that degree growth is interrupted; it is the second cortex which, on careful consideration, we find produces all the exterior parts of the plant, either gradually in the stem, or all at once in the flowers and fruit. But only the subordinate function of producing the petals was ascribed to it by Linnaeus. The important production of the male staminal apparatus fell, on the other hand, to the wood; but it may easily be observed, on the contrary, that the wood itself is brought to a state of repose by its solidification, and, durable as it is, it is incapable of performing vital operations. The pith, finally, is supposed to accomplish the principal function, that of producing the female reproductive organs and a numerous progeny. The doubt which has been cast upon the great importance of the pith, and the reasons upon which this doubt is grounded, are to me weighty and decisive. The style and fruit present merely a superficial appearance of originating from the pith, because these structures, when they first make their appearance, are in a soft, ill-defined, pith-like, parenchymatous condition, and are crowded together just in the centre of the stem, where we are accustomed to see only the pith.

XVIII. SUMMARY

§ 112

I hope that the present attempt to interpret the metamorphosis of plants may contribute something to the solution of this enigma, and may give occasion for additional investigations and deductions. The scattered observations on which it is based have already been collected and arranged in order[143]; and it will soon be decided whether the step which we have here taken constitutes an approach to the truth. We will now as shortly as possible, summarise the principal results of the foregoing discourse.

§ 113

If we consider a plant in so far as it expresses its life force, we see that this force reveals itself in two directions — first, in *vegetative growth,* when it produces stem and leaves, and then in *reproduction,* which is completed in flower- and fruit-formation. If we inspect growth more closely, we see that, since the plant carries forward its existence from node to node and from leaf to leaf as it vegetates, a reproduction may be said to take place.

140. FERBER *in* Praefatione Dissertationis Secundae de Prolepsi Plantarum. [The full reference is FERBER, J. J. (1763): *Prolepsis plantarum, in* LINNAEUS, C., *Amoenitates Academicae,* Lugduni Batavorum, vol. 6, No. cxx, *Praefatio,* p. 365. (A.A.)]

141. "Cortex" is used as a translation of "Rinde", but there is no exact English equivalent for this term, which, in GOETHE's sense, includes epidermis, bark, cortex, phloem, and cambium. (A.A.)

142. GOETHE no doubt included what we now call the cambium in "die zweyte Rinde". (A.A.)

143. BATSCH, Anleitung zur Kenntniss und Geschichte der Pflanzen. Theil I, Cap. 19. [For fuller reference see p. 70 (A.A.)]

This type of generation distinguishes itself, by the fact that it is *successive,* from the reproduction through the flower and fruit, which happens *suddenly;* being successive, it shows itself in a sequence of individual developments. This vegetative force, gradually expressing itself, bears an extremely close relation[144] to that which manifests itself once and for all in a conspicuous reproductive phase. A plant can be compelled, under various conditions, to *vegetate continuously,* while, on the other hand, one can *hasten the flowering phase.* The former result occurs when crude saps flood the plant; the latter when more rarefied forces predominate.

§ 114

When in this way we have named the *vegetative shoots* as representing successive reproduction, and *flower and fructification* as representing simultaneous reproduction, we have, in so doing, indicated the manner in which they both express themselves. A plant which *vegetates,* spreads itself more or less, and develops a stalk or stem; the intervals from node to node are generally noticeable; and its leaves spread out from the stem on all sides. On the other hand, a plant which *flowers* has contracted all its parts; increase in height and breadth is, as it were, arrested; and all its organs are in a highly condensed state and developed in close proximity to one another.

§ 115

When now the plant vegetates, blooms, or fructifies, so it is still *the same organs* which, with different destinies and under protean shapes, fulfil the part prescribed by Nature. The same organ which on the stem expands itself as a leaf, and assumes a great variety of forms, then contracts in the calyx — expands again in the corolla — contracts in the reproductive organs — and for the last time expands as the fruit.

§ 116

This operation of Nature is at the same time bound up with another — the *assembling of different organs round a centre,* according to definite numbers and proportions, which, however, in many flowers may often be, under certain circumstances, much modified and variously changed.

§ 117

In like manner in the *formation* of flowers and fruit an *anastomosis* operates, whereby the extremely delicate fructification parts, closely crowded against one another, are most intimately united, either throughout their whole duration, or only for part of this time.

§ 118

These phenomena of *approximation, arrangement round a centre*[145], and *anastomosis,* are not, however, peculiar to flowers and fructifications. We may, indeed, perceive something similar in cotyledons; and other plant members will give us ample material for similar considerations in the sequel.

§ 119

Just as we have now sought to explain the protean organs of the vegetating and flowering plant all from a single organ, *the leaf,* which commonly unfolds itself at each node; so we have also attempted to refer to leaf-form those fruits which closely cover their seeds.

§ 120[146]

It goes without saying that we must have a general term to indicate this variously metamorphosed organ, and to use in comparing the manifestations of its form; we have hence adopted the word *leaf.* But when we use this term, it must be with the reservation that we accustom ourselves to relate the phenomena to one another *in both directions.* For we can just as well say that a stamen is a contracted petal, as we can say of a petal that it is a stamen in a state of expansion. And we can just as well say that a sepal is a contracted stem-leaf, approaching a certain degree of refinement, as that a stem-leaf is a sepal, expanded through the intrusion of cruder saps.

§ 121

In the same way it may be said of the stem[147] that it is an expanded flowering and fruiting phase, just as we have predicated of the latter that it is a contracted stem.

§ 122

I have moreover at the conclusion of this essay considered the development of the *buds,* and through them have sought to explain compound flowers and unenclosed fruits.

§ 123

And in this way I have laboured to expound, as clearly and completely as I could, an idea which in my eyes has much that is convincing. If, in spite of all, it is still not fully in accordance with the evidence; if fault may still be found with it for some inconsistencies; and if the foregoing manner of interpretation does not seem to be universally applicable: so much the more will it be my duty to note all objections, and to treat this subject more exactly and circumstantially in the sequel, in order to make this way of looking at things more lucid, and to earn for it a more general approval than it can perhaps expect today.

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144. "Verwandt" misprinted "vewrandt" in the first issue of the first edition. (A.A.)

145. This expression is used for "Centralstellung", which is translated "concentrations" by Soret. (A.A.)

146. The translation here given for the early part of this paragraph is made somewhat freely, in order to convey the meaning, which cannot be understood without reference to the previous paragraph. (A.A.)

147. One is tempted here and elsewhere to translate "Stengel" as "vegetative shoot," but to do so would modernise Goethe's phraseology unduly. (A.A.)

THE OPENING OF A HORSE-CHESTNUT BUD (*Aesculus Hippocastanum* L.), PROBABLY AN ORIGINAL SKETCH BY GOETHE. — From SCHUSTER, J. (1924): *l.c.*, fig. 8, p. 100 (*See* p. 80 of text).

SKETCH BY GOETHE, SHOWING AT THE RIGHT, "FOLGE DER KNOTEN" (SEQUENCE OF NODES) AND LEFT, "ZUSAMMENZIEHUNG" (THE CONTRACTION FROM THE STEM-LEAVES TO THE CALYX; ON THIS CONTRACTION SEE P. 75 OF TEXT). — Sophien-Ausgabe, II, 13 (from TROLL, W., 1926): *l.c.*, p. 143. (These and other scribbled notes by GOETHE mentioned on p. 79 of text).

THE METAMORPHOSIS OF PLANTS.

Thou art confused, my beloved, at, seeing the thousand
fold union

Shown in this flowery troop, over the garden dispers'd;
Any a name dost thou hear assign'd; one after another

Falls on thy list'ning ear, with a barbarian sound.
None resembleth another, yet all their forms have a likeness;

Therefore, a mystical law is by the chorus proclaim'd;
Yes, a sacred enigma! Oh, dearest friend, could I only

Happily teach thee the word, which may the mystery solve!
Closely observe how the plant, by little and little progressing,

Step by step guided on, changeth to blossom and fruit!
First from the seed it unravels itself, as soon as the silent

Fruit-bearing womb of the earth kindly allows Its escape,
And to the charms of the light, the holy, the ever-in-motion,

Trusteth the delicate leaves, feebly beginning to shoot.
Simply slumber'd the force in the seed; a germ of the future,

Peacefully lock'd in itself, 'neath the integument lay,
Leaf and root, and bud, still void of colour, and shapeless;

Thus doth the kernel, while dry, cover that motionless life.
Upward then strives it to swell, in gentle moisture confiding,

And, from the night where it dwelt, straightway ascendeth to light.
Yet still simple remaineth its figure, when first it appeareth;

And 'tis a token like this, points out the child 'mid the plants.
Soon a shoot, succeeding it, riseth on high, and reneweth,

Piling-up node upon node, ever the primitive form;
Yet not ever alike: for the following leaf, as thou seest,

Ever produceth itself, fashioned in manifold ways.
Longer, more indented, in points and in parts more divided,

Which. all-deform'd until now, slept in the organ below,
So at length it attaineth the noble and destined perfection,

Which, in full many a tribe, fills thee with wondering awe.
Many ribb'd and tooth'd, on a surface juicy and swelling,

Free and unending the shoot seemeth in fullness to be;
Yet here Nature restraineth, with powerful hands, the formation,

And to a perfecter end, guideth with softness its growth,
Less abundantly yielding the sap, contracting the vessels,

So that the figure ere long gentler effects doth disclose.
Soon and in silence is check'd the growth of the vigorous branches,

And the rib of the stalk fuller becometh in form.
Leafless, however, and quick the tenderer stem then up-springeth,

And a miraculous sight doth the observer enchant.
Ranged in a circle, in numbers that now are small, and now countless,

Gather the smaller-sized leaves, close by the side of their like.
Round the axis compress'd the sheltering calyx unfoldeth,

And, as the perfectest type, brilliant-hued coronals forms.
Thus doth Nature bloom, in glory still nobler and fuller,

Showing, in order arranged, member on member uprear'd.
Wonderment fresh dost thou feel, as soon as the stem rears the flower

Over the scaffolding frail of the alternating leaves.
But this glory is only the new creation's foreteller,

Yes, the leaf with its hues feeleth the hand all divine,
And on a sudden contracteth itself; the tenderest figures

Twofold as yet, hasten on, destined to blend into one.
Lovingly now the beauteous pairs are standing together,

Gather'd in countless array, there where the altar is raised.
Hymen hovereth o'er them, and scents delicious and mighty

Stream forth their fragrance so sweet, all things enliv'ning around.
Presently, parcell'd out, unnumber'd germs are seen swelling,

Sweetly conceald in the womb, where is made perfect the fruit.
Here doth Nature close the ring of her forces eternal;

Yet doth a new one, at once, cling to the one gone before,
So that the chain be prolonged for ever through all generations,

And that the whole may have life, e'en as enjoy'd by each part.
Now, my beloved one, turn thy gaze on the many-hued thousands

Which, confusing no more, gladden the mind as they wave.
Every plant unto thee proclaimeth the laws everlasting,

Every flowered speaks louder and louder to thee;
But if thou here canst decipher the mystic words of the goddess,

Everywhere will they be seen, e'en though the features are changed.
Creeping insects may linger, the eager butterfly hasten,—

Plastic and forming, may man change e'en the figure decreed!
Oh, then, bethink thee, as well, how out of the germ of acquaintance,

Kindly intercourse sprang, slowly unfolding its leaves;
Soon how friendship with might unveil'd itself in our bosoms,

And how Amor, at length, brought forth blossom and fruit
Think of the manifold ways wherein Nature hath lent to our feelings,

Silently giving them birth, either the first or the last!
Yes, and rejoice in the present day! For love that is holy

Seeketh the noblest of fruits,—that where the thoughts are the same, Where the opinions agree,—that the pair may, in rapt contemplation,

Lovingly blend into one,—find the more excellent world.

1797.

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Review / Revue

Goethe and the ABC model of flower development[1]

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Abstract – About 10 years ago, the ABC model for the genetic control of flower development was proposed. This model was initially based on the analysis of mutant flowers but has subsequently been confirmed by molecular analysis. This paper describes the 200-year history behind this model, from the late 18th century when Goethe arrived at his idea of plant metamorphosis, to the genetic studies on flower mutants carried out on *Arabidopsis* and *Antirrhinum* in the late 20th century. © 2001 Académie des sciences/Éditions scientifiques et médicales Elsevier SAS

organ identity / plant development / flower / genes / metamorphosis

Résumé – Goethe et le modèle ABC de développement de la fleur. Le modèle ABC qui supporte le contrôle génétique du développement floral a été proposé il y a une dizaine d'années. Il a été initialement établi à partir de l'analyse de mutants du développement et a été confirmé ultérieurement par l'analyse moléculaire. Cet article retrace deux siècles d'histoire à l'origine de ce modèle: de la fin du 18^{e} siècle, lorque Goethe proposa le concept de métamorphose des plantes, jusqu'à celle du 20^{e} siècle, au cours duquel les études génétiques de mutants du développement floral ont été réalisées chez *Arabidopsis* et *Antirrhinum.* © 2001 Académie des sciences/Éditions scientifiques et médicales Elsevier SAS

identité d'organe / développement végétal / fleur / gènes / métamorphose

1. Introduction

At three in the morning on the 3rd September 1786, Johann Wolfgang Goethe jumped into a coach, assumed a false name, and set off for Italy. Goethe had just turned 37. In his youth, he had achieved great success with the publication of a tragic novel, *The Sorrows of Young Werther*. The book was so popular that a cult industry rapidly grew around it. There were Werther plays, operas and songs; even pieces of porcelain were made showing Werther scenes. In spite of his outstanding literary success, Goethe chose at the age of 26 to serve for a period in the court of Weimar, at the invitation of the Duke. At various times during the next eleven years he assumed responsibilities for the mines, the War Department, and the Finances of the Duchy. However, life in Weimar eventually proved too restrictive and by the time he was 37 Goethe felt impelled to escape incognito to a new environment.

Goethe travelled around Italy for about 20 months [1]. During this time he developed various scientific theories concerning the weather, geology and botany. It may come as a surprise that so famous a poet should have concerned himself with science. Goethe though, had far ranging interests in nature. His scientific work was particularly important to him, and he spent much of his time seriously dedicated to it. The aspect that most concerns us here is an important botanical idea he had during his Italian journey.

2. A unifying theme

To understand Goethe's idea and how he came to it we need to go back a few years to a discovery he made during

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[1]This paper is based on chapter 4 from *the Art of Genes* (1999) by Enrico Coen, with permission of Oxford University Press.

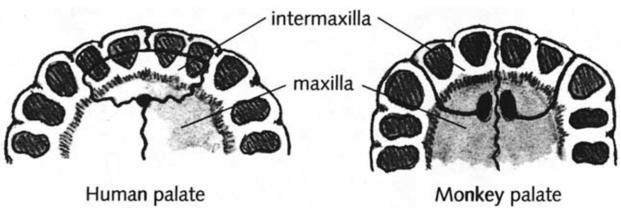

Figure 1. Intermaxillary bone of humans and monkey.

his period at Weimar at the age of 34 [2]. Goethe had been struck by fundamental similarities in the structures of different organisms and became convinced that they were all formed in a common way. One of the most obvious illustrations of this was the similar arrangements of bones in the skeletons of many different animals. For instance, the human thigh bone or femur, had an easily identified counterpart in a dog, bull, lion or any other mammal. However, although such a one to one correspondence could be established for most bones in the body, there were some apparent exceptions. For example, monkeys had a bone in the middle of their face, called the intermaxilla, which appeared to be lacking in man (this bone is also known as the premaxillary). This was often taken to be an important distinguishing mark that separated man from ape. But Goethe's belief in a fundamental unity between organisms encouraged him to look much more closely at the human skull. Eventually he discovered that the intermaxillary bone was also present in man but it had been overlooked because it was tucked away in the upper jaw and was closely joined with other bones (*figure 1*). His conviction in the commonality of forms had led him to discover something that others had missed. He was able to show that rather than being a distinguishing mark, the intermaxillary bone was a connecting link that unified man with other animals.

One piece of evidence that Goethe used to support his identification of the bone came from abnormalities. He noted that in individuals born with a cleft palate, the cleft almost always ran along the join between the proposed intermaxillary region and the surrounding bones, pointing to the intermaxillary bone as being a separate entity. He was using a rare congenital defect, the cleft palate, as a way of more clearly revealing what was normally going on. It was a type of argument he was to employ again in support his botanical theories.

During his time at Weimar, Goethe also developed a profound interest in botany, helped by teachers from the nearby Academy at Jena. The local forests, gardens and estates provided an extensive flora for him to practice and apply his botanical knowledge. But it was only when he went to Italy that a unifying idea about plants started to crystallise, as he explained in an autobiographical essay later in life: "everything that has been round about us from youth, with which we are nevertheless only superficially acquainted, always seems ordinary and trivial to us, so familiar, so commonplace that we hardly give it a second thought. On the other hand, we find that new subjects, in their striking diversity, stimulate our intellects and make us realise that we are capable of pure enthusiasm; they point to something higher, something which we might be privileged to attain. This is the real advantage of travel and each individual benefits in proportion to his nature and way of doing things. The well-known becomes new, and, linked with new phenomena, it stimulates attention, reflection and judgement." [3]

Exposed to a new flora during his Italian journey, Goethe was stimulated to think about their deeper significance. As with his work on skulls, he was searching for a fundamental unity that lay behind the surface of things. He came to realise that there was a single underlying theme to plants, epitomised by the leaf. It seemed to him that the same theme occurred again and again throughout the life of every plant:

"While walking in the Public Gardens of Palermo, it came to me in a flash that in the organ of the plant which we are accustomed to call the leaf lies the true Proteus who can hide or reveal himself in all vegetal forms. From first to last, the plant is nothing but leaf, which is so inseparable from the future germ that one cannot think of one without the other.

Anyone who has had the experience of being confronted by an idea, pregnant with possibilities, whether he thought of it for himself or caught it from others, will know that it creates a tumult and enthusiasm in the mind, which makes one intuitively anticipate its further developments and the conclusions towards which it points.

Knowing this, he will understand that my vision had become an obsessive passion with which I was to be occupied, if not exclusively perhaps, still for the rest of my life". [1]

On returning to Germany, Goethe wrote up his idea in an essay on *The Metamorphosis of Plants*, published in 1790 [4]. He began by describing the typical life of a plant. After germination of the seed, a tiny shoot bearing one or two small leaves, emerges from the ground. As the seedling grows, foliage leaves are successively produced, spaced out around the axis of the stem. At this stage all there is to the plant is stem and leaves (Goethe was not concerned with roots in his account). Eventually, however, the plant starts to form flowers. The question was how flowers might be related to the rest of the plant. Goethe proposed that the different parts of a flower were fundamentally equivalent to foliage leaves; it was just that instead of being spaced out along a stem, the parts of a flower were all clustered together.

A flower typically has several types of organs, clustered around each other in concentric rings or whorls (*figure 2*). Here a whorl means a region or zone of the flower that normally includes organs of one type (this is not quite the same as a botanist's definition but it will be more useful for our purposes). Many flowers have four whorls of organs. The outermost whorl comprises the sepals, usually small green leaf-like structures that protect the flower when it is in bud. Within these is a whorl of petals, usually the most obvious and attractive parts of a flower. Next come the

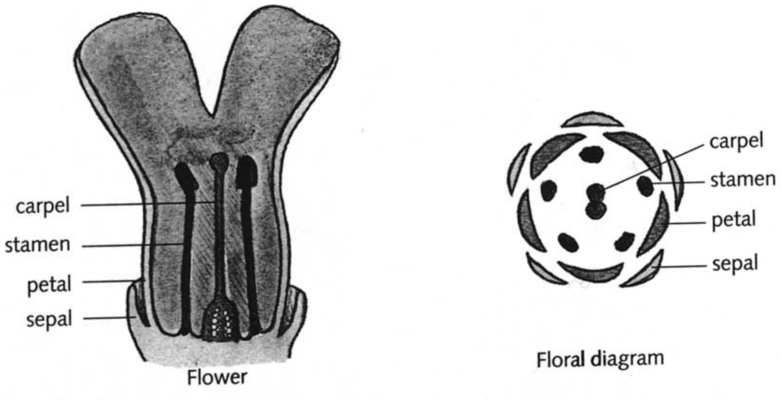

Figure 2. Section through a typical flower (left) showing organs arranged in concentric whorls of sepals, petals, stamens and carpels. The overall arrangement is shown in diagrammatic form on the right.

stamens, the male sex organs that bear pollen. Finally, in the centre are the carpels, the female organs that when pollinated will grow to form fruits containing seeds. This concentric arrangement is shown diagrammatically in the right part of *figure 2*.

Goethe proposed that the floral organs as well as all the foliage leaves, were simply different manifestations of a common underlying theme. This theme could be realised in different ways during plant growth: first as foliage leaves, then as the organs of a flower: sepals, petals, stamens and carpels. It seemed as though an underlying organ was simply passing through a series of different forms. He called this process of change metamorphosis, by analogy with the changes many insects experience (unlike insect metamorphosis where the whole organism undergoes a change, Goethe's version is more abstract and refers to only parts of the organism expressing a change, the various leaf-like organs). Accordingly, above ground level, a plant was made solely of stems and a series of different types of organs based on a common theme.

In support of his claim, Goethe emphasised the many similarities between flower organs and foliage leaves. It is perhaps not too difficult to imagine that sepals are equivalent to leaves because they usually have a very leaf-like appearance. Petals are also not so different from leaves give or take a bit of shape and colour. But what about the sex organs? Apart from simply being plant appendages, the male organs (stamens) do not bear any obvious resemblance to leaves. In the case of the female organs (carpels) we sometimes get a faint leaf-like appearance when they have been fertilised and grow into fruits or pods containing seed: a pea pod could be thought of as a leaf that has been folded lengthways and had the edges stuck together. But what about a tomato? Slice a tomato cross-wise and you will see two or more segments, each containing seed. Is a tomato several leaf-like organs joined together? The tomato segments do not look like leaves, so it is not at all obvious that they are the same sort of thing. As with his studies on the human skull, Goethe turned to abnormalities to help resolve the issue.

3. Helpful monsters

Monstrous flowers are curiously attractive. For years gardeners have selected varieties with extra petals, sometimes called double-flowered forms. Roses, for example, have only five petals in the wild, yet many of the commonly cultivated garden varieties have many more than this. They have been selectively bred for their appeal to humans. In some cases, these abnormal flowers have extra petals at the expense of sex organs so they can no longer reproduce properly by sexual means (many of them are propagated vegetatively, by taking cuttings).

Although considered attractive to gardeners, most botanists viewed these abnormalities with suspicion, as unruly freaks of nature that would not repay further study. The 18th century philosopher Jean-Jacques Rousseau, also a keen botanist, warned young ladies against the dangers of such flowers:

"Whenever you find them double, do not meddle with them, they are disfigured; or, if you please, dressed after our fashion: nature will no longer be found among them; she refuses to reproduce any thing from monsters thus mutilated: for if the more brilliant parts of the flower, namely the corolla [petals], be multiplied, it is at the expense of the more essential parts [sex organs], which disappear under this addition of brilliancy." [5]

Rather than shunning these monstrosities, Goethe realised that they could provide important clues to understanding how flowers normally form. To Goethe, the monstrous flowers with extra petals in their centre suggested that the sex organs could somehow been transformed into petals. Surely this showed that the different organs of a flower were inter-convertible and so fundamentally equivalent. If this conclusion was granted, then the obvious similarity between foliage leaves and at least some of the flower organs (sepals and petals) indicated that all of the organs of a plant should be lumped into the same equivalence group. The various parts of a flower were equivalent to each other and to other types of leaves; they were all variations on a common theme. As further confir-

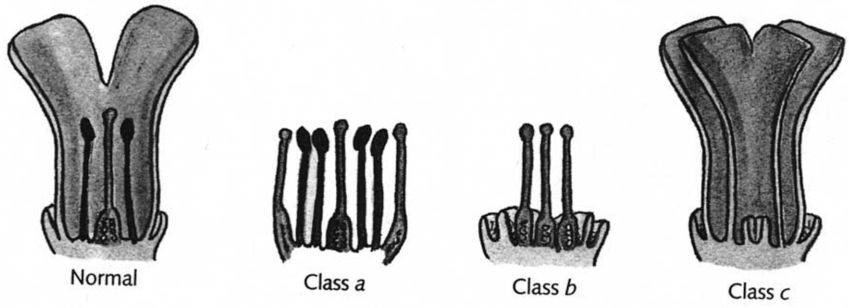

Figure 3. Normal flower compared to three classes of mutant, *a*, *b* and *c*.

mation of this idea, Goethe cited abnormal roses which, instead of sex organs, had an entire shoot emerging from their centre, bearing petals and leaves. Here was a clear illustration of the equivalence between floral organs and leaves.

At the time Goethe wrote his essay on plant metamorphosis, he was not aware that some of the ideas had been arrived at 20 years before him, by Caspar Friedrich Wolff. Wolff was one of the founding fathers of the theory of epigenesis, the view that organisms develop by new formation rather than being preformed in the egg. At the age of 26, Wolff had produced a doctoral dissertation at the university of Halle, *Theoria Generationis*, which was remarkable in its scope and insights for such a young man. It included a range of original microscopic studies on the development of plants and animals. From his plant work, he had been struck by how various parts, such as leaves and floral organs, arise in a similar way at the growing tips of the plant (Wolff was the first to describe the plant growing tip). A few years later, in 1768, he considered this in the light of abnormal flowers:

"one observes that the stamens in the Linnaean Polyandria [species with lots of stamens in their flowers] are frequently transformed into petals, thereby creating double flowers, and conversely that the petals are transformed into stamens; from this fact it may be concluded that the stamens, too, are essentially leaves. In a word, mature reflection reveals that the plant, the various parts of which appear so extraordinarily different from one another at first glance, is composed exclusively of leaves and stem, inasmuch as the root is part of the stem." [3]

Wolff had come to the same conclusion as Goethe: the various parts of a flower could be thought of as equivalent to leaves and thus the whole plant above ground was made up of only stem and leaf-like organs. Later on, Goethe came across this work and acknowledged Wolff's precedence. Nevertheless, Goethe developed the idea of the equivalence of plant organs much more extensively than Wolff, and put it forward more coherently as a theory of plant development.

The reception of Goethe's theory was mixed. Some biologists regarded his ideas as of the utmost importance, and viewed him as a founding father of morphology (Goethe coined the term), the scientific study of shape and form. Others were less generous and saw Goethe's contribution as over-idealistic, trying to make nature conform to his poetic views, rather than being a serious scientific theory based on hard facts: they were the dabblings of an amateur rather than an important scientific effort. As mentioned previously, Goethe's own view was that his work on science was much more than a mere adjunct to poetry. He took his scientific studies very seriously and continued with them for the rest of his life, dedicating much of his later time to the study of optics.

One of the problems with assessing Goethe's botanical ideas has been that until quite recently, his theory could not be followed up experimentally. He was much more concerned with giving a general intuition of how plants were formed than with laying the foundations of an experimental programme of investigation. It was only with the advent of new approaches to the study of flower development that many of his ideas have come to be appreciated again from a fresh perspective. Some of this recent work will be described before returning to consider Goethe's contribution in the light of this.

4. Identity mutants

Many of the flower abnormalities of the type described by Goethe are caused by mutations in particular genes. Their significance became much clearer during the 1980s, when a systematic collection of such mutants was obtained by screening many thousands of plants for exceptional individuals with abnormal flowers. The screens were mainly carried out in two species: *Arabidopsis thaliana* and the snapdragon, *Antirrhinum majus*. To see how these studies helped illuminate the nature of floral monstrosities, three important classes of mutant that emerged from these screens, called *a*, *b* and *c*, need to be described.

A flower normally has four concentric whorls of organs, which proceed from outside to inside in the order sepals, petals, stamens and carpels. In mutants of class *a*, the sepals and petals, which normally occupy the outer two whorls, are replaced by sex organs: carpels grow in place of sepals and stamens in place of petals (*figure 3*). If we were to give a formula for the normal flower as sepal, petal, stamen, carpel, the class *a* mutant would be carpel, stamen, stamen, carpel (the organs that are altered compared to normal have been underlined). In other words, structures that are normally restricted to the inner regions of the flower, the stamens and carpels, have now taken over the outer positions as well. It should be emphasised that this does not involve any organs actually moving or changing position. Rather, the outer organs develop with an altered identity: as carpels and stamens rather than sepals and petals. Each organ grows and develops in the same location as in a normal flower, but the organs in the outer whorls assume the same identity as those that are normally found in the inner whorls.

In mutants belonging to the next class, *b*, the identity of a different pair of organ types is affected: petals are replaced by sepals, and stamens are replaced by carpels; giving the formula sepal, <u>sepal</u>, <u>carpel</u>, carpel (*figure 3*). As with the previous class, two whorls are affected but in this case it is the pair lying between the outermost and innermost whorls, where the petals and stamens normally form.

In mutants of class *c*, the two inner whorls of the flower are affected: stamens are replaced by petals, and carpels are replaced by sepals, giving sepal, petal, <u>petal</u>, <u>sepal</u> (*figure 3*). This is essentially the opposite of what happens in class *a* mutants: inner reproductive organs are now replaced by outer sterile organs. Some garden varieties with extra petals, may belong to this class. In some cases, you can get numerous petals in this way because the normal flower contains many stamens, each of which is replaced by a petal. (It should be mentioned that there are some additional complications with interpreting garden varieties. In some cases the transformations towards petals may not be complete, so you get only a proportion of the sex organs being replaced, sometimes imperfectly. This may be because the mutations have not fully inactivated the relevant gene. A further complication is that class *c* mutants can also have extra whorls within the flower, on top of the usual four, for reasons that are not yet fully understood.)

5. The ABC of hidden colours

What is remarkable about all these mutations is that they seem to result in almost perfect transformations in the type of organ made. We normally think of mutations as messing things up in some way, but here stamens, for example, appear to be replaced by perfectly formed petals. That is why roses with numerous petals in place of stamens can seem very attractive to us: their petals are still well-formed. How is it that a mutation, the inactivation of a gene, can lead to such a neat conversion?

The genes affected in the mutant flowers have a special type of role that can be understood in terms of defaults. To see how this works, a simple model that was designed to account for three mutant classes *a, b* and *c*, needs to be described. This model was arrived at independently by two research groups in the late 1980s [6–8]. There are various ways of presenting this model, but here it will be described in terms of what shall be referred to as hidden colours. It is important to bear in mind that these are abstract, rather than real colours. Their only justification is to provide a convenient way of explaining the different types of floral mutant.

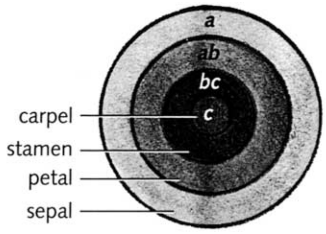

Figure 4. Concentric rings of colour, corresponding to four organ identities in a normal flower.

According to the model, the flower can be symbolised as four concentric rings of hidden colour, corresponding to the four whorls of organs: sepals, petals, stamens, carpels (*figure 4*). These colours are themselves built up from a combination of three basic colours, called *a, b* and *c*. The outermost ring is coloured *a*, the next ring in is coloured with the combination *a* + *b*, third in is *b* + *c* and finally *c* is in the centre. These basic colours and their combinations therefore give a different colour signature to each whorl. Starting from the outer whorl and moving towards the centre, the combinations are: *a*, *ab*, *bc*, *c*, representing the identities sepal, petal, stamen, carpel respectively.

The key feature of the model is that if you remove one or more colours, the identity of the organs will change to a default determined by the remaining colours. Suppose, for example, that colour *b* is missing (*figure 5*). Instead of the colours being *a*, *ab*, *bc*, *c*, the flower will now have colours *a*, *a*, *c*, *c*. Remembering that colour *a* alone corresponds to sepal identity, and *c* alone signifies carpel identity, a flower with rings *a*, *a*, *c*, *c* will have sepals in the outer two whorls and carpels in the inner two, giving the formula sepal, sepal, carpel, carpel. This is essentially what the mutant flowers belonging to the *b* class look like. The model has been expressly designed to account for the *b* class of mutants in terms of the loss of a particular hidden colour: *b*.

The *a* and *c* classes of mutants can be explained in a similar manner, through loss of their respective colours. In this case, though, there is an additional complication. To predict the correct pattern of organ identities, we must assume that the *a* and *c* colours are not completely independent but oppose each other in some way. If for some reason colour *a* is missing, then the *c* colour appears in its place. Similarly, if *c* is missing, the *a* colour will substitute. Thus, in a mutant that lacks *a*, the *c* colour appears in all

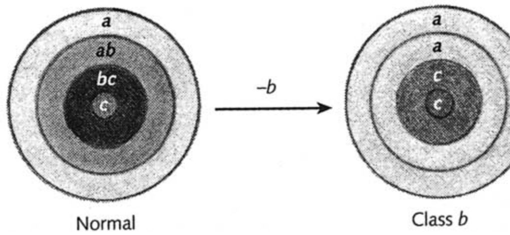

Figure 5. Effect of losing the *b* colour on organ identity.

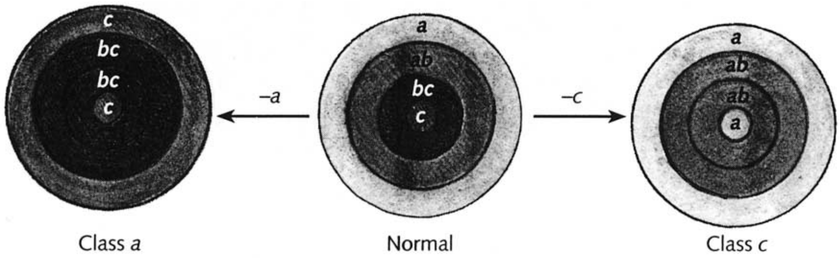

Figure 6. Effect of losing *a* colour (left) or *c* colour (right) on organ identity.

rings but the *b* colour is not affected, giving the colours *c, bc, bc, c* (*figure 6*), left). This would signify a flower with the formula carpel, stamen, stamen, carpel, agreeing with the appearance of class *a* mutants. On the other hand, if we take *c* away, the *a* colour appears everywhere and we get *a, ab, ab, a*, signifying a flower that is sepal, petal, petal, sepal, as observed with class *c* mutants (*figure 6*, right).

The model therefore gives us a set of rules for predicting what type of organs will be made when a distinctive regional quality, symbolised by a colour, is lost. We can even predict what would happen if two hidden colours were missing. Suppose both colours *b* and *c* are absent: the flower would only be left with *a*, and because their is no *c* to oppose it, *a* will appear in all rings, predicting a flower that and only consists of sepals. This is precisely what is seen when class *b* and *c* mutations are combined in the same plant.

6. Identity genes

So far the effects of hidden colours have been described in a rather negative sense, by showing what happens when they are removed. This is because of the reverse way in which we learn the DNA language through mutations, looking at what happens when a particular gene is defective. From a positive viewpoint, we could say that there are a specific set of genes in the plant, what I will call organ identity genes, that are dedicated to producing the set of *a*, *b* and *c* colours. The positive significance of these genes is to ensure that particular colours are made. Mutations that render one of these genes ineffective result in the loss of a colour, and so change the identity of the whorls of organs that develop.

It is important to emphasise that neither these genes nor the colours they produce represent instructions for how to construct a particular type of organ. They simply provide distinctions between regions. It might be thought, for example, that because *a* + *b* results in an organ developing with the identity of a petal, then this colour combination specifies how a petal should be made. To see why this is not the case, look at *figure 7*, which compares flowers from *Antirrhinum* with *Arabidopsis*. The basic organisation of the two types of flowers is the same: they are both comprised of concentric whorls of sepals, petals, stamens and carpels. This reflects a similar distribution of *a*, *b* and *c* hidden colours in concentric rings. Nevertheless, the structure of the various organs is quite different, allowing us to distinguish the two species quite easily. For one thing, the *Antirrhinum* organs are much larger, being about ten times the size of *Arabidopsis* in the linear dimension (for size comparison, see the tiny *Arabidopsis* flower within the circle at the bottom right corner of *figure 7*). But even adjusting for size, the organs obviously have a different structure. The five petals of an *Antirrhinum* flower are united together for part of their length to form a tube. At the end of the tube, the petals become more separate forming five lobes, the lower ones providing a platform for bees to land on and prize open the flower, as shown in the side view of *figure 7*. In contrast, the petals of *Arabidopsis* are more spoon-shaped and are entirely separate from each other. Together, they form symmetrical cross (hence the name Cruciferae, for the family of plants this species belongs to). Similar comparisons could be made for the sepals, stamens and carpels: in each case there are numerous differences in anatomy and shape that distinguish corresponding organs of *Antirrhinum* from *Arabidopsis*. So even though the identity of the organs in both species depends on a similar set of hidden colours, the structure of the organs is different.

The point is that if the *a*, *b* and *c* hidden colours were giving precise instructions on how to make each type of organ, the organs should be identical in both species. If the details of how to make a petal were specified by the *a* + *b* combination, a petal of *Antirrhinum* should look the same as one from *Arabidopsis*. Clearly the colours are not giving instructions of this sort. They merely provide a distinction between different regions, allowing organs with separate identities to develop. It is as if the colours provide a common underlying pattern, but how this becomes manifested in the final organs of a flower can vary greatly according to the species.

In some cases, this variety of forms may go so far as to contradict some familiar notions. We normally think of petals as being the largest and most attractive organs of the flower. Yet in some species, this is a feature of the outer whorl of organs, the sepals rather than the petals. In flowers of the genus *Hydrangea*, for example, the sepals are often much more conspicuous than the petals, so the colourful display we enjoy in garden varieties is almost

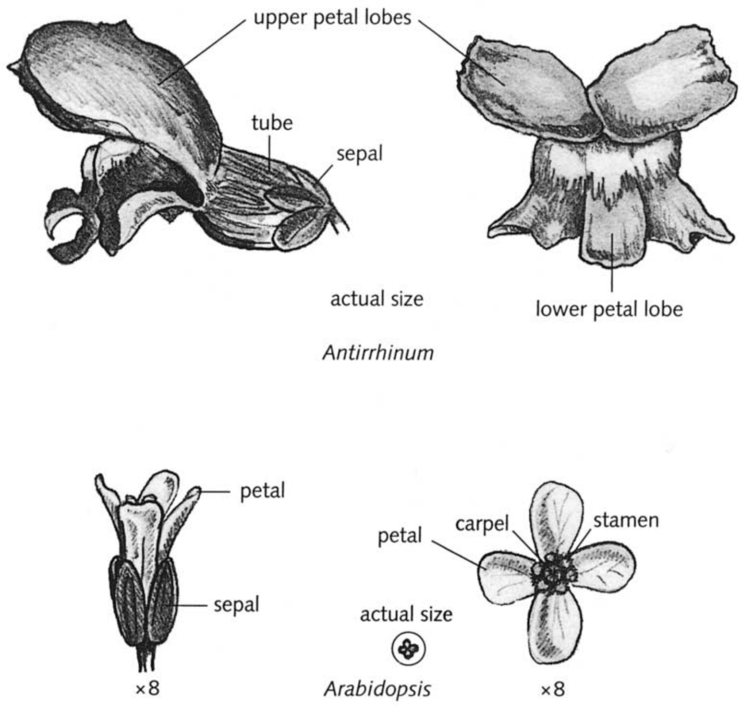

Figure 7. Comparison of *Antirrhinum* and *Arabidopsis* flowers, adjusted to the same size, each shown in side and face view. For size comparison, look at smaller *Arabidopsis* flowers inset within the circle in the right bottom corner.

entirely due to the sepals (*figure 8*). Although the relevant genes from these species have yet to be studied, it is reasonable to suppose that they will have a comparable set of *a*, *b* and *c* hidden colours to those in *Antirrhinum* or *Arabidopsis*. It is just that in the case of *Hydrangea*, this pattern becomes manifested in a different way.

7. A change in outlook

Looking back on Goethe's views from our present perspective, we can see that many of his ideas turned out to be insightful. The idea that the different organs of a plant might be variations on a theme has a modern resonance with the various hidden colours that confer distinct organ identities. In my view, though, Goethe's greatest insight was his clear perception of how the study of abnormalities, what we now call mutants, could be used to understand the normal course of development. As he stated in his essay on plant metamorphosis:

"From our acquaintance with this *abnormal* metamorphosis, we are enabled to unveil the secrets that *normal* metamorphosis conceals from us, and to see distinctly what, from the regular course of development, we can only infer. And it is by this procedure that we hope to achieve most surely the end which we have in view." [4, my italics].

He clearly saw that this reverse form of logic, arguing from the abnormal to the normal, was a valid and important way to proceed in unravelling development. Perhaps it was Goethe's breadth of mind, his desire to understand the underlying unity of nature without too much concern for experimental details, that led him to this remarkable insight. This does not mean that everything Goethe said about plants was gospel. Some of his ideas, like his notion that organs change in appearance due to a sap being gradually purified as plants develop, are of little modern significance. But his clear appreciation of the significance of abnormalities was certainly ahead of its time.

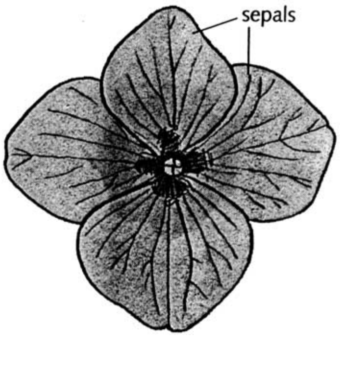

Figure 8. Flower of *Hydrangea* showing large showy sepals.

References

[1] Goethe J.W., Italian Journey, Translated by W.H. Auden and E. Mayer, Penguin Classics, London, England, 1970.

[2] Fink K.J., Goethe's History of Science, Cambridge University Press, 1991.

[3] Goethe J.W., Natural Sciences in General, Morphology in Particular, Vol. 1, No. 1, Translated by Mueller, B. in Goethe's Botanical Writings, University of Hawaii Press, 1952.

[4] Goethe J.W., The Metamorphosis of Plants. Translated by A. Arber as Goethe's Botany, Chronica Botanica 10 (1946) 67–115.

[5] Rousseau J.-J., Letters on the Elements of Botany. Translated by T. Martyn, John White, London, 1807.

[6] Bowman J.L., Smyth D.R., Meyerowitz E.M., Genetic interactions among floral homeotic genes of *Arabidopsis*, Development 112 (1991) 1–20.

[7] Coen E.S., Meyerowitz E.M., The war of the whorls: genetic interactions controlling flower development, Nature 353 (1991) 31–37.

[8] Carpenter R., Coen E.S., Floral homeotic mutations produced by transposon-mutagenesis in *Antirrhinum majus*, Genes Dev. 4 (1990) 1483–1493.