

Over two hundred years ago, the great German thinker Johann Wolfgang von Goethe used his brilliant holistic intuition to grasp the nature of plants and the diversity of their forms, particularly the various manifestations of their most prominent organs: the leaves. Plant leaves, with their obvious symmetries yet unexpected variations, in unusual agglomerations or colossal sizes, inspired Goethe's theory of plant morphology. The shapes of plants, the limits they impose on space and the way they explore it, evoke artistic creations with astonishing profiles, outlines and metallic sheen. Their familiar homogeneous nature is thereby transformed into a plethora of powerful, captivating shapes. Yet Goethe, who was also an artist, regarded leaves as a unifying theme for understanding the extremely varied forms of plants and proposing his scientific theory on their metamorphosis.

PLANT FORMS:
VARIATIONS ON A THEME

The theme: leaves

Goethe revealed his admiration for nature from the time he was a young man, as the author of *The Sorrows of Young Werther*. This tragic novel, which

soon attracted the attention of his contemporaries, inspired poems, plays, operas and even porcelain designs. In this literary work, the writer, who was still under twenty-five, already shows the seeds of his professional transformation that would subsequently turn him into the father of scholars of plant and animal forms and morphology. Fascinated since his youth by the various manifestations of nature and aware of man's belonging to it, he wrote in this novel:

Nature! We are enveloped and embraced by it, unable to emerge from it and yet incapable of penetrating it more deeply. Unbidden and unwanted, she receives us in the circuits of her dance, she herself drifts forward with us until we tire and fall from her arms.

Despite his literary successes, Goethe decided to serve the court of Weimar by assuming various responsibilities and it was then that he developed his profound interest in botany, with the help of his teachers from the nearby Academy of Jena. The local forests and gardens both inspired him and enabled him to practice and apply his theories. But it was not until his trip to Italy that his unifying theory on plant forms began to crystallize.

In an autobiographical essay, he remarks:

...Everything that surrounds us since youth, yet with which we are only superficially acquainted, begins to seem ordinary and trivial to us; it is so familiar and common that we hardly ever stop to think about it. On the contrary, we think that new subjects, with their impressive diversity, stimulate our intellects and make us realize we are capable of feeling pure enthusiasm. They point towards something higher that we may have the privilege of reaching. This is the true advantage of travel and each individual benefits from it in keeping with his nature and way of doing things. The great connoisseur becomes a novice and contact with new phenomena encourages him to pay attention, reflect and have common sense.

Goethe's travels provided him with the inspiration for his theory on the metamorphosis of plants that over two hundred years later, with the recent advances in molecular biology, have been able to be experimentally tested.

Johann Wolfgang von Goethe experienced a crisis of vocation at the age of thirty-seven and decided to change his life. Early on the morning of September 3 1786, he jumped off his sofa, assumed a false name and set off to seek his fortune in Italy, where he immersed himself in the study of nature. Botany became one of his passions. Indeed, one of his contributions in this field was conceived during this trip. Goethe had always been interested in discovering the common features of living creatures.

He was determined to find the fundamental unit underlying the varied surfaces of their shapes. His discovery of various new shapes during his journey to Italy enabled him to corroborate the fact that plants shared a common morphology of construction and that plants had a single unifying theme epitomized by the leaf. It occurred to him that the same theme was repeated over and over again throughout the lifetime of all plants. This idea is summarized in the following quote from Goethe:

As I walked through the public gardens of Palermo, I was struck by the idea that underlying the organ of plants we call the leaf is the true Proteus (the sea god of Greco-Roman mythology who assumes various shapes) that can be hidden or revealed in all plant forms. From start to finish, a plant is nothing more than a leaf, which is so inseparable from the future germ that it is impossible to conceive of the one without the other. Anyone who has had the experience of being faced with an idea that is full of possibilities, either because he has thought of it himself or because he has heard about it from others will know that it creates a tumult and enthusiasm in the mind, that it makes one anticipate its subsequent developments and the conclusions to which it points.

Knowing this, he will readily understand that my vision became an obsessive passion with which I was to be occupied, if not exclusively, then at least continuously for the rest of my life.

The theme of leaves in plants can be divided into sub-themes ranging from the enormous agave leaves that blend into the surrounding space, proving, as Chillida said, that “limits are the true protagonists of space,” to the various forms of palm leaves, split by shafts of light, and of ferns of spiraling veneration, with their capricious shapes. There are also themes that dominate in the circular, floating leaves of flowering water lilies or the banana leaves that mark the limits of white space with dramatic imperfections. We also find the themes of calla lily leaves or other Araceae that resemble structures made from inert materials such as wax, cement or plaster.

The diversity of plant forms led Goethe to the conclusion that the unifying theme in plant variety was the leaf. He developed this idea in depth in *The Metamorphosis of Plants*, which he published on his return to Germany four years after his trip to Italy. This work begins with a description of the typical life cycle of a plant. Following the germination of a seed, a small shoot with one (monocotyledons, such as maize, rice, grasses and palm trees) or two (dicotyledons, such as most of the flowers we know) embryonic leaves (i.e., cotyledons) emerges from the soil. As the seedling grows, leaves are successively produced, spaced out around the axis of the stem. Until that point, the plant merely consists of a stem and leaves. It is interesting to note that Goethe was not in the least concerned with the

plant's root, which is usually the organ that anchors it to the soil and through which it absorbs nutrients and water although in most cases it remains hidden underground. In some plants, such as mangroves, the roots are visible in astonishing formations that support the latter on riverbanks.

In his description of the life cycle of plants, Goethe went on to say, “Eventually, however, the plant begins to form flowers,” and in his view, the various parts of flowers were fundamentally equivalent to leaves, except that, rather than being spaced out around the stem like leaves, they are compressed. In flowers, the transformed leaves are distributed around concentric rings. Since then, these rings of similar organs in flowers have been known as verticils (whorls).

Variations or floral forms of the plant Proteus

Goethe proposed, then, that flower organs, like the variously shaped leaves, were merely different expressions of an underlying common theme. This theme could be developed in several ways during the growth of plants, first as green leaves and then as the organs of the flower, such as sepals, petals, stamens and carpels, almost as though the same organ simply adopted a series of different shapes during the plants' life cycle. Goethe called this process of change “metamorphosis” by analogy

with the changes many insects experience during their lives. Unlike insects, however, whose entire organism undergoes changes, Goethe's version of metamorphosis is far more abstract and refers solely to the parts of the organism that reflect changes and give rise to the various transformed organs on the basis of a common plan: that of the leaf. According to this theory, the aerial parts of plants are nothing more than the stems and a series of organs based on a common theme, namely the leaf.

To support his theory, Goethe argued that some floral organs were extremely similar to leaves. This is obviously so in the case of sepals and perhaps petals. But in the case of the sexual organs, the "proteus" of the plants is hidden. All plants with flowers, or angiosperms, have four whorls of floral organs. In virtually all of them, approximately a quarter of a million of different species, the whorl of the sepals is located on the periphery of the flower. Inside the sepals lie the petals, generally the most attractive part of flowers and, although leafy, usually colored rather than green. Finally, the two whorls in the center of the flower contain the elements that sustain the reproductive organs and the germ cells, first the male cells, called stamens and then the carpels in the center. The grains of pollen are the male sex cells—something like plant sperm—located in sac-shaped structures (anthers) usually found at the tip of the stamen filaments. In the center of the flower are the carpels, structures

containing ovules or female gametes which, once combined with the male gametes, produce seeds. After fertilization, the carpels are transformed into fruits with seeds inside. Once they are dispersed and germinate again, the seeds repeat the plants' life cycle.

It is difficult to think of stamens and carpels as modified leaves. Take the case of tomatoes, for example. It is hard to envisage this fleshy fruit as one or more modified leaves. If we cut it in half, however, we see that it consists of a series of thick slices wrapped around each other forming various cavities linked to the center of the fruit. Each of these cavities contains seeds. The thick slices inside a tomato are in fact modified leaves, and the walls of the carpels in the rest of the plants with flowers are also modified leaves. This is much more obvious in the case of the fruits of legumes, such as beans, runner beans and peas. Not only because they are green before drying out, like leaves, but because they have a foliar consistency and a clearly-visible central vein of was once a leaf, to which the seeds are attached. This modified leaf folds over on itself to form what is known as a pod.

In support of Goethe's theory, there are modified leaves resembling petals. The flamboyant flowers of the common Poinsettias and Bougainvilleas are not really such; as it happens, the most colorful parts of these "flowers" are modified leaves of different colors: red, purple, orange.... These leaves

surrounding the actual flowers are known as bracts. The leaves that form those striking shapes in the flowering heliconias of rain forests are also bracts. Despite these variants, the evidence that Goethe had of wild forms to support his scientific proposition was limited. We will see now how aberrations in wild forms provided him with the most conclusive data.

*Rousseau and the "enchanted" roses
Or the surrealism of nature*

Wild roses have only five petals. For years, however, roses with many petals have been cultivated for their beauty. These abnormal flowers with extra petals, sometimes at the expense of their reproductive organs, have been bred by gardeners using cuttings and plant shoots for hundreds of years. Yet most 18th and 19th century botanists regarded them as aberrant and hardly worth studying. The 18th century botanist and philosopher Jean-Jacques Rousseau warned young ladies of the dangers of these flowers:

Never play with them if you find them doubled, they are disfigured... nothing of nature remains within them. It refuses to reproduce anything from such mutilated monsters: because if the brightest parts of the flower, the corolla [meaning just the petals in this

case] multiply, they do so at the expense of the most essential parts [the sex organs] which disappear as a result of this addiction to brilliance.

For Goethe, however, these monstrosities were not unworthy aberrations of nature. On the contrary, and ahead of his time, he found crucial evidence for his theory in them. Roses with more than the usual number of petals suggested to him that under certain circumstances, whose nature he was as yet unable to understand, even reproductive organs could be converted or transformed into organs that were more similar to leaves, namely petals. These aberrations showed that the flower's organs were mutually interchangeable and that those that were not so leafy, such as carpels and stamens, could become petals that looked more like leaves.

Despite the support that Goethe found in the wild, aberrant forms of flowers, it was only very recently that his ideas could be experimentally tested. Many of the abnormalities in flowers and other parts of plants are caused by changes or mutations in particular genes. Genes are the basic units of hereditary material, which is why offspring resemble their parents. The analysis of these aberrations and the genes affected is precisely what supports modern scientific practice for understanding the genetic basis of the development of the flower and other complex structures of living creatures.

Although molecular tools have only been avail-

able to scientists for the past thirty years, the variants that underpin contemporary models of the genetics of development were described and named much earlier. A century after Goethe, the English naturalist William Bateson coined the term “genetics”. Regarded as the father of this science, Bateson stated that the study of the variation of living forms was the basis for understanding biological evolution. Bateson described many plant variants, despite being a zoologist. The main classes of variants include precisely those that resemble the *ABC* mutants of flowers. In this type of variants or mutants, the identity of certain parts is altered in both plants and animals. Bateson wrote:

Facts of this kind, so common in plants with flowers, yet in their more extreme expressions, so rare in animals, occupy a place in the study of variation, similar perhaps to that occupied by the prism in the study of light.

Bateson also coined the term “homeosis” to refer to this type of variation in which a member of a serial class assumes the characteristics normally associated with another member. In other words, homeosis occurs when one structure adopts the identity of another, which generally develops or is formed in another place. It is rather like the Belgian painter René Magritte’s *Red Model* in which the shoes take on the identity of the feet, although for the effects

of the painting, this conversion was only partial. The mutant flowers used to decipher floral morphogenesis are also homeotic and in them, organs adopt the wrong identities.

Three types of monstrous flowers with homeotic transformations have attracted the notice of contemporary scientists. These three types, called *A*, *B* and *C*, form the basis of the *ABC* model of floral development which, in simple terms, states that, from the periphery to the center, the combinations of genetic functions that define the four rings of the flower are: *A* (sepals), *AB* (petals), *BC* (stamens) and *C* (carpels). The importance of this simple model is that it predicts how the identities of whorls will change when one of the three functions that correspond to each of the three types of mutants identified fails. If they lack the *B* function, the floral organs’ identity will be provided by the action of the *A* function in the two outer whorls, where only sepals will differentiate. In these *B* mutants, the differentiation of the two internal whorls will be governed solely by the *C* function, and therefore, carpels will differentiate in them. Thus, in these mutants, the floral formula will change to: *A* (sepals), *A* (sepals), *C* (carpels) and *C* (carpels). In the case of the mutants lacking the *C* function, the stamens and carpels are transformed, through homeosis, into petals and sepals respectively. These mutants also lose the determination of the floral meristem and the cells in the center of the flower

continue to divide in order to produce flowers within flowers with sepals and petals. This is precisely the case of the roses that Rousseau regarded as “bewitched”.

This simple model provides us with rules for predicting what type of floral organ will be differentiated in each whorl or ring when one of the regional functions disappears. It even predicts the floral arrangement of the mutants lacking two of the *ABC* functions or even all three. In the mutants lacking the three functions, the flower only has organs that are very similar to leaves. This result certainly supports Goethe’s theory of metamorphosis, since all the floral organs remain in a state that could be described as a default or basal state when they lose the *ABC* functions. This is the state that corresponds to the leaf. Thus, these three genetic functions, whose molecular nature has recently been described, are essential to the differentiation of the flower’s various organs from the basal state that apparently coincides with that of leaves. In order to complete Goethe’s theory, however, one question has yet to be answered. Are the genes underlying these functions, that are apparently essential for the plant to run the development program that produces the flower’s organs, sufficient to turn leaves into floral organs?

The answer is “no”. However, researchers have recently discovered additional genes to the *ABC* which, when expressed at the same time as the lat-

ter in leaves, through the modern techniques of molecular biology, transform the leaves into the various floral organs. Rather like Goethe’s cherished dream! It took two hundred years for scientific and technological advances to catch up with Goethe’s holistic genius.

Goethe’s idea was that all of a plant’s appendices are variations on a single theme. Certainly while sepals, petals, stamens, carpels and leaves may appear to be very different from each other, they share an underlying similarity that we now know depends on the interactions of a series of genes, which in turn “dictate” protein synthesis. Goethe needed a term to refer to the theme that unified the various organs of a plant and he chose “leaf”.

A general term is obviously required to refer to that organ of varied metamorphoses and to be used to compare the expressions of its shape, which is why we have adopted the word “leaf.” But when we use that term, it should be with the proviso that we tend to relate phenomena to each other in two directions. We can therefore say that a stamen is a contracted petal, in the same way that a petal is a stamen in a state of expansion. Likewise, we can also say that a sepal is a contracted leaf of a stem...just as we can say that a leaf from a stem is a sepal.

Goethe used the word “leaf” in an unusual way to refer to the implicit theme behind each organ.

This theme, we now know, is determined by the action of various genes whose activities are combined in various ways to give rise to the formation of different organs. As in Goethe's concept, there is no particular direction. Once the necessary genes are taken into consideration, organs can be compared and exchanged in either direction. Goethe summarized this equivalence by saying that the various organs were variations on a theme; in other words, they were all different types of leaves. Unfortunately, by choosing this term to refer to the underlying theme, he created confusion in certain minds, since we use the same word to refer to one of the variants: the leaves of the stem. But Goethe did not mean leaves *stricto sensu*, the green leaves of stems were an explicit theme on the basis of which all the other organs developed. He was using the term "leaf" to refer, more implicitly, to a theme that was common to both the green leaves of the stem and the flower's organs. This is precisely what has now been proved through experiments in the molecular era. There are a series of genes whose joint functions are expressed in several ways to define the different metamorphic states of Goethe's leaf. The Goethian leaf or implicit theme is expressed in various ways in the different parts of a plant. From this point of view, plant leaves that were the ancestors of plants with flowers should represent other variations of the same theme.

The leaves of ferns, contemporary representa-

tives of certain older lineages that appeared before the lineages now represented by plants with flowers, enable us to abound on the theme of leaves and their variations. Although ferns do not have flowers, they reproduce sexually. This shows that fern leaves are not the ancestral forms that would later give rise to flower organs, as would be implied if one misunderstood Goethe's concept as an explicit theme. Conversely, the leaves or large fronds of ferns are both green leaves and organs that support spores in round structures called sori. These are found on the underside of the fronds or leaves of ferns. Ferns produce the male and female sex cells that fuse to continue the ferns' life cycle. Fern fronds are therefore typical, green, leaves that capture the sun's energy yet at the same time resemble flowers, since they support sex cells. In flowering plants, that evolved later, specialized structures originated for each of these two vital plant functions.

Although we can now transform leaves into petals and petals into leaves, thereby proving Goethe's theory of metamorphosis, this is only the beginning of the understanding of the mechanisms that "translate" the information from genes into plant forms. This is summarized by the name of the model of floral development: we can only understand the *abc*, the essentials. The mechanisms are far more complex and many questions remain unanswered. Let us use an example to ex-

plain this: *ABC* genes belong to a same family of sequences. We have recently discovered that virtually identical sequences characterize the genes that regulate the development of the heart in humans! This result suggests that there are functional restrictions that have preserved the sequence of the genes involved in very different processes over many years. This example shows that understanding the simple nature of molecules, let alone that of the master genes of development, enables us to understand how a flower or a heart develops from a cluster of undifferentiated cells. Understanding the form and evolution of such spectacular creations of nature will be the task of future explorations.

C O R O L L A R Y :

"The limit is the real protagonist of space, just as the present, another limit, is the true protagonist of time."

By way of a title for a corollary, I have borrowed this quote from a lecture by Eduardo Chillida at the International Conference on Sculpture in Dublin fourteen years ago. In Chillida's work, I have glimpsed some of the concepts that Goethe developed in his theories on living forms which could in fact be universal for the creators of artistic works and also of scientific knowledge. Both types of cre-

ators have to cope with the unknown and with matter and its forms, both inanimate and living. In the words of this Basque sculptor:

From space, with its brother, time, under the incessant force of gravity, experiencing matter as a slower form of space, I wonder about what I do not know.

Returning to the theme of limits, this universal theme could well lie behind biological themes. In the end, living forms are nothing more than forms forged by evolution from matter, which, although it lives, reproduces, recombines, inherits, responds to stimuli, dies, and is selected or changes at random from generation to generation, also has and is defined by limits and their interrelations, which are the main factors in time and space. Limits are perhaps what underlies the themes of the diverse display of living forms. Artistic creation also depends on the same matter and, as Chillida says, "Nature is not the basis of an artistic action but the essence and condition that enables it to occur." The same can be said of the evolution of living forms. Form, we know well, is not something that is superimposed but rather something that is generated by matter itself, which reveals itself in it. Form, as Nietzsche states, is for the artist what the non-artist calls content.

Chillida's work is indeed propelled by the impetus of the confrontation of opposites, which com-

plement each other, returning to the unity involved in the transgression of limits. As Chillida says:

I like things that are distinct and clear-cut... with deviations, total changes that create distance and cause these silences or vacuums, whatever you like to call them, in which the form can vibrate [...]. In most of my sculptures, the positive and the negative alternate.

There are other coincidences, in addition to the most obvious one: Chillida professed his admiration for Goethe and dedicated one of his alabaster works to him. Both of them specialized in questions and perception, rather than experience. Chillida expressed this as follows:

The desire to experience, to discover, often makes me work at an uneven pace, which may be due to the fact that I am more interested in experimenting than

experiencing. I also prefer knowing to knowledge. I don't believe in experience. I feel that it is conservative. I believe in perception, which is quite different. It is more risky and more progressive.

Chillida's main interest was perception which, as he said, always acts in the present with one foot in the future, rather than experience, which always does so with one foot in the past.

For scientists, as for artists, every creation emerges from a dark universe that encompasses everything that we do not know. This explains why the exploration of the dark lacks a set route. It also explains one of Eduardo Chillida's searching questions, "Isn't being frequently disoriented one of the essential qualifications of an artist?"

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