On the Origins and Renaissance of Goethe's Morphology

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Summary

The science of morphology proposed by Goethe was initially conceived as both an autonomous and auxiliary discipline within the still emerging field of biology of his time. By tracing morphology back to its origins, some historical aspects of its agenda and development are presented in order to reassess potential contributions of Goethe's morphological approach to contemporary botany. Additionally, I will argue, based on recent studies in floral evolutionary developmental biology (Evo-Devo), that Goethe's morphology is not only at the inception of such research, but also if rightly comprehended, it can be both descriptive and explanatory, since it provides a more process-oriented thinking with its unique notion of form and causality.

Zusammenfassung

Der von Goethe begründete Wissenschaftszweig «Morphologie» wurde ursprünglich in der sich neu entfaltenden Biologie sowohl als autonome als auch als Hilfsdisziplin aufgefasst. Einige historische Aspekte der Morphologie, ihre urprüngliche Agenda und ihre Entwicklung, werden vorgestellt, um potentielle Beiträge von Goethes morphologischem Ansatz für die moderne Botanik abzuschätzen. Ausserdem werde ich – gestützt auf neue Arbeiten aus der evolutionären Entwicklungsbiologie der Blüte – die Ansicht vertreten, dass Goethes Morphologie nicht nur am Anfang dieser Disziplin steht, sondern – wenn sie richtig aufgefasst wird – sowohl deskriptiven als auch erklärenden Wert hat. Mit ihrem besonderen Begriff von Form und Kausalität führt sie zu einem stark prozessorientierten Denken.

Keywords: history of botany, floral morphology, Goethe, process ontology, Morpho-Evo-Devo.

> *"Geschichte der Wissenschaften: der reale Teil sind die Phänomene, der ideale die Ansichten der Phänomene."*
>
> (*Goethe* 1833)

1. Introduction

Since *Albert Wigand's* seminal "Kritik und Geschichte von der Lehre der Metamorphose der Pflanzen" (1846), Goethe's morphological work and its scientific contributions as a whole have been subject of reappraisal by several historians of biology (*Hansen* 1919, *Schmid* 1935, *Arber* 1946, 1950,

Kuhn 1962, *Leonir* 1982, *Jahn* 2000, *Richards* 2002, *Levit et al.* 2015) and Goethean biologists (*Portmann* 1956, *Kranich* 1989, *Suchantke* 2002, *Wirz* 2008, *Holdrege* 2014, *Ginefra Toni & Richter* 2017). However, even though Goethe's morphology has received a considerable amount of attention by Goethean scholars, its conceptual foundations still remain poorly read in modern biology.

In the context of evolutionary developmental biology and phylogenetic research, where development and generative processes of organismal form are taken into account, the Goethean motto: "Form as Formation (*Bildung*) and Transformation (*Umbildung*)" provides morphology with a new meaning. In these terms, morphology has become a keyword among some contemporary biologists and philosophers of biology proclaiming its renaissance in our understanding of evolution (*Müller & Newman* 2003, *Richter & Wilkner* 2014, *Niklas & Kutschera* 2016, *Abzhanov* 2017, *Ledford* 2018, *Minelli* 2018). Moreover, Goethe has been cited by plant developmental geneticists, due to a number of findings that corroborate some of the ideas foreseen in his essay *An attempt to explain the metamorphosis of plants* published in 1790 (*Meyerowitz et al.* 1989, *Coen & Carpenter* 1993, *Bowman* 1994, *Coen* 2001). These findings are those of the ABC Model of flower development. The model explains the control mechanism of identity of floral organs. Some of the authors were surprised that such a model conformed with Goethe's concept of regular (normal) and irregular (abnormal) metamorphosis and his hypothesis that flower organs are transformed leaves (foliar theory). Goethe proposed these ideas more than 200 years ago, and of course, without any kind of molecular tool from plant developmental genetics. In their experiments, plant geneticists found that a triple mutant of *Arabidopsis thaliana* produced flowers bearing only vegetative leaves.[1] This would be an example of abnormal or irregular metamorphosis. Nowadays this type of metamorphosis is associated with the modern concept of homeosis[2], a term introduced by *Bateson* in 1894.

1 Actually Goethe did not mean that a petal, is homologous to a leaf, in a historical sense, but rather in a dynamic-typological one. Leaf and petal are related in the same way that leaves can be also related to shoots (partial shoot theory). *Classen-Bockoff* (2016) pointed out that the ABC model perhaps does not support Goethe's interpretation of the flower. As she wrote: "one should question how far the triple mutant in *Arabidopsis thaliana* indeed confirms the shoot concept of the flower. Does the loss of ABCDE function only affect the development of the lateral appendages or does it rather induce a reversal of the whole flower meristem into a vegetative stage?"

2 Homeosis: the total or partial replacement of one part by another of the same organism.

However, such conclusions in the context of plant molecular biology were developed by overlooking the epistemological and methodological foundations of Goethe's Morphology, since the scientist-poet brought forth some unique notions of form and causality, and his morphological contribution to plant research should not be reduced to only foliar theory in the context of the ABC model of floral organ identity.

Therefore the aim of this paper is, beside celebrating the 200 years of the publication of Goethe's morphological journal "*Zur Morphologie*", firstly to trace back Goethe's original dynamic way of seeing biological form by revisiting the historical-conceptual and empirical foundations of his morphology; and secondly to prospect for its place and role in contemporary research and education in plant biology.

2. The principle of autobiographical form in Goethe's "Zur Morphologie"

Although morphology was already practiced long before Goethe by Aristotle, Theophrastus, Jung, Wolff, and later by De Candolle (*Arber* 1950, *Cusset* 1982, p. 33) the term *Morphologie* and its conceptual framework as an autonomous and auxiliary scientific discipline was established by Goethe in July 1817 in his "Zur Naturwissenschaft überhaupt, besonders zur Morphologie" ("On Natural Science in general, Morphology in particular"). Some months later, the rubric was formally introduced in German academic institutions by *K. F. Burdach* with his publication "Über die Aufgabe der Morphologie" (*Schmid* 1935, *Nyhart* 1995). Therefore, in our present scientific context, one could ask: what was actually new in Goethe's morphological approach which has been recently neglected by modern plant biologists? Goethe would answer this question along the following lines:

> *"In Morphology we propose to establish a science new not because of its subject matter, which is already well known, but because of its intention and method, which lends its principles to their unique form and gives it a place among the other sciences."*
>
> (*Goethe* 1995, p. 57)

There are three keywords in the above cited passage: intention, method and principles. These are, according to Goethe, the core aspects of his morphology that grant its originality in the history of science. At its Goethean inceptions, morphology was first intended to become an autonomous (*selbständige*) discipline among other biological sciences, i.e., "a theory in itself and for itself" (*Goethe* 1995, p. 57). If we do not grasp this unique form given by Goethe to Morphology, we will have difficulties answering

the second question, namely, what is the place and role of Goethe's morphology in modern biology?

In philosophy of biology, the consensus that the necessity of reassessing our modes of thinking about living formations and their evolution by bringing the organism back into the focus of biological research seems to be symptomatic (e.g., *Nicholson* 2015). However such a claim can be traced back to the biological epistemology of *Hans Driesch* (1908 p. 7), in a rather more fundamental sense: *"It is form particularly which can be said to occupy the very centre of biological interest; at least it furnishes the foundation of all biology."*

Actually Goethe's attempt to found a proper *Wissenschaft* of living nature, under the rubric of Morphology, had the concept of form (morphé) at centre-stage in his biological interest. The forms of life, as the philosopher of biology and Goethean scholar Ronald Brady argued:

> *"[…] are not 'finished work' but always forms becoming, and their 'potency to be otherwise' is an immediate aspect of their internal constitution – i.e. of their representative function – and not something to be added to them. Their 'potency' is 'self-derived,' in that it is inherent in their identity with the whole. The becoming that belongs to this constitution is not a process that finishes when it reaches a certain goal but a condition of existence – a necessity to change in order to remain the same. Of course, at some time the leaf or bone loses this capacity – it no longer participates in the continual becoming of its generation and therefore does not remain the same – i.e. does not remain alive".*
>
> (Brady in: *Amrine* 1982, p. 287)

Such notion of form, i.e., form as metamorphosis, is Goethe's solution for integrating in the very same method both the descriptive and explanatory dimensions of his morphology. For Goethe, form is causal and should have an ontological status in biology. As Brady has further argued, "how form can be a 'making' principle rather than a 'thing made' and can be spoken of in language that implies causal efficacy, however, is not a linguistic problem but a conceptual one". Goethe's concept of plant form is based on his principle of *Bildung*, and attempts to follow the changes that lead to and from each plant form, remaining, as he remarks later, "as active and as plastic as the example she [nature] provides us." The aim of such a research approach was to realize how the pattern formation (or the formal law) entered into "the transitory, something which he expected to trace through his own act of cognition, and such *Bildung* constituted his way of participating in nature's activity" (*Brady* 1982).

Goethe's *Metamorphosis of Plants* was his first scientific publication and it did not have any modifications in its two subsequent editions. In the second edition, published in the first issue of his *Zur Morphologie* (1817), Goethe used the same method of investigating nature to present his ideas on metamorphosis, by way of an autobiographical form of account expressed in the subtitle "Erfahrung, Betrachtung, Folgerung durch Lebensereignisse verbunden" of that journal. In such a mode of presentation, Goethe gives us the possibility to retrace the development of his morphological thinking in the content of the "Zur Morphologie". Therefore, to study the history and philosophy of morphological thought also creates an opportunity for striving to make Goethe's unique approach to living form, as well as to scientific thinking in general, better known and understood by the public at large (*Matthews* 1994).

3. The morphological principle of Bildung and its genetic method: a process ontology

In modern plant biology, morphology has been interpreted in either a narrow or a broad sense (e.g., *Sattler* 1978). In the narrow sense, morphology refers only to external form or structure (see, e.g., *Bell* 1991). In the broad sense, it comprises structure at all organizational levels, i.e. the structure of whole organisms, organs, tissues, cells, organelles, molecules and domains. Thus Morphology *sensu lato* includes anatomy and even structural biochemistry. However, regardless of whether morphology is defined narrowly or broadly, *it deals primarily with the change of form over time*, during evolutionary development. Morphology *sensu stricto* does not comprise morphogenesis (the development of form), but rather it is, in its core and origin, the study of morphogenesis itself (*Sattler & Rutishauser* 1997). Goethe had already explicitly made this point at the inception of Morphology by giving the title "Bildung und Umbildung organischer Naturen" to the opening of the first volume of his "Zur Morphologie" (*Goethe* 1817).

The Goethean morphological concept of *Bildung* carries in its core an educational aspect, which invites the morphologist to engage her/his cognitive capacities in an intentional process called "exakte sinnliche Phantasie". Goethe described its meaning in the following words:

> *"If I look at the created object, inquire into its creation, and follow this process back as far as I can, I will find a series of steps. Since these are not actually seen together before me, I must visualize them in my memory so that they form a certain ideal whole. At first I will tend to think in terms of steps, but nature leaves no gaps, and thus, in the end, I will have to see this progression of uninterrupted activity as*

> *a whole. I can do so by dissolving the particular without destroying the impression.*"
>
> (*Goethe* 1790 in: 1995, p. 75)

So in order to grasp the flow of life and its specific qualities in a plant or an animal, we have to work to also make our thinking fluid or process-oriented (*Holdrege* 2005, 2013).

Such a genetic method, which searches for the genesis or origination of organismal form, involves a different philosophical attitude towards biodiversity, and its practice brings forth an aesthetic appraisal (*Steigerwald* 2002). In this view, morphology has its place of birth exactly at the confluence of art and science, a necessary dialogue in present scientific praxis which can enhance methodological awareness in biological research and also provide an epistemological alternative concerning environmental educational issues.

4. Goethe's morphology and floral evo-devo: a continuum?

After having elucidated some of the key aspects regarding the origins and nature of Goethe's morphology, i.e., its epistemological autonomy, it is time to survey its auxiliary role among other contemporary biological disciplines.

Should morphologists and morphology *sensu stricto* be reconsidered at center stage in the synthesis of evolution and development? E.g., *D. Wake* (1982) proclaimed the "renaissance" of morphology in modern biology; *M. Wake* (1992) examined the field of "evolutionary morphology" and recognized five then-current subareas of analysis: functional morphology, biomechanics, ecomorphology, developmental morphology, systematics and phylogenetics of morphology. She predicted integrative evolutionary morphology as a sixth field. *Sattler & Rutishauser* (1997), *Minelli* (2018) and *Rutishauser* (this issue) demonstrated that morphology, understood as a "process morphology", has fundamental relevance to plant evo-devo research. *Stuessy et al.* (2003) proposed a "deep morphology" as a renaissance of the morphological method in plant systematics. *Williams & Ebach* (2008), in their "Foundations of Systematics and Biogeography", traced important morphological concepts in homology and classification from the 19th century to the present through the provision of an anthology of scientific writings from Goethe and other naturalists such as Agassiz, Geoffroy St. Hilaire, Owen, Naef, among others. *Ronse De Craene & Wanntorp* (2011) argued in favor of re-establishing morphology as center stage in contemporary botanical research. They warned about the lack of support and interest for the formation and education of professional morphologists in the vocation of biology and related areas dominated by molecular approaches. *Riegner*

(2013) described a "new ancestor of an archetypal biology" by re-thinking the dynamic way of seeing in Goethe's morphology and its compatibility with the conceptual framework of Evo-Devo, and *Wanninger* (2015) in a similar gesture also proposed a "Morpho-Evo-Devo" approach to molecular Evo-Devo and phylogenomics.

In the present essay, three main topics of floral evo-devo studies, namely, homeosis, heterochrony and synorganization in flowers, will be discussed from a morphological perspective in order to provide a more accommodating framework for rethinking Goethe's conceptual contribution to modern approaches to floral morphology.

4.1 Metamorphosis and homeosis in flowers

Goethe distinguished two main types of metamorphosis: regular (or progressive) and irregular (retrograde) metamorphosis. Regular metamorphosis is illustrated through his whole work by taking the annual plant as a model. By modification of the same organ – the leaf – the plant ascends, through an alternation of expansions and contractions, from the very first node with the cotyledons towards the last node with the carpel development and its subsequent fructification and seed formation. However, in the irregular metamorphosis, a flower, e.g., a rose, modifies its development by producing more petals at the position normally occupied by stamens. These abnormal organs can develop completely into petals or only partially, and in this last case, intermediate forms between petals and stamens arise. About the study of this second type of metamorphosis Goethe wrote:

> *"We shall be able to bring to light what the regular type keeps hidden from view and to distinguish clearly what otherwise we are allowed only to conjecture. It is by this procedure that we have the best prospect of attaining our purpose."*
>
> (*Goethe* 1989, p.32)

However, Goethe's booklet on metamorphosis provided mainly an ontogenetic perspective on flowers, and it is helpful to put it in an evolutionary context, in order to address contemporary questions regarding the relationship between development and evolution of angiosperms. E.g., the concept of irregular metamorphosis is of particular interest in evo-devo because it is closely related (although not identical) to the one of *homeosis* introduced by *Bateson* (1894). In his "Materials for the Study of Variation", Bateson (who also coined the word *genetics*) understood homeosis as *"the assumption by one member of a meristic series, of the form or characters proper to other members of the series"*; such a narrow definition would imply homology

among the members of the series. Leavitt originally used the term *morphic translocation* for the phenomenon designated as homeosis by Bateson, but afterwards he adopted and redefined the term homeosis by giving many examples in plants, which do not necessarily imply homology (*Leavitt* 1909). One example given by Leavitt is the advancing petaloid modification of the calyx of *Ranunculus bulbosus*. In a series of four sepals, the first normal one is green and hairy on the back, while the petal is glabrous and yellow. The other three remaining sepals are progressively invaded by yellowness and glabrouness (and other corolla characters), until all that remains of the sepal's nature in the last sepal is hairiness and slight greenness in the median line of the back (*Leavitt* 1909, p. 41)[3]. *Čelakovský* (1901) also described many other examples of these intermediate formations and called them *anamorphoses*. *Sattler* (1988) interpreted this as a *developmental introgression*.

Later, *Sattler* (1994) defined homeosis broadly, as the total or partial replacement of one part by another of the same organism. Replacement may be partial or complete, and structures replacing each other do not need to be homologous. The question whether two homeotic structures are homologous is superfluous according to *Sattler* (1988), since homeosis includes both phenomena. Such broad definition of homeosis is to be preferred over a narrow one, where replacement must be between two homologous organs, since it allows one to deal with a broader range of phenomena and because it is not always possible to recognize the homology of structures that look very different morphologically (*Ronse De Craene* 2003). The difference between two homeotic structures is seen as a matter of degree because one can recognize a continuous series in between, e.g., a petal and a stamen. Homeosis thus involves structural change as well as a transfer of function between the two organs (*Corner* 1958, *Sattler* 1988, *Kirchoff* 2000). In an evolutionary developmental genetic context, homeosis can also be restricted to the one-to-one replacement of an organ by another (total replacement), such as stamen and petals; and in that case homeosis is synonymous of *homeoheterotopy*, i.e., a homologous transfer of function via heterotopy, in which the expression of genes typical of one structure in another structure constitutes the sharing of genetic identity between those structures (*Baum & Donoghue* 2002).

However, when we focus on some of the contemporary research in the emerging field of floral evolutionary developmental morphology (*Ginefra Toni* 2017), the definition of Sattler is considered much broader, since it

3 Despite the words used by Leavitt (reproduced here), the four sepals are just a morphocline and do not occur as a series in the calyx of the same flower.

allows the inclusion of partial transfer of genetic identity, i.e., mixed homology (*Ronse De Craene* 2003), thus expanding Goethe's foliar theory into a more encompassing meaning. E.g., petals are a relatively recent evolutionary novelty in angiosperms (*Endress* 2006). The question of their morphological and phylogenetic origin is also debated. The classical theory, which was later supported by the ABC model, suggests a distinction between bracteopetals and andropetals (e.g., *Hiepko* 1965), i.e., it implies that petals can either have a bract-derived origin or are derived from staminodes, respectively. It also implies that core eudicots have basically stamen-derived petals. However, more recent research shows that petal origins are highly diverse in core eudicots with little indication for a staminodial origin, except for a few clades, such as Rosales and Caryophyllales, where petals have been previously lost (*Ronse De Craene* 2007, *Ronse De Craene & Brockington* 2013). It has been suggested that the evolution of the perianth in Rosaceae may have occurred through a process of homeosis, where the upper outermost stamen primordia were transformed into petals (*Ronse De Craene* 2003).

The same hypothesis was tested in the case of a probable secondary lost of petals within the wind-pollinated tribe of Rosaceae: the Sanguisorbeae (*Ginefra Toni* 2017). It was shown that in this group, the petal was lost developmentally through two different processes: homeosis (in the narrow sense) and total loss. Despite having lost their petals, flowers of the subtribe Sanguisorbinae were able to reinvent "petalness" in manifold ways. One fascinating example is provided by the species *Sanguisorba hakusanensis*. The total suppression of the formation of petal primordia in the second whorl of the perianth of *S. hakusanensis* could be interpreted as a compensation or developmental trade-off, since the lack of petals is balanced by a strong petaloidy in the remaining floral organs. Therefore, petals have been lost, but flowers have the potential to re-create the same quality and function by other means such as morphic translocation (sensu Leavitt), developmental introgression (sensu Sattler) or homeoheterotopy (sensu Baum & Donoghue). In other words, the morphogenetic processes active in the second whorl of these flowers were lost, but as compensation they have been *internally* (i.e., ontogenetically) *reorganized* into the other whorls. By so doing, another shift in their mode of pollination (a back and forth between wind- and insect pollination), or as Ron Brady put it "*their potency to be otherwise*", became evident in this group of "metamorphosed roses".

4.2 Archetypal form, heterochrony and floral synorganization

Goethe's notion of the plant archetype is a dynamic one, since it is intrinsically intermingled with the idea of metamorphosis, i.e., the modification of the same organ into a variety of forms. Archetype, in this sense, is not a

structural and static schema, but a condition of existence, or in other words, the necessity of a given form to change in order to remain itself. However, it can only be manifested by way of two other interconnected principles in the plant's ontogeny: polarity and intensification. Polarity, in this sense, means the successive modular alternation of opposite formative qualities (e.g., expansions and contractions) during plant organogenesis which leads naturally to its own enhancement or intensification in what one, in the act of perception, calls flower and fruit. In the formation of a flower, the organs that have been previously formed in this successive alternation of expansions and contractions, are now more or less simultaneously formed by a contraction in the floral axis and calyx, an expansion in the corolla together with a contracting androecium. In fruit formation, the gynocieum is expanded in its ovary(ies) at the same time as seed formation takes place inside of it, as the maximum actualization of that very conceptual breathing of polarity and intensification. The beginning is an end and the end is a beginning. Philosophically speaking, Kant called this process *intrinsic teleology*. Life has an end in itself and not for something else. In other words, life means autonomy. Organisms are self-determined and only by such self-determinacy they can be modified by something external.

Goethe was highly aware of this teleological problem proposed by Kant, and through the development of his morphological thinking, the poet-scientist was able to uncover a dialectical pair of concepts (Archetype-Metamorphosis/Polarity-Intensification) by a thorough reflection of the processes of transformation during angiosperm ontogeny.

Things become more difficult when one tries to see this rationality in a more complex level of phenomena such as flower evolution. However, the flower morphologist Peter Endress has drawn our attention to two fundamental and contrasting principles of floral diversification and stability: (1) the progressive elaboration of flowers especially by *synorganization* and fixation at certain formative levels and the opening of flexibility at new formative levels, and (2) simplification by *reduction* and loss of fixation by reversals (*Endress* 2011). They appear to work together as a kind of polarity and intensification but now act as key innovations on an evolutionary level.

Synorganization is thus a major evolutionary developmental trend responsible for the increase of complexity and integration of floral organs, resulting in functionally fitting positions of all floral organs and covariation of fitting parts. Such new complex structures or "hyperorgans" in synorganized flowers can be found especially in the highly nested monocots and eudicots (e.g., the gynostemium in orchids and the gynostegium in asclepias). An essential precondition to synorganizational processes in flowers is the transition of the spiral anthotaxis to a whorled one, leading consequently

to an increased proximity (tangential and radial) of the organs and interaction among them (*Endress* 2015). And in order for this transition to occur, a change in developmental timing of the shoot apex meristem and of the initiation of the floral organs (heterochrony) is necessary.

At this point Goethe's morphology can be very fruitful since another concept, that of *subordination,* can shed light on the phenomena of synorganization in the evolution of flowers. In one of his introductory essays of the first issue of his "Zur Morphologie", Goethe presents this new morphological concept in the following manner:

> *"Each living creature is a complex, not a unit; even when it appears to be an individual, it nevertheless remains an aggregation of living and independent parts, identical in idea and disposition, but in outward appearance identical or similar, unlike or dissimilar. These organisms are partly united by origin; partly they discover each other and unite. They separate and seek each other out again, thus bringing about endless production in all ways and all directions.*
>
> *The more imperfect a creature is, the more do these parts appear identical or similar to each other and the more do they resemble the whole. The more the creature is perfected, the more dissimilar its parts become. In the first case, the whole is more or less identical to the parts.; in the second case, the whole is dissimilar to the parts. The more the parts resemble to each other, the less they are subordinated to each other. Subordination of the parts betokens a more perfected creature."*
>
> (*Goethe* 1817 in: 1989, p. 24)

Subordination, in this sense, is a parameter for perfection, and here, the latter means the degree of dissimilarity and integration of parts in relation to the whole, in other words, the capacity for self-transformation, determination and diversification. Now I would like to give some examples of how this concept of subordination can been portrayed in the evolution of the perianth in flowers:

Two common and extreme types of perianth organization form an interesting polarity in the floral morphospace. In the first type, a polymerous perianth is composed of very similar parts (called tepals), variable in number, and the parts are initiated in a spiral sequence. This type of perianth is found in basal angiosperms, e.g., *Illicium* and *Magnolia*. In the second type, the perianth is mainly dicyclic (two-whorled), with elements occurring in fixed numbers – mostly in four or five – with elements from differentiated categories: the outer ones called sepals and the inner ones called petals. This type of perianth is found in the more phylogenetically derived eudicots, e.g.,

the rosids and asterids. It is generally assumed that whorled flowers have been derived from spiral ancestors by a progressive cyclisation and reduction of organ numbers. A two-whorled perianth of undifferentiated parts called perigone evolved in the monocotyledonous flowering plants and is associated with trimery. A two-whorled perianth in which the first whorl is initiated in a spiral sequence is found in some rosids (e.g. *Rosaceae*). The latter intermediate organizational types share both the phylogenetically primitive and derived character states. Furthermore, there is an evolutionary trend of increased differentiation, complexity and subordination of the parts, creating in some cases extremes of synorganization and change to monosymmetry, e.g., *Salvia*, *Lamiaceae* and other Sympetalae. Reversals by way of loss of fixation occur as well, e.g. in *Cactaceae*, (which is an eudicot); the perianth is again polymerous and spirally arranged.

Such disparities in the floral morphospace, created by polymerization vs. oligomerization, differentiation vs. undifferentiation, spiral- vs. whorled arrangement and poly- vs. monosymetry, seem to appear recursive within some clades as the taxonomic resolution becomes coarser (e.g., the labile *Ranunculaceae*), and thus, they can be considered compatible with Goethe's dynamic notion of archetypal form. In this sense, I agree with Rudolf Steiner, who called Goethe "*the Kepler and Copernicus of the organic world*", since his morphology contributes above all towards *new ways of thinking biological organization* in modern biology.

Conclusions

In the transition of the 20th to the 21st century, morphology has once again become a keyword among biologists and Goethe has been often cited in developmental genetic research. However, such studies were not published without sacrificing the original and unique epistemological notions of form and causality in Goethe's morphology. From a Goethean perspective, comparative morphology is not only descriptive but also explanatory, and complements molecular approaches in the study of Evolutionary Developmental Biology (EVO-DEVO).

Thus, by developing its method in adequacy with the object of study, morphology aims to contribute towards *a rational organicism* in order to investigate the dynamic-causal nature of organisms, i.e., the dialetics between archetypal form (robustness) and metamorphosis (plasticity), and its consequences in the generation of evolutionary novelties and biological organization. This approach, known as Evolutionary Developmental Morphology (MORPHO-EVO-DEVO), is of special concern not only for academic researchers but also for high school teachers engaged in biology education.

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