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# WHITHER MORPHOLOGY?[1]

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I am deeply conscious of the honour you have done me. I express my sincere thanks to the Executive Council and Members of the Indian Botanical Society for the award of Vishwambhar Puri Medal.

Morphology is defined as the study of form and structure. Today, it no more enjoys the commanding position it once held. Its position is such that it does not appeal much to the younger generation of botanists. Since the advent of physiology and genetics, it has failed to attract students of botany. So it is not only necessary for the morphologists alone but also those engaged in other disciplines of botany to give a deep thought to the present sorry state of morphology and to make an attempt so that it becomes again the centre of attraction, because without the study of morphology, there cannot be any approach to evolution. In fact, Charles Darwin called morphology as the very soul of natural history. So the question arises, "How such a soul of natural history suffer in the later period of 20th century?" The answer lies in the study of botanical history with special reference to morphology.

Agnes Arber (1950) in her excellent thought provoking book, "The Natural Philosophy of Plant Form" and Wardlaw (1952) in his book, "Phylogeny and Morphogenesis" and to some extent Sinnott (1960) in his book, "Plant Morphogenesis" have discussed this subject. All morphologists and even students of other disciplines of botany should give deep consideration to the views expressed in these books.

When we start from the great scientific thinker and philosopher Aristotle, we find that his scope of form was broad and it covered the whole of the intrinsic nature of an organism. The scope of morphology was not limited merely to characters of superficial shape as at present. Even we find today that the adjective 'formal' is considered as mere triviality.

Aristotle says, "The main seat of the nutritive psyche is central plainly to be both in plants and animals. In plants, it is manifested in the phenomenon presented by the germination of seeds and by grafts and cuttings." Theophrastus in his "Historia" while dealing with the general scope of botany, states that one has to take into consideration: (1) parts of plants, (2) their qualities, (3) the way in which their life originates, and (4) the course which their life follows. In modern terms, these objectives can be included under (1) morphology, (2) physiology and biochemistry, (3) the study of reproduction and development, and (4) the study of life-histories.

Let us now survey the period of development of morphology from Grew to Goethe and de Candolle. After the invention of microscope, Grew was the first to undertake a detailed study of anatomy of plants. He published his work in 1672 and 1682. He also took keen interest in the developmental aspect of plants. His work on seedlings particularly those of bean was the first of its kind. In 1675 and 1679,

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there appeared Malpighi's great book, "Anatomie Plantarum" in two volumes. A posthumous volume was published in 1697. In his study, he also laid emphasis on the developmental aspect. He described wheat embryo and the seedling in several stages. He studied the development during the first four days and then at six and eleven days and a month. This means that he recognised the full significance of time element in such segments. But even today when refined techniques and sophisticated instruments are available, a very few embryologists have paid attention to the time element. Both Grew and Malpighi studied not only development of the plant as a whole but also that of the individual shoot. Grew also demonstrated the foliar nature of sepals and petals. Wolff (1768) supported Grew and also considered stamens and pericarp as modified leaves. It should be remembered that his was probably the first statement that all floral parts are foliar in nature. In the words of Agnes Arber, "This thesis is at least a step towards the truth, is suggested by the fact that it has been reached independently by so many botanical thinkers." Althogh Goethe was not aware of the ideas of Grew and Wolff, he put forward more or less similar views in his book on metamorphosis in plants in 1790. He formulated his theory of metamorphosis, in which all the various and divesrse appendages of the shoot in higher plants were regarded as the metamorphosed products of a single fundamental organ, the ideal leaf. His theory made a great impact on the contemporary botanists. He stated, "My only concern was to trace back the separate phenomena to a general fundamental law." It should be noted that Goethe's study went beyond the individual members of the flower. In fact, not only Goethe but de Candolle also thought that there is a common basic scheme of organisation, underlying both the leafy shoot and the reproductive system; but in recent time, this has been repudiated by some. What was Goethe's concept of the organisation type? His type appendage was called by him leaf (Blatt). According to Agnes Arber, for this the term 'phyllome' should be preferred. Like the archetypal plant, the type phyllome is a valid concept if it is used consistently on an abstract plane, but unfortunately this has not been always done.

The work on teratology can be carried out with two objects: (1) the study of abnormalities for its own sake, and (2) tracing the ancestral history by using data on abnormal forms. de Candolle (1827) could think of the regular order lying hidden in abnormalities. Geoffrey Saint-Hillaire (1832-36) studied teratology so as to acquire deeper knowledge of the normal. Hofmeister (1857) added considerably to our knowledge of morphology of mosses, liverworts, ferns, gymnosperms, and angiosperms. His work on higher cryptogams was really a land mark in the progress of botany. His work was not descriptive. He was not content with mere observations of a regular succession of characteristic changes in form and structure that had taken place. He had a keen desire to know how the observed form came to be and to what processes of growth the structural development that he observed, could be connected. He went into the question of the internal and external factors responsible for the specific structural organisation. Sachs (1875) followed him and elaborated his views on causal morphology.

We may think that Hofmeister's objective enquiries and his critical search for relationship between physiological processes and the development of specific form of pattern and the subsequent work of Sachs might have been mainly responsible for the establishment of broad and firm foundation wherein morphology and physiology were inseparable. Had such a broad view prevailed afterwards and carried further, our knowledge about the factors governing the development of form and structure would have been well advanced. But unfortunately, this is not the case. One may ask, "Why?" The answer lies in the impact of Charles Darwin's book, "Origin of Species" published in 1859.

Darwin's book had tremendous influence on the contemporary and later botaanists. This led them to make a comparative study of plants with an object of constructing a phylogenetic system or family tree. They laid emphasis on details of plant structure together with such information that could be obtained from the fossil record. These data were the materials for the comparative studies and for constructing the family or genealogical tree. However, they had inadequate knowledge of the developmental processes. They had no idea about the factors determining form and structure. If a contemporary worker tries to make good this inadequacy, it is likely that he would neglect the phylogenetic aspect. There is relationship of one to the other, although the nature of the relationship may not be often clearly understood. Such an attitude of the post-Darwinian workers caused a very marked swing away from the causal outlook which was characteristic of Hofmeister's later work. They ignored the question of how the observed form comes to be in terms of nutritional, physical and other factors. They only focussed their attention on finding out family relationships on the basis of the observed form and made an attempt on the basis of these data to trace the course of evolution.

The place of general or causal morphology of Hofmeister was taken by the special or comparative morphology. It is true that no study or interpretation of evolution in plants or animals is possible without comparative morphology. But a bad feature of the phylogenetic period was that plant morphology and physiology were mostly considered as separate disciplines. There was a tendency among morphologists including anatomists to give flexible-pseudophysiological explanations of the function and adaptive value of tissues or organs. What they assumed was not tested by experiment. Haberlandt was, however, a notable exception.

Haberlandt's book, "Physiologische Pflanzenanatomie" (Physiological Plant Anatomy) was published in 1884 and the English translation by M. Drummond in 1914. Haberland recognised the physiological basis of different plant tissues having characteristic structural delineations. He made an attempt to find out correlation between these diverse structures and functions. When such correlations become obvious, it then becomes possible to formulate the necessary explanation as to how the plant or its part which acts within the limits of its structural peculiarities becomes more reasonably understandable. His researches have indicated that the study of various cells and tissues of the plant body clearly reveals the fact that the physiological activity is dependent upon the general structure of the organism and individual anatomical characters, just as the special mode of action of every machine is the result of its particular type of construction. Since any specific physiological function seems to an observer to be the aim and object of the correlated structural characters, every experimental proof between structure and function assumes a teleological aspect. At the same time, one must not forget that the value of a teleological explanation depends entirely on the philosophical attitude of its author.

Sometimes, when there is a change in function, functionless characters appear and their occurrence is partly due to the influence of heredity. It does not mean, however, that all the morphological characters that are correlated with the function undergo a change necessarily in such a way. Haberlandt observed that in the organisation of the plant, one and the same tissue system may be capable of construction to several distinct plans, none of which gives an appreciable advantage as compared with the rest. He remarks, "Nature, as it were, takes a pleasure in ringing the changes indefinitely upon the possible variations of structural detail; in this way arises the inconceivable diversity which prevails with regard to the details of anatomical structure." He points out that the two types of structure may be mutually exclusive as regards their occurrence within a group of closely related plants (e.g., Ranunculaceae) or both may occur in the same individual; so there is not even the slightest ground to suppose that the two varieties of structure represent special adaptations. In cases of physiological adaptation, the morphological feature which is being studied—whether a localised structure or an entire tissue system—is assumed to perform a physiological function, that is, to play a definite role in the internal economy of the plant. There also exist numerous ecological or biological adaptations which are developed in connection with many needs of plants in response to the environmental factors such as climate, habitat on the one hand and the animals on the other. He maintains that the recognition of the fact that plants show adaptations in regard to their internal structure is quite independent of the various suggestions and hypotheses which have been put forward to explain the origin of this adaptation. He states that frequently it is impossible to determine the principal function of a tissue with certainty from anatomical evidence alone. In such circumstances, he feels that resort must be had to experiment. He, however, admits that there are many questions regarding the relation between structure and function which do not admit of experimental treatment at all (e.g., cuticular ridges of guard cells). His statement that the physiological experiments expose an organism or a portion thereof, to combinations which are always artificial and often unnatural is noteworthy. This statement applies more especially to the so-called method of *extirpation* which frequently represents the only experimental resource with the anatomist. He considers the comparative and experimental methods of equal value to the physiological anatomist. He wants us not to forget that every cell represents a unit not only in the morphological but also in the physiological sense. It is a functional as well as a structural unit.

In fact, Haberlandt was prompted to undertake the work of physiological anatomy as he was attracted by Schwendener's classical treatise, "Das mechanische Prinzip in anatomischen Bau der Monocotyleen" (The mechanical principles underlying the anatomical structure of Monocotyledonous plants) published in 1874. This treatise showed how it was important to take into consideration physiology while dealing with anatomical characters. It indicated the necessity of a new demarcation and classification of the various tissues with reference to physiological conceptions. But alas ! After Haberlandt, no notable contributions were made in this new branch. Even today, though many research papers have appeared on epidermis, ontogeny and structure of stomata, foliar sclereids, peristome structure in mosses, spore morphology, anatomical changes in seed coat, nodal and floral anatomy, none of them has taken into consideration physiological aspects.

Although attempts to avoid an official split between plant morphology and physiology succeeded at the meeting of the British Association held at Oxford in 1894, it seems that in reality the split still continues. What we, in fact, observe is that the morphologist tells with some over-emphasis but as Wardlaw remarks not without justification, that when he refers to the text books of physiology to get information relevant to his own work, he is disappointed since such books give him almost negligible information. At the same time, the modern physiologist complains that he does not get specific information required by him from the morphological literature. In this connection, Wardlaw remarks, "Moreover, there is a tendency among physiologists to regard the morphologist as a relic of an earlier phase and as a less inventive botanist who is still plodding along in an overlooked field." It is interesting to imagine what would have been the present state of botany if the views of workers like Hofmeister and Haberlandt would have prevailed. Morphology and physiology would have then made an advance, as if symbionts, giving conscious treatment to the same problems in such a way that they would have appeared as the inseparable aspects of the same phenomena. There would have been no such thing as the purely morphological concept. Physiologists with a broader outlook would have applied their mind to a wider field so as to form a more mature background for specialization in the several disciplines of today's botany.

There appeared an excellent treatise by D'Arcy Thompson on "Growth and Form" in two volumes in 1917 with a mathematical approach. In his Preferatory Note to the first volume, he wrote that he had written the book as an easy introduction to the study of organic form, by methods which are the common places of physical science which are by no means novel in their application to natural history but which nevertheless naturalists are little accostomed to employ. He, however, stated, "It is not the biologist with an inkling of mathematics, but the skilled and learned mathematician who must ultimately deal with such problems." He has quoted Kant, "It is nature herself, and not the mathematician who brings mathematics into natural philosophy." Although three editions of D'Arcy Thompson's treatise were published, neither the mathematician nor the biologist paid any noteworthy attention in solution of the problems dealing with growth and form. Recently, Sinnott (1966) in the Compilation of Essays under the title, "Trends in Plant Morphogenesis" presented to C. W. Wardlaw on his 65th birthday, has in his essay, "The Geometry of Life" has focussed the attention to the work of D'Arcy Thompson. He has indicated how a fruitful field is available here for cultivation.

A study of form in both the plants and animals clearly shows that there is an orderly and specific pattern. In other words, there is regularity in protoplasmic activity which is exhibited under the close developmental control. Growth has a geometric basis and we can learn much about this aspect from the work of D'Arcy Thompson and his followers. Some structures can be analysed in terms of geometry. The consideration of absolute size also involves geometry.

The subject of phyllotaxy depends upon mathematical properties. Two parts or dimensions of an organism keep in tune. This fact indicates the unity and integration of the organism. This has been very well demonstrated by D'Arcy Thompson. He has laid stress on the the polarity in development.

Symmetry, another important non-specific factor is considered by D'Arcy Thompson. Symmetry results when the axis of a geometrically homogeneous mass of material modifies the homogeneity in a regular manner.

D'Arcy Thomson says, "Organic evolution has its physical analogue in the universal law that the world tends, in all its parts and particles, to form certain less probable configuration or states. This is the *second law of evolution of the world*, and we call it after Clausias the Principle of *Entropy*, which is a literal translation of Evolution in Greek." He further states, "How far even the mathematics will suffice to describe, and physics to explain, the fabric of the body, no man can foresee. It may be that all the laws of energy, and all the properties of the matter, and all the chemistry of all the colloids are as powerless to explain the body as they are important to comprehend the soul. For my part, I think it is not so."

About his object, D'Arcy Thompson writes, "My sole purpose is to correlate with mathematical statement and physical law certain of the simpler outward phenomena of organic growth and structure or form, while all the while regarding the fabric of the organism, *ex hypothesi*, as a material and mechanical configuration .... one does not come by studying living things for a life time to suppose that physics and chemistry can account for them all."

As regards the terms growth and form, D'Arcy Thompson says, "The terms Growth and Form are to be considered as I need hardly say, in their relation to the study of organisms. We want to see how in some cases at least, the forms of living things, and of the part of living things, can be explained by physical considerations, and to realise that in general no organic forms exist save such as are in conformity with physical or mathematical laws. And while growth is a somewhat vague word for a very complex matter, which may depend on various things, from simple imbibition of water to the complicated results of the chemistry of nutrition, it deserves to be studied in relation to form. Whether it proceeds by simple increase of size without obvious alteration of form, or whether, it so proceeds as to bring out a gradual change of form and the slow development of a more or less complicated structure." I have quoted D'Arcy Thompson with the hope that some of the young botanists would be tempted to read his book and think of entering into this fruitful field. In order to make the science of embryo development precise, the great French embryologist Souèges enunciated laws of embryo development such as law of numbers, law of disposition. In this case, the application of mathematics following D'Arcy Thompson, i.e., analysis of geometric basis of organic form in relation to these laws would really help to make embryogeny more precise.

During the last few decades, there has been extensive botanical research covering various new aspects Special and refined techniques have also been developed and they have helped present botanical workers to a large extent. But in spite of this advance, the fact remains that the process of splitting of branches and labelling them as specialised and separate fields has taken place. At present, the tendency of a botanist is to be labelled systematist, morphologist, anatomist, palaeobotanist, physiologist, ecologist, mycologist, plant pathologist, phycologist, cytologist and geneticist, even in genetics, classical and molecular geneticist and cytogeneticist. Under all these specialisations, the assumption is that the worker of a particular discipline is a specialist and can be little else. As a result of this process of splitting and specialisation, progessive disintegration of botanical science as a whole has taken place. Time has now come to find out ways and means to stop this disintegration. It is necessary to bring morphology back to its past glory since it is the basis of all botanical disciplines. A noteworthy attempt has been made in this direction by botanists like Wardlaw, Sinnott, Wetmore and others by emphasising an experimental approach in the field of morphology. Such a study has been termed as *Morphogenesis*. Some of the botanists who have no more attraction for comparative morphology and treat phylogeny contemptuously have developed some fascination for morphogenesis since it is a promising field and where still there has been little work.

In the words of Wardlaw, "The aim of study of morphogenesis is to explain how, at each stage in the development of the individual, the distinctive form comes to be what it is. In other words, it attempts to answer the question : How in the process of development is the characteristic form or succession of forms produced, and what are the factors involved? But if we had this information for representative species of the several major groups of plants, to what use would we put it? One answer, at least seems clear. We should return with the new knowledge to a reconsideration of the problems of comparative morphology, of phylogeny, and more generally of the evolution of plants. In brief, the wider vision requires consideration of both morphogenesis and phylogenesis. These studies may be separate disciplines—they have been certainly inspired by different mental qualities—but they are after all, no more than different aspects of the same theme, i.e., the origin of species as reflected in the individual development." This aim is really laudable. But in this case also, we have to be cautious. Although there has been considerable advance in our knowledge and it has become possible to examine and analyse extremely smaller amounts of material biochemically as well as microscopically, some morphologists seem to have lost perspective and outlook on the plant. They have forgotten that a plant at all stages or any stage of develoment is an organism, that the organs of plant have meaning only if they perform their essential roles in the complex organisation and since they are functioning parts of the integrated whole plant, their evolutionary survival depends on the continuity of integration in structure and function throughout the sequential changes that take place during the plant development. Though the basic pattern is controlled by genes, the range of expression within this pattern depends on the total milieu of its development.

It is now necessary to think how to get the proper perspective and outlook on the plant. In this respect, we have to turn to the pioneers like Aristotle, Goethe, Hofmeister and Sachs. Even today, we can gain much from Aristotle in regard to the fundamental concepts than any other author of a later period. We have to follow him for the proper interpretation of plant morphology. He recognises four primary causes as follows:

1. *The material cause:* The matter or substrate of the thing.
2. *The efficient cause:* The source of motion, or the cause of change in the thing.
3. *The final cause:* The purpose or end

of the thing.

4. *The formal cause:* The essence or essential nature of the thing (quoted from Agnes Arber, 1950).

In order to explain these causes, let us take an example of the construction of a road. We require the earth, stones, sand, tar etc. in the making of the road. This is the material cause. We have to employ labour to use these materials. When they start work, the forces are set in motion which ultimately lead to the completion of work. This is the efficient cause. The purpose of constructing the road is to facilitate travel from one place to the other. This is the final cause. What was the idea of road making which had already been in the mind? This is the formal cause.

When we apply the above mentioned four causes while studying the organic form, we may group them into two categories: (1) the mechanical or physico-chemical causes, i.e., material+efficient causes, and (2) the teleological causes, i.e., final+formal causes.

When we go through the pages of history of science, we find that at any period, there is generally emphasis either on physico-chemical causes or on teleological causes. Teleology means the doctrine of final causes. In the case of the former, the organism is considered as a machine and in the case of the latter, the trend is towards an interpretation in terms of purpose. There began a period in the seventeenth century when the emphasis was laid on material and efficient causes. Even, today, such is the case. There is no doubt that the mechanistic approach has certain advantages. With this approach, it has become possible to bring the study of nature within the orbit of experimental methods. This has led to the advancement in techniques and manipulative skills with the result that extensive data are now available. But most of these data are, however, based on the physico-chemical methods of studying the plant. So they have their own limitations. In fact, such a type of study cannot yield anything which is outside the scope of physics and chemistry. Even a modern thinker like Bertlanffy states, "The physico-chemical description of vital processes does not exhaust them." In short, the mechanistic view of the organism or plant is very narrower than Aristotle's concept. He not only emphasised the final cause but also realised the importance of the efficient cause. Theophrastus was also in agreement with the duplex view. He was aware that the plant had to depend on the physical conditions. His ideas were on lines of teleology. Kant said that the mechanism without teleology is blind, while teleology without mechanism is empty.

We have now to find out the way so that there would be synthesis of mechanistic and teleological views. When we consider the final cause in connection with the organism, it is to be defined (after Agnes Arber) as the extrinsic directivity of the organism itself. When we think of the final cause in this light, we have to develop certain concepts. Let us take an example of sunflower We observe the plant. This observation carries a certain notion in the brain, which is based on the characters of this individual plant. A mental picture is then formed which is retained in the memory. After making observations in respect of several plants, a general idea of a thing called sunflower emerges. This is associated with characteristic features common to several individual plants seen and thought over. But this notion is not, however, a composite picture. It is the abstraction of the idea of "sunflowerness". Such general notions are called universals or concepts. It should be remembered that the formal cause differs in its nature from 'cause' which is generally used to mean something which precedes its effects. Formal causes coexist and it is therefore reasonable to use them in preference to causes.

We should follow Agnes Arber in thinking of reason and consequence instead of cause and effect. One may ask, "What is the example of the action of the formal cause?" To answer this question, let us consider the process of development from the egg to the maturity of plant. In this process, differentiation of cells takes place in due relation to another. There is co-ordination in the roles performed by cells individually as well as in different parts. This cooperation is continued till the mature structure with all its complexities is formed. This process is entirely determinate. When we consider such a process on the basis of formal cause, it is better to subdivide the formal cause, as suggested by Agnes Arber, in accordance with the distinction made by Goethe between *Bildung*, which is dynamic and *Gestalt*, which is the static view. Let us again turn to the example of road construction. The formal cause was the idea of road construction already prevailing in the mind. If the road had been a living organism, the formal cause would have prevailed within the organism, instead of in a mind external to it. This example leads us to the conclusion that the organisation type and *Gestalt* are the expressions of the formal cause. In this connection, Agnes Arber points out, "We should recognise that the Formal cause being immanent in the organism, considered as a discrete individual, and the Final cause being immanent in the organism considered as a part of the whole. If we take this view, many of the difficulties of telelogy, vanish, since most of these difficulties arise out of the fact that the purely extrinsic is unthinkable." Physico-chemical concepts are applicable to the phenomena while aim of the morphological concepts is to penetrate the thing itself.

Goethe has used the word *Anschuung*. It means interpretative portrayal or internalised representation. The morphologist has not only to describe the features of a plant but also to present its interpretative portrayal. A painter who is a master in his art does not simply draws a portrait of an individual but adds his intellectual insight in such a way that the personality of the individual is revealed. There has not been much work on pollination mechanism where plant and insect agency are to be thought in terms of formal and final cause so that one would be able to make an internalised interpretation or draw an interpretative portrayal. With this view in mind, even one can use one's camera skilfully. It seems that there is a certain correlation between artistic power and morphological insight. We have to think with mind's eye. Here I am tempted to quote Agnes Arber. She says, "While the *physico-chemical* study of form is achieved by means of conceptual reason, and together with causal analysis, the morphological position is reached through combining conceptual reason, and thought which is visual and tactual. The first of these two modes of approach towards the understanding of form, involves reliance upon the Material and Efficient causes alone, while the second invokes the reinstatement of Aristotle's Formal cause, with its corollary of thinking with the mind's eye. Though these two approaches seem, in our present limited view, to be parallel and disconnected yet—since the four causes are all abstractions—the two paths must converge at last upon the ultimate concrete synthesis of the work of the eye and the intellect."

If the morphology has to regain its exalted position back, the morphologists have to think in terms of four primary causes of Aristotle and *Anschuung* of Goethe. They have also to get help of other disciplines. At the same time, workers in other disciplines must not forget that morphology is the very soul of natural history. It is necessary to have a joint effort so that there will be again integration of the botanical science. It must not also be forgotten that both phylogeny and ontogeny are subjects which compel an effort of understanding. The study of morphological processes should be used to correlate ontogeny and phylogeny wherever possible in the plant kingdom. Then alone morphology will be able to get its place as a unifying and integrative discipline.

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