

## REVIEW

### Flower morphology, a source of evidence for evolution as a physiological process

by

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Evolution has for a century and a half been the subject of both speculation and research. It has been approached from almost every imaginable side. However, while on the one hand the fossil evidence has provided us with the main lines of development both of characters and of taxa, and on the other comparison of living organisms mutually and experiments of various kinds have given us some insight into the processes which may play a part in the mechanism of evolutionary development, the two methods of research are still separated by a wide gap and in spite of many efforts we are far from understanding what is really happening and what the admittedly necessary connection between the framework and the skin may be.

In a recently published book the Swiss artist-botanist Erich Nelson has offered a contribution to the static (or short-time) side of the problem. It must be admitted that his considerations are bearing on a part of the field only (*viz.* Angiosperm flowers) and that an ample, though by no means exclusive use is made of facts which were already known, this does not lessen the merit of the author that he has contrived to open up a new and promising field of research by expounding a rather bold but consistently argued theory which seems well worth considering.

Nelson justly points out that traditional morphology seems to be inclined to think of "characters" as constant, static manifestations of the genome. Of course, theoretically everybody knows that this is not so, but it must be admitted that in practice morphology deals with flower parts as organs of a definite shape and position. As will be mentioned underneath similar opinions are expressed by Nelson regarding the genetical side of characters but here, I think, his views are less likely to be generally appreciated. Yet both the morphologist and the geneticist cannot but profit by paying due attention to Nelson's numerous observations.

By these observations the mind of Nelson the artist-painter was extended to that of Nelson the scientist. If I am not mistaken, his original hobby was painting wild flowers (especially orchids), which he did under the benign sun of the Mediterranean and the Near East between 1923—1929. His gift of accurate observation aroused his scientific interest. This made him pursue his observations along logical lines even to artistically less alluring objects and this again made him look for a reasonable explanation of their mutual connections, which ultimately led him up to a theory of comparative flower morphology and organogenesis in particular and of evolutionary mechanism in general. This could, of course, not be attained without a thorough scientific basis and this the author managed to procure during a study of several years at the university of Zürich and elsewhere. Although Nelson has, so far as I know, not been graduated, his book clearly shows that he cannot be considered an amateur; he has happily combined high-standard art with high-standard science.

Without going so far as Markgraf who in the prospectus declares that since Eichler flower morphology has not made any such progress, it must be admitted that our knowledge of intimate flower morphology has been considerably augmented by Nelson's book. Nobody, so far as I know, has ever gone into so much detail regarding

shape, colour patterns, and positions of flower plants, their variability and inter-relations.

Nelson's material is variability. For him evolution is not accidental, it is primarily a physiological process. It is not a competition between the indifferently developing genome (by haphazard mutation) and selection by the environment; it is a struggle between the genome and "younger formative physiological impulses". Nelson's idea is that the genome is far more plastic than is generally assumed. No or very little appreciation is shown for the idea of an autonomous development of the genome. Mutations, whether or not induced by environmental factors, are supposed to pave the way for the activities of the "physiological impulses" which may, for instance, be caused by positional or nutritional influences exerted by neighbouring organs, and which become gradually genetically fixed and thus represent the evolutionary mechanism (p. 17).

The induced mutations are taking part in the continuation of "orthogeneses" (e. g. series from actinomorphy to zygomorphy, and from Liliiflorae to Orchidaceae, p. 18); the random ones play their part regarding minor characters such as colour patterns, variations in shape and pubescence, etc.. Nelson's theory shows traces of both darwinism and lamarkism, but the latter seems to prevail by a marked tendency to the acceptance of heredity of acquired characters.

In my opinion the most important part of the work is its contribution to flower morphology both by the detailed descriptions and by the beautiful pictures of which a large number (230 out of almost 700) are coloured.

This does not mean that his theory is of a lesser quality. The two cannot be compared but it would seem that the theory, some points of which will be indicated underneath, is still somewhat immature. Both the evolutionary and the genetical basis are insufficiently pondered.

An other weak point is that long range phylogeny has been entirely neglected. This has inevitably influenced some of Nelson's homologisings (stamens, obdiplostemony), which might have turned out differently, had he realised that Angiosperms organs must have had a very long history behind them. He does not express a definite opinion regarding the question whether mutations can result in transspecific (or transgeneric) alterations but he seems inclined to deny this possibility. Should this possibility exist, he says, then the process is necessarily primarily a physiological one: the form is secondary. This is one of the problems which are not sufficiently dwelt upon and they leave the reader unsatisfied.

Numerous morphological problems have been passed in review. Here are some examples giving an idea of Nelson's opinions and conclusions, with some comment of the reviewer (Rev.).

"The" Angiosperm flower is a shortened specialised axis. This shortening results in a close contact of flower parts and this again in a superposition between sepals and stamens, which causes an excessive sectorial tension. Shifting on account of disturbances in the equilibrium of nutritious transport results in a gradually acquired alternation of and equidistance between flower parts (p. 34).

Nelson circumstantially discusses various theories on phyllotaxis (p. 39 ss.), but he fails to mention Plantefol's revolutionary views, which are unfortunately based on but a few selected examples. He denies that in the growth point the limit divergence prevails and only later on leads up to one of the known types of phyllotaxis. He seems to think that in early stages the organ primordia are variably arranged as to local possibilities, including the distribution of organic substances, and that only later on, through continued physiological action, the arrangement of lateral organs gains some regularity though even then local shifting remains possible on the basis of the primordial plasticity. He speaks of "differentiated alternation" as the general principle of what he calls "Gruppenstellung" (aggregation) of organs. These aggregations, brought about by hampering influences by older on younger organs, mean disturbances of the (physiological) equilibrium, which during evolution is getting regulated in various ways.

Deviations of the ideal picture are actually general; in fact the theoretical divergences are rare, they represent averages or ideal cases; the Fibonacci figures appear everywhere in broken series. Relationships are suggested by transitional series between types. Assuming that such transitional series which can be construed between recent groups and also appear sometimes during ontogeny, have a similar reality in (short-range) phylogeny, the implication is that a phenotypical alteration in the organisation

of a flower has become a genotypical one (p. 78). Nelson's conclusion is that somatic processes ("physiological impulses") have played an important part in these genotypisations (p. 88).

Transitions (ontogenetical and phylogenetical) between helicoid (spiral) and whorled phyllotaxis are possible and can actually be observed in either direction, though helicoid to whorled seems by far the more frequent one, particularly in flowers. Its counterpart is to be found in the transition between opposite cotyledons and spirally arranged leaves (p. 79). It seems questionable, however, that such opposite cotyledons are forming a true whorl; it seems more likely that they form a false whorl, brought about by the lack of space in the seed.

A traditional opinion is that the epipetalous position of stamens of Monochlamydeae is due to the abortion of one whorl of phyllomes. According to Nelson nobody has apparently thought of this kind of superposition as primitive character. He expresses this view and finds support to it in the regularly decreasing percentage of Monochlams for the Cretaceous (p. 33). Here his neglect of long range phylogeny avenges itself. Nelson has apparently not come across those papers, which advocate the axial nature of certain stamens, nor does he quote the reviewer's publications in which the same opinion has been expressed with the suggestion that in these and other cases of stachyosporous the stamen is to be considered a fertile axis axillary to a phyllome. Nor does he mention the so far unexplained phenomenon of centrifugal stamens, described by Corner and others. Nelson says that the Monochlams have not yet "invented" full alternation in their flowers.

Yet, wondering what "the" Angiosperm stamen should be considered to represent "organophyletically", Nelson arrives at a conclusion not too much different from that which stachyosporous demands. He supposes that filament and connective are a sort of outgrowth of the sporangia or, which is the same in other terms, a sporangium stalk or sporangiophore (p. 94). Even petaloid stamens and petals are not considered phyllomes. All evidence for the latter interpretation is simply argued away. I am afraid he goes a little too far here, but it is interesting to notice that an almost classical view like this still finds an adversary and, for that matter, one from the camp of what I use to call static morphology! Even a proliferated *Drosera* flower with tentacled leaves instead of petals and carpels cannot convince him that they are phyllomes. I must admit that, to me at least, the argument in favour of the phyllome homology is not a strong one. The fact that small but perfectly developed *Drosera* leaves are inserted above what is clearly a calyx, does not necessarily imply their homology with petals, stamens, and carpels; in fact, they are ordinary leaves.

According to Nelson the sporophyll has contributed nothing or very little to "the" Angiosperm stamen; its plastique is the plastique of the sporangium ("sporanges Gewebe") (p. 96); filaments and connective protrusions are "secondary structures". Phylogenetically (long range) speaking, this is nonsense, the sporangium does not show a plastique of any importance; as the reader may know, I distinguish sporophylls (phyllomes) and sporogenic axes (sporangiophores) (Rev.).

Nelson refutes the phyllomatic nature of the petals (p. 132 ss). On the strength of numerous examples he concludes that they are generally metamorphous stamens. The enormous plasticity and polymorphy of the corolla can be better understood if we drop the concept of its phyllomatic nature. Petalisation of the stamens is only possible at the cost of the sporangia (p. 148). This is phylogenetically speaking probably a very old and fundamental phenomenon: a telome is, ever since the Devonian, either fertile or sterile (Rev.). The influence of sporangia on the shape of leaves is already discernible in *Selaginella*, ferns, etc. (p. 269). It also shows in double flowers (Rev.).

The plastique of the corolla is much increased by lateral insertion of the flower and by the acquisition of zygomorphy. Nelson speaks of dorsiventrality but I prefer to reserve this expression for a deplanation in the transverse plane (Rev.). The fact that the calyx is much less involved in zygomorphy than the corolla, is, according to Nelson, due to its "vegetative" character (p. 157).

Differences between terminal and lateral flowers are physiologically determined. Terminal flowers show a closer phyllotaxial relation with the leaves than lateral flowers where the phyllotaxial gap is more sharply marked. This is why in plants with decussate phyllotaxis the terminal flower is more often 4-merous, while the lateral ones are 5-merous (p. 26).

Zygomorphy is extensively discussed (p. 158 ss.). It is both influenced by position (topology) and by gravitation. As a rule zygomorphy is hypotrophic, i. e. the lower side of the flower is furthered (p. 167), but epitrophic zygomorphism, primary or secondary, is known as well. In false zygomorphy (Compositae, Iberis, Viburnum) the plastique is not increased; their androecium remains actinomorphic (p. 223).

A related phenomenon is the resupination of flowers, notably when they are epitropically zygomorphous (Orchids) (p. 208).

In peloria atavism is an interpretation of a very relative value only, the main agents being physiological influences. Though this may be true to a certain extent, I am afraid, that Nelson in cases like these as well as in teratology generally minimises the genometric factors in an inadmissible degree.

Teratisms are primarily explained as being brought about by "morphogenetic substances" (p. 234 ss.). Calycanthemy, for instance, is not an atavism — sepals and petals not being homologous — but is considered a secondary phenomenon induced by physiological action, emanating from the corolla. Nelson speaks here of "Annäherung", meaning the formative influence of one organ on another which is inserted close to it (p. 241).

Nelson considers the Helobiae without much arguing the most primitive Monocotyledons. The latter should have originated "from the Polycarpicae" by the following secondary processes: 1. acquisition of the cyclical arrangement of flower parts; 2. petalody ("korollinische Annäherung"); and 3. acquisition of trimery (p. 266).

His interpretation of the monocotyledonous perigone, though logically following from his circumstantial reasonings, seems rather fantastic: the original condition should be a quincuncial (vegetative) calyx, to which one phyllome is added by the androecium. He mentions in support of this rather surprising construction a teratism in *Lilium* in which a terminal flower was found to be quincuncial. Curiously enough Nelson considers this case an atavism (p. 268).

Apparently Nelson rather naively sees the phylogenetical system as a linear arrangement: Pteridophyta-Gymnospermae-Haploclamydeae-Diploclamydeae (p. 270), but this point is not explicitly stressed and falls outside the real scope of the work.

The tendency of inflorescences to develop into pseudoflowers is brought under the viewpoint of "Annäherung", and the impulse towards the effect mentioned is supposed to emanate from the flowers, no teleological or final factor being involved. The same is assumed for coloured leaves and bracts such as those of *Bougainvillea*, *Cornus*, *Petasites*, etc. There seem to be a correlation between the rise of petaloid bracts and suppression of marginal flowers (p. 270).

"Orthogenesis" is used in the very restricted sense of continuation of a tendency ad absurdum, inside a group of related species, e.g. regarding the lateral lobes of the *Ophrys*-labellum (p. 276). There seems to be a contradiction here to an earlier statement (p. 18).

The above points, though few in number and only briefly mentioned, may give the reader some idea of the contents of this work which is undoubtedly an important addition to our knowledge of Angiosperm flower morphology. Though, as has been stated above, the theoretical side is perhaps still somewhat immature, it is stimulating in that it evokes self-defense in well-established and generally accepted concepts and draws the attention to a dynamic side of the mechanism of micro-evolution which has so far been all too much neglected. It may arouse new research in the field of morphogenetics and the connected fields of pure genetics and biochemistry.

The book is not easy to read for though the framework has been built up along very logical and consistent lines, the style is often somewhat heavy. Despite this the work is warmly recommended to all botanists interested in problems of phyllotaxis, flower morphology, organogenesis (ontogenetical and phylogenetical), and micro-evolution. It concludes with a bibliography of about 400 titles, which is apparently not complete. European and, in particular, German titles are predominant.

The size is a stout quarto, the print clear, the paper excellent, and the illustrations, particularly the coloured ones admirable, both from an artistic and from a scientific viewpoint, but the price is, in spite of a liberal grant from the "Schweizerische Nationalfonds zur Förderung der Wissenschaftlichen Forschung", so high that it is to be feared that many private botanists have to refrain from purchasing the work. This is the more regrettable since the book is undoubtedly worthy of a wide interest.

If I should appear to have failed in giving it full justice, the author and the reader may blame me for an insufficient insight in some of the fields, which are reaching beyond the scope of the reviewer's specialised study. My main purpose was to draw to Nelson's work the attention it deserves.

### Litterature quoted

- CORNER, E. J. H., Centrifugal stamens — *J. Arn. Arb.*, 27, 1946, 423—437.  
LAM, H. J., L'évolution des plantes vasculaires — *Coll. Int. du Centre Nat. de la Rech. Sc. Paris Mai 1952* (*Ann. Biol.* 28, fasc. 5—6, 1952, C. 57—C. 88).  
NELSON, E., Gesetzmässigkeiten der Gestaltwandlung im Blütenbereich, ihre Bedeutung für das Problem der Evolution. 4°. XII + 302 p., 689 Abb. — Verlag E. Nelson, Chaux-de-Fonds-Montreux, 1954 — Price Sfr. 81.10.  
PLANTÉFOL, L., L'ontogénie de la fleur, Paris 1949.