FLOWERS FREE FROM THE ENVIRONMENT?

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At the jubilee of Professor Lam it seems suitable to contribute a paper on the flower as a functional unit, though it is in the form of a kind of book-review.

Lam himself wrote on the more fundamental connections between flowering and lower plants and on the basal morphological elements of the flower. He gave general schemes for relations among the flowering plants, in which he aimed at a synthesis between materialism and metaphysics, micro-evolution and macro-evolution, autonomous orthogenesis and selectivistic adaptation.

In recent times the distinguished phytogeographer Prof. R. Good published a book *) of more one-sided scope, criticizing the existing conceptions on the forces of evolution as insufficient and maintaining only one, autogenesis.

The main part of the book is an immense amount of reflections of a, seemingly, negativistic and sceptic nature, which may confuse the unprepared reader. Only at the end we find the conclusions which may justify the preceding enumerations. I resume some of them:

a) The evolution of green plants may be regarded, because of their autotropism, as having been independent, while the evolution of animals must have been conditioned to some extent by that of plants.
b) In the Flowering Plants evolution appears motiveless, change because change is the innate order of nature rather than because of biological superiority — an automatic impetus.
c) This brings an element of repetition into floral forms, so that much of their evolution is kaleidoscopic elaboration.
d) Little or nothing supports the view that they are the product of selection.

This anti-selectionistic standpoint is in the line of Goebel, who emphasized that primary pluriformity is used by the environment as material, that structure determines function. He recognised, however, the functional connection with the environment, so that he sees parts as organs. He investigated the physiological connections experimentally and said that a pure, "idealistic" morphology should not be able to use the term "organ".

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*) R. Good — Features of evolution in the Flowering Plants. 1956, Longmans, Green and Co., London.

Good ignores Goebel and goes much farther, neglecting practically all bonds with the environment — as if a flower were not an organ entirely directed at the outside world.

I do not venture into the realm of metaphysical, deeper connections, do not wish to promote selectionistic or Lamarckistic views but wish as an ecologist to emphasize that the bond between flower and pollinating agent cannot be ignored with impunity.

The passivity of the plant

This conception is of course true in the main, but is not so completely true, even for the search for food, that the whole course of evolution in plants should be independent and different from the one in animals — as presumed in the book. It seems especially dangerous to extend this view to the flower, which is certainly not independent.

The flower, though immobile, is in its way active. Choosing is probing the environment and rejecting what is unwanted. The random dispersal of seeds is perhaps not so basically different from what happens in an animal brain. The eutropous flower determines in a way how it will attract and which pollinators it will attract. We still fail to understand fully how this proceeds and have to admit that this specialization often seems dangerous, but it exists.

In contrast to Good's idea that the plant leads and that the animal follows, we will see later on that often the flower lags behind. It was born in contact with the only pollinators present at the time, the beetles, but both flowers and pollinators changed since then. I already remarked on this in an earlier paper (1957), also stressing that what seems independent or senseless now, may have been adaptive in a more primitive environment.

Repetition

Good mentions many instances of superficial resemblance in parts of plants from heterogeneous groups, where "repetition" seems an expression of comparable morphological factors, with "absence of any general system of correlation between them". As instance no. 1 we find quoted the well known vegetative similarity between succulent Cactaceae, Stapelieae and Euphorbiae. Though we have to recognize that other families in the same desert-like environment did not develop this habit and that a certain innate possibility must be present, this convergence seems perfectly determined by the environment and of adaptive value.

As one of the main instances in flowers Good considers the pluriformity in the Asclepiaceae, where innumeral recombinations occur of the possibilities present in the flowers of the flowering plants as a whole. I remark that only total neglect of floral biology can maintain "absence of any correlation between them". The "frequent instances of superficial resemblance between members of different genera" are undoubtedly mostly convergent adaptations within the possibilities of the family, but directed by and towards specific pollinators, so that there is in the first place correlation with the environment.

Vogel (1954) already gave a preliminary classification of the ecological floral types in the family, which disproves the blind, kaleidoscopic "elaborative evolution". Let us only consider the class of "sapromyophilidae" (pollinated by carrion-flies and the like), so common in the family. No wonder that its characteristics emerge everywhere in the enumeration of Good. (Cf. my study on this class (1953) and Vogel). I quote only four, as Good paid no attention to the characteristic smell, viz. 1. purple colour or purple-spotted; 2. lantern-type with slits by fusion of tips of lobes; 3. tails (filiform appendages); 4. *Flimmerkörper* (vibrating hairs). These and other characteristics are strongly correlated into a syndrome, which occurs in many tribes and also in many other families (cf. Plate IV of Vogel).

On p. 366 Good remarks that there is even a parallelism between many Aroids and Aristolochiaceae. This reposes on the common occurrence of the above mentioned adaptive syndrome. The development of this syndrome stands outside the realm of pure or autonomous morphology. This follows from the fact that, e. g. the ecologically comparable tails, have often (even in one genus) morphologically nothing in common (as demonstrated by v. d. Pijl, 1953). Troll already pointed to the convergence between Ceropegia and Aristolochia, which has the same background.

Another instance of this kind of "repetition" is the conspicuous combination of red and yellow mentioned (p. 328) for a number of flowers from very divergent families. All these flowers, however, are clear cases of ornithophily, mostly proven cases, with the colour combination as part of the syndrome of ornithophilous characters. A glance on Vogel's plate V shows still more cases of this combination.

The cited resemblance in shape between *Ribes speciosum,* Fuchsia species and *Pitcairnea staminea* (p. 340) is not blind "repetition", but common adaptation to colibris.

The "repetition" in Isotoma and Clerodendron (p. 352) becomes clear ecological convergence after a glance on Vogel's plate III, with a number of sphingophilous flowers. The "repetition" in Saponaria-Silene-Phlox (p. 343) belongs to the same category.

Lam (1946) mentioned (p. 63) other cases of convergence, e.g. between the flowers of a Labiate and an orchid and thought that there was no function behind this development. He ascribed it to the limited number of possibilities in nature. I think this explanation should restrain both morphologists and ecologists from far-fetched conclusions, but I doubt whether it is necessary here. I already described a striking convergence between Canavallia and Labiatae due to common pollination by large bees (1954).

The mangrove-plants are mentioned in the book, but their convergencies are not discussed. These are clearly adaptive.

Taking into account the unity of plan in the Flowering Plants we cannot be astonished that in families with dry fruits suddenly some species develop fleshy fruits and v.v. It seems far fetched to consider this (as Good does) as autonomous repetition and to leave the ecological significance out of consideration (p. 329—335). The fruit is the youngest organ of all and, over and above the organisation-type of the family in the ovaries, the mature fruits develop everywhere parallel differentiations for parallel ways of dispersal.

The author criticizes selectionistic conceptions with the argument that not a single character can be advantageous as all characters apparently lead to viable flowers. He ignores the opinion of modern selectionists, like Stebbins (1951), that the selective value is rarely due to one factor in the flower, but to the combination, which forms an "adaptive peak". Stebbins also remarked that if one character changes, the selective value of another character may change also.

We have to admit that there are many neutral, allotropous flowers and that in eutropous flowers each of the separate characters of a syndrome may fail in clearly adapted flowers while the whole functions nevertheless. We have also to admit that there is an apparently superfluous duplication of contrivances. Such a luxuriant development seems a kind of autogenesis, but it was originally guided by ecology.

We may recognise evolutionary trends, progressing in the same direction in different sub-groups and giving there parallel phases. These are, however, not mere kaleidoscopic repetitions of factors. The images of a kaleidoscope have no directed connection.

Besides organisation-types evolved from historical elements, we may distinguish in the flowers "architectural classes" and the "biological classes" mentioned before. The former may relate to more fundamental processes of pollination in general, the latter to special (later) pollinators, but the so called morphological, architectural types, like tubulate, labiate, papilionate and capitulate flowers, were also guided by ecological factors — as said before (v. d. Pijl, 1957). Vogel gave an extensive discussion of this point.

Monocotyledones

Chapter 3 is devoted to a fine analysis of the differences between Monocotyledones and Dicotyledones. The conclusion is that these are just two parallel series, a repetition on a grand scale without implication of higher or lower or better adapted. The possibility is left open (p. 358) that the Monocotyledons are a simplification, with perhaps a prevalence in geophily.

The latter new seems to me just the refuted ecological background to many of the differences, being a consequence of specialization in habitat. I see before me a rain forest, with tall gymnosperm and dicotyledonous trees in the upper stories and monocotyledonous semi-herbs in the lowest story, originally spread over periodically dry regions and swamps.

I might mention the names of Sargant, Němějc, Bews and Schlitter, but will only point out the work of Holttum (1955). The gist of their work is the following interrelation of processes in geophily: shortening of permanent stem, loss of secondary growth, change of vascular construction, constant renewal of subterraneal stem parts by sympodial outgrowth, while temporal, unbranched aerial systems care for propagation and assimilation. These parts often broaden and strengthen their leaf sheaths, which obtain intercalary growth and many veins. The taproot becomes superfluous, the roots too lose their cambium and adventitious roots arise constantly anew.

Some differential characteristics remain unexplained and apparently a-ecological — e. g. monocotyly and trimery. Goebel (1915—18), however, pointed already (p. 1232, 1236) to a correlation between monocotyly and geophily. Trimery may be just an incidental character inherited from Ranalian ancestors and fixated in the group, not as a repetition but as an archaism.

Surely there is correlation in every respect.

Compositae

The crucial chapter 10 is devoted to this family. It contains a comparison between a capitulum of Cosmos and a flower of Anemone, which are alike in many points. I cite: "It is hard to see what possible benefit the Composite form and the presumed immense amount of evolutionary change confers upon its possessor."

This somewhat simplistic opinion can simply be refuted by another comparison, viz. in the range fish-mammal-whale.

Anemone is a specialized Ranalian, an early parallel of, not a precursor of Cosmos.

We shall further see that this opinion suffers from the idea that the environment in regard to flowers has always been the same or was of no importance.

When a certain environmental factor has once left its stamp on an organism, it is possible (cf. the whale) that later on a different, even a more ancient, factor obtains opportunity to alter the shape. (For Composites I point to secondary anemophily in Ambrosia). If then a shape arises like the one of Anemone in Cosmos this means the same answer to the same challenge, though made necessary by the organism itself in its urge of specialization.

Morphologically the changes in the capitulum can perhaps also be seen as autogenetic, as a progressing integration, which after aggregation and differentiation leads to a new whole. I hesitate to call such a process "repetition", and prefer the term "evolutive cycle" in the spiral ascension of living forms. In the future we may perhaps expect capitula with characters as in the flowers of orders higher than the Ranales, but then all of the second order, as centralized nectaries (already present in Barnadesia), central stigmatization, sympetaly, epigyny and syncarpy (already present in rubiaceous inflorescences).

But the pluriformity is at the same time ecologically understandable. As the usual analyses of relations in the family (cf. Cronquist) abstain from floral biology I venture to introduce here this element.

The group originated in the beetle-era and seems the culmination in this phase. It shows the aggregation of flowers in a plane that still occurs so often in beetle-flowers, fitting to pollinators that are lazy fliers and apparently like to crawl over the flowers. This can still be seen in Umbelliferae, Cornus, Viburnum, Sambucus, and some Rosaceae like Spiraea, Crataegus, Sorbus, etc. amongst the later beetle-flowers. (In the Arales the aggregate remained cylindric with a special covering). Some of the

Compositae stuck to beetles. An investigation in a region as N. Zealand, which as a whole seems to stick to beetles, might illustrate this. We know it from this country in Brachyglottis and further in Adenostyles and of *Cenia turbinata* (S. Africa). The primitive capitula of the arboreal Vernonieae deserve special attention in this respect. Vogel (p. 77) suspects cantharophily in many more S. African Compositae. In some temperate forms like *Tanacetum vulgare* and *Achillea millefolium* (still favourites of beetles) the aggregated capitulae formed anew a plane. Though the capitulae grew large, most Compositae did not specialize strongly into new directions (remaining allotropous flowers). This stands in contrast with other families, even part of the Ranales, which had not imposed on themselves an aggregate and could apparently easily rebuild their single flowers in accordance with new pollinators. The Composites lag in this respect one phase behind, so that Cosmos, though morphologically on a higher level, can have the shape and ecological level of a Ranalian which just rose above the beetle-level.

Just as in the case of trimerous and pentamerous flowers, where Good sees no advantage, it is dangerous to assume that one shape of flower is as good as the other, ignoring the vast literature on experiments in regard to insect preferences. We know, now, that development of ray florets is not only important for enlargement of surface but also for a more dissected contour.

The arrangement of flowers in a plane seems not ideal for higher insects and birds. Experiments showed that bumble bees have a marked preference for three-dimensional "flowers" with "*Tiefenwirkung*".

Vogel (p. 306), to whom I may refer for details and names, already pointed to beginnings of eutropy (limitation of visitors) in the family. There is some anemophily, melittophily, sphingophily, myophily and ornitophily. Here, however, the modifications are not so much in the flower-parts, which remain remarkably fixated, but also in the capitulum-parts.

Many of the phenomena of blind "repetition" in the capitulum, mentioned by Good, may be reconsidered in this light. I refrain from a detailed discussion but mention: increase of and deeper position of nectar (ornithophily in Barnadesia), zygomorphy, apetaly, uniflory, fleshy involucrum, pendent position, tubiformity, and unisexuality. They go along with the signs of general integration mentioned above.

I refrain from a discussion of the fruit, though here too we have early fixation and late reorganization.

To leave the, almost last, word to Good I cite his question (p. 307): "Can we believe that the simpler Vernonia condition is in any material way less surely and adequately functional than that of others?"

I have some objections against this question. We have to assume that this capitulum is primitive, not simplified. Further I think that the question is biologically unsound, and might be put with the same right in regard to Amoeba and Homo. Nevertheless the answer is: Yes, I can. It is like other relics viable in the tropical rain forest, but it may be a relative relic in a changed world.

Finally I quote with agreement what Lam — our "*jubilaris*" — (p. 66) wrote about the bond flower-pollinator: "Autogenesis alone fails us here, mutations are difficult to imagine, with autogenesis plus selection we go quite a stretch, but much remains above our mind."

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