

1991

## Parallelism, It's Evolutionary Origin and Systematic Significance

K. Kubitzki

*Universität Hamburg*

P. von Sengbusch

*Universität Hamburg*

H. Poppendieck

*Universität Hamburg*

Follow this and additional works at: <http://scholarship.claremont.edu/aliso>



Part of the [Botany Commons](#)

---

### Recommended Citation

Kubitzki, K.; von Sengbusch, P.; and Poppendieck, H. (1991) "Parallelism, It's Evolutionary Origin and Systematic Significance," *Aliso: A Journal of Systematic and Evolutionary Botany*: Vol. 13: Iss. 1, Article 8.

Available at: <http://scholarship.claremont.edu/aliso/vol13/iss1/8>

PARALLELISM, ITS EVOLUTIONARY ORIGIN AND  
SYSTEMATIC SIGNIFICANCE<sup>1,2</sup>

K. KUBITZKI, P. v. SENGBUSCH AND H.-H. POPPENDIECK

*Institut für Allgemeine Botanik und Herbarium Hamburgense  
Universität Hamburg, 2000 Hamburg 52, FR Germany*

ABSTRACT

Parallelism as one of the forms of biological similarity is investigated in the light of recent findings from developmental and molecular biology. From the organismic point of view, functional constraints and evolutionary canalization are well established as causes of parallelism. To these may be added, from the molecular perspective, (a) erratic activations of repressed genes; (b) activations of alternative pathways under the influence of homoeotic genes; and (c) horizontal gene transfer, for which a simple mechanism is proposed. The control of gene expression through the action of transposable elements, reversible to some degree, appears to be an evolutionarily important and frequent phenomenon, which may account for many cases formerly interpreted as losses or irreversible changes of genes. It is suggested that this mechanism, which seems to be optimized in angiosperms, may account for the great evolutionary plasticity of this plant group. It may also provide an explanation for so-called reversals which appear as artifacts of character analyses and are biologically barely explicable. Events of horizontal gene transfer, creative for evolution but disturbing for classification, appear less frequent, or otherwise the structure of the taxonomic hierarchy would not be perceptible. Increasing knowledge in the fields of molecular and developmental biology tends to blur the borderline between homology, homoiology, parallelism, and perhaps convergence, phenomena formerly thought to be more or less distinct.

Key words: cladistics, convergence, gene control, homoeotic genes, homology, horizontal gene transfer, parallelism, phylogeny, silent genes, transposable elements.

---

INTRODUCTION

Organismic similarity has different forms. The biologically most important one is homology, which implies structural or molecular equivalence due to common ancestry. Much care has been taken to clarify the conceptual and operational basis of homology (see, for instance Roth 1984; Sattler 1984; Stevens 1984; Tomlinson 1984). Analogy, in contrast, is the appearance of structural similarity in different lineages on a nonhomologous basis and in adaptation to similar functions and/or environmental conditions. If, in the course of evolution, members of a lineage become dissimilar we speak of divergence; if members of different lineages become similar through the acquisition of analogous traits, we speak of convergence. In the general opinion of biologists, convergence is explained exclusively by natural selection.

A different phenomenon is parallelism. In the definition of Simpson (1961) this is "the independent occurrence of similar changes in groups with a common ancestry and *because* they have a common ancestry." In this context Plate (1928) spoke of "homoiology," a concept which applies to the independent appearance of similar traits within a group of closely related taxa whose common ancestor did not have this trait. Consequently, a common genetic basis for parallelism had to be postulated, similar to Vavilov's (1922) "law of homologous series" and Baur's (1930) "parallel mutations."

Parallelism does not only pose a problem for developmental genetics but also

for our understanding of evolution and the practice of classification. It is difficult to see how a character not present in the common ancestor and appearing in some but not consistently all of its descendants can be "nearly" homologous ("homoiologous") because of its "loose" common genetic basis. If frequent, parallelism may both impede the practice of classification and the reconstruction of phylogeny. Other phenomena such as convergences and atavisms aggravate the amount of reticulate character distributions. On top of these well-known phenomena the process of nonsexual horizontal gene transfer, first envisaged by Went (1971), and the erratic activation of "silent" genes may also be responsible for classificatory and evolutionary "noise." Therefore it may be interesting to investigate these phenomena in relation to molecular biology, which in the last years has provided a vast amount of knowledge pertinent to development and differentiation. We are convinced that this knowledge is not only applicable at the molecular and cellular level but at the organismic level as well. In the following, a first attempt is made to bridge the gap between different approaches that usually stand apart from each other but ought to be complementary.

Among many other practicing taxonomists Rolf Dahlgren (1970), when studying *Aspalathus* and related genera, had to cope with the problems of parallelism and convergence, and it seems especially germane to dedicate this paper to his memory.

#### FUNCTIONAL CONSTRAINTS

In his "Mechanisch-physiologische Theorie der Abstammungslehre," which Karl von Naegeli published in 1884, with regard to plant organization he distinguished between "organizational" (or "constitutive") characters and "adaptive" characters, in which he was followed by nearly all botanists. Organizational characters are such as the structure of the flowers, fruits, inflorescences, and anatomical traits, on which taxonomic classifications generally are based. In contrast, traits related to growth form, the kind of foliage, spinescence, water storage in different organs and so on are considered as adaptive characters. Since representatives of quite different lineages of land plants living under the same environmental conditions may exhibit very similar convergent traits, adaptive characters must be evolutionarily rather plastic, while constitutive characters appear more or less invariable. As will be deduced later, these statements are in agreement with and may be due to the existence of high and low ranking genes. While the integrity and action of high ranking genes are maintained by strong selective pressures, low ranking genes can accumulate through mutational change.

In spite of this invariability, constitutive characters are, like the adaptive ones, exposed to functional constraints, and they may also have different evolutionary origins. The consistent presence of the fundamental organs of the cormus, leaf, stem, and root, is a foremost example. Since the most ancient representatives of the three subgroups of the pteridophytes were probably rootless, one may assume that in the lycopods, horsetails, and true ferns roots have originated independently; in view of the differences in the organization of their leaves and stems this may be true also for their other "fundamental organs" (Zimmermann 1959; Sporne 1962). This underlines that the construction of a land plant as a cormus must be a very efficient adaptation for the exploitation of the light-air space (see also Raven 1977). Obviously convergence very often must have its basis in functional constraints, and much similarity must be due to convergence.

Functional constraints may also be heavily involved in pollen evolution. A rather intriguing phenomenon is the appearance of columellate exines which, according to widespread consensus, seem to have evolved from a granular, or completely compact exine in parallel in various evolutionary lines. The co-occurrence of columellaless and columellate exines for example in the Nymphaeaceae, Canellaceae, and in various genera of the Annonaceae (Le Thomas 1980/81) and Myristicaceae (Walker and Walker 1980, 1981) would imply the multiple transition from the noncolumellate to the columellate state. Even if one invokes the functional aspect—storage of substances involved in sporophytic self-incompatibility reactions in the inter-columellar space (Heslop-Harrison 1976)—a completely independent and multiple origin of the columellate structure is difficult to understand since its origin would appear as a preadaptation for the evolution of an—in this case—sporophytic self-incompatibility system. Therefore, the possibility cannot be excluded that the granular and finally interstitia-free condition is a reductive development from an ancestral columellate condition, if one does not prefer to invoke a widespread presence of genes for columellate exines in primitive angiosperms.

Another most instructive example is the succession of tricolpate to pantocolpate to pantoporate pollen grains that has occurred in parallel within various lineages of which the most well known are the families of the Caryophyllales and the genera of the Papaveraceae (van Campo 1976; van Campo and Vernier 1984). In several taxa, such as *Phyllanthus* (Köhler 1967), *Hypericum* (Clarke 1975), and *Trientalis europaea* L. (Punt, van Weenen, and Oostrum 1974) this trend is known to be associated with changes of the ploidy level. When polyploid cytotypes produce pantocolpate pollen in contrast to the tricolpate grains of the diploids, one might argue that the genes for the pantoporate configuration should be present in the diploids as well. In this case, the effect could be attributable to gene dosis effects, in which a threshold of gene activities has to be overcome before the progressive phenotype is expressed. However, the situation becomes more complicated through known cases of anthers containing grains with different aperture types (van Campo and Vernier 1984); developmental and perhaps also selective processes (Clarke 1975) so far poorly understood, possibly related to the sheer size of the grains, may interfere as well.

#### EVOLUTIONARY CANALIZATION

Apart from extrinsic influences, plant evolution is also subject to intrinsic constraints which may lead to evolutionary canalization. The study of this topic has a long tradition and has recently been the subject of a symposium (J. Linn. Soc., Biol. 39(2):99–193, 1990). When a certain stage is reached in the evolutionary history of an organism, this clearly restricts the possibilities for further evolutionary change so that, in the extreme case, under the necessity for further evolutionary change, only one option remains. If this happens in a series of subsequent evolutionary steps, the result may be interpreted in terms of orthogenesis, a concept discredited through the use of neo-Lamarckists towards the end of last century and in our century through authors like Croizat (1964). (For a discussion along the lines of Croizat's reasoning, see Grehan and Ainsworth [1985].)

Meristic fixation of floral parts is a foremost example of evolutionary canalization. The occurrence of trimerous flower structures, common in the monocot-

yledons and frequent in magnolialean families, has often been interpreted as an ancient (plesiomorphic) character (see, for instance, Dahlgren 1983). However, due to the fact that many ancient representatives of the Magnoliales have a spiral anthotaxis following the limiting divergence of  $137^\circ$ , a meristic fixation of the flower inevitably leads to trimerous or pentamerous (rarely dimerous) whorls. Such a transition is documented in extant species of *Magnolia* and genera of several magnolialean families (for details, see Kubitzki 1987; Endress 1987). Therefore, trimery is not a plesiomorphy of the monocotyledons and Magnoliales, but has originated in a parallel manner along various evolutionary lines as a consequence of evolutionary canalization.

The same principle is obviously operative in other fields of evolutionary character change as well. Abbreviation of biosynthetic sequences is a common phenomenon in the micromolecular evolution of land plants (Gottlieb 1982). It may be related to the fact that in the interplay between herbivores and plant defense substances certain groups of secondary metabolites may become ineffective and a switch to a new major group of substances requires the evolution of a novel precursor (Cronquist 1977; Gardner 1977). In the angiosperms as a whole, these necessities may be responsible for the retrograde biosynthetic sequence of the primary precursors of the shikimate-phenylpropanoid pathway and the final switch to the mevalonate and acetate pathways (Kubitzki and Gottlieb 1984a, b).

#### VARIABLE EXPRESSIONS OF CHARACTERS

In the current discussion of parallelism sometimes reference is made to relatively trivial traits such as the density of the indumentum, the texture and dissection of leaves and bracts, etc., or obviously reductive characters are used that result from adaptations to environmental stress such as the reduction in number of pinnae of a leaf. The following examples refer however to qualitatively different traits for which an independent evolutionary origin is highly unlikely. First, in the more ancient families of conifers, Araucariaceae and Podocarpaceae, the wood rays are solely composed of parenchyma cells. An innovation, the additional appearance of tracheidal cells, is found in most, but not all genera of the Pinaceae (lacking in *Abies*, *Keteleeria*, and *Pseudolarix*); it is not consistently present in all species of the genera where it occurs (as in *Pinus*, *Cedrus*, *Picea*, and *Pseudotsuga*). In the Taxodiaceae tracheidal ray cells occur only in two genera, and in the Cupressaceae only in a few species (Greguss 1955). Since the taxonomy of the conifer families is based on a wide array of characters and hardly to be challenged, we are forced to conclude that this innovation originated early in the evolution of conifers, but that its genetic potential is not realized in all members of the group.

Another example refers to the conversion of calyx lobes to leaflike structures which is characteristic of many members of the Rubiaceae. In the periphery of the inflorescences one finds flowers with outward directed calyx lobes which are converted into foliaceous semaphylls of red or white coloration (Leppik 1977). In some species, the enlarged calyx lobes are transformed into a wing of the fruit. The continual recurrence of enlarged calyx lobes runs across the tribal classification of the Rubiaceae and is not even constant at the generic level. In *Mussaenda* and *Pentas*, for instance, some species have enlarged calyx lobes and some have equal ones (Verdcourt 1958). Reclassification following the character states of the calyx

would result in much less ordered character distributions and would increase the amount of parallelism and is therefore to be excluded. Again one is forced to assume that the genetic potential for the formation of these semaphylls has originated in the common ancestor of the tribes where this structure occurs, while these genes are not transcribed in all its descendants.

In other words, part of the genetic information of lineages of land plants can be expressed during certain phases of their evolutionary history and not so during others. This recalls the phenomenon of differential gene activation that, during ontogeny, is responsible for the coordinated and harmonic development of every organism.

#### GENOME SIZE, NUMBERS OF GENES, AND "SILENT" GENES

It is a well-known fact that all eukaryotic genomes contain much more DNA than would be essential for instructing the development and maintaining the functions of an organism. In angiosperms a strong correlation exists between the total DNA amount and a number of developmental variables such as cell size, mitotic cycle, and life form (Bennett 1972). In some instances the DNA content has been shown to vary in correlation with phenological strategies (Price 1987). This means that the total amount of DNA on the one hand and the number of genes on the other are independent variables subject to different selective control.

Indeed the genome of eukaryotic cells contains three classes of DNA sequences: highly repetitive, intermediately repetitive, and single (unique) sequences. There is some evidence that the intermediate repetitive DNA, which is dispersed throughout the genome, is involved in gene regulation (Britten and Davidson 1969). With a few exceptions genes are confined to the single sequence fraction. The portion of repetitive sequences can vary considerably. In higher plants values between 18 and 95% were recorded. Molecular mechanisms are known that explain the selective replication (=amplification) of the highly repetitive sequences (=heterochromatin). Thus the total DNA amount per genome can vary within wide limits.

If we try to relate estimates of the number of genes with the available amounts of nonrepetitive DNA, we can start from the generally accepted assumption that 50,000 genes are required to code for all proteins in man, while the estimate is 5000 for invertebrates such as *Drosophila*. Thus certainly not more than 5000–10,000 protein-coding genes are required for a higher plant, the structural complexity of which is far less than that of an animal. However, the *Drosophila* genome contains 0.1 pg DNA per haploid equivalent (1 C-value), the human genome 2.9 pg, while the vast majority of angiosperms contain more than 1 pg (Bennett and Smith 1976; Bennett, Smith, and Heslop-Harrison 1982).

For these reasons it is inevitable to conclude that the angiosperm genome contains much more genetic information than would be required for coding for all essential functions. The high DNA amount of angiosperms may be a heritage from their ancestors, although the minimal value in gymnosperms (and in ferns as well) has been shown to be more than one order of magnitude higher than that of angiosperms (Sparrow, Price, and Underbrink 1972; Price 1976).

It is very likely then that most of the genes of angiosperm genomes must reversibly or irreversibly be silenced through powerful repression mechanisms and can be individually reactivated through a wide variety of internal and external

influences. Cell cultures have proven as an especially well-suited tool for demonstrating that the genetic potential of plant cells is often higher than, or at least different from, that of the intact plant living under normal conditions (Böhm 1977). Thus cell cultures of *Ricinus communis* L. under special growth conditions produced rhodoxanthin, a retro-carotenoid not present in the whole plant and otherwise known only from a limited number of different nonrelated species of green land plants (Kayser and Gemmrich 1984). While intact plants of species of *Weigelia*, *Lonicera*, *Symphoricarpus*, and *Hydrangea* contain secologanin, cell cultures did not, but had the capacity of transforming added loganin to secologanin (Tanahashi, Nagakura, Inouye, and Zenk 1984). Cell cultures of *Akebia quinata* Decne., *Cinchona ledgeriana* Moens and *Tabernaemontana elegans* Stapf all produced an array of triterpenes, anthraquinones and indole alkaloids, respectively, but among the individual substances of these classes some were unknown from the whole plants (Ikuta and Itokawa 1986; Robins, Payne, and Rhodes 1986; van der Heijden, Brouwer, Versoote, Wijnsma, Beek, Harkes, and Svendsen 1986). Cell cultures of *Ochrosia elliptica* Labill. under certain laboratory conditions were found to produce mainly alkaloids known from the whole plant (Kouadio, Creche, Chemieux, Rideau, and Viel 1985), while under different conditions, i.e., mainly in another culture medium, compounds were produced most of which are closely related to, but different from metabolites known from the whole plant (Pawelka and Stöckigt 1986). The finest example pertinent to this problem has been provided by Wink and Witte (1983) who worked with quinolizidine alkaloids which are known mostly from Leguminosae. By adding various substances to the culture medium, or simply transferring the cells into fresh medium, they were able to induce quinolizidine alkaloid accumulation in cell cultures of species belonging to the Chenopodiaceae, Umbelliferae, Boraginaceae, and Solanaceae, which are known to produce no alkaloids at all or only other alkaloids. The conclusion of Wink and Witte was that the genes for the synthesis of quinolizidine alkaloids are obviously not restricted to the Leguminosae but must be widely distributed in higher plants.

#### LEVELS OF GENE CONTROL

Plant morphologists are well aware of cases where similar changes appear in nonrelated lineages and even in nonhomologous organs. One example is the "tortuosa" syndrome, which leads to tortuous growth of the branches or sometimes even the leaves; it has been identified in a number of woody and herbaceous plants, such as the shoots of *Corylus avellana* L., *Fagus sylvatica* L., and *Robinia pseudoacacia* L., and the leaves of *Juncus effusus* L. Although in this case the molecular and developmental background has not yet been analyzed, we are convinced that phenomena like this one must have a common developmental basis.

The general concept of gene control is well established at the molecular level. It depends on the existence of a particular class of proteins that bind to specific DNA sequences, thus reversibly affecting their expression. The action of these regulatory proteins is modulated by a number of chemical and physical signals. In plant development, hormones and red light ( $\lambda = 680$  nm), among others, have a profound influence on their activity. Consequently, the mechanism of gene expression allows quick response to environmental signals. Regulatory proteins,

which themselves are gene products of particular regulatory genes, can also influence the expression of other regulatory genes, whose products in turn influence a further set of genes etc. Thus a cascade is formed in which genes display their activities at successive hierarchical levels. A "high ranking" regulatory gene controls a large number of "low ranking" or "subordinate" genes and thus a number of characters in the phenotype. Thus changes in the expression of a single high ranking regulatory gene can have profound effects as exemplified by the "tortuosa" syndrome and by phenomena known from the development of *Drosophila* and other animals.

The development of multicellular organisms (plants as well as animals) in general proceeds through a one-way activation of particular genes or sets of genes, while others are repressed at the same time. This kind of gene control acts through successive switches that are typical of any program of differentiation. Plants are usually characterized as open systems, and their development can be described as a repeated production of modules, such as internodes, leaves, flowers, etc. The change from one module to another is induced by the expression of a particular gene. As soon as a decision of this kind is taken, other "lower ranking" genes are required for the realization of the particular characters of the module in question. Genetic programs may change at all hierarchic levels. Changes of "low ranking" genes can affect special traits in the realization of the module; changes in "high ranking" genes can affect the production of the whole module.

Genes affecting early decisions of the developmental program have been called *homoeotic genes*. Although different genes of this category perform quite diverse functions in shaping the phenotype, a conspicuous molecular link between them has been uncovered recently: Corresponding nucleotide sequences have been identified in three homoeotic genes of *Drosophila* and it has been shown that these sequences are also present in homoeotic genes of frogs and mammals, indicating that these sequences are widespread and highly conserved (McGinnis, Garber, Wirz, Kuroiwa, and Gehring 1984; Carrasco, McGinnis, Gehring, and DeRoberts 1984).

Gene activities are usually limited to certain developmental stages of particular organs or tissues. Under special circumstances their expression can influence an organ that is usually dependent on other genes. The ontogeny of phylloclades provides a pertinent example. In several lineages of xerophytic plants the leaves are strongly reduced and photosynthesis takes place in phylloclades. In *Semele androgyna* (L.) Kunth and other members of the Asparagaceae these organs resemble pinnate leaves, as judged by their size, arrangement and number of pinnae, and development (Cooney-Sovetts and Sattler 1986). Obviously the "leafy" traits of the phylloclade are determined by a homoeotic gene that is normally involved in leaf development.

In such instances homoeotic genes may override controls, thus providing "rescue mechanisms" which allow stem primordia to differentiate into leaflike phylloclades that substitute leaves. Similar situations may occur in reproductive organs and Troll (1928) had pointed to several examples of straight similarity between flowers and pseudanthia.

These examples illustrate that the action of "high ranking" genes can be independent from those that are essential for the fine-tuning of developmental processes; when these two sorts of genes are "recombined" in an unusual way, their action may result in what Sattler (1984) has called "partial homology."

## TRANSPOSABLE ELEMENTS AS GENERATORS OF DIVERSITY

Apart from the genes that are involved in the regular developmental program, the category of unstable or labile genes has to be considered, which in plants lead to phenomena such as mosaicism, variegation, and position effects, and which are known from animals (*Drosophila*) as well. In maize these genes are responsible for a conspicuous pigmentation pattern in the endosperm, the genetic background of which was analyzed by McClintock (1950). She came to the conclusion that mobile "controlling elements" are present in the maize genome which can cause gene inactivation and chromosomal rearrangements. More recently it was shown that the "controlling elements" are distinct DNA segments which under certain circumstances can change their place in the genome and can inhibit the transcription of the nucleotide sequences in which they are inserted. These DNA segments are now called *transposable elements* or "*jumping genes*" (Nevers and Saedler 1977; Döring and Starlinger 1984; Fedoroff 1984; Nevers, Shepherd, and Saedler 1986). They have been isolated and characterized at the molecular level from a number of higher plants such as maize, teosinte, snap-dragon, and soybean, from *Drosophila* and from yeast and bacteria. It becomes increasingly clear that they are widespread and frequent in all kinds of organisms and that they play an important role as diversity generators. As predicted by McClintock they do not only control gene expression, but are also instrumental in controlling chromosomal rearrangements and chiasma frequency, phenomena which in turn are closely linked to evolutionary change (Stebbins 1950). When transposons are excised from a nucleotide sequence they leave behind them a small sequence as a footprint. The introduction of such sequences into a gene may alter permanently its expression rate or its information content or may remain without any effect at all. This depends among other things on the site of insertion of the transposable element either in a promotor region, an intron, or an exon.

In conclusion, many of the effects, elicited through the action of transposable elements on the spur of the moment seem to be destructive, thus hardly supporting stable evolutionary novelties. However, when recalling that many evolutionary trends in angiosperms are reductive (Takhtajan 1976), transposable elements indeed provide a conclusive explanation. In comparison with ferns and gymnosperms, angiosperms have a much higher evolutionary plasticity, which allows them to adapt to a wider variety of environmental conditions, and it is tempting to speculate that they have developed mechanisms for a more efficient use of the transposition system.

Since the process of "gene silencing" through transposable elements to some degree is reversible, the original genetic information may recover independently in more or less closely related lineages. As an evolutionary mechanism this is superior to the loss or irreversible change of genes. Gene losses have been demonstrated in a few cases, and all of them are accompanied by a very high degree of specialization (Price and Bachmann 1975; Bachmann, Chambers, and Price 1979).

## THE DISSOLUTION OF THE CONCEPT OF THE GENE

It has been said that it is not gene combinations but individual genes that have evolutionary continuity. In the light of modern developments even the integrity

of the gene has to be challenged, and ideas referring to "proteins in pieces" and "genes in pieces" have been put forward. How far the nucleotide sequence of a gene can be rearranged becomes clear from the following example. In plants, especially in legumes, specific carbohydrate binding proteins (lectins) exist, for instance Concanavalin A in *Canavalia ensiformis* DC., which has a single polypeptide chain consisting of 237 amino acid residues. In *Vicia faba* L. another lectin with a different sugar binding specificity, favin, is present. A comparison of the two proteins revealed a circular permutation of extensive homologous sequences. Favin is made up of two polypeptides; its  $\alpha$ -chain corresponds to residues 70–119 of Concanavalin A, and the  $\beta$ -chain corresponds to the remaining sequences 120–237 followed by 1–69. Its gene thus is a fusion product of the two terminal sections of the Concanavalin A gene (Cunningham, Hemperley, Hopp, and Edelman 1979). A third lectin, again with different binding specificity, is known from soybean; in its sequence arrangement it is identical with favin, but its polypeptide chain is uninterrupted. Thus, it corresponds to a fusion product of the  $\alpha$ - and  $\beta$ -chain of favins (Lis and Sharon 1986).

From this follows that nucleotide sequences can be rearranged in the course of evolution, which leads to products with changed properties. To a large extent this recombinational potential is due to the organization of eukaryotic genes which contain transcriptional units (exons) that are separated by nontranscriptional sequences (introns). Exons can be combined in various ways, and through this process whole protein families may originate (Dayhoff 1972), all members of which may have the same catalytic activity, while differing through their substrate specificity. One of the most impressive examples of this process is the rise of the NAD-dehydrogenase family (Eventoff and Rossmann 1976).

#### HORIZONTAL GENE TRANSFER

To our knowledge Went (1971) was the first to postulate ample nonsexual gene transfer between nonrelated organisms. With this process he tried to explain striking similarities in growth form, leaf shape, leaf and flower pigmentation, and so on, which are prominently represented in geographically restricted regions. Without trying to discuss the validity of Went's specific examples, it appears to us that his suggestions cannot be dismissed, although in the light of contemporary knowledge two of Went's assumptions appear unlikely: (a) Transfer of plant DNA by viruses cannot be very important since most plant viruses are RNA viruses that cannot transmit DNA. (b) Went's idea that whole groups of genes can be transmitted is improbable: If one assumes that transmission is a statistical process, one would expect nucleotide sequences of different length as a result of this process. This would imply a great variability in the characters transmitted to various recipients so that common traits hardly could be recognized.

If one assumes, in contrast, that only single genes or functional pieces of them are transmitted, the process of gene transfer does not only become more likely but its result will be more readily identifiable. We do not postulate special vectors for gene transfer, such as aphids, viruses, etc., but rather favor the possibility of direct transfer of DNA into plant cells. Everywhere in the environment of living organisms great amounts of extracellular DNA exist, which are released from decaying organic material and disperse over the surface of living organisms. It is true that neither viruses nor extracellular DNA can invade completely intact,

healthy plant organs. However, local minor injuries of the epidermis that originate from the movement of passing animals, from rubbing of the leaves against each other in the wind and so on, can create the sites of uptake of alien nucleic acids. The virulence of plant viruses, which have no mechanism for active entrance in plant cells, demonstrates that an uptake of macromolecules and macromolecular complexes into plant cells can take place. Under laboratory conditions DNA and RNA have repeatedly been introduced into living cells. Once they have come in contact with the plasmalemma, they are ingested by phagocytosis. Certainly incorporation of alien DNA into the genome of the nucleus is a difficult step, but that it *can* occur has not only been demonstrated by experiments with transformed protoplasts, but is also evident from the exchange of genes between the nucleus, plastids, and mitochondria that has taken place in the course of evolution. *The relative simplicity of the methods used for transformation in plant genetic engineering suggests that this process may exist in nature as well.* Nevertheless, efficient conservative mechanisms exist that try to keep small the frequency of such events, so that the genetic programs of cells are not disrupted. As in bacteria, there are protective mechanisms in higher plants that usually prevent the uptake and incorporation of alien nucleic acid into the genome. Nucleases are common and are frequently secreted over the surface of the organisms producing them, thereby acting as extracellular enzymes. In plants, which as a rule are capable of vegetative propagation, transformed cells can become part of the gene pool. In animals, horizontal gene transfer will have little impact since vegetative propagation is rare and soma and germ line are strictly separated.

#### THE ENIGMA OF PLANT HEMOGLOBINS

Most remarkable is the occurrence and distribution of plant hemoglobin, which is known so far from eight families of dicotyledons which are not closely inter-related, including the Leguminosae, Ulmaceae, Rhamnaceae, Datisceae, etc. (Landsmann, Dennis, Higgins, Appelby, Kortt, and Peacock 1986). Most of these plants have a symbiotic relationship with N-fixing bacteria or actinomycetes. Through its binding capacity for oxygen, hemoglobin is capable of creating anaerobic spaces in which the nitrogenase can act. The plant gene has a 4 exon-3 intron structure, while in vertebrates exons 2 and 3 are fused, forming a long internal exon (see Lewin 1985). In the arthropod gene there are no introns at all. Hence the suggestion that plant hemoglobin originated from transfer from insects is very unlikely. In view of its highly complicated structure, an independent, convergent origin of hemoglobin in eight plant families must be gauged as highly unlikely either. In order to account for the erratic distribution of plant hemoglobin, two possibilities remain: (a) the occasional expression of a widely distributed, ancient and repressed gene, and (b) horizontal gene transfer from vertebrates. According to the first possibility the globin gene family must be expected not only to be widespread in modern plants but to have its evolutionary origin in the ancestor common to modern plants and animals. Landsmann et al. (1986) argue for a cryptic expression of this gene in nonsymbiotic tissue of plants in order to explain its "survival" during evolution. In our opinion this suggestion is unnecessary since, as it was pointed out before, all eukaryotic genomes contain unexpressed DNA sequences in abundance. Obviously there is no selection pressure to discard them. But one should keep in mind that protein synthesis is extremely

energy consuming, and that it is more advantageous to store unexpressed genes and to express them only on demand. The second possibility—horizontal gene transfer—would imply a change in the exon-intron structure of vertebrate hemoglobin in plants, which appears less likely albeit not impossible.

Although at present it cannot be decided whether the presence of hemoglobin in plants is due to vertical or horizontal gene transfer, both alternatives would provide examples of striking parallelism.

#### CONSEQUENCES FOR CLASSIFICATION AND EVOLUTIONARY RECONSTRUCTION

Problems connected with parallelism and related phenomena have been a constant challenge for many biologists, among them as thoughtful ones as Wernham (1912), Arber (1925), Cronquist (1963), Hennig (1982), Meyen (1973), and Stevens (1986). It is apparent from their work that the discussion of parallelism cannot be divorced from that of homology. Not only in the contemporarily leading school of biological classification, cladistics, but in all scientific approaches to plant classification the concept of homology has a central position. In order to accommodate what he considered to be nonhomologous variation, Simpson (1961) took up the concept of "homoplasy"; this term covers parallelism, convergence, analogy, mimicry, and chance similarity. It is only recently that the use of this concept has been taken up by cladists in order to quantify the amount of traits which are in conflict with those that support a suggested pattern (e.g., Dahlgren and Bremer 1985; Doyle and Donoghue 1986; Johnson and Briggs 1984). In other words, homoplasy corresponds to what can loosely be described as evolutionary and classificatory noise. While admittedly a careful analysis will be able to resolve some of these conflicts, the presence of extensive homoplasy presents a challenge both for methodology and for biological explanation (Stevens 1986, 1987). It is ironic that homoplasy can only be analyzed, or even detected, in a kind of classification in which its massive amount may impede its construction.

With our insight from molecular biology we can now say that parallelism may be, and certainly often is, due to one of the following alternatives: (a) erratic activation or inactivation of genes; (b) activation of alternative pathways under the control of regulatory genes; or (c) horizontal gene transfer. The influence from developmental biology on morphological thinking has led to relaxed definitions of homology. One notable example is the definition given by Roth (1984) who wants to base homology on the sharing of pathways of development, which are controlled by genealogically related genes. Sattler (1984) pleads for different degrees of homology, which agrees with the idea that nucleotide sequences in the course of evolution not only can be altered by point mutations, but can also be separated and rearranged, apart from being activated or inactivated. Another corollary of the foregoing is that parallelism cannot be classified with certainty as a nonhomologous phenomenon; the contrary may frequently be true. This is reflected in Roth's notion that a distinction between homology and parallelism may be impossible not only for methodological, but also for biological reasons, and that one must acknowledge that the course of evolution may not be as orderly as the algorithms that are used to delineate the patterns of character distributions. Indeed the two current algorithmic approaches to plant classification—cladistics and phenetics—may both be appropriate in contrasting situations. This is because reversible silencing of genes, by increasing the amount of randomly

distributed character sets, creates "phenetic" situations, while strictly ordered character distributions lend themselves for cladistic treatments.

Apart from parallelisms, reversals may afflict patterns equally frequently. It appears to us that they need not only be artifacts of the process of classification, as many believe, but at least in part may represent instances of neoteny (Johnson and Briggs 1984). Other reversals that appear biologically unfounded, and which Johnson and Briggs (1984) therefore do not wish to admit, may be easily explained as switching off or on alternative pathways.

It is evident that molecular biology will take over a leading part in the explanation of observable patterns. However, in the absence of information from molecular biology it would be meaningless to discuss whether disjunct traits (such as the occurrence of plant hemoglobin in eight angiosperm families, or of betalains in the Centrospermae and certain fungi) were due to the activation of ancient genes, of horizontal gene transfer or were acquired independently.

#### CONCLUSION

In spite of the perturbing influence of the abovementioned processes, their impact on evolution seems to be small, or otherwise the taxonomic structure of families, genera, and species would not be perceptible. Indeed evolution by and large must have worked orderly and resulted in hierarchically organized entities, a fact that could not be anticipated from the stochasticity at the molecular level. It is difficult to decide whether (a) this is due to the rarity of processes such as reactivation of silenced genes or horizontal gene transfer, whether (b) the consequences of such events are shielded by the stability of the epigenetic system, or whether (c) stabilizing selection works to admit only a limited number of the many possible phenotypes. The role of developmental canalization, fervently discussed and focussed on in several recent symposia (e.g., see Humphries 1988, and *J. Linn. Soc., Biol.* 39(2):97-191. 1990), can scarcely be overemphasized. Each level of investigation, the molecular, the developmental, the morphological, and the taxonomic one, calls for appropriate methods, but it should always be borne in mind that these levels of investigation are complementary. The fact that homology, homoiology, parallelism and perhaps analogy and convergence "converge" into each other on the molecular level does not undermine their utility on the morphological one. But it may be responsible for some of their lack of exactitude.

#### ACKNOWLEDGMENTS

The authors are most grateful for the valuable suggestions received from Drs. J. Praglowski and M. H. Zenk, and two anonymous reviewers.

#### ADDENDUM

This paper had been prepared for the Rolf Dahlgren Memorial Symposium at the International Botanical Congress at Berlin in 1987 and submitted for publication in the same year. In the meantime, there has developed a strong interest in the topics raised here, leading to a large number of publications, of which the following are especially pertinent here. Sanderson and Donoghue (1989) have shown that the amount of homoplasy is more or less correlated with the size of

the taxon under study, and not with its biology. Roth (1988) extended and clarified her earlier concepts of homology, pointing out that difficulties with homology usually point to biologically interesting problems. The justification for publishing our paper with such a long delay may be sought in the fact that papers discussing the biological background of parallelism with reference to plants are still rare. Of special importance are therefore Sattler's (1988) essay on homoeosis in plants, Harborne's (1990) paper on the constraints of biochemical pathways, and Endress's (1990) article on patterns in floral construction.

*Added in proof:* Recent and important contributions to the topics covered in this paper have been published in a series of articles in *Science* 250:923–966, 1990, and in *Aust. Syst. Bot.* 3:1–163, 1990.

## LITERATURE CITED

- Arber, A. 1925. *Monocotyledons. A morphological study.* Cambridge University Press, Cambridge. 258 p.
- Bachmann, K., K. L. Chambers, and H. J. Price. 1979. Genome size and phenotypic evolution in *Microseris* (Asteraceae, Cichorieae). *Pl. Syst. Evol., Suppl.* 2:41–66.
- Baur, E. 1930. *Einführung in die Vererbungslehre.* 7–11. Aufl. Verlag Gebr. Bornträger, Berlin. 478 p.
- Bennett, M. D. 1972. Nuclear DNA contents and minimum generation time in herbaceous plants. *Proc. Roy. Soc. London, Ser. B, Biol. Sci.* 181:109–135.
- , and J. B. Smith. 1976. Nuclear amounts in angiosperms. *Philos. Trans., Ser. B* 274:227–274.
- , ———, and J. S. Heslop-Harrison. 1982. Nuclear DNA amounts in angiosperms. *Philos. Trans., Ser. B* 216:179–199.
- Böhm, H. 1977. Secondary metabolism in cell cultures of higher plants and problems of differentiation, pp. 104–123. *In* M. Luckner, L. Nover, and H. Böhm [eds.], *Secondary metabolism and cell differentiation.* Springer, Heidelberg.
- Britten, R. J., and E. H. Davidson. 1969. Gene regulation for higher cells: a theory. *Science* 165:349–357.
- Campo, M. van. 1976. Patterns of pollen morphological variation within taxa, pp. 125–135. *In* J. K. Ferguson and J. Muller [eds.], *The evolutionary significance of the exine.* Academic Press, London.
- , and D. Vernier. 1984. Les grains de pollen. *Séries morphologiques et structures de l'exine.* *Giorn. Bot. Ital.* 118:255–270.
- Carrasco, A. E., W. McGinnis, W. J. Gehring, and E. M. DeRobertis. 1984. Cloning of an *X. laevis* gene expressed during early embryogenesis coding for a peptide region homologous to *Drosophila* homeotic genes. *Cell* 37:409–414.
- Clarke, G.-C. S. 1975. Irregular pollen grains in some *Hypericum* species. *Grana* 15:117–125.
- Cooney-Sovetts, C., and R. Sattler. 1986. Phylloclade development in the Asparagaceae: an example of homoeosis. *J. Linn. Soc., Bot.* 94:327–371.
- Croizat, L. 1964. *Space, time form: the biological synthesis.* Published by the author, Caracas.
- Cronquist, A. 1963. The taxonomic significance of evolutionary parallelism. *Sida* 1:109–116.
- . 1977. On the taxonomic significance of secondary metabolites. *Pl. Syst. Evol., Suppl.* 1:179–189.
- Cunningham, B. A., J. J. Hemperley, H. P. Hopp, and G. M. Edelman. 1979. Favin versus Concanavalin A: circularly permuted amino acid sequences. *Proc. Natl. Acad. U.S.A.* 76:3218–3222.
- Dahlgren, R. 1970. Parallelism, convergence, and analogy in some South African genera of Leguminosae. *Bot. Not.* 123:551–568.
- . 1983. General aspects of angiosperm evolution and macrosystematics. *Nord. J. Bot.* 3:119–149.
- , and K. Bremer. 1985. Major clades of the angiosperms. *Cladistics* 1:349–368.
- Dayhoff, M. O. 1972. *Atlas of protein sequence and structure, Vol. 5.* Nat. Biochem. Res. Found., Washington, D.C. 542 p.

- Döring, H. P., and P. Starlinger. 1984. Barbara McClintock's controlling elements: now at the molecular level. *Cell* 39:253-259.
- Doyle, J. A., and M. J. Donoghue. 1986. Seed plant phylogeny and the origin of angiosperms: an experimental cladistic approach. *Bot. Rev. (Lancaster)* 52:321-431.
- Endress, P. K. 1987. Floral phyllotaxis and floral evolution. *Bot. Jahrb. Syst.* 108:417-438.
- . 1990. Patterns of floral construction in ontogeny and phylogeny. *J. Linn. Soc., Biol.* 39:153-175.
- Eventoff, W., and M. G. Rossmann. 1976. The structure of dehydrogenases. *Trends Biochem. Sci.* 1:257-260.
- Fedoroff, N. 1984. Transposable genetic elements in maize. *Sci. Amer.* 250:65-74.
- Gardner, R. O. 1977. Systematic distribution and ecological function of the secondary metabolites of the Rosidae-Asteridae. *Biochem. Syst. Ecol.* 5:29-35.
- Gottlieb, O. R. 1982. *Micromolecular evolution, systematics and ecology.* Springer, Heidelberg. 170 p.
- Grehan, J. R., and R. Ainsworth. 1985. Orthogenesis and evolution. *Syst. Zool.* 34:174-192.
- Greguss, P. 1955. *Xylotomische Bestimmung der heute lebenden Gymnospermen.* Akademiai Kiado, Budapest. 308 p., 350 pl.
- Harborne, J. B. 1990. Constraints in the evolution of biochemical pathways. *J. Linn. Soc., Biol.* 39:135-151.
- Heijden, R. van der, R. L. Brouwer, R. Versoote, R. Wijnsma, R. A. van Beek, P. A. A. Harkes, and A. Baerheim Svendsen. 1986. Indole alkaloids from a callus culture of *Tabernaemontana elegans*. *Phytochemistry* 25:843-846.
- Hennig, W. 1982. *Phylogenetische Systematik.* Parey, Berlin. 246 p.
- Heslop-Harrison, J. 1976. The adaptive significance of the exine, pp. 27-37. *In* J. K. Ferguson and J. Muller [eds.], *The evolutionary significance of the exine.* Academic Press, London.
- Humphries, C. J. (ed.) 1988. *Ontogeny and systematics.* Columbia University Press, New York. 236 p.
- Ikuta, A., and H. Itokawa. 1986. Triterpenoids of *Akebia quinata* callus cultures. *Phytochemistry* 25:1625-1628.
- Johnson, L. A. S., and B. Briggs. 1984. Myrtales and Myrtaceae—a phylogenetic analysis. *Ann. Missouri Bot. Gard.* 71:700-756.
- Kayser, H., and A. R. Gemmrich. 1984. Hormone induced changes in carotenoid composition in *Ricinus* cell cultures. I. Identification of rhodoxanthin. *Z. Naturf.* 39c:50-54.
- Köhler, E. 1967. Über die Beziehungen zwischen Pollenmorphologie und Ploidiestufen im Verwandtschaftsbereich der Gattung *Phyllanthus* (Euphorbiaceae). *Feddes Repert.* 74:159-165.
- Kouadio, K., J. Creche, J.-C. Chemieux, M. Rideau, and C. Viel. 1985. Alkaloid production by *Ochrosia elliptica* cell suspension cultures. *J. Pl. Physiol.* 118:277-283.
- Kubitzki, K. 1987. Origin and significance of trimerous flowers. *Taxon* 36:21-28.
- , and O. R. Gottlieb. 1984a. Micromolecular patterns and the evolution and major classification of angiosperms. *Taxon* 33:375-391.
- , and ———. 1984b. Phytochemical aspects of angiosperm origin and evolution. *Acta Bot. Neerl.* 33:457-468.
- Landsmann, J., E. S. Dennis, T. J. V. Higgins, C. A. Appelby, A. A. Kortt, and W. J. Peacock. 1986. Common evolutionary origin of legume and non-legume plant hemoglobins. *Nature* 324:166-168.
- Leppik, E. E. 1977. Calyx-borne semaphylls in tropical Rubiaceae. *Phytomorphology* 27:161-168.
- Le Thomas, A. 1980/81. Ultrastructural characters of the pollen grains of African Annonaceae and their significance for the phylogeny of primitive angiosperms. *Pollen & Spores* 22:267-342; 23:5-36.
- Lewin, R. 1984. Surprise finding with insect globin genes. *Science* 226:328.
- Lis, H., and N. Sharon. 1986. Lectins as molecules and tools. *Annual Rev. Biochem.* 55:35-67.
- McClintock, B. 1950. The origin and behavior of mutable loci in maize. *Proc. Natl. Acad. U.S.A.* 36:344-355.
- McGinnis, W., R. L. Garber, J. Wirz, A. Kuroiwa, and W. J. Gehring. 1984. A homologous protein-coding sequence in *Drosophila* homeotic genes and its conservation in other metazoans. *Cell* 37:403-408.
- Meyen, S. V. 1973. Plant morphology in its nomothetical aspects. *Bot. Rev. (Lancaster)* 39:205-260.

- Naegeli, C. v. 1884. *Mechanisch-physiologische Theorie der Abstammungslehre*. R. Oldenbourg, München und Leipzig. 822 p.
- Nevers, P., and H. Saedler. 1977. Transposable genetic elements as agents of gene instability and chromosomal rearrangements. *Nature* 268:109-115.
- , N. S. Shepherd, and H. Saedler. 1986. Plant transposable elements. *Adv. Bot. Res.* 12:103-203.
- Pawelka, K.-H., and J. Stöckigt. 1986. Indole alkaloids from *Ochrosia elliptica* plant cell cultures. *Z. Naturf.* 41c:381-384.
- Plate, L. 1928. Über Vervollkommnung, Anpassung und Unterscheidung von niederen und höheren Tieren. *Zool. Jahrb. Physiol. (Festschr. Hesse)*: 745-798.
- Price, H. J. 1976. Evolution of DNA content in higher plants. *Bot. Rev. (Lancaster)* 42:27-52.
- . 1987. Variation in DNA of maize. XIV Internat. Botanical Congress, Berlin (Abstract 3-10-3).
- , and K. Bachmann. 1975. DNA content and evolution in the Microseridinae. *Amer. J. Bot.* 62:262-267.
- Punt, W., J. S. de Leeuw van Weenen, and W. A. P. Oostrum. 1974. Northwest European pollen flora. 3. Primulaceae. *Rev. Palaeobot. Palynol.* 17: NEPF 31-70.
- Raven, J. A. 1977. The evolution of vascular plants in relation to supracellular transport processes. *Adv. Bot. Res.* 5:153-219.
- Robins, R. J., J. Payne, and M. J. C. Rhodes. 1986. The production of anthraquinones by cell suspension cultures of *Cinchona ledgeriana*. *Phytochemistry* 25:2327-2334.
- Roth, V. L. 1984. On homology. *J. Linn. Soc., Biol.* 22:13-29.
- . 1988. The biological basis of homology, pp. 1-26. *In* C. J. Humphries [ed.], *Ontogeny and systematics*. Columbia University Press, New York. 236 p.
- Sanderson, M. J., M. J. Donoghue. 1989. Patterns of variation in levels of homoplasy. *Evolution* 43:1781-1795.
- Sattler, R. 1984. Homology—a continuing challenge. *Syst. Bot.* 9:382-394.
- . 1988. Homeosis in plants. *Amer. J. Bot.* 75:1606-1617.
- Simpson, G. G. 1961. *Principles of animal taxonomy*. Columbia University Press, New York. 247 p.
- Sparrow, A. H., H. J. Price, and A. G. Underbrink. 1972. A survey of DNA-content per cell and per chromosome of prokaryotic and eukaryotic organisms: some evolutionary considerations. *Brookhaven Symp. Biol.* 23:451-494.
- Sporne, K. R. 1962. *The morphology of pteridophytes*. Hutchinson, London. 191 p.
- Stebbins, G. L. 1950. *Variation and evolution in plants*. Columbia University Press, New York and London. 643 p.
- Stevens, P. 1984. Homology and phylogeny: morphology and systematics. *Syst. Bot.* 9:395-409.
- . 1986. Evolutionary classification in botany, 1960-1985. *J. Arnold Arbor.* 67:313-339.
- . 1987. Pattern and process: phylogenetic reconstruction in botany, pp. 155-179. *In* H. M. Hoenigswald and L. F. Wiener [eds.], *Biological metaphor and cladistic classification*. University of Philadelphia Press, Philadelphia.
- Takhtajan, A. 1976. Neoteny and the origin of flowering plants, pp. 207-219. *In* C. B. Beck [ed.], *Origin and early evolution of angiosperms*. Columbia University Press, New York and London.
- Tanahashi, T., N. Nagakura, H. Inouye, and M. H. Zenk. 1984. Radioimmunoassay for the determination of loganin and the biotransformation of loganin to secologanin by plant cell cultures. *Phytochemistry* 23:1917-1922.
- Tomlinson, P. B. 1984. Homology: an empirical view. *Syst. Bot.* 9:374-381.
- Troll, W. 1928. *Organisation und Gestalt im Bereich der Blüte*. Springer, Berlin. 413 p.
- Vavilov, N. J. 1922. The law of homologous series in variation. *J. Genet.* 12:47-89.
- Verdcourt, B. 1958. Remarks on the classification of the Rubiaceae. *Bull. Jard. Bot. État* 28:209-290.
- Walker, J. W., and A. G. Walker. 1980. Comparative pollen morphology of the mainland African genera of Myristicaceae (*Cephalosphaera*, *Coelocaryon*, *Pycnanthus* and *Scyphocephalum*). *Amer. J. Bot.* 67:603-611.
- , and ———. 1981. Comparative pollen morphology of the Madagascan genera of Myristicaceae (*Mauloutchia*, *Brochoneura* and *Haematodendron*). *Grana* 20:1-17.
- Went, F. W. 1971. Parallel evolution. *Taxon* 20:197-226.
- Wernham, H. F. 1912. Floral evolution with particular regard to the sympetalous dicotyledons. IX. Summary and conclusions. *New Phytol.* 11:373-397.

- Wink, M., and L. Witte. 1983. Evidence for a wide-spread occurrence of the genes of quinolizidine alkaloid biosynthesis. *FEBS Lett.* 159:196.
- Zimmermann, W. 1959. *Die Phylogenie der Pflanzen.* G. Fischer, Jena. 777 p.

## FOOTNOTES

<sup>1</sup> Dedicated to the memory of Rolf Dahlgren (1932–1987).

<sup>2</sup> Based on a presentation by K. Kubitzki given at the XIV International Botanical Congress in Berlin, 1 August 1987, as part of the Rolf Dahlgren Memorial Symposium entitled "Steps toward the natural system of the dicotyledons," chaired by R. F. Thorne and H. Huber.