

Erwin Baur or Carl Correns: Who Really Created the Theory of Plastid Inheritance?

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Historical reviews of the field of non-Mendelian genetics and many other publications credit Erwin Baur and Carl Correns equally for the development of the theory of plastid inheritance. However, a study of the original literature indicates that this conclusion is not correct. Analysis of the relevant articles leads to the conclusion that Baur alone deserves credit for the theory of plastid inheritance. In his classic article on the inheritance properties of white-margined *Pelargonium* plants, Baur (1909) stated: (1) The plastids are carriers of hereditary factors which are able to mutate. (2) In variegated plants, random sorting-out of plastids is taking place. (3) The genetic results indicate a biparental inheritance of plastids by egg cells and sperm cells in *Pelargonium*. By contrast, Correns held the view that in variegated plants there is a maternally transmitted labile state of the cytoplasm which switches either to a permanently “healthy” state (allowing the “indifferent” plastids to become green chloroplasts) or to a permanently “diseased, ill” cytoplasmic state (causing white plastids and cells). Otto Renner supported Baur’s theory and worked out important characteristics of plastid inheritance in the genus *Oenothera*. In the 1930s Renner reported many more observations, which established plastid inheritance as a widely accepted genetic theory.

Plastid Genetics as an Integral Part of Current Genetic Research

Research involving plastid as well as mitochondrial genetics has contributed to recent advances in both basic and applied research. Over the past 15 years the complete DNA sequences of several plastid genomes from higher and lower plants have been determined. In addition, extensive studies on the expression of plastid genes, their mutations, their regulation, and interaction with the nucleocytoplasmic compartment have advanced our knowledge of the role of plastid genes within the genetic system of plants.

Recent molecular work also has provided new insights into the evolution of plastids from formerly free-living cyanobacteria. Nowadays a wealth of genetic, biochemical, and cytological data support the idea that the endosymbiotic uptake of a cyanobacterium by a pre-eukaryotic cell was followed by the gradual transformation of the endosymbiont into a plastidlike cell organelle—a process accompanied by massive gene transfer from the plastid genome to the chromosomes in the cell nucleus. In addition to their importance in

basic research, plastids have also attracted the attention of plant biotechnologists due to the recent development of transformation technologies for higher plant chloroplasts, which enable the expression of foreign genes in the plastid compartment (Bock and Hagemann 2000).

In contrast to the general importance of research on plastid genetics, many textbooks of genetics (irrespective of their country of origin) almost completely ignore the field of plastid genetics: it is mentioned on at most two or three pages in a total text of 500 or 800 pages and, moreover, the text frequently contains erroneous statements. (The situation regarding mitochondrial genetics is slightly—but not much—better.)

This article addresses this problem by providing a review of the original literature from the turn of the 20th century. This summary of the German literature may also be useful to scientists within the discipline of organelle genetics who have questions concerning the history of this field, how this discipline has evolved from its very beginning, and who was the discoverer of the basic principles of plastid inheritance.

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Discovery of Non-Mendelian (Extranuclear) Inheritance by Carl Correns and Erwin Baur

In one issue (no. 3) of Volume 1 of the “Zeitschrift für induktive Abstammungs- und Vererbungslehre” (the first international journal of genetics and the progenitor of *Molecular and General Genetics*), Correns and Baur separately published articles on non-Mendelian inheritance of variegated phenotypes in plants. Correns (1909a) emphasized in a footnote to his article: “The simultaneous publication of this paper with the following article by E. Baur is based on mutual agreement; however, each of us had no knowledge of the contents of the other ones paper.” The titles of the two articles are

Correns, Carl. Vererbungsversuche mit blass(gelb)grünen und buntblättrigen Sippen bei *Mirabilis jalapa*, *Urtica pilulifera* und *Lunaria annua*. Zeitschr f ind Abst u Vererbungsl 1909;1:291–329. (Inheritance experiments with pale (yellow) green and variegated varieties of *Mirabilis jalapa*, *Urtica pilulifera* and *Lunaria annua*.)

Baur, Erwin. Das Wesen und die Erblchkeitsverhältnisse der “Varietates albomarginatae hort.” von *Pelargonium zonale*. Zeitschr f ind Abst u Vererbungsl 1909;1: 330–351. (The nature and the inheritance properties of horticultural varieties of *Pelargonium zonale* having white borders.)

For different plant species both authors reported the non-Mendelian mode of inheritance of green-white or green-yellow leaf variegations.

Following crosses between variegated, yellow, and green plants (or branches) of *Mirabilis*, *Urtica*, and *Lunaria*, Correns found that the leaf color trait (green versus yellow) is inherited through the mother only, that is, that there is a purely maternal inheritance: green branches always produced seeds that gave rise to green seedlings, seeds from yellow branches yielded only yellow offspring, while the variegated branches produced green, yellow, and green-yellow variegated seedlings in widely varying ratios. In contrast, the pollen-providing parent had no influence on the phenotype of the progeny.

Baur found another type of non-Mendelian inheritance in his crossing experiments with *P. zonale*. He crossed green and periclinal chimeric white-margined plants (or white shoots from otherwise white-margined plants). Reciprocal crosses revealed a biparental, but non-Mendelian, inheritance of the leaf color trait

green versus white. The F₁ progeny consisted of green, green-white variegated, and white seedlings. In many crosses there was a bias in the F₁ toward the phenotype of the maternal parent.

Thus, in 1909, Baur and Correns simultaneously discovered and described the occurrence of non-Mendelian inheritance in higher plants. Their conclusion that in addition to the Mendelian inheritance of genes in the cell nucleus, there are other hereditary factors outside the nucleus (i.e., in the protoplasm) which exhibit a non-Mendelian mode of inheritance marks a milestone in genetics and the date of birth for a new field of research. Although credit for the initial observations should be shared between Baur and Correns, their subsequent theoretical interpretations distinguish their contributions to the field.

The Foundation of the Theory of Plastid Inheritance

The authors of numerous monographs, review articles, and textbooks express the opinion that, in 1909, Erwin Baur and Carl Correns contributed equally to the establishment of the theory of plastid inheritance. However, a careful study of the original literature indicates that this interpretation does not reflect the history of plastid genetics correctly. Below, the original sources in the genetic literature are analyzed.

The Position of Erwin Baur

The theory of plastid inheritance and of random sorting out of plastids. In his article Baur (1909) was the first to provide the explanation that chloroplast defects in *P. zonale* and their mode of inheritance are cases of plastid inheritance: The green and the white shoots of variegated plants differ in the genetic constitution of their plastids (Baur used the term “chromatophores”). One plastid type is green (normal, nonmutated, capable of becoming green during ontogenetic development); the other type is white (mutated, incapable of becoming green).

In his 1909 paper, Erwin Baur (Figure 1) explained the green-white variegation of seedlings and the formation of branches in the F₁ plants with different phenotypes (green, variegated, white; periclinal or sectorial chimeras) by the theory that somatic segregation and sorting out of plastids had occurred: variegated plants developed from zygotes containing two distinct types of plastids, namely green plastids (from one parent) and white plastids

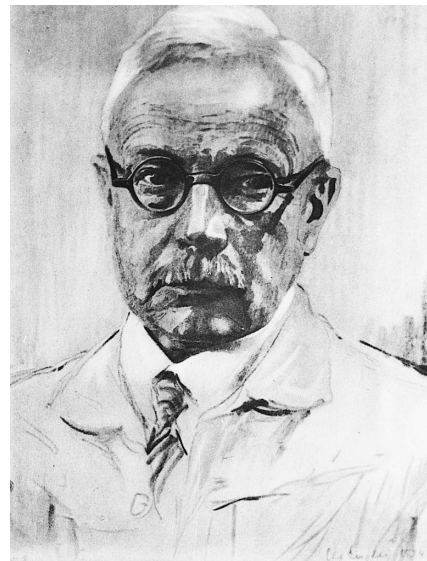


Figure 1. Erwin Baur (1875–1933).

(from the other parent). In the course of the subsequent cell divisions, plastids segregate randomly. This random segregation regularly results in sorting out of the two types of plastids and—during ontogenetic growth of the plants—in the formation of pure green and pure white areas in one and the same plant.

Baur's development of this theory is documented by the following citations from his 1909 paper (in English translation):

I have, on the basis of these observations, formed a theory which shall serve as a working hypothesis for the following investigations [...] The *P. zonale* races with white-margined leaves are chimeras with a periclinally divided growing point. The peripheral two or three cell layers of the shoot apex have only albino plastids, which entirely lack the capacity of chlorophyll formation. The central cells of the shoot apex, however, contain entirely normal plastids capable of turning green.

The fertilized egg cell, as generated through the union of a ‘green’ with a ‘white’ gamete cell, thus contains two types of plastids, green and white. During the cell divisions leading from the egg cell to the embryo, the plastids are distributed to the daughter cells entirely randomly. Whenever a daughter cell receives only white plastids, this cell subsequently will have only white descendent cells, and will give rise to a white sector within the mosaic; whenever a daughter cell receives only green plastids, a solid green sector will arise from it. Cells with both types of plastids will be capable of segregating further, and so on.; probably, I need not explain this in greater detail. If the cell, which will give rise to cotyledons and the growing point, receives only green plastids during one of the first divisions, then a seemingly pure green hybrid will be produced. If only white plastids segregate into that cell, seemingly white progeny will be generated, etc. Furthermore, a simple consideration—which I need not explain through

lengthy or detailed writing—leads us to realize that, after a large number of divisions, cells with both types of plastids will decrease in percentage as compared to cells with only one type of plastid.

This hypothesis is well in accordance with all facts that, thus far, have been determined empirically; it will have to be tested by further investigations which, however, I do not at all wish to reserve for myself.

[Original German text in Baur (1909:349–351) and in Hagemann (2000:102). Baur always used the term “chromatophores,” which has been translated into “plastids.”]

Hypothesis of biparental transmission of plastids in Pelargonium. In the first decade of the 20th century, among botanists, the opinion was held that in higher plants the plastids are transmitted to the next generation only by the mother plant. Baur immediately realized the inconsistency of his experimental genetic findings with this widely held opinion. Trusting his experimental results he proposed that his crosses might indicate that, in *Pelargonium*, plastids are transmitted biparentally to the next generation (i.e., by the female as well as by the male parent):

The hypothesis makes—to emphasize this once again—just one assumption, that is not yet proven, namely that the fertilized egg cells generated through fusion of a ‘white’ with a ‘green’ gamete cell, carry two types of plastids: white ones and green ones. [...] According to the currently dominant scientific dogma, the plastids of the fertilized egg cell descend only from the mother; whether or not this is really absolutely certain, shall remain undiscussed here. If the plastids should indeed always come only from the mother and, hence, if the currently dominant opinion is correct, then we are faced here with extremely curious modes of inheritance. It then must be the case that, in a white \times green cross, part of the white plastids of the egg cell are converted into green plastids under the influence of the male sexual nucleus, and, in the reciprocal cross, part of the green plastids of the egg cell must turn into white plastids under the influence of the male sexual nuclei stemming from a white plant. Of course, theoretically, something like that can be imagined, however, to the best of my knowledge, there is no inheritance phenomenon known which would be analogous to this in any respect.

But should it—in contrast to the hitherto ruling doctrine—turn out that the male sperm cells are also able to transmit plastids into the egg cells, then the hereditary processes of the white-margined plants (of *Pelargonium*) would be fully understandable.

Only further investigations will enable discrimination among these possibilities. It is definitely necessary that the developmental processes regarding the plastids of higher plants have to be carefully studied with newer methods in a continuous series from the sexual cell (through the developing organism) to the sexual cell of the next generation.

[Original German text in Baur (1909:350) and in Hagemann (2000:103).]

In his following publications, Baur (1911, 1919) described several additional experiments and observations from his studies with *Pelargonium zonale* which were in full agreement with his initial suggestions outlined in the article of 1909.

Studies on green-white variegated plants of Antirrhinum majus. Simultaneously with the *Pelargonium* studies, Baur performed experiments with green-white variegated plants of snapdragon (*Antirrhinum majus*) (Baur 1910a,b). In this species he found (by conducting reciprocal crosses) the same mode of non-Mendelian inheritance as Correns (1909a,b) had described for *Mirabilis jalapa*: In *A. majus*, the difference between green and white is inherited through the mother only: green branches give rise to green seedlings only, white branches produce only white offspring, while the variegated branches produce green, white, and variegated seedlings in widely varying ratios. The genetic constitution of the pollen had no effect on the phenotype of the progeny.

Initially Baur only pointed out the accordance of his findings with the results that Correns had obtained for *Mirabilis*. However, in the third edition of his textbook of genetics, Baur (1919) clearly stated that the examples of green-white variegation in *Pelargonium* (biparental inheritance) as well as in *Antirrhinum*, *Mirabilis*, and *Primula* (maternal inheritance) are cases of plastid inheritance. Baur referred to, accepted, and supported the view of Ö. Winge (1919) that variegation in the aforementioned species are examples of plastid inheritance. The only difference is that in the case of maternal inheritance, the plastids are transmitted only by the egg cells, whereas, in the case of biparental inheritance (*Pelargonium*), the plastids are transmitted by both the egg cells and the sperm cells of the pollen. Baur held this view in all of his later publications on this issue.

Although Thomas Hunt Morgan was very skeptical regarding many reports on the phenomenon of “cytoplasmic inheritance,” in his book *The Physical Basis of Heredity*, Morgan (1919) expressed his agreement with the theory that plastids are carriers of hereditary factors.

The Position of Carl Correns

By contrast with the interpretations of Baur, Carl Correns (Figure 2) developed a rather different hypothesis. His line of ar-

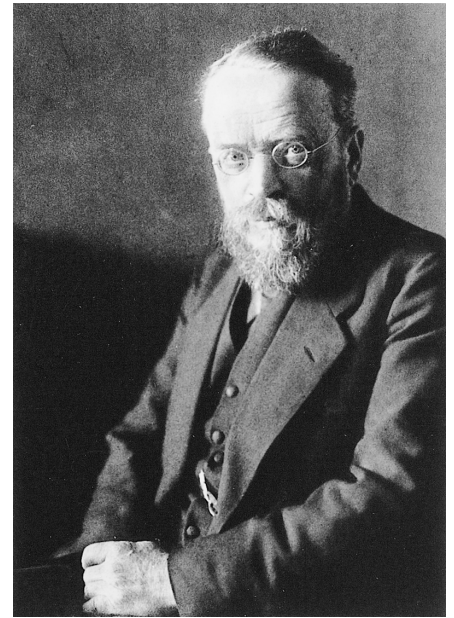


Figure 2. Carl Correns (1864–1933).

gument was based on the terms “healthy” and “ill” (“diseased”). In his articles of 1909 (a,b), he expressed the view that the factor determining green or yellow (or white) plastids was due to the relative health of the cytoplasm: “The basis of the white leaf color is a diseased state of the cytoplasm, a non-infectious chlorosis.” Correns assumed the existence of two types of cytoplasm, a healthy cytoplasm and an ill one. When (indifferent) plastids are introduced into a healthy cytoplasm, they develop into normally green chloroplasts; however, when they are introduced into an ill cytoplasm, then they remain (or become) white or yellow. “Thus, the cell nuclei of the whole plant would be uniform and healthy. However, the cytoplasm, depending on the mosaic, ill or healthy. [Original German text in Correns (1909a:322).]

Correns was well aware of Baur’s contrasting argument (1) that the plastids themselves are the carriers of the genetic differences between “green” and “white” and (2) that, in *Pelargonium*, pollen and egg cells transmit plastids to the next generation, while in *Antirrhinum* and *Mirabilis*, only the egg cells transmit plastids. However, he was reluctant to accept Baur’s view. “I cannot believe that the two experimental organisms (*Pelargonium*—*Mirabilis*) should behave so fundamentally differently in this respect” (Correns 1909b:340).

In some publications, Correns (1909b, 1928) even compared the “illness of the cytoplasm” in such variegated plants with the action of the agents causing tubercu-

losis or with spirochetes. In his later articles on non-Mendelian inheritance, Correns (1922, 1928) added to his hypothesis one important new idea: He assumed that in plants that later will become green-white variegated, the cytoplasm of the “embryonic cells” (i.e., the zygote and early meristematic cells) is in a “labile cytoplasmic state.” During early development of the seedlings, this “labile state” switches either to a normal, permanently “healthy state” (allowing the formation of green chloroplasts) or to a permanently “diseased state” (causing white plastids and cells).

Correns summarized his view in his lecture for the Fifth International Congress of Genetics in Berlin (September 1927). He held this opinion until his death in 1933.

Instead of attributing the primary cause for the different colors to the chloroplasts and assuming that the healthy green and the ill white plastids are located in a cytoplasm which would be neutral in this respect, one could search for the cause in the cytoplasm itself that then would occur in two different states, a healthy one in which the chloroplasts can turn green, and an ill one which prevents them from greening. This assumption would let us understand the absence of ‘mixed’ cells, particularly in mature tissue, because the behavior of all plastids always would be determined by the cell cytoplasm. Besides this, single exceptions that occur more or less frequently, depending on the specific cytoplasm, probably can be explained.

However, this theory would have to refrain from explaining the mosaic of the final differentiated stage by tracing it back to a mosaic in a single cell. Even though we could assume the presence of the two types of cytoplasm in the initial cell, an unequal distribution of them according to that of the two types of chloroplasts is too improbable, a mixing would be expected to occur all too soon.

By contrast, the cytoplasm of the embryonic cells (in such albomaculata-colored plants) could be in a labile state, capable of adopting the healthy or the ill state as a consequence of reasons that we call ‘random’ (1922). The genome would remain unaltered; however, a cell that once would be differentiated in the one or the other way, would retain its characteristic cytoplasm [...] It can and will undergo further divisions: depending on whether the decision about it is made sooner or later, here or there, closer to or farther away from the definitive state of the organ, it will give rise to a larger or a smaller area of white or green tissue, from entire branches down to single cells.

The purely maternal transmission would occur through the cytoplasm (which is subject to constant changes) and would give rise to entirely green and completely white seedlings. Plastids that are transmitted with the sperm nucleus would adjust to the egg cytoplasm and depending on that would become either healthy or ill. [...] The colored seedlings, however, would stem from egg cells that were still in the labile state (which would be in accordance with their position in mosaics of *Taraxacum* and *Se-*

necio); already after one of the first divisions of the embryo a decision could be made leading to a clear mosaic.

[Original German text in Correns (1928:144–145) and in Hagemann (2000:111, 113).]

One of the main arguments of Correns against Baur’s theory was the presumed lack of “mixed cells” within variegated leaves. If somatic segregation of green and white plastids would take place at random, one has to expect (according to Baur’s theory) not only cells with green plastids and those with white plastids, but also cells that contain both types of plastids. Unless the two plastid types are mutually exclusive, “mixed cells” (Mischzellen) should be found containing both green chloroplasts and white plastids side by side within one and the same cell.

Correns repeatedly stated that such “mixed cells” had not been found in a sufficient quantity or not at all. However, Correns cited three authors who had reported the finding of “mixed cells”; among them was his coworker Funaoka (1924) who observed “mixed cells” in variegated leaves of *Stellaria media* “relatively frequently” (Correns and F. von Wettstein 1937:17, 22). Later, such “mixed cells” were found by light microscopy and by electron microscopy in many species. I have summarized these findings, including all relevant references, in several previous reviews (e.g., Hagemann 1964, 1965).

The Foundation of the Theory of Plastid Inheritance

In view of these original statements by Baur and Correns in their publications from 1909 to 1933, we must come to a clear conclusion concerning the foundation of the theory of plastid inheritance: The only founder of the theory of plastid inheritance was Erwin Baur (cf. Hagemann 2000). With his classic article on *P. zonale* in 1909 he laid the groundwork for the currently flourishing discipline of “plastid genetics.”

The Further Development of the Theory of Plastid Inheritance by Otto Renner

Baur’s experiments with *Pelargonium* were based on so-called loss mutations (“Defekt-Mutationen”), plastid mutations causing an inability of the plastids to become green (in any nuclear background that had been tested); some of these plastid mutations led to yellow plastids and

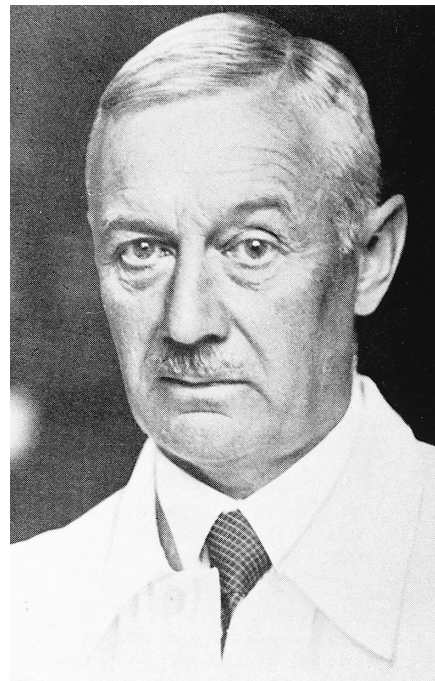


Figure 3. Otto Renner (1883–1960).

leaves, whereas most of them caused white plastids and leaves).

Starting in 1922, Otto Renner (Figure 3) published numerous articles on plastid inheritance. He performed crosses between different species of the genus *Oenothera* (subgenus *Euoenothera*). Their analysis led him to the discovery of a new phenomenon in plastid genetics: hybrid (plastid) deficiency (“Bastardbleichheit”). Different species of the genus *Oenothera* do not only differ in their genotypes, but also in the genetic constitution of their plastids (the plastome). Evolution involved not only mutations in the genome complexes, but also a genetic diversification of the plastomes. The differences in the plastomes are manifested by specific plastid types being unable to green when interacting with certain genome complexes; however, when interacting with their native genome complexes, these plastids develop into normal green chloroplasts.

Here, occurrence of a chlorophyll deficiency is clearly not due to a plastid “loss mutation.” Instead, during evolution of the genus *Oenothera*, “differentiation mutations” (“Differenzierungs-Mutationen”) occurred that led—paralleled by nuclear mutations during species evolution—to genetic differences in the interactions between the nucleus and the plastids. The genetic details of these interactions between different nuclear genomes and five different types of wild-type plastids subsequently were defined by Renner’s for-

mer student and coworker W. Stubbe (1960). Moreover, Renner (1936) and Schwemmler (1940) also found “plastid loss mutations” in *Oenothera* which caused white plastids (comparable to the white plastid mutants studied by Baur in *Pelargonium* and *Antirrhinum*).

All results of crosses in the genus *Oenothera* convincingly proved the biparental inheritance of plastids. In *Oenothera* (and also in *Hypericum*), reciprocal crosses between green and white plants or branches lead to distinct reciprocal differences with a strong bias toward the plastids of the maternal parent. Crosses of green × white yield variegated, many green, and (almost) no white seedlings; whereas crosses of white × green yield variegated, many white, and (almost) no green seedlings. These results were confirmed with both white plastome mutants and hybrid deficient plastids.

In several papers and reviews from 1922 to 1937, Renner dealt with different aspects of plastid inheritance. He always emphasized that his results are in full accordance with the theory of plastid inheritance as formulated by Erwin Baur. Renner (1934) expressed his view in a convincingly lucid and expressive style:

The explanation provided by E. Baur (1909) for the inheritance pattern of the green-white-variegated *Pelargonium* plants is very straightforward and persuasive: The non-nuclear-conditioned reactions that lead to chromatophores of different colors are attributed right from the beginning to the plastids themselves. A variegation (= a variegated plant) arises by the pollen tube introducing plastids into the egg upon fertilization; those plastids differ significantly in their properties from the plastids of the egg and, during the course of development, the two types of plastids are distributed among different cells and, consequently, among different tissue areas. In the green-white variegated *Pelargonium* plants, under the conditions of the experiments, only one type of plastid is healthy and capable of greening, the other one is always ill and incapable of forming chlorophyll.

That is to say: In Baur’s hypothesis, all details of the variegation phenomena of the *Pelargonium* type are brought to such a perfect agreement with the developmental history of the shoot that one could deduce the cell division processes at the shoot apex—if they were not known—from the variegation patterns. In turn, if only the cell division processes were known and the chromatophores were submicroscopically small, one could infer from the phenomena of colored-leaf plants, the existence of distinct carriers of the chlorophylls.

How happy would we be if, in other cases, we would see only half as clearly the relationship between the hereditary material of the germ cell and the phenotype of the mature organism! And this clarity would be clouded by the introduction of a labile state of cytoplasm just be-

cause we do not see the plastids creeping out of the pollen tube into the egg cell. That we cannot see this transition means, as compared to the significance of the variegation phenomena, almost as little as the invisibility of the chromosomes in mature germ cells as compared to the significance of the chromosome number during the division of the zygote nucleus.

Skepticism is good, but should be measured!

The development of the chromosome theory of Mendelian inheritance has shown that scientists were on the right track that, after having reached a certain body of evidence, did not further question every aspect of the importance of the chromosomes, but believed in the theory. From their experimental data, these believers have erected the foundation of the current theory of inheritance, to which the doubters have contributed nothing significant ever since.

In my opinion, this evidence for the autonomy of plastids is nowadays so well supported that it is worth formulating a theory on this autonomy and taking this theory as the basis for further deductive treatments of this problem.

From the experiences with the sudden appearance of colorless tissue areas in lines that had been purely green for generations, one has to conclude that the plastids can change their constitution by themselves, without an influence of the nucleus. This change is practically irreversible and I do not know any reason why one should not call this process plastid mutation.

[Original German text in Renner (1934:243, 251) and in Hagemann (2000:124–125).]

In the years 1934–1937, the concept of plastid inheritance as founded and espoused by Baur and Renner became a fully established and generally accepted genetic theory. This was demonstrated impressively by the statements of Fritz von Wettstein (1937), who was a former coworker and admirer of Correns and became his successor as the director of the Kaiser-Wilhelm-Institute of Biology in Berlin. F. von Wettstein took over the responsibility for the posthumous publication of the book *Nicht mendelnde Vererbung* (Non-Mendelian Inheritance) which Correns had intended to publish as a volume of the *Handbuch der Vererbungswissenschaft* (Handbook of Hereditary Science). He edited the manuscript very carefully and always tried to do this in accordance with the initial intentions of Correns. However, to the chapter on non-Mendelian variegation, he added the following postscript:

The publications of Renner (1922, 1924, 1929, and above all 1936) have informed us of a huge amount of experimental material and results on this subject; the details are dealt with there.

These results make it clear that the plastids possess characteristic and specific traits and a specific make-up, which guarantee their genetic independence of the nucleus. Renner has coined the term “plastome” for this indepen-

dent element. Furthermore Renner (1936) tries to show that the other cases of non-Mendelian variegation are consistent with this explanation. The differences result primarily from the mode of transmission of the plastids by the pollen tube. It seems that a broad range of plastid transmission is possible from cases with ample transmission of plastids by the pollen tube to those in which no paternal plastids are donated to the egg cell. The sorting-out occurs with different speeds, which may be due to different properties of the cytoplasm. [...] According to all results that have been published thus far, I (= F. von Wettstein) have come to the conclusion that the explanations of Renner are well founded for many cases; many reservations, which Correns expounded, can be dispelled now.

[Original German text in Correns and von Wettstein (1937:42, 45) and in Hagemann (2000:123–124).]

This statement indicates that Fritz von Wettstein had decided to revise Correns’ position and to accept the convincing results and the clear arguments of Renner thus agreeing on Baur’s theory of plastid inheritance.

The Way to Molecular Genetics of Plastids

The foundation and refinement of the theory of plastid inheritance was based on clear-cut genetic results, that is, large-scale reciprocal crosses in several species, their careful analysis as well as intense cytologic investigations that ultimately provided important supportive evidence. This classical work has been summarized in detail in a number of comprehensive reviews (Hagemann 1964, 1965; Kirk and Tilney-Bassett 1967, 1978).

At the end of the 1950s a number of researchers reported the identification of specific DNA in plastids. Since 1963–1964, it generally has been accepted that plastids contain their own organelle-specific genetic information (plastid DNA) which provides the material basis for the hereditary factors of the plastids, termed plastome (Kirk 1986).

In the following decades, the plastid DNAs of many plant species were intensely characterized regarding their buoyant density, GC content, contour length, physical size (kbp) and renaturation behavior. In the 1970s, the discovery of restriction enzymes and the growing methodological spectrum of gene technologists paved the way for the rise of plastid molecular genetics. Over the past two decades our knowledge concerning all aspects of plastid biology has benefited immensely from the power of molecular genetics.

Erwin Baur investigated—as mentioned earlier—green-white variegations of *Antirrhinum majus* which exhibited a purely maternal inheritance. Our plastid research group at the University of Halle studied several of such variegated lines. We obtained one line from Professor Hans Stubbe, Gatersleben, who was a PhD student and coworker of Erwin Baur. The mutant plastids of this line, designated *en.alba-1*, carry a specific deficiency in photosystem I, and thus have a total block in photosynthesis. The combination of PCR and SSCP (single-strand conformation polymorphism) analysis, followed by DNA sequencing, revealed that this plastome mutant has—as compared with the wild-type—a single base-pair substitution at codon 136 (TAT→TAG) within the plastid gene *psaB*. This point mutation in plastid DNA produces a new stop codon that leads to a truncated PsaB protein, which prevents the assembly of a functional photosystem I complex (Schaffner, Laasch, and Hagemann 1995).

Comparable investigations were performed with the yellow-margined variety “Mrs. Pollock” of *Pelargonium zonale* which had been used already by Erwin Baur’s PhD student Ludwig Roth (1927). This yellow plastome mutant also exhibits a deficiency in photosystem I (Hagemann 1979; Herrmann et al. 1976).

These examples show that the plastome mutants, initially investigated by Baur and his coworkers, have become—after many decades—valuable tools for studies in the field of plastid molecular genetics.

Molecular research on plastid biology continues to produce exciting findings and to generate stimulating ideas (Hagemann et al. 1981–1998). As this research proceeds, it should be borne in mind that this whole development is founded on the brilliant classical genetic analyzes and the visionary ideas of Erwin Baur and Otto Renner.

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