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# Variation and evolution in plants and microorganisms: Toward a new synthesis 50 years after Stebbins

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"The present book is intended as a progress report on [the] synthetic approach to evolution as it applies to the plant kingdom" (ref. 1, p. *ix*). With this simple statement, G. Ledyard Stebbins formulated the objectives of *Variation and Evolution in Plants* (1), published in 1950, the last of a quartet of classics that, in the second quarter of the 20th century, set forth what became known as the "synthetic theory of evolution" or "the modern synthesis." The other books are Theodosius Dobzhansky's *Genetics and the Origin of Species* (2), Ernst Mayr's *Systematics and the Origin of Species* (3), and George Gaylord Simpson's *Tempo and Mode in Evolution* (4). The pervading theory of these books is the molding of Darwin's evolution by natural selection within the framework of rapidly advancing genetic knowledge. Stebbins said it simply: "In brief, evolution is here visualized as primarily the resultant of the interaction of environmental variation and the genetic variability recurring in the evolving population" (ref. 1, p. *xi*).

*Variation and Evolution in Plants* distinctively extends the scope of the other books to the world of plants. Dobzhansky's perspective was that of the geneticist. Mayr's was that of the zoologist and systematist. Simpson's was that of the paleobiologist. All four books were outcomes of the famed Jesup Lectures at Columbia University. Plants, with their unique genetic, physiological, and evolutionary features, had been left out of the synthesis until then. In 1941, the eminent botanist Edgar Anderson was invited to write botany's analogue to Mayr's *Systematics and the Origin of the Species* and to publish it jointly with Mayr's book. Anderson did not fulfill the task, and Stebbins was thereafter invited to deliver the Jesup Lectures in 1947. *Variation and Evolution in Plants* is the outgrowth of those Lectures.

The mathematical underpinnings of the modern synthesis were set between 1918 and 1931 by R. A. Fisher (5) and J. B. S. Haldane (6) in Britain, and Sewall Wright (7) in the United States. According to Darwin, evolutionary change occurs by natural selection of small individual differences appearing every generation within any species. Any change effected by selection is typically small, but it may amount to major change over time. In contrast, Thomas Huxley and Francis Galton, among Darwin's most dedicated supporters, argued that evolution occurs by selection of discontinuous variations, or sports, and that evolution proceeds rapidly by discrete leaps. In Huxley's view, natural selection, operating on only gradual differences among individuals, could hardly account for the gaps between existing species evident in the paleontological record. According to Galton, evolution proceeds by "jerks," some of which imply considerable organic change, rather than as a smooth and uniform process.

In the latter part of the 19th century, the biometricians Karl Pearson and W. F. R. Weldon believed, like Darwin, in the primary importance of common individual differences. William Bateson, like other geneticists, argued for the primary importance of discontinuous variations. The controversy was acrimonious. The rediscovery of Mendelian inheritance in 1900 might have served as the common grounds to resolve the conflict. Instead, the dispute between biometricians and geneticists extended to continental Europe and to the United States. Bateson was the champion of the Mendelians, many of whom accepted the mutation theory proposed by De Vries (8), and denied that natural selection played a major role in evolution. The biometricians argued that Mendelian characters were sports of little significance for the evolutionary process. Fisher, Haldane, and Wright advanced theoretical models of evolutionary processes based on the natural selection of genetic changes (mutations) that are small when considered individually but are cumulatively of great consequence.

Theodosius Dobzhansky was the first to complete the mathematicians' theoretical propositions with a wealth of biological knowledge and empirical support, and Mayr, Simpson, and Stebbins (and, less notably, many others) soon followed. Stebbins was particularly suited to bring in the evidence from plants. He was born in 1906 and became interested in natural history during his childhood. He started studying botany in his early teens while he was a student at Cate School in Santa Barbara, CA. As an undergraduate at Harvard (1924–1928), he came under the influence of Merritt Lyndon Fernald (1873–1950), a charismatic teacher and distinguished botanist, whom Stebbins accompanied on field trips to study the New England flora. In 1928, Stebbins became a graduate student at Harvard and worked on the cytology, geographic variation, and seed development of *Antennaria*, a genus that bore several apomictic species that could be collected in nearby localities. He would focus on the distinctive evolutionary role of vegetative reproduction in plants throughout his life.

The 17 papers that follow were presented at the colloquium "Variation and Evolution in Plants and Microorganisms: Toward a New Synthesis 50 Years After Stebbins." The colloquium celebrated the 50th anniversary of the publication of Stebbins' classic book. Professor Stebbins, although frail for the last few years, intended to attend the colloquium. Alas, he became ill about 1 month before the colloquium was held and died on January 19, 2000, 2 weeks after his 94th birthday. The "Appreciation" that follows this introduction was delivered by Peter Raven, on January 28, at the time that had been reserved for Stebbins (9). The 16 papers following the "Appreciation" are organized into five successive sections: Early Evolution and the Origin of Cells, Viral and Bacterial Models, Protoctist Mod-

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This paper is the introduction to the following papers, which were presented at the National Academy of Sciences colloquium ''Variation and Evolution in Plants and Microorganisms: Toward a New Synthesis 50 Years After Stebbins,'' held January 27–29, 2000, at the Arnold and Mabel Beckman Center in Irvine, CA.

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els, Population Variation, and Trends and Patterns in Plant Evolution.

## Early Evolution and the Origin of Cells

Darwin noticed the sudden appearance of several major animal groups in the oldest known fossiliferous rocks. “If [my] theory be true, it is indisputable that before the lowest Cambrian stratum was deposited . . . the world swarmed with living creatures,” he wrote, noting that he has “no satisfactory answer” to the “question why we do not find rich fossiliferous deposits belonging to these assumed earliest periods” (ref. 10, ch. 10). In his colloquium article, J. William Schopf (11) points out that, one century later, one decade after the publication of Stebbins’ *Variation and Evolution in Plants* (1), the situation had not changed. The known history of life extended only to the beginning of the Cambrian Period, about 550 million years ago. This state would soon change, notably due to three papers published in *Science* in 1965 by E. S. Barghoorn and S. A. Tyler (12), Preston Cloud (13), and E. S. Barghoorn and J. W. Schopf (14). Schopf speaks of the predecessors who anticipated or made possible the work reported in the three papers, and of his own and others’ contributions to current knowledge, which places the oldest fossils known, in the form of petrified cellular microbes, nearly 3,500 million years ago, seven times older than the Cambrian and reaching into the first quarter of the age of the Earth.

Lynn Margulis, M. F. Dolan, and R. Guerrero set their thesis in the title of their contribution: “The chimeric eukaryote: Origin of the nucleus from the karyomastigont in amitochondriate protists” (15). The karyomastigont is an organellar system composed of at least a nucleus with protein connectors to one (or more) kinetosome. The ancestral eukaryote cell was a chimera between a thermoacidophilic archaebacterium and a heterotrophic eubacterium, a bacterial consortium that evolved into a heterotrophic cell, lacking mitochondria at first. Cells with free nuclei evolved from karyomastigont ancestors at least five times, one of them becoming the mitochondriate aerobic ancestor of most eukaryotes. These authors aver that only two major categories of organisms exist: prokaryotes and eukaryotes. The Archaea, making a third category according to Carl Woese and others (16), should be considered bacteria and classified with them.

The issue of shared genetic organelle origins is also indirectly a subject of the colloquium paper by Jeffrey D. Palmer and colleagues (17). The mitochondrial DNA (mtDNA) of flowering plants (angiosperms) can be more than 100 times larger than mtDNA of animals. Plant mitochondrial genomes evolve rapidly in size, by growing and shrinking. Within the cucumber family, for example, mtDNA varies more than sixfold. Palmer and collaborators have investigated more than 200 angiosperm species and uncovered enormous pattern heterogeneities, some of which are lineage specific. The authors reveal numerous losses of mitochondrial ribosomal protein genes (but only rare losses of respiratory genes), virtually all in some lineages, yet most ribosomal protein genes have been retained in other lineages. High rates of functional transfer of mt ribosomal protein genes to the nucleus account for many of the losses. The authors show that plant mt genomes can increase in size, acquiring DNA sequences by horizontal transfer. Their striking example is a group I intron in the mt *cox1* gene, an invasive mobile element that may have transferred between species more than 1,000 independent times during angiosperm evolution. For more than a decade, we have known that the rate of nucleotide substitution in angiosperm mtDNA is very low, 50–100 times lower than that in vertebrate mtDNA. Palmer *et al.* have now discovered fast substitution rates in *Pelargonium* and *Plantago*, two distantly related angiosperms.

## Viral and Bacterial Models

Andrés Moya and colleagues (18) point out advantages offered by RNA viruses for the experimental investigation of evolution; notably, the phenotypic features (“phenotypic space”) map fairly directly onto the “genetic space.” In other organisms, from bacteria to humans, the expression of the genetic make-up in the phenotype is mediated, to a lesser or greater degree, but always importantly, by complex interactions between genes, between cells, and the environment. The model that these authors use is the vesicular stomatitis virus (VSV), a rhabdovirus containing 11.2 kb of RNA encoding five proteins. The authors grow different viral clones under variable demographic and environmental conditions, and measure the evolution of fitness in these clones by competition with a control clone. Fitness generally decreases through the serial viral transfers from culture to culture, particularly when bottlenecks associated with transfers are small. Fitness may, however, increase when the transmission rates are high, although the response varies from clone to clone. Moya *et al.* conclude with an examination of the advantages and disadvantages of traditional population genetics theory for the description of viral evolution vis-à-vis the quasi-species concept, which proposes that the target of natural selection is not a single genotype but rather a cloud of mutants distributed around a most frequent one, the “master sequence.”

Robin M. Bush and colleagues (19) had noticed in their earlier reconstruction of the phylogeny of influenza A virus, based on the hemagglutinin gene, an excess of nonsilent nucleotide substitutions in the terminal branches of the tree. They explore two likely hypotheses to account for this excess. The first is that these nucleotide replacements are host-mediated mutations that have appeared or substantially increased in frequency during passage of the virus in the embryonated eggs in which they are cultured; this hypothesis can account at most for 59 (7.9%) of the 745 nonsilent substitutions observed. The second is that sampling bias is induced by the preference of investigators for sequencing antigenetically dissimilar strains for the purpose of identifying new variants that might call for updating the vaccine, which seems to be the main factor accounting for the replacement excess in terminal branches. The authors point out that the matter is of consequence in vaccine development and that host-mediated mutations should be removed before making decisions about influenza evolution.

Bruce R. Levin and Carl T. Bergstrom (20) note that adaptive evolution in bacteria compared to plants and animals is different in three respects. The two most important factors are (*i*) the frequency of homologous recombination, which is low in bacteria but high in sexual eukaryotes, and (*ii*) the phylogenetic range of gene exchange, which is broad in bacteria but narrow (typically, intraspecific) in eukaryotes. A third factor is that the role of viruses, plasmids, and other infectiously transmitted genetic elements is nontrivial in the adaptive evolution of bacteria, while it is negligible in eukaryotes.

## Protoctist Models

The mitochondrial genome of kinetoplasts is a highly derived genome in which frameshift errors in reading frames are corrected at the mRNA level. “RNA editing” refers to these posttranscriptional modifications, of which two types are known. One consists of the precise insertion or deletion of U residues, so as to produce open reading frames in the mRNAs encoded in the organelle DNA known as the maxicircle. The other editing system is a modification of 34 Cs into 34 Us in the anticodon of tRNA molecules that can decode the UGA stop codon as tryptophan. Larry Simpson and colleagues (21) seek to unravel the evolution of these two peculiar genetic systems. With support from computer simulations, the authors elaborate an evolutionary scenario that proposes an ancient but unique evolutionary origin for both systems, which may have arisen shortly after the divergence of the trypanosomes and their relatives from the euglenoids.

Stephen M. Rich and Francisco J. Ayala (22) summarize data showing absence of synonymous nucleotide polymorphisms in diverse genes from *Plasmodium falciparum*, the agent of malignant malaria. The inference is that the extant world populations of *P. falciparum* originated from a single ancestral cell in recent times, estimated to be less than 50,000 years. At first, this inference seems incompatible with the existence of numerous amino acid and other polymorphisms in the antigenic genes of the parasite. Rich and Ayala analyze allelic sequences of antigenic genes and conclude that they are consistent with a recent origin of the world populations of *P. falciparum*. The antigenic polymorphisms come about rapidly by mass natural selection acting on sequence variations originated at high rates by intragenic recombination of short DNA repeats.

## Population Variation

Nina Fedoroff (23) notices that the publication 50 years ago of Stebbins' book roughly coincides with the first reports by Barbara McClintock that there are genetic elements capable of transposing from one to another chromosomal location in maize. Today we know that transposable elements make up a large fraction of the DNA of agriculturally important plants, such as corn and wheat, of animals such as mice and humans, and perhaps of all species of mammals and many other vertebrates. Fedoroff reviews the history of the discovery of transposing elements and advances the hypothesis that the mechanisms controlling transposition are an instance of "the more general capacity of eukaryotic organisms to detect, mark, and retain duplicated DNA through regressive chromatin structures."

Grasses (family Poaceae) and their cultivated relatives encompass a gamut of genome size and structural complexity that extends from rice at the lower end to wheat and sugarcane at the higher end, which have nuclear DNAs more than 30 times larger than rice's. Maize is toward the middle, with about six times more nuclear DNA than rice, embodied in 10 pairs of chromosomes. The maize genome is replete with chromosomal duplications and repetitive DNA sequences, as Brandon S. Gaut and his collaborators tell us (24). This complexity has motivated these authors to focus on maize as a model system for investigating the evolution of plant nuclear genomes. More than 11 million years ago, after the sorghum and maize lineages had split, the maize genome became polyploid, which accounts for much of the difference in DNA content between these related species. The polyploid event was followed by diploidization and much rearrangement of the genome, so that maize is now a diploid. But there remains "extra" DNA in maize, mostly consisting of multiple repetitions of retrotransposons that account for 50% of the nuclear genome. This multiplication has occurred within the last 5–6 million years and has also contributed to the genome differentiation between maize and sorghum. The evolutionary complexities of cultivated maize extend to individual genes that have been variously impacted by domestication and intensive breeding.

Michael T. Clegg and Mary L. Durbin (25) trace the development of flower color in the morning glory, from the molecular and genetic levels to the phenotype, as a model for analyzing adaptation. Most mutations determining phenotypic differences turn out to be attributable to transposon insertions. Insect pollinators discriminate against white flowers in populations where white flowers are rare. This would provide an advantage to white genes through self-fertilization in white maternal plants. The pattern of geographic distribution of white plants indicates that such an advantage is counteracted by definite, but undiscovered, disadvantages of the white phenotype. The authors conclude by proposing that floral color development is an area of special promise for understanding the complex gene interactions that impact the phenotype and its adaptation, precisely because "the translation between genes and phenotype is tractable . . . [and] the translation between environment and phenotype is more transparent for flower color than in most other cases."

Barbara A. Schaal and Kenneth M. Olsen (26) point out that Stebbins was largely responsible for the investigation of individual variation within populations, which became part and parcel of the study of plant evolution. For many years beyond 1950, the focus of investigation was the phenotype: morphology, karyotype, and fitness components. Protein electrophoresis opened up the identification of allozyme variation and thus the study of allelic variation at individual genes. Restriction analysis and DNA sequencing have added the possibility of reconstructing the intraspecific genealogy of alleles. The mathematical theory of gene coalescence has provided the analytical tools for reconstruction and interpretation. Schaal and Olsen put all of these tools to good use in several model cases: the recent rapid geographic expansion of *Arabidopsis thaliana*, with little differentiation between populations; the recolonization of European tree species from refugia created by the Pleistocene glaciation; and the origin and domestication of cassava (manioc), the main carbohydrate source for 500 million people in the world tropics.

## Trends and Patterns in Plant Evolution

The study of angiosperm fossils has experienced a "paradigm shift" during the last three decades. In 1950, when *Variation and Evolution in Plants* was published, angiosperm paleobotany consisted of matching fossils, mostly leaves, to extant genera, contributing little toward understanding patterns and rates of plant evolution. Angiosperms from the Cretaceous and early Tertiary are now known that have become extinct or are only distantly related to living genera. The evolutionary biology of angiosperms is nowadays largely addressed on the basis of detailed character-based analyses that follow cladistic methodologies. According to David Dilcher (27), three basic radiation nodes have been identified: the closed carpel and radially symmetrical flower, the bilateral flower, and fleshy fruits with nutritious nuts and seeds. The genetic systems of the angiosperms promoted their evolution toward outcrossing reproduction, with the strongest selection directed toward flowers, fruits, and seeds.

COLLOQUIUM

There is a variety of reproductive systems among the 250,000 known species of vascular plants. Evolutionary explanations of this variety have in the past been based on population-level differences. Thus, selfing or asexual plants are said to be more highly adapted to immediate circumstances but less able to adapt to changing environments than sexual outcrossers. Kent E. Holsinger (28) argues that, to understand the origin and persistence of particular reproductive styles, we must relate them to differences expressed among individuals within populations. Holsinger points out that selfers have fewer genotypes within populations, but greater genetic diversity among populations, than sexual outcrossers. Therefore, selfers and asexuals may be less able to respond adaptively to changing environments, and they also accumulate deletion mutations more rapidly. Sexual outcrossers suffer from a cost of outcrossing and may be impacted by circumstances that handicap the union of gametes produced by different individuals. These costs of outcrossing and reduced reproductive assurance lead to an over-representation of selfers and asexuals in newly formed progeny, which may displace sexual outcrossers unless these enjoy compensating advantages in survival and reproduction.

The damage wrought by invasive species costs $122 billion per year in the United States. Successful plant and animal invasions impact ecologically and demographically the endemic flora and fauna and may have considerable evolutionary import. Norman

C. Ellstrand and Kristina A. Schierenbeck (29) note that invasions typically involve long lag periods before they become successful and require multiple introductions. The authors' explanation is that hybridization between the invaders and resident populations is a stimulus often required for successful invasion. Hybrid progenies may enjoy genetic advantages over their progenitors. Ellstrand and Schierenbeck show that, as predicted by their model, invasiveness can evolve.

Stebbins devoted two chapters to polyploidy. Pamela S. Soltis and Douglas E. Soltis (30) set forth the genetic attributes that account for the great success of polyploid plants: about 50% of all angiosperm species and nearly 95% of all ferns. Polyploids maintain higher levels of genetic variation and heterozygosity, and exhibit lesser inbreeding depression, than diploids, possibly because most polyploid species have arisen more than once, from genetically different diploid parents, in addition to the presence of more than two homologues. Genome rearrangement seems to be a common attribute of polyploids and many plant species may be ancient polyploids (see maize in ref. 24). Soltis and Soltis conclude that, the advances of the last 50 years notwithstanding, much remains unknown about polyploid plant species, including their general mode of formation.

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