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Volume 22

MOLECULAR GENETICS of PLANTS

Edited by
John G. Scandalios

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PREFACE

During the past decade, enormous technological advances have occurred in biology that have led to significant and revolutionary developments. New techniques allow genetic transformations through cell fusion and by the insertion or modification of genetic information through the cloning of DNA. Methods are now available for manipulating organs, tissues, cells, or protoplasts in culture, for regenerating plants, and for testing the genetic basis of novel traits. Whether these techniques can be successfully applied to all species, and not merely to a few, is currently the focus of numerous investigations. However, the potential for exploiting modern molecular biological technology for plant breeding and genetics is vast and virtually untapped.

The recent developments in genetic engineering permit the plant breeder to bypass the various natural breeding barriers that have limited control of the transfer of genetic information in higher organisms. Recombinant DNA technology allows for the selection and production of amplified copies of specific DNA segments that can then be transferred by appropriate vectors into specific plant cells. The *Ti* (tumor-inducing) plasmid carried by *Agrobacterium tumefaciens* has, to date, proven to be the most efficient vector in transferring DNA in higher plants (discussed in this volume). The full benefits of genetic engineering of plants, or any eukaryotes, will be realized only if adequate systems of selection for desired traits and transfer of specific desirable sequences of DNA are effected, and only if these sequences can be properly regulated for expression in the desired tissue at the proper time during development.

In his Preface to Volume 1 (1947), the founding Editor, Dr. Milislav Demerec, stated, "*Advances in Genetics* has been started in order that critical summaries of outstanding genetic problems, written by competent geneticists, may appear in a single publication." The goal set for the series was "to have articles written in such form that they will be useful as reference material for geneticists and also a source of information to nongeneticists." Over the years, the goals set forth have been more than satisfied, and a tradition of excellence was established first under Demerec, and subsequently under Dr. Ernst W. Caspari. I am pleased to have been invited to join Dr. Caspari in carrying on this series.

Because of the diversity of genetics as a science, *Advances in Genetics* has adhered to a policy of publishing in each volume a series of outstanding but largely unrelated articles. Although it is felt that this tradition should be maintained, we will on occasion depart from this format and periodically review a central topic in a highly "topical" or "thematic" volume. We feel this is essential in view of the extremely rapid developments in genetics, which have led to an unparalleled information explosion in recent years. The present volume is to be the first aperiodic "thematic" volume in the series, and is devoted to a review of some current developments in plant molecular genetics.

The intent of this volume is not to present a comprehensive review of the area. Rather, each author was asked to critically summarize and highlight some of the more interesting and, hopefully, significant advances in his own area of expertise. The four articles composing this volume include "state-of-the-art" discussions on the structure and function of mitochondrial genomes, the structure and expression of nuclear genes, chromatin structure and gene regulation, and the molecular genetics of crown gall tumorigenesis. Our purpose is not just to inform but also to stimulate the reader, whether a beginning or an advanced researcher, to explore, question, and, whenever possible, test various hypotheses advanced herein. We hope we have covered some material of lasting value in view of the very rapid developments in this field.

I wish to acknowledge with gratitude the generous cooperation of the individual contributors. I thank numerous colleagues who aided me in the review process, and the Academic Press staff for their gracious cooperation.

It is fitting that I dedicate this volume to the memory of a visionary scientist and great geneticist, the founding Editor, Dr. Milislav Demerec, who was also my scientific mentor and friend.

JOHN G. SCANDALIOS

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P. J. J. HOOYKAAS AND R. A. SCHILPEROORT

STRUCTURAL VARIATION IN MITOCHONDRIAL DNA

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I. Introduction: Structural Variation and Functional Conservation of Mitochondrial Genomes

Although the function of mitochondria in oxidative phosphorylation is common to virtually all eukaryotic systems, the great diversity of the mitochondrial genomes of plants, animals, fungi, and protozoa is both fascinating and bewildering. In these systems, the basic mitochondrial functions appear highly conserved, whereas the size, organization, and structure of the genomes vary greatly. The size and internal structure of mitochondrial genes also vary greatly in different mitochondrial genomes.

This article is intended to review the structural diversity of mitochondrial chromosomes, particularly the variations of size and structure resulting from rearrangements in mitochondrial DNA (mtDNA). The observed diversity reflects both functional constraints and mechanisms of genetic variation that underlie the divergent paths taken by these unusual organelle genomes. In addition to unitary mitochondrial chromosomes, many additional or supernumerary DNA elements, such as plasmids and plasmidlike molecules, are found in mitochondrial genomes. These additional DNA elements are extremely diverse, are found in mtDNA of widely different groups, and may be important in the organization and evolution of mitochondrial genomes. The comparison of these diverse systems is directed toward a better understanding of the evolution of mtDNA and toward suggesting directions for future research.

Many reviews and books have recently covered many aspects of the structure and function of mitochondrial genomes. "Mitochondrial Genes" (Slonimski *et al.*, 1982) and the "12th Bari Conference" (Kroon and Saccone, 1980) are among the most recent. Gray (1982) and Wallace (1982) recently reviewed mitochondrial genome diversity and organelle evolution. Several reviews of plant mitochondrial genome organization and expression have recently been published (Leaver and Gray, 1982; Levings and Sederoff, 1981; Levings *et al.*, 1983). The evolution of mitochondrial DNA with respect to the origin of mitochondria has been reviewed by Gray and Doolittle (1982) and was a major subject of a symposium of the New York Academy of Sciences (Fredrick, 1981). The genetics and biochemistry of yeast mtDNA have been reviewed by Borst and Grivell (1978, 1981), Tzagoloff *et al.* (1979), Gillham (1978), Tzagoloff (1982), Borst (1981), and Butow and Strausberg (1981). Several recent reviews of kinetoplast DNA structure and function have also been published (Borst *et al.*, 1981b; Englund *et al.*, 1982a; Englund, 1981; Borst and Hoeijmakers, 1979a).

Most animal mitochondrial genomes are found as monomeric circular DNA molecules of about 16 kb (Borst and Flavell, 1976; Wallace, 1982) (Table 1). Throughout the animal kingdom, relatively little variation is found in size or organization. In contrast, mitochondrial DNAs of fungi are diverse in size, ranging from about 18 kb to over 100 kb, and vary greatly in organization (Clark-Walker and Sriprakash, 1982). Major differences in the organization of sequences, or in the amount of DNA in the mitochondrial genome, are found in closely related species. Intervening sequences, absent from animal mtDNA, are common in fungal mtDNA and have important roles in the expression of specific genes (Dujardin *et al.*, 1982; Borst, 1981; Borst and Grivell, 1981). In some species, amplification of specific DNA sequences as small circular molecules may occur in the development of senescence in *Podospora anserina* (Wright *et al.*, 1982; Esser *et al.*, 1980; Belcour *et al.*, 1981) or as mutations in fungi (Locker *et al.*, 1979; Faugeron-Fonty *et al.*, 1979; Lazowska and Slonimski, 1977; Heyting *et al.*, 1979b; Lazarus *et al.*, 1980a,b).

In higher plants, the diversity of mtDNA molecules is even greater (Levings and Pring, 1978; Levings and Sederoff, 1981; Leaver and Gray, 1982). Estimated genome sizes range from about 100 to 2400 kb in dicotyledonous plants alone (Bendich, 1982). mtDNA populations can be heterogeneous mixtures of linear and circular molecules, some of which may be greatly amplified with respect to other mitochondrial genes (Levings and Sederoff, 1981; Dale, 1982).

Complete linear mitochondrial chromosomes with fixed ends have been found in groups as divergent as *Paramecium*, *Chlamydomonas*, and yeast (Grant and Chiang, 1980; Weslowski and Fukuhara, 1981; Cummings and Pritchard, 1982). In some cases, the chromosomes are always linear, e.g., in *Paramecium*; however, in *Chlamydomonas*, the linear molecules appear to arise from site-specific cleavage of circular molecules. The most unusual mitochondrial genomes are the kinetoplast DNAs, which are composed of large maxicircles with inter-

TABLE 1

Sizes of Mitochondrial Genomes

Organism	Length (μm)	Md	kb	Structure	Method	References[a]
Vertebrates						
Homo sapiens			16.569	Circular	Sequence	1
Pan troglodytes (chimpanzee)			16.4	Circular	Contour length	2
Cercopithecus aethiops (guenon: African green monkey)			16.4	Circular	Contour length	2
Lagothrix cana (wooly monkey)			16.3	Circular	Contour length	2
Galago senegalensis (bush baby)			16.5	Circular	Contour length	2
Macaca mulatta (rhesus)	5.5				Contour length	3
Mus musculus (mouse)			16.295	Circular	Sequence	4
Rattus norvegicus (Norwegian rat)			16.4	Circular	Contour length	2
Rattus rattus (rat)			16.4	Circular	Contour length	2
Bos taurus (bovine)			16.338	Circular	Sequence	5
Ovis aries	5.4	10.8		Circular	Contour length	3,6
Mesocricetus auratus (hamster)			16.3	Circular	Contour length	2
Oryotolagus cuniculus (rabbit)			17.3	Circular	Contour length	2
Canis familiaris (dog)	5.0				Contour length	3
Cavia porcellus (guinea pig)	5.6	11		Circular	Contour length	3,10
Gallus domesticus (chicken)	5.4	10.8	16.2	Circular	Contour length	3,7,10
Gallus ferrugineus (jungle fowl)			(16.2)		Restriction	7,8
Acryllium vulturinum (guinea fowl)			(16.2)		Restriction	7
Phasianus torquatus (ring-necked pheasant)			(16.2)		Restriction	7
Meleagris gallipavo (turkey)			(16.2)		Restriction	7
Anas platyrhynchos (Pekin duck)	5.1	10.2		Circular	Contour length	3
Sauromalus ater (chuckwalla)	5.3			Circular	Contour length	3
Terrapene ornata (turtle)	5.3	10.6		Circular	Contour length	3
Cnemidophorus tigris mundus			17.6	Circular	Contour length	9
Cnemidophorus inornatus			17.4	Circular	Contour length	9
Cnemidophorus neomexicanus			17.3	Circular	Contour length	9

Cnemidophorus tesselatus			17.5	Circular	Contour length	9
Rana pipiens (leopard frog)	5.8	11.6		Circular	Contour length	10
Xenopus laevis (clawed frog)	5.8	11.7		Circular	Contour length	10
Xenopus mulleri (clawed frog)	5.8	11.7		Circular	Contour length	3
Siredon mexicanum (axolotl)	4.7	9.4		Circular	Contour length	10
Necturus maculosus (mud puppy)	4.8			Circular	Contour length	10
Ictalurus punctatus (channel catfish)	5.1				Contour length	3
Carrassius carrassius (carp)	5.4				Contour length	3
Echinoderms						
Lytechinus pictus (white sea urchin)	4.7	9.4	15.7		Contour length	2
Strongylocentrotus purpuratus (purple sea urchin)			15.7		Contour length	2
Insects						
Drosophila						
melanogaster (fruit fly)		12.35		Circular	Contour length	12
simulans		11.9		Circular	Contour length	12
mauritiana		11.7		Circular	Contour length	12
yakuba		10.28		Circular	Contour length	12
teissieri		10.04		Circular	Contour length	12
erecta		9.92		Circular	Contour length	12
lucipennis		10.96		Circular	Contour length	12
suzukii		10.37		Circular	Contour length	12
takahashii		10.75		Circular	Contour length	12
birchii		11.01		Circular	Contour length	12
kikkawai		10.68		Circular	Contour length	12
auraria		10.81		Circular	Contour length	12
denticulata		10.44		Circular	Contour length	12
ficusphila		10.68		Circular	Contour length	12
eugracilis		10.31		Circular	Contour length	12
elegans		10.40		Circular	Contour length	12
bipectinata		10.05		Circular	Contour length	12
ananassae		10.17		Circular	Contour length	12

(continued)

TABLE 1 (*Continued*)

Organism	Length (μm)	Md	kb	Structure	Method	References[a]
saltans		10.04		Circular	Contour length	12
lutea		10.67		Circular	Contour length	12
willistoni		10.13		Circular	Contour length	12
pseudo-obscura		10.19		Circular	Contour length	12
tripunctata		10.32		Circular	Contour length	12
funebris		10.34		Circular	Contour length	12
mercatorum		10.09		Circular	Contour length	12
neohydei		9.90		Circular	Contour length	12
hydei		10.34		Circular	Contour length	12
robusta		10.61		Circular	Contour length	12
americana		10.06		Circular	Contour length	12
montana		10.32		Circular	Contour length	12
virilis		10.12		Circular	Contour length	12
balioptera		9.91		Circular	Contour length	12
hawaiensis		10.00		Circular	Contour length	12
silvarentis		10.01		Circular	Contour length	12
grimshawi		10.00		Circular	Contour length	12
gymnobasis		10.01		Circular	Contour length	12
duncani		10.11		Circular	Contour length	12
buskii		9.95		Circular	Contour length	12
lebanonensis		10.20		Circular	Contour length	12
Locusta migratoria			~16		Restriction	56
Musca domestica (house fly)	5.2			Circular	Contour length	3
Rhynchosciara hollaenderi	9.0			Circular	Contour length	13
Other animals						
Artemia salina (brine shrimp)	5.1	10.2		Circular	Contour length	3
Ascaris lumbricoides (roundworm)	4.8	9.6		Circular	Contour length	3
Ascaris suum (roundworm)	5.0			Circular	Contour length	11

Hymenolepis diminuta (tapeworm)	4.8	9.6		Circular	Contour length	3
Urechis caupo	5.9	11.8		Circular	Contour length	3
Fungi						
Aspergillus nidulans			32–33	Circular	Restriction	14,15
nidulans var *echinulatus*			38	Circular	Restriction	15
var *quadrilineatus*			31	Circular	Restriction	15
Brettanomyces anomalus CBS 77	18.15		57.7	Circular	Contour length	16
			56.5		Restriction	16
Brettanomyces custersii			108		Restriction	16
Candida parapsilosis	11.1	23		Circular	Contour length	8,17
Cephalosporium acremonium			26.7	Circular	Restriction	55
Dekkera bruxellensis CBS 74			75		Restriction	16
Dekkera intermedia CBS 4914			63.5		Restriction	16
Hanseniaspora vineae CBS 2171			26.7		Restriction	16
Hansenula mrakii	17.5	37	55	Linear	Restriction	18
Hansenula wingei	8.2	17	25.5	Circular	Contour length	17
Kloeckera africana CBS 277	8.33		26.5	Circular	Contour length	16
			27.1		Restriction	16
Kluyveromyces lactis	11.4	24	37	Circular	Contour length	17
Neurospora crassa			62	Circular	Contour length	3,8
Podospora anserina	31		95		Restriction	20,21
Pachytichospora transvaalensis CBS 2186			41.4		Restriction	16
Saccharomyces cerevisiae KL 14-4A			77.8	Circular	Restriction	23
Saccharomyces cerevisiae NCYC 74	24.7			Circular	Contour length	22
NCYC 74			68.0	Circular	Restriction	23
Saccharomyces cerevisae (Danish maltese cross)	26.6			Circular	Contour length	22
Saccharomyces exiguus CBS 379	7.47		23.4	Circular	Restriction	16
			23.7		Contour length	16

(*continued*)

TABLE 1 (*Continued*)

Organism	Length (μm)	Md	kb	Structure	Method	References[a]
Saccharomyces lipolytica (*Candida lipolytica*)		30.5	44		Contour length	19
Saccharomyces telluris CBS 2685			34.8		Restriction	16
Saccharomyces unisporus CBS 398	8.63		27.4	Circular	Restriction	16
Saprolegina (sp.)	14	28	42	Circular	Contour length	3
Schizosaccharomyces pombe EFL			19	Circular	Contour length	24
Schizosaccharomyces pombe 50h⁻			17.3	Circular	Restriction	24
Torulopsis glabrata CBS 138	5.95		18.9	Circular	Contour length	16
Torulopsis glabrata Phaff 71-91			20.3	Circular	Restriction	16
Ustilago cynodontis		50	75	Circular	Restriction	25
Slime molds						
Physarum polycephalum	19	41		Circular	Contour length	26,8
Dictyostelium discoideum		35–40		Circular	Contour length	8
Water mold						
Achlya ambisexualis			49.8	Circular	Restriction	51
Higher plants						
Zea mays						
B37N (maize)			484		Restriction (minimum estimate)	27
cms-T			463		Restriction	27
cms-C			494		Restriction	27
cms-S			489		Restriction	27
WF9-N			650		Cosmid mapping	28
Sorghum bicolor (sorghum)		150–200			Restriction	30
Glycine max (soybean)		150			Restriction	52,53
Linum usitatissimum (flax)		106			Restriction	32
Pisum sativum (pea)		240			Reassociation	29
Vicia faba (broadbean)		190			Restriction	33

Vicia villosa		250			Restriction	33
Triticum aestivum (wheat)		140	210		Restriction	31
		230			Restriction	34
Citrullus vulgaris (watermelon)		220			Reassociation; restriction	29
Cucurbita pepo (zucchini)		560			Reassociation; restriction	29
Cucumis sativus (cucumber)		1000			Reassociation	29
Cucumis melo (muskmelon)		1600			Reassociation	29
Nicotiana tabacum (tobacco)		260–290			Restriction	35
Brassica napus N		136.5			Restriction	36
Brassica napus (*cms*)		140.3			Restriction	36
Solanum tuberosum (potato)		90			Restriction	31
Oenothera berteriana (evening primrose)		180–190			Restriction	37
Lactuca sativa (lettuce)		140			Reassociation	8
Parthenocissus tricuspidata (Virginia creeper)		165			Restriction	31
Algae						
Chlamydomonas reinhardtii		10	15	Linear/circular	Contour length	38
Chlorella pyrenidosa		53			Renaturation	39
Euglena gracilis		40–50		Circular	Contour length	40,41,42,43
Protozoa						
Acanthamoeba castellanii	12.8	27	40	Circular	Contour length	44
Plasmodium lophurae	10.3	21.5	18.5	Circular	Contour length	54
Tetrahymena pyriformis						
ST		30		Linear	Contour length	45
GL		32.6		Linear	Contour length	45
W		25.8		Linear	Contour length	45
Parameciuum aurelia	14		40	Linear	Contour length; restriction	46
Crithidia luciliae	11.3		35	Maxicircle	Contour length; restriction	47

(*continued*)