Contents

Introduction 1

1 The Modern Corn Plant 5

2 Theories on the Origin of Maize 11
The Pod-Corn Theory 11
The Teosinte Theory 11
The Theory of a Common Ancestry 12
Minor Theories 12
The Tripartite Theory 13
Tripsacum a Hybrid of Maize and *Manisuris* 13
Geographical Origins 14

3 Teosinte, the Closest Relative of Maize 15
Historical Records 15
Botanical Relationships 17
Nomenclature and Taxonomy 19
Geographical Distribution 20
Morphology 21
Physiological Characteristics 23
Chemical Analyses 23
Resemblances in Teosinte and Maize Chromosomes 24
Sterility of F_1 Hybrids 26
Races of Teosinte 26
Teosinte's Role in the Origin of Maize 26

4 The Genetic Nature of Teosinte 37
Early Experiments on Maize-Teosinte Hybrids 37
Crossing over between Maize and Teosinte Chromosomes 38
Linkages of Genetic Differences with Marker Genes 38
Additional Linkage Experiments 38
Genetic Differences between Teosinte Varieties 38
Extracting Blocks of Genes from Teosinte 39
Linkage Relations of Extracted Blocks of Genes 40
A Second Cycle of Transferring Blocks of Genes 42
Polygene Segments as Supergenes 42
Failure to Reconstitute Teosinte 43
Mendelian Segregation in F_2 Generations 43
Five Races of Teosinte Analyzed 45
What Is Teosinte? 48
Criticisms of the Theory of the Hybrid Origin of Teosinte 48
Alternative Possibilities 49

5 *Tripsacum*, a More Distant Relative of Corn 53
Descriptions of the Species 54
Cytology of *Tripsacum* Species 56
Crossing Relationships 58
Zea × *T. dactyloides* (2n) 60
A Comparison of Diploid and Triploid Hybrids of *Zea* and *Tripsacum* with the Parental Genera 63
The Progeny of the Triploid Hybrid 64
Crossing Over between Maize and *Tripsacum* Chromosomes 69
The Trigenomic Hybrid of Zea, *Tripsacum*, and Teosinte 69
Failure to Hybridize Teosinte × *Tripsacum* 70

6 Corn's Old World Relatives 71
Crossing Relationships 72
Other Andropogoneae Possibly Related to Maize 73

7 Pod Corn, the Ancestral Form 75
History of Pod Corn 75
An Experimental Verification of an Historical Reference 76
Other Early References 76
Pod-Corn on Uniform Genetic Backgrounds 79
Various Expressions of the Pod-Corn Locus 79
Producing a Fertile, True-breeding Pod Corn 79
The Genetically Reconstructed Ancestral Form, the First Model 81
The Reconstructed Ancestral Form in a Simulated Wild Habitat 84

8 The Nature of the Pod-Corn Locus 87
The Locus Dissected and Reconstructed 87
Postscript to the Dissection Experiment 88
A Comparison of *Tu-tu* Genotypes in Isogenic Stocks 89
Characteristics of Additional Genotypes at the *Tu-tu* Locus 91
The Components of Wild Corn 92
Wild Corn a Pod Corn 93
The Genetically Reconstructed Ancestral Form: Later Models 93
A Tuncinate Teosinte 98

9 Races of Maize 101
Previous Classifications of Maize 101
Other Countries Follow Mexico's Example 103
The Pointed Popcorns 105
The Sweet Corns 107

10 The Concept of Lineages 113
Eight-Rowed Corn 113
Kculli 114
The Chapalote-Nal-Tel-Pollo Complex 117
Pira Naranja 118
Chromosome Knobs of Races of Maize 118
Summary 120

11 The Role of Hybridization in Corn's Evolution 121
Interracial Hybridization 121
Hybridization of Maize and Teosinte 122
Anatomical Evidence of Teosinte Introgression 125
Archaeological Evidence of Teosinte or *Tripsacum* Introgression 125
The Evidence of Introgression from *Tripsacum* 127
Cryptic Genes for Tripsacoid Characteristics in Latin-American Races of Maize 127

12 Mutations 133
The Mutagenic Effects of Hybridizing Maize and Teosinte 133
Mutations in Long-Inbred Strains of Maize 139
Introgression and Mutation Systems 140
Summary 141

13 Genetic Drift and Selection 143
Waxy Maize 143
Flour and Sweet Corns 144
Gene Frequencies in Mexico and United States 144
Natural and Artificial Selection 145
Summary 145

14 Archaeological Evidence of Corn's Evolution 147
Bat Cave, New Mexico 147
Radiocarbon and Other Dating 148
Bat Cave Revisited 149
La Perra Cave, Northeastern Mexico 152
The Caves of Infiernillo Canyon, Mexico 154
Swallow and Other Caves, Northwestern Mexico 157
Richards' Caves and Tonto Monument, Arizona 160
Cebollita Cave, New Mexico 161
Spread of an Eight-Rowed Maize from Mexico and the Southwest 162
Summary 163

15 Prehistoric Wild Corn and Fossil Pollen 165
Remains of Prehistoric Wild Corn 165
Coxcatlan and Purron Caves 166
El Riego Cave 166
San Marcos and Tecorral Caves 166
Cultural Zones and Dating 167
The Remains of Maize 167
The Nature of Wild Corn 167
Early Cultivated Corn 169
Hybridization Plays a Role 170
Corn at the Time of Christ 173
Wild Corn Reconstructed 178
Fossil Pollen 181
Summary 185

16 Corn in Prehistoric Art 187

17 Corn's Spread to the Old World 201
Pre-Columbian Maize in Asia? 201
New "Evidence" on Prehistoric Maize in India 204
Pre-Columbian Corn in Africa? 205
Pre-Columbian Maize in the Phillipines? 205
Pre-Columbian Corn in Europe? 206

18 The Prehistoric and Modern Improvement of Maize 207
Corn Breeding before Columbus 207
Pre-Columbian Hybridization 209
Corn Breeding in Early Historical Times 209
The Period of the Corn Shows 210
Ear-to-Row Breeding 211
The History of Hybrid Corn 211

19 The Nature of Heterosis 215
Dominance of Linked Factors 215
Overdominance 216
Epistasis 217
Genic Balance a Factor in Heterosis 218
Heterosis and Genetic Homeostasis 218
Inbreeding Depression in Maize 218
Inbreeding Depression in Popcorns 220
Inbreeding Depression in Teosinte 220
Types of Heterosis in Maize 221
Evidence of Overdominance 222
Evidence for Epistasis 223
Agreement between Mathematical and Biological Models 224

20 Modern Breeding Techniques 227
Convergent Improvement 227
Recurrent Selection 229
Gamete Selection 233
Homozygous Lines from Monoploids and Parthenogenetic Diploids 235
The *Oenothera* Method of Establishing Homozygous Lines 236
The Use of Exotic Germ Plasm 236
Inventory of Exotic Races 238
Using Exotic Races 238
Using Exotic Germ Plasm from Diverse Sources 239
The Use of Cytoplasmic Male Sterility 239
Breeding Corn for Improved Protein Quality 240

Bibliography 245

Index 253

Corn

Its Origin
Evolution
and Improvement