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4th Edition
David Briggs , S. Max Walters
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Plant Variation and Evolution

FOURTH EDITION

We are in the midst of a biological revolution. Molecular tools are now providing new means of critically testing hypotheses and models of microevolution in populations of wild, cultivated, weedy and feral plants. They are also offering the opportunity for significant progress in the investigation of long-term evolution of flowering plants, as part of molecular phylogenetic studies of the Tree of Life.

This long-awaited fourth edition, fully revised by David Briggs, reflects new insights provided by molecular investigations and advances in computer science. Briggs considers the implications of these for our understanding of the evolution of flowering plants, as well as the potential for future advances. Numerous new sections on important topics such as the evolutionary impact of human activities, taxonomic challenges, gene flow and distribution, hybridisation, speciation and extinction, conservation and the molecular genetic basis of breeding systems will ensure that this remains a classic text for both undergraduate and graduate students in the field.

David Briggs is Emeritus Fellow of Wolfson College at the University of Cambridge. He has a lifelong interest in evolution, genetics, conservation and taxonomy. He is also the author of *Plant Microevolution and Conservation in Human-Influenced Ecosystems* (Cambridge, 2009), which won the British Ecological Society's 2011 Marsh Book of the Year award.

S. Max Walters (1920–2005) was a leading British field botanist, and the author and editor of major works on the classification and identification of both wild and garden plants. He served as Director of Cambridge University Botanic Garden from 1973 until his retirement in 1983.

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FOURTH EDITION

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and

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This edition revised by David Briggs

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PREFACE

In writing the earlier editions of *Plant Variation and Evolution*, with my great friend Max Walters (1920–2005), our approach to this complex subject was clearly set out in the preface to the Third Edition. 'When it was first proposed to establish laboratories at Cambridge, Todhunter, the mathematician, objected that it was unnecessary for students to see experiments performed, since the results could be vouched for by their teachers, all of them of the highest character, and many of them clergymen of the Church of England' (Bertrand Russell, 1931). While Russell's mischievously anti-clerical comments do not entirely reflect the views of Todhunter (Todhunter, 1873; Macfarlance, 1916), they do provoke us to take a critical look at the way scientific advances are made, in every historical period, through questioning the opinions of various 'authorities'. In many texts on evolution a judicious mixture of concepts, mathematical ideas and the results of laboratory and field experiments are combined in an elaborate pastiche to provide a more or less complete edifice. Perhaps one or two areas of uncertainty may be indicated, but the general impression is of a house well built, but awaiting the placing of the last few roof-tiles. Conversations with research biologists, however, quickly reveal a different picture. While the broad outlines of evolution are supported by an increasing body of evidence, almost nothing is completely settled: current views represent a provisional framework, and even some parts of the subject, long held to be clarified, are suddenly overturned by new discoveries. Teaching experience reinforces our view that students of science should be shown the way in which, slowly and painstakingly, our present partial pictures have been built up, how and to what extent they are testable by experiment and observation, and in what way they remain vague or defective. A healthy scepticism in the face of the complexities of organic evolution is the best guarantee of real progress in understanding its patterns and processes.

The aim of this new edition is to provide, as before, an authoritative introductory university text, while at the same time satisfying the general reader with a real interest in the subject, showing how the study of variation and evolution of flowering plants has developed over the last 400 years. This development has been increasingly scientific, leading to the realisation of the crucial importance of hypothesis and experiment.

Throughout the book, I have tried to provide a critical but concise overview of current excitements and advances, while at the same time paying attention to difficulties and uncertainties. Furthermore, I have intentionally introduced and shown the connection between many complex subjects, and have therefore provided references to important research papers and books, in order that the reader may build on the framework provided.

As in previous editions, I emphasise the logical and historical framework of early observation and experiment, which is almost wholly neglected in some university courses. Sapp (2003) stresses this important point when he writes, 'many teachers of science have noted, [that] scientific problems are usually much better understood from studying their history rather than their logic alone'. Accordingly this book shows how, building on historical foundations, modern investigative methods are providing new insights into past and present patterns of variation in nature and the processes that give rise to them.

ACKNOWLEDGEMENTS

First, I pay tribute to my co-author and mentor Max Walters, formerly Director of Cambridge University Botanic Garden. My family and I thank Max and his wife Lorna for lifelong friendship and many kindnesses.

I wish to thank those teachers, colleagues and friends who gave me encouragement and provided many life-changing opportunities: Ada Radford (my first biology teacher), Donald Pigott, David Valentine, Harry Godwin, Harold Whitehouse, Percy Brian, Richard West, John Burnett, Jack Harley, David Lewis and Peter Ayres.

Over the years, I have discussed many issues about evolution and conservation with a large number of friends and colleagues. To all of them I offer my thanks: John Akeroyd, Janis Antonovics, Elizabeth Arnold, John Barrett, David Bellamy, Alex Berrie, John Birks, May Block, Margaret Bradshaw, Tony Bradshaw, Arthur Cain, Arthur Chater, Judy Cheney, David Coombe, Gigi Crompton, Quentin Cronk, Jim and Camilla Dickson, Jeff Duckett, Trevor Elkington, Harriet Gillett, Peter Grubb, Mark Gurney, John Harper, Joe Harvey, John Harvey, Peter Jack, David Kohn, Andrew Lack, Vince Lea, Elin Lemche, Roselyne Lumaret, Terry Mansfield, Hugh McAllister, Pierre Morisset, Gina Murrell, Peter Orris, Philip Oswald, John Parker, Joseph Pollard, Duncan Porter, Chris Preston, Oliver Rackham, John Raven, Tom ap Rees, Peter Sell, Alison Smith, Betty Smocovitis, Edmund Tanner, Andrew and Jane Theaker, John Thompson, Lorna Walters, Alex Watt, David Webb, John West and Peter Yeo.

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I pay special tribute to my family for encouraging me to write this book, my parents Mabel and Tom Briggs, Nancy Briggs, Jonathan Briggs, Nicholas Oates, Alastair Briggs, Catherine, Miranda, Ella, Judith and Adrian Howe, Norman Singer and Geoffrey Charlesworth.

Without my wife Daphne's support, tolerance and unfailing commitment, this book would never have been written. With good humour and constant encouragement, she has helped me bring this project to fruition. I thank her for all her help, especially for hours of painstaking checking and proofreading.

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NOTE ON NAMES OF PLANTS

Scientific names are generally in accordance with the third edition of Stace, C. (2010) *New Flora of the British Isles* for British plants; and, for European plants not in the British flora, Tutin *et al*. (1964–93) *Flora Europaea*. In the cases not covered by either work we have used the name we believe to be correct. Where an author has used a non-current name, this is noted in brackets.

While some botanists continue to use long-standing names for important families, increasingly others use names derived from the type genus (e.g. Compositae/Asteraceae; Cruciferae/Brassicaceae, etc.). We give alternative names in the text.

ABBREVIATIONS

AFLP	amplified fragment length polymorphism
APG	Angiosperm Phylogeny Group
BGCI	Botanic Gardens Conservation International
BP	before the present
BSC	Biological Species Concept
CMS	cytoplasmic male sterility
CNI	cytonuclear incompatibilities
cpDNA	chloroplast DNA
ENM	ecological niche modelling
ESM	Earth System Model
FAO	Food and Agriculture Organization of the United Nations
FISH	fluorescence *in situ* hybridisation
GISH	genomic *in situ* hybridisation
GM	genetically modified
HGT	horizontal transfer of genetic information
IPCC	Intergovernmental Panel on Climate Change
ISH	*in situ* hybridisation
ISSRs	inter simple sequence repeats
IUCN	International Union for Conservation of Nature
K–T	Cretaceous–Tertiary (K–T) boundary
LGM	Last Glacial Maximum
mtDNA	mitochondrial DNA
MVP	Minimum Viable Population
Mya	million years ago
OTU	operational taxonomic unit
PCA	principal component analysis
PCO	principal coordinates analysis
PCR	polymerase chain reaction
ppb	parts per billion
ppm	parts per million
PVA	population viability analysis
QTLs	quantitative trait loci
RAPD	random amplified polymorphic DNA
RFLP	restriction fragment length polymorphism
SNP	single nucleotide polymorphism
SSRs	simple sequence repeats
SSSI	Site of Special Scientific Interest in UK
STR	short tandem repeat
UNEP	United Nations Environmental Programme
WGD	whole genome duplication
WCMC	World Conservation Monitoring Centre