Bryophyte Biology provides a comprehensive yet succinct overview of morphology, systematics, ecology, and evolution of hornworts, liverworts, and mosses. A distinguished set of contributors provide state-of-the-art summaries of the most recent advances in bryology, with rich citation of the current literature. Revised classifications for the liverworts and mosses are presented that depart significantly from previous arrangements. These novel classifications reflect the results of recent phylogenetic analyses and include exhaustive lists of accepted genera with their familial placements. Accessible and well-illustrated overviews of morphology are provided for each group, with subsequent contributions focusing on current areas of active research, including developmental biology, molecular genetics, ecology, and microevolution. In addition to reviews of the most current literature, the chapters provide abundant reference to classical studies in bryology that will help those new to the topic to develop an historical perspective within which recent developments can be viewed.

A. Jonathan Shaw is Associate Professor of Botany at Duke University, North Carolina, and Curator of the L. E. Anderson Bryophyte Herbarium. His research has covered monographic work, developmental anatomy, population genetics and, most recently, the molecular systematics and evolution of peat mosses. He teaches courses in evolutionary biology and speciation, as well as bryology.

Bernard Goffinet is Assistant Professor in the Department of Ecology and Evolutionary Biology at the University of Connecticut where he teaches bryology and plant morphology. His research focuses on the evolutionary biology and systematics of mosses, and he also maintains a strong interest in lichenology. He is the holder of the 1995 A. J. Sharp Prize, award by the American Bryological and Lichenological Society.
Contents

List of contributors page vii
Preface ix

1 Anatomy, development, and classification of hornworts 1
Karen S. Renzaglia and Kevin C. Vaughn

2 Morphology and classification of the Marchantiophyta 21
Barbara Crandall-Stotler and Raymond E. Stotler

3 Morphology and classification of mosses 71
William R. Buck and Bernard Goffinet

4 Origin and phylogenetic relationships of bryophytes 124
Bernard Goffinet

5 Chemical constituents and biochemistry 150
Rüdiger Mues

6 Molecular genetic studies of moss species 182
David Cove

7 Control of morphogenesis in bryophytes 199
Michael L. Christianson

8 Physiological ecology 225
M. C. F. Proctor

9 Mineral nutrition, substratum ecology, and pollution 248
J. W. Bates

10 Peatlands: ecosystems dominated by bryophytes 312
Dale H. Vitt

11 Role of bryophyte-dominated ecosystems in the global carbon budget 344
K. P. O’Neill
vi Contents

12 Population ecology, population genetics, and microevolution  369
   A. JONATHAN SHAW

13 Bryogeography and conservation of bryophytes  403
   BENITO C. TAN and TAMÁS PÓCS

Index 449
Contributors

Dr J. W. Bates
Department of Biology, Imperial College at Silwood Park, Ascot, Berkshire, SL5 7PY

Dr W. R. Buck
New York Botanical Garden, Bronx, NY 10458–5126, USA

Dr M. L. Christianson
Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, KS 66045, USA

Dr D. Cove
Leeds Institute of Plant Biotechnology, University of Leeds, Leeds, LS2 9JT

Dr B. Crandall-Stotler
Department of Plant Biology, Southern Illinois University, Carbondale, IL 62901–6509, USA

Dr B. Goffinet
Department of Ecology and Evolutionary Biology, U-43 75 North Eagleville Road, University of Connecticut, Sorrs, CT 06268–3043, USA

Dr R. Mues
Universität des Saarlandes, PO Box 151150, D-66041 Saarbrücken, Germany

Dr K. P. O’Neill
Nicholas School of the Environment, Duke University, Durham, NC 27708, USA
viii  Contributors

Dr T. Pócs
Department of Botany, Esterházy College, EGER, Pf.43, H-3301, Hungary

Dr M. C. F. Proctor
Department of Biological Sciences, Hatherley Laboratories, University of Exeter, Prince of Wales Road, Exeter, EX4 4PS

Dr K. S. Renzaglia
Department of Plant Biology, Southern Illinois University, Carbondale, IL 62901–6509, USA

Dr A. J. Shaw
Department of Botany, Duke University, Durham, NC 27708, USA

Dr R. E. Stotler
Department of Plant Biology, Southern Illinois University, Carbondale, IL 62901–6509, USA

Dr B. C. Tan
Department of Biological Sciences, National University of Singapore, Singapore 119260

Dr K. C. Vaughn
USDA-ARS Southern Weed Science Laboratory, Stoneville, MS 38776, USA

Dr D. H. Vitt
Department of Biological Sciences and Devonian Botanic Garden, University of Alberta, Edmonton, AB T6G 2E1, Canada
Interest in bryophytes has undergone a resurgence in the last decade. This renewed focus on the mosses, liverworts, and hornworts has converged from diverse quarters within the scientific community. With recent advances in DNA sequencing technology and analytical approaches to phylogeny reconstruction, systematists have made unprecedented progress toward reconstructing the “tree of life.” One of the truly monumental events in the history of life was the origin of land plants, or Embryophytes. The bryophytes have long been considered a pivotal group positioned at or near the base of the embryophytes and a great deal of molecular work has recently been aimed at resolving relationships among the disparate groups of bryophytes, and their relationships to the tracheophyte clade (see chapter 4). At the same time, the utility of bryophytes, especially mosses, for analyses of plant function and development has been increasingly appreciated and capitalized upon (see chapter 7). Haploidy and structural simplicity among land plants gives the mosses “added value” for research in functional genomics and several species are presently being utilized as model systems (see chapter 5). The ecological importance of bryophytes has long been appreciated, but recent concerns about the implications of global climate change has focussed renewed attention on some bryophyte-dominated ecosystems, especially boreal peatlands (see chapters 10 and 11).

The idea for this volume came about from two divergent directions. Schofield’s recent textbook of bryology\(^1\) is no longer in print, and students in bryology classes have few other succinct options. In addition, growing attention to bryophytes by ecologists and molecular biologists

---

raises the need for an accessible but inclusive reference on the biology of bryophytes. Fulfilling these rather disparate needs provided the stimulus for this book. Bryology students need a readable overview of bryophyte biology, and it is our opinion that students are well served by rich citation of both current and classic research. We envision that this volume will be especially appropriate for advanced undergraduate and graduate-level bryology students. For ecologists, geneticists, and other researchers who use bryophytes as model systems, we hope to provide a one-stop overview that provides entry into current literature from the spectrum of bryophyte research, as well as descriptions of basic biological characteristics. We tried to find the best compromise between these goals.

Mishler and Churchill\(^2\) presented the first formal cladistic analysis of mosses, liverworts, and hornworts in relation to the tracheophyte clade that includes all other land plants. Their conclusion that the “bryophytes” comprise a paraphyletic basal grade rather than a monophyletic group has been supported by most recent molecular analyses (see chapter 4). What the three groups do have in common is a pleisomorphic life cycle that is nevertheless unique among land plants. The gametophytes of bryophytes are typically large and free-living, perennial, and photosynthetic, while the sporophytes remain attached to the gametophytes and are photosynthetic for a relatively short time. Although the bryophytes do not form a natural group in the sense of monophyly, their comparable life cycles promote a cohesive field of scientific study: bryology. The word bryophyte is used throughout this book in an informal sense in reference to those basal land plants that share the haploid-dominant dibiontic life cycle.