Preface

Pollen studies make important contributions to our knowledge in many interdisciplinary arenas. Pollen identification is widely used in reconstruction of, e.g., vegetation, the climate of the past, and plant biodiversity. Studies concerning pollen structure, size and form are key issues in basic sciences, as, e.g., plant taxonomy and evolution, but are also of importance in applied fields as, e.g., plant breeding. In pollination studies pollen is generally used specifically to identify food sources of visitors and to reconstruct their foraging routes. Fewer have been devoted to pollen collection mechanisms and to the structure and content of pollen in relation to its function.

A computerized search of the current literature reflects these general trends. A search done on December 1st 1999 showed the following: In Agricola the term pollen was mentioned 13354 times, pollination 7184, the combination pollen + pollination 36, and pollen + ecology 17. In Biosis the results were: 15515, 3985, 57 and 3; and in Bioscience 53886, 20187, 502 and 38, respectively.

The present volume, filling a gap, is an attempt to produce a comprehensive interdisciplinary text as a bridge between scientists who study various aspects of pollen biology: physiologists, botanists, ecologists, zoologists and neurophysiologists. We aim to consider the functional ecology of pollen in relation to its structure and constituents as a framework towards a better understanding of evolutionary processes that mold pollination biology.

The 16 papers, all of which were commissioned especially for the present volume, could be roughly classified, by their interdisciplinary nature, into three main themes: pollen structure and constituents, pollen evolutionary ecology and the pollen-pollinator interface. Several papers overlap somewhat or are perhaps even somewhat contradictory and reflect the author's own ideas and experience. Some could be understood more deeply by consulting other closely related articles. The reader is strongly referred to the respective literature list of each article.

The last steps of anther ripening and pollen development (Pacini) and the mature pollen wall structure (Hesse) are key factors to understand pollen dispersal mechanisms in biotic pollination (Stroo) as well as abiotic pollination (Ackerman). Pollen size, shape, wall stratification and the micro-topography of its surface as well as the composition and structure of the pollenkitt have an important role in pollen-connecting mechanisms (Thorp) and also in the dispersal mechanism in which electrostatics is an important factor. Pollen electrostatics (Vaknin et al.) is reviewed from theoretical as well as practical aspects in relation to natural and agricultural systems. Special attention is devoted to the importance of the flower's morphological features that confer adaptiveness to electrostatic pollination.

Abiotic pollination is discussed by Ackerman, who surveyed definitions and terminology of the phenomenon. Pollen physical characteristics are evaluated in relation to its functional ecology and the evolutionary relationships between plant morphology and fluid dynamics. His findings are closely related to those on pollen structure (Hesse), electrostatics (Vaknin et al.), and content (Pacini, Nepi and Franchi) as well as to viability and longevity

(Dafni and Firmage) and adaptation to special pollinators (Stroo).

Pollen constituents are viewed from two complementary angles: pollen cytochemistry (Nepi and Franchi) and pollen nutritional value (Roulston and Cane). Pollen cytochemistry (Nepi and Franchi) deals with the application of cytochemical methods to mature pollen with special reference to reserve material. The chapter on pollen cytochemistry serves as a basic background to understanding pollen physiological behaviour and chances for germination and fertilization. The chemistry of the pollenkitt is a key factor in understanding pollen dispersal (Ackerman; Hesse et al.) as well as in pollen odour (Dobson and Bergström) and colour (Lunau). The inner pollen composition is related to its viability (Pacini; Dafni and Firmage) as well as to its value as a food for consumers (Roulston and Cane).

Pollen viability and longevity is discussed from practical, ecological and evolutionary viewpoints. The article by Dafni and Firmage surveys the advantages and disadvantages of the existing methods to asses pollen viability and examines the current hypotheses that link pollen longevity and pollination biology.

Pollen may attract flower visitors by visual (Lunau) as well as by odoriferous cues (Dobson and Bergström). In general, our attention is focused on petals (and sepals) as the main attractants of flowers. Lunau draws our attention to the importance of visual pollen signals. While considering evolutionary, ecological, sensory-physiological and behavioral aspects of flower-pollinator interaction, the various strategies of angiosperms for attracting pollinators to the site of rewards are elucidated with special reference to pollen. Floral odours are important cues even as a long distance signals that flowers emit. Dobson and Bergström discuss pollen odours in relation to bee foraging behavior, location of pollen sources, discrimination of pollen amounts and specific recognition of flower resources. Their work includes a review of the current knowledge as well as new experimental evidence and chemical analyses concerning pollen odours.

Cruden deals with the intriguing question of why there are so many pollen grains? This article examines the selective forces that affect pollen number.The author analyses the relationships among other floral traits of animal-pollinated plants, including pollen size, stigma area and depth, and the pollen-bearing area of the pollinator that may affect pollen number, and also provides a model to examine how change in one trait may elicit change in other traits.

Pollen as a food for its consumers is a widely neglected topic. The article by Roulston and Cane covers the mechanisms of pollen digestion by animals; the efficiency of removal of pollen content and the taxonomic distribution of pollen content. All these aspects are discussed in relation to adaptive hypotheses that associate pollen chemistry with pollinator rewards. Roulston and Cane surveyed the digestion and nutrient content of pollen, which is an outcome of pollen cytochemistry (Nepi and Franchi). They discuss mechanisms of pollen digestion and its efficiency and the range and taxonomic distribution of pollen nutrients. All these address adaptive hypotheses concerning pollen chemistry and pollinator reward. Pollen digestibility is, to a large extent, an outcome of the pollen wall structure (Hesse) and content (Pacini).

The various mechanisms of pollen collection by bees are surveyed by Thorp. Pollen is an essential food of many pollinators especially bees due to its nutritive contents (Roulston and Cane; Pacini) especially bees. Thorp surveys the various structures and behavioral adaptations for acquiring and transporting pollen by bees.

Pollen structure and packaging have coevolved in relation to transfer functionality and pollinator's specificity. Stroo reviews the pollen morphological evolution in bat- pollinated flowers. An analysis of pollen size, shape, aperture number and type and ornamentation type is used to test previous hypotheses concerning the characteristics of bat-pollinated pollen. Orchid pollinaria structure is discussed in relation to its functionality (Johnson and Edwards). Aspects as attachment to vectors, mechanisms of pollen deposition, pollen longevity (see also Dafni and Firmage), pollen:ovule ratio (see also Cruden), spatial dispersal patterns and outcrossing in relation to pollen export are also discussed. This contribution is a key to elucidating Roubik's paper on a new deceptive mechanism in orchids involving Meliponini bees as pollinators. It is assumed that the relationship is based either on mimicry of rewarding resources or on a bee pheromone.

Various thread-forming structures in pollen anthers are discussed by Hesse et al. in relation to their role in pollination ecology. These unique structures may function as pollen-connecting vectors in forming pollen dispersal units and/or playing a role in pollen presentation.

Beetles are important pollen-eaters, Bernhardt reviews the convergent evolution and adaptive radiation of beetle- pollinated angiosperms. His survey stresses the diversity of beetle-pollinated flowers and their shared and peculiar adaptations contributing to the syndrome of cantharophily and its evolution.

We would like to acknowledge here all those who have made possible the publication of this volume. We are very grateful to all our contributors for their effective co-operation, and to all our reviewers for their careful revisions and for their efforts to return quickly their comments and suggestions. We would like to thank especially the staff of our publisher, Springer-Verlag in Vienna, for the help and support during the preparation of this special issue of Plant Systematics and Evolution. It is hoped that this interdisciplinary volume will promote multifaceted studies leading to a better understanding of pollination evolutionary ecology. Floral rewards, such as pollen and nectar, are only one aspect of the multidimensional pollination kaleidoscope. Any attempt to evaluate the role of pollinators attraction and behaviour has to be considered in relation to the reward's content, composition, and physical and chemical properties, all this in relation to environmental conditions as well as the agent's efficiency as a disperser of a functional pollen.

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Guest Editors