

Floral Diagrams

Floral morphology remains the cornerstone for plant identification and studies of plant evolution.

This book gives a global overview of the floral diversity of the angiosperms through the use of detailed floral diagrams. These schematic diagrams replace long descriptions or complicated drawings as a tool for understanding floral structure and evolution. They show important features of flowers, such as their relative position in an inflorescence, the positions of the different floral organs, their fusion, symmetry and structural details. In addition, the book contains a wealth of information as a comprehensive synthesis of the diversity of families. The relevance of the diagrams is discussed, and pertinent evolutionary pathways are illustrated. The range of plant species represented reflects the most recent classification of flowering plants based mainly on molecular data, which is expected to remain stable in the future. This book will be invaluable for researchers and students working on plant structure, development and systematics, as well as being an important resource for plant ecologists, evolutionary botanists and horticulturists.

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Floral Diagrams

An Aid to Understanding Flower Morphology and Evolution

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To Catherine, Camille and Alexandre, with love



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Foreword

This very welcome addition to the literature on the structure and evolution of flowers provides a valuable and practical new perspective on a classical botanical theme. It focuses on the relationships between flower structure and the evolutionary diversification of plants as reflected in the latest system of classification.

Floral diagrams provide one of the best examples of the idea that a picture is worth a thousand words. They provide a stylised system for describing and communicating the arrangement of floral organs with great simplicity, regardless of the structural complexity of the particular flower. It is therefore no surprise that floral diagrams have stood the test of time and remain as effective today as when they first began to be used. The German botanist August W. Eichler is generally credited with their introduction in the late nineteenth century and they were rapidly adopted, soon becoming a familiar feature of numerous botanical textbooks. Eichler was also a pioneer in the field of classification of flowering plants and one of the first botanists to base a system of classification upon evolutionary principles. Whilst the utility of floral diagrams has remained unchanged since their invention, we now use very different methods to establish the evolutionary relationships between different groups. For most of the twentieth century plant classification relied on the comparison of morphological characters and numerous different schemes competed for attention. The advent of classifications based upon the analysis of DNA sequence data rather than on traditional morphological characters resulted in revolutionary advances. An international collaboration by the Angiosperm Phylogeny Group has provided a new and much more stable framework. Although we might expect some minor changes to take place as new gene sequences begin to be integrated into the analysis, the classification we have today is unlikely to change much in the future.

Louis Ronse de Craene, a research botanist who has made a significant contribution to the study of evolutionary development in flowers, has therefore



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written a very timely book. Here he reconnects the tradition of floral diagrams as a concise shorthand notation with the latest understanding of plant evolutionary relationships. The book will provide an invaluable tool for anyone who wishes to understand the form of flowers and use them, for example, to identify unfamiliar plants.

Stephen Blackmore Regius Keeper Royal Botanic Garden Edinburgh



Preface

Flowers are extremely attractive to us as a source of inspiration and happiness. It is no wonder that various technical textbooks in plant science tend to enhance their front page with some glamorous illustrations of flowers. Despite this wide interest, our knowledge about the diversity of floral structures is still limited and relies mostly on research carried out in the nineteenth century.

A floral diagram is a basically schematic cross-sectional drawing of a flower. However, floral diagrams are more than just a two-dimensional representation. There are more than 250 000 species of angiosperms and their flowers vary in many ways. The arrangement of flowers in inflorescences, the number, position, identity and shape of floral organs and the symmetry of the flower as a whole are rarely identical between different families, genera or even species. Floral diagrams are a rich source of data for identification purposes and for understanding structures, but can also be used to express a hypothesis of evolution. The information contained in floral diagrams is potentially immense and replaces complex descriptions.

Students often struggle with the identification of flowers, mainly because they fail to look at the structures hidden in the bud. However, the spatial arrangements of organs in the flower, as well as the number of whorls, are an essential indication of systematic relationships. This information is particularly important for identifying plants in the field and tells us much about the key characters of a specific group of plants. The educational merits of floral diagrams in the classroom are obvious. Used together with floral formulae, they convey information in a rigorous and clear way. They are important for systematists or evolutionary botanists in providing information for databases dealing with morphological data (e.g. Morphbank: http://www.morphbank.net/) or for clarifying phylogenetic questions. In paleobotanical research floral diagrams are a useful resource in reconstructing the shape of fossilized flowers.



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Researchers in evolutionary developmental genetics will find appropriate questions about the nature of floral organs to investigate. Finally, horticulturists or amateur botanists will find this book valuable to understand general patterns of flower construction and floral diversity.

It is more than 130 years since August Wilhelm Eichler (1839–1887), then professor of botany in Kiel, produced a book in two parts, in 1875 and 1878. This book, entitled *Blüthendiagramme Construirt und Erlaütert*, is a major reference work, concentrating the information about flowers known at that time. As such, it represents a treasure trove, detailed and often accurate, and even today extremely valuable as a source of data. Eichler's work was an inspiration for later generations of morphologists, such as Arthur W. Church (1865–1937) and Agnes Arber (1879–1960). A particularly fine example of a book using floral diagrams is *Types of Floral Mechanism* published by Church (1908) and intended as a series, but limited to a single volume by lack of interest and funds (Mabberley, 2000). Since Eichler's book was published, much progress has been made in documenting flower morphology, especially during the last decades of the twentieth century, when there was a renewed interest in floral morphology coupled with the use of the scanning electron microscope.

However, information about flowers is scattered in scientific papers that are not readily accessible to the general public, providing little scope for a broad overview of the flowering plants. Alternatively it dates from important work carried out in the nineteenth century that is in danger of being forgotten. Floral diagrams were used sparingly in different textbooks as illustrative material (e.g. Baillon, 1868–1894; Engler and Prantl, 1884–1909), but never to the extent of Eichler's book. More recent examples are Melchior (1964), Sattler (1973), Graf (1975) and Stützel (2006). The most recent major textbooks on angiosperm phylogeny (e.g. Judd *et al.*, 2002; Soltis *et al.*, 2005; Simpson, 2006) lack any floral diagrams. Spichiger *et al.* (2002) did include diagrams for major families, but the diagrams are oversimplified and riddled with mistakes.

The system of classification used by Eichler is outdated, as it is based on the Englerian concept that simple, unisexual catkin-like flowers are ancestral and that more elaborate bisexual flowers are derived. Recent changes in the phylogeny of flowering plants based mainly on molecular evidence have created the need for a new book on floral diagrams. It is essential to link obvious morphological characters to any molecular phylogeny. I hope this book fulfils this purpose.



Acknowledgments

The idea for this book has matured over several years. Discovering the variation in flowers has always been a major passion for me, and there is no better way to present this variation than by floral diagrams. Besides the possibility of describing flowers and their structures by photographs or drawings, floral diagrams bring another dimension that I enjoyed exploring. The book allowed me to compile more than twenty years of research on flowers.

My special thanks go to Paula Rudall, Livia Wanntorp, Erik Smets and David Harris for critically reviewing an early draft of the book and for their helpful suggestions. Several colleagues were inspirational and helpful through previous contacts, such as Peter Endress, Greg Kenicer, Peter Linder, Gerhard Prenner, Rolf Sattler, Dennis Stevenson, Wolfgang Stuppy, the late Cyrille Vandenberghen and Philip Smith, among others. Without the vast living collections at the Royal Botanic Garden Edinburgh, the extent of my book would be meagre indeed. I thank the horticultural staff, especially Fiona Inches, for their help in identifying specimens. Aleck Yang, Colin Belton, David Harris, Euridice Honorio, Paulina Hechenleitner, Peter Linder, Tony Miller, Mark Newman, Rolf Rutishauser, Tory Tokuoka and Peter Wilkie contributed to obtaining material for study. Frieda Christie and the technical staff of the Royal Botanic Garden Edinburgh have been very helpful in assistance with preparing and observing some specimens used in this study. The curators of the pickled collections of the Swedish Museum of Natural History, the National Herbarium of the Netherlands in Wageningen and the Royal Botanic Garden Kew were helpful in allowing me to visit the collections and use the material. Finally, I thank my daughter Camille for her creative help in designing parts of the book. The writing of this book would not have been possible without the constant support and patience of my dear wife Catherine. Finally, I owe much to the generosity of my parents who allowed me to pursue my career in botany.