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## Introduction: Establishing the state of the art – the role of morphology in plant systematics

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### 1.1 Outlook

Scientific biological research is dominated by genetics and molecular studies nowadays. This research is extremely important and has led to a tremendous advance in the fields of systematic botany and evolutionary developmental genetics. Nevertheless, from the start the molecular approach grew at the expense of more traditional approaches, such as morphology, embryology, palynology and cytology, and today molecular Barcoding and phylogenetic studies often appear to be the dominant, sometimes exclusive, research areas. Despite this, most systematists would agree that morphological and molecular data are complementary and should, when possible, be used together in phylogenetic and evolutionary investigations. A common approach used in systematics, combining the molecular and morphological methods, routinely maps unexplored morphological characters or putative synapomorphies on well-supported phylogenetic trees in order to study the evolution of these characters. There is an important problem with this approach, that morphological characters can be wrongly defined or are often unknown or superficially assessed. However, understanding the characters used for phylogenetic studies is crucial for understanding evolutionary processes in plants.

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A general appreciation of floral morphology is also becoming difficult to grasp, with the disappearance of generalists, and this is not helped by the fact that there is little or no funding for any PhDs that are non-molecular. With the cutback of traditional botany in university education, lack of interest and funding from decision-making bodies, floral morphology is left increasingly aside. This is tragic, because it represents a loss of knowledge, which needs to be 'rediscovered' (as currently happens with the oblivion of obscure nineteenth century observations in even more obscure journals) and a non-appreciation of the value of morphology in contributing to solving the biodiversity crisis. Alas, morphology and general botany are increasingly scrapped from university curricula in the constricted atmosphere of 'efficient' research funding, with retiring experts not being replaced and with an increased specialization in botany on offer. Very few universities still have a morphology-based, integrative botany course. Recent developments such as genetic Barcoding are undoubtedly useful, but they remove interest and funding from other studies, such as those focusing on floral morphology.

There is an urgent need to stop the continuous erosion of expertise in morphology and systematics that has been going on for several decades. However, researchers in disciplines dealing with living organisms are increasingly confronted with a lack of knowledge of structures, with dire consequences for inaccurate interpretations and lack of perspective to their research. The understanding of the morphology of organisms in a broad range of taxa is essential to make links between observed patterns and helps the researcher to connect with the real world.

Flowers have always been the first pole of attraction to botany. While the beauty of flowers is part of human appreciation, the underlying parts and mechanisms of flowers have become the domain of floral morphology. Floral morphology is the reflection of an ongoing evolutionary process that started some 130 million years ago, and is continuously progressing with time. It is the accomplishment of close co-evolution with pollinating agents or physical mechanisms that lead to a single goal: fertilization and production of offspring. As a science, morphology is highly synthetic, even holistic. It finds unifying features in the great diversity of life (cf. Classen-Bockhoff, 2001; Kaplan, 2001). Floral morphology has a long and rich tradition in botany. Starting with herbals, it evolved into a major science that found its heydays in the nineteenth century, mainly in Germany and France. At the end of the twentieth century, morphology (especially of flowers) had become a well-established component in systematic research, as a major tool to reconstruct phylogeny, with far-reaching speculations about the evolution and significance of organs (e.g. Cronquist, 1981; Takhtajan, 1997). However, misconceptions grew out of a superficial approach to floral morphology, where things may look the same, but are not. Conspicuous

examples of these generalizations are the derived nature of inferior ovaries, multistaminate androecia and the nature of petals. The rise of cladistics and molecular systematics was a great milestone in the understanding of relationships of plants, but it did not help in stopping a trend of a progressive demise of morphology. Important shifts were proposed in the classification systems that were originally considered to be sacrosanct. The acceptance of the important principles of parsimony and the understanding that only apomorphies can be considered valid led to increasing suspicions on the legality of floral morphology, as a nest of convergences and homoplasy.

Despite this, the advantages of investigating morphological characters with the help of molecular phylogenetic trees have become more evident during the past years.

The use of molecular methods is undeniably valuable and has helped botany to put order in the system, but its expansion went at the expense of traditional botany, of which floral morphology is a major component. The appreciation that producing molecular phylogenies for the sake of creating trees is hardly practical without 'real' or 'visual' characters, has led to a reconsideration of morphology. It is now generally understood that the support of phylogenetic trees is usually improved by combining molecular data with morphological data. The increased use of fossil evidence in phylogenies makes the use of structural data more important, as fossils possess no retrievable DNA (Endress, this volume; Doyle and Endress, 2010). Morphology is increasingly used as the basis of the molecular phylogenies, to understand how patterns evolve. This is useful to a certain extent but becomes doubtful when the morphological characters are not well understood or even wrongly assessed. When the principle of parsimony is used, some assumptions of morphological change quickly become listed as 'reversals', as characters are reconstructed along the nodes. This can lead in some cases to changes that are difficult to explain on morphological grounds. Especially at the level of their genetic mechanisms, the expression of morphological characters can be switched on and off very easily along the nodes of a tree.

However, with increased stability of the angiosperm tree of life, the value of flower morphology becomes increasingly obvious as a worthy counterpart to molecular characters in phylogenetic studies and as a source of data that help clarifying floral evolution and the underlying mechanisms of flower development. There are still major parts of the tree that need to be explored. For example, there are angiosperm groups whose positions in the system are yet unresolved and genera (even families) whose flower morphology and ontogeny is either poorly or completely unknown. This lack of knowledge is limiting our current understanding of the evolution of flowers and their structures considerably, as well as our general comprehension of the systematics of angiosperms. However, the complexity of floral morphology is increasingly being investigated, thanks to the development

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of evo-devo research, and our understanding of underlying structural and genetic factors does not fail to impress researchers.

## 1.2 Contents

*Flowers on the Tree of Life* aims to be a celebration of floral morphology by representing a compilation of articles from eminent researchers in the field of floral morphology. This volume is the proceedings of a symposium 'Flowers on the tree of life', organized by the editors and supported by the UK Systematics Association. This symposium was part of an international conference, entitled 'Systematics', organized by the Systematics Association and the Federation of European Biological Systematic Societies in Leiden from 10–14 August 2009. The symposium was built around three major themes: use of floral characters in phylogeny reconstructions, theoretical background for morphological characters and case-studies of specific groups of angiosperms whose flower morphology is controversial, unexplored or in need of further research. The symposium has clearly demonstrated that there is a great potential to re-establish floral morphology as centre-stage in botanical research and on the tree of life, putting more emphasis on the definition of sound characters that can be used to clarify relationships of plants and the intrinsic evolution of their flowers. Morphology is hugely important because it is a synthetic science that builds on information from multiple sources.

Chapters 2–4 deal with questions of relationships in angiosperm origins and early evolution of flowers.

A central subject to our understanding of flowers is how and when they diverged in evolution. This question has been pursued from several angles such as molecular phylogenetics and evolutionary developmental genetics, as well as morphology, including extant taxa and fossils (e.g. Bateman, Hilton and Rudall, 2006; Doyle, 2008; Doyle and Endress, 2010; Endress and Doyle, 2009; Friis, Pedersen and Crane, 2010; Frohlich, 2006; Soltis et al., 2009; Soltis and Soltis, 2004; Theissen and Melzer, 2007).

Bateman, Hilton and Rudall (Chapter 2) explore the relationships of bisexual angiosperm flowers with their gymnosperm relatives. A major obstacle to our understanding of flowers comes from the fact that gymnosperms are unisexual. The authors analyse this question from a historical as well as a developmental-genetic perspective and conclude that changes in gender from gymnosperm ancestors are inversely proportional to divergence between male and female developmental programmes.

Maria von Balthazar and co-workers (Chapter 3) explore the diversity of fossil Lauraceae and demonstrate how characters of extant Laurales are represented in the fossil record, but in different combinations.

James Doyle and Peter Endress (Chapter 4) discuss the origin and early evolution of the angiosperm flowers by mapping morphological characters on a phylogeny based on molecular data. They demonstrate that reconstructions of floral evolution depend on the phylogenetic framework, but also on morphological aspects of floral organizations.

Chapters 5 and 6 analyse the significance of morphological characters for phylogenetic reconstructions on the tree of life. Peter Endress (Chapter 5) discusses how the role of flowers has changed away from phylogenetics to a better understanding of evolutionary processes. However, increased use of fossil evidence increases the role of morphological data in phylogenetic reconstructions. The flexibility of changes in morphological characters is illustrated by several examples and highlights the importance of exploring morphology at deeper levels. A genetic predisposal can be treated as a character in its own right, even if it is not always expressed in a clade. The understanding of these underlying genetic systems will undoubtedly clarify our concepts of character evolution. This corresponds to a distinction between cladistic homology and biological homology as discussed by Endress.

Understanding key characters at deep phylogenetic nodes becomes an important part of morphological research. Paula Rudall (Chapter 6) explores characters that are significant at deeper nodes of the angiosperm tree of life. The centrifugal direction of stamen development is shown to be partially significant, but not at the level of Corner's (1946) prediction. This update of our knowledge of stamen development puts a final nail in the coffin of Cronquist's belief of centrifugal stamen development as a basic character for his subclass Dilleniidae. We now have a much better understanding of the relationship of centrifugal stamen development and polyandry (see also Ronse De Craene and Smets, 1992).

The next chapters (7–12) are examples of specific groups of plants where morphological investigations have a major impact, in understanding the phylogenetic relationships of palms with polyandry (Chapter 7) and genera making up the family Nitrariaceae (Chapter 8), and the understanding of the evolution and significance of floral morphological characters (Chapters 9–12).

Sophie Nadot and co-workers (Chapter 7) explore how the optimization of floral characters on a supertree of palms helps in understanding the evolution of the androecium in the diversification of the family.

Julien Bachelier, Peter Endress and Louis Ronse De Craene (Chapter 8) analyse how newly explored floral characters support the recent amalgamation of *Nitraria*, *Peganum* and *Tetradiclis* in a family Nitrariaceae of Sapindales.

Livia Wanntorp and co-workers (Chapter 9) study the variation in merism in *Conostegia* (Melastomataceae) and explore how changes in petal and stamen numbers correlate with increases in carpel numbers.

Alexandra Ley and Regine Classen-Bockhoff (Chapter 10) study the variation in the elaborate pollination mechanism of Marantaceae. By mapping major

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transformations of characters on a phylogenetic tree they are able to reconstruct the evolution of this unique pollination mechanism throughout the family.

The contribution of Gerhard Prenner (Chapter 11) studies a special case of high stamen and carpel numbers in *Acacia celastrifolia* and how this appears to be a concerted increase, linked with specific pollination strategies.

Finally Louis Ronse De Craene (Chapter 12) demonstrates on floral developmental evidence that petals of *Napoleonaea* (Lecythidaceae) represent a true corolla and not staminodes as previously suggested. This study also shows the value of comparative floral development in interpreting morphological structures.

In conclusion, flower morphological and ontogenetic studies have been and are going to remain an important contribution to systematics. This book clearly demonstrates that there is a great potential to re-establish floral morphology as centre-stage in botanical research and on the tree of life, putting more emphasis on the definition of sound characters that can be used to clarify relationships between plants and the intrinsic evolution of their flowers. New methods for working with flower morphological characters, such as synchrotron X-ray tomographic microscopy and more traditional light and electron microscopy techniques, as well as new ways of storing and making morphological data available to the community, such as the use of databases, are facilitating the use of such characters. This together with the necessity to use morphological characters as a complement to molecular data will ensure, whenever possible, that the morphological tradition will not be forgotten. As the world's flora is under increasing threat, understanding of plant structure becomes increasingly vital and experts with a global view on biodiversity become a necessary breed. Let us hope that there is room for a renaissance in morphology and that the present symposium becomes commonplace in the future.

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# 2

## Spatial separation and developmental divergence of male and female reproductive units in gymnosperms, and their relevance to the origin of the angiosperm flower

RICHARD M. BATEMAN, JASON HILTON AND PAULA J. RUDALL

### 2.1 Introduction: aims and terminology

It is now generally accepted that angiosperms are monophyletic and are derived from a gymnospermous ancestor. It is also widely recognized that, among extant seed-plants, angiosperm reproductive units are typically bisexual (= bisporangiate, hermaphrodite) and are termed flowers, whereas putatively comparable units produced by the four groups of gymnosperms represented in the extant flora are typically unisexual, either functionally dioecious (cycads, *Ginkgo*, gnet-aleans) or a more complex admixture of dioecious and monoecious taxa (conifers) (e.g. Tandre et al., 1995). Individual extant gymnosperms are either monoecious, bearing male and female units on separate axes of the same plant, or dioecious, each individual bearing units of only one gender (note: in this chapter, the terms 'male' and 'female' are used consistently as colloquial shorthand for the ovuliferous and (pre)polleniferous conditions, respectively). A positive correlation

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with dispersal mechanism is evident, monoecious extant gymnosperms typically producing dry, wind-dispersed seeds and dioecious gymnosperms bearing fleshy, often animal-dispersed seeds (cf. Givnish, 1980; Donoghue, 1989).

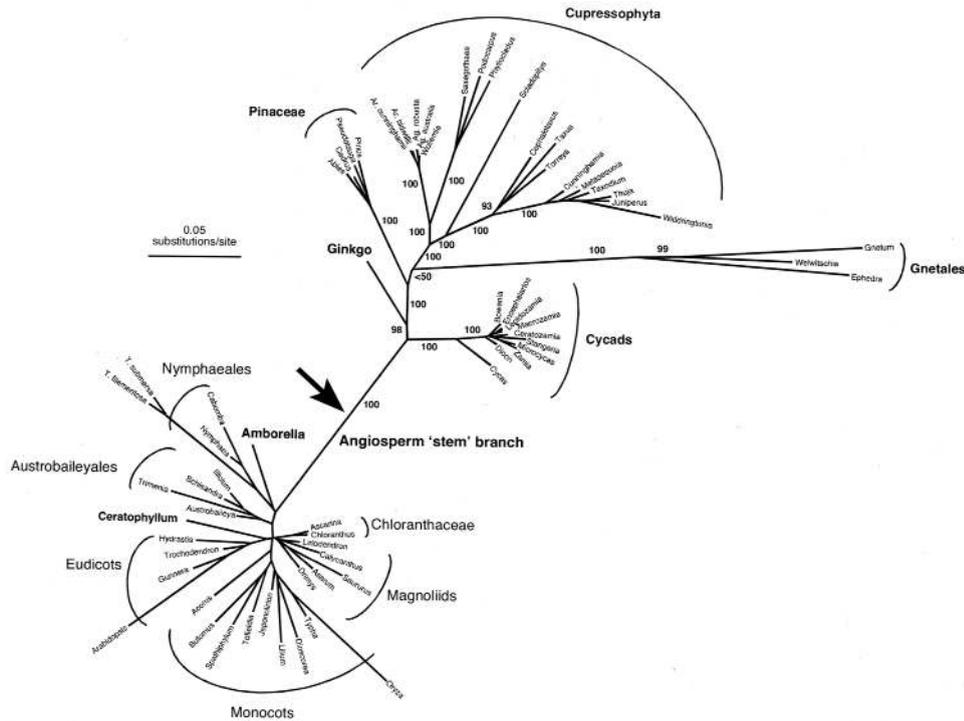
Further terminological clarifications are needed. Bateman et al. (2006, p. 3472) reviewed relevant definitions before defining a flower as ‘a determinate axis bearing megasporangia that are surrounded by microsporangia and are collectively subtended by at least one sterile laminar organ’. Accepting this controversial definition means that the angiosperm flower is not unique; comparable hermaphrodite structures occur in at least one other group of seed-plants, specifically a putatively highly derived clade within bennettites (Crane, 1988). Extending this logic, the term inflorescence could also be applied more widely, to encompass axial systems that bear multiple reproductive units of gymnosperms. However, we have chosen to use throughout this chapter the more phylogenetically neutral term ‘truss’ to describe any reproductive shoot, unbranched or branched (we recognize that this usage of ‘truss’ contradicts that employed in the telome theory of Zimmermann, 1952).

Returning to the topic of gymnosperm–angiosperm relationships, the transition from unisexual to bisexual (bisporangiate, dimorphic, hermaphrodite) reproductive units, thereby spatially – though by no means always temporally – unifying male and female expression, has been consistently implicated as a key step in the long-debated origin of the angiosperm flower (reviewed by Bateman et al., 2006; Endress and Doyle, 2009; Specht and Bartlett, 2009). In contrast, the likelihood that the earlier origin of the gymnosperms involved the physical *separation* of male and female genders has received less consideration. In this paper we review the evidence for, and assumptions that underlie, these assertions of contrasting but equally radical shifts in the spatial location of male and female expression. We critically assess several scenarios emerging from recent evolutionary-developmental genetic studies in the light of: (a) the reproductive morphology of fossil gymnosperms and (b) teratological reproductive structures found in extant gymnosperms.

## 2.2 The enlarged phylogenetic gap between extant angiosperms and extant gymnosperms

Cladistic analyses conducted during the last three decades have consistently revealed vast morphological (e.g. Crane, 1985, 1988; Doyle and Donoghue, 1986; Donoghue and Doyle, 1989; Nixon et al., 1994; Rothwell and Serbet, 1994; Hilton and Bateman, 2006; Endress and Doyle, 2009; Rothwell et al., 2009) and molecular (e.g. Rydin et al., 2002; Burleigh and Mathews, 2004; Rai et al., 2008; Graham and Iles, 2009; Mathews, 2009) disparities between extant angiosperms and extant

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**Fig 2.1** Unrooted phylogeny of extant seed-plants (modified after Graham and Iles, 2009, Fig 2). The arrow indicates the most common location of the tree root.

gymnosperms, irrespective of detailed topology (Fig 2.1). This exceptional phylogenetic divergence not only challenges the credibility of root placement in such trees but also represents a potentially insurmountable barrier to the important goal of reconstructing the phenotype and/or genotype of the angiosperm ancestor.

Similar ambiguity surrounds the characteristics of the hypothetical ancestor of the angiosperm crown group (i.e. the next node towards the apex of the seed-plant tree). Although it has not yet been quantified to our satisfaction, there appears to be greater morphological diversity among early-divergent extant angiosperms (termed by many authors the ANITA grade plus the magnoliids) than subsequently diverging and far more species-rich taxa of monocots and eudicots. This interpretation is encouraging in suggesting that the early-divergent extant angiosperms represent a genuine residue of the initial angiosperm radiation. However, the comparatively high level of morphological diversity also brings more negative consequences, as it renders very uncertain any attempted reconstruction of the shared ancestor of the crown group; when addressing this important question we can expect only limited help from 'top-down' angiospermo-centrism (Bateman