

Introduction

Darwin and the evolution of flowers

With the ubiquity of flowers in our everyday lives, it is sometimes easy to overlook their central importance in the production of food and other materials on which human survival depends. The origin of flowering plant (angiosperm) diversity, which is intimately connected to the diversification of floral form and floral biology, is also of great interest because as the dominant autotrophs of terrestrial environments, angiosperms provide the energy on which most of the rest of biological diversity depends. The evolution of flowers and flowering plants is therefore both of fundamental significance and of contemporary relevance.

The Discussion Meeting reported in this volume presents recent and emerging ideas on the evolution of flowers and their function while also highlighting the influence of Darwin on this field. The meeting was timed to bridge two important celebrations. Publication of this Discussion Meeting was timed to coincide with the beginning of the celebrations of the 350th anniversary of the Royal Society, recognizing that the biology of flowers was investigated scientifically by some of the most well-known scientists in the early history of the Society. The Discussion Meeting itself took place a little over six months earlier, in May 2009, and was timed to coincide with the celebrations at the Royal Society and elsewhere around the bicentenary of the birth of Charles Darwin and the sesquicentenary of the publication of '*Origin of species*...' (Darwin 1859). The aim was to examine Darwin's key contributions to understanding the biology of flowers in light of current knowledge, but also to feature emerging areas of research and the advances now possible with new ideas and approaches.

The Discussion Meeting brought together plant organismal biologists with broad interests in the evolution of flowers from many different perspectives. The disciplines represented included plant palaeontology and systematics, plant morphology and development, and plant reproductive and conservation biology. The Meeting sought to highlight renewed interest in the theoretical aspects of pollination biology, which continues to refine the concepts first explored by Darwin. It also sought to emphasize the impact of modern phylogenetics, which is illuminating

the evolutionary diversification of flowers and flowering plants with a level of specificity that Darwin could never have imagined. Well-resolved phylogenies (at many taxonomic levels), coupled with improved insights from the fossil record and from studies of living plants, are providing increasingly precise and specific evidence regarding the evolution of floral structure and biology. At the same time, advances in understanding the genetic control of floral development based on studies of model systems are now being applied in an explicit evolutionary context, and across a much broader systematic front. These advances offer new possibilities for understanding how the bewildering floral variety of angiosperms has been generated by modifications of fundamentally similar developmental processes.

Darwin's interest in plants sprang from many sources: the botanical interests of his grandfather and father, the guidance of John Henslow, his mentor at Cambridge, and the lifelong influence of his close friend Joseph Hooker. Throughout his life, he maintained a fascination with plants. He collected plant specimens as a young man on the Beagle expedition and ideas about the evolution of plants persist in his correspondence up to the time of his death. He considered domesticated plants in '*The variation of animals and plants under domestication*' (Darwin 1868) and he explored the form and function of carnivorous plants for 15 years before eventually bringing together his experiments and observations in '*Insectivorous plants*' (Darwin 1875). Darwin's botanical interests were wide ranging, but he also appreciated the value of plants as experimental organisms. He recognized that they could be observed, manipulated and experimented on with relative ease and he used them to develop and test his evolutionary ideas.

Darwin was also impatient to see certain key questions of plant evolution resolved. His famous letter to Joseph Hooker, in which he describes the relatively late and apparently sudden appearance of flowering plants as 'an abominable mystery', was written towards the end of his life in July 1879 (Darwin in letter to J. D. Hooker, 22 July 1879; see also Friedman 2009). He commented that he would like 'to see this whole problem solved'. The papers by Mathews *et al.* (2010), Friis *et al.* (2010) and Rudall & Bateman (2010), in this volume provide modern perspectives on different aspects of the origin of flowers.

Mathews *et al.* consider the question of the relationship of flowering plants to other seed plants using a

One contribution of 16 to a Discussion Meeting Issue 'Darwin and the evolution of flowers'.

duplicate gene rooting approach. The results point towards a close relationship between angiosperms and cycads. Friis *et al.* review the palaeobotanical evidence for the very early evolution of flowers. They present the first unequivocal evidence of monocots in some of the earliest mesofossil assemblages that contain flowers and other angiosperm reproductive structures. These early monocots include forms that are clearly related to modern subgroups of living Araceae.

Rudall and Bateman raise the question of the origin of flowers more directly, emphasizing in particular the difficulties of distinguishing among the different evolutionary and developmental pathways that can potentially give rise to flower-like reproductive structures. This is a topic that has assumed new importance with the discovery of very simple flowers among early fossil angiosperms and the recent recognition that extant *Trithuria*, the sole genus of the living family Hydatellaceae, is a member of the Nymphaeales with surprisingly divergent and enigmatic reproductive units. As the sister group to all other extant angiosperms except *Amborella*, Nymphaeales are a key lineage for interpreting early patterns of floral evolution, but in *Trithuria*, and also in some key fossils from the Early Cretaceous, the flowers are far from 'typical' of angiosperms as a whole.

Darwin had relatively little to say about the origin of the angiosperm flower, but the evolutionary diversification of floral form and its evolutionary significance was central among his botanical interests. As Barrett (2010) points out in the first paper in this volume, Darwin was striving to answer a single key question—what evolutionary advantages do different kinds of flowers confer in the struggle for existence? This question is still at the heart of our thinking about the origins of floral diversity, and Darwin's three major books, which tackled this question from different perspectives, are the foundation for our modern understanding of evolutionary reproductive biology in plants. Barrett places Darwin's legacy in its modern context focusing particularly on the evolution and maintenance of polymorphic breeding systems in plants, a topic that traces its intellectual foundations to Darwin's final book on flowers, '*On the different forms of flowers on plants of the same species*' (Darwin 1877).

Darwin's first book on floral biology '*On the various contrivances by which British and foreign orchids are fertilized by insects and the good effects of intercrossing*' (Darwin 1862) established for the first time that the great variety of form in orchid flowers had arisen by natural selection through different mechanisms to facilitate pollination and fertilization of one flower by another. Darwin's insights placed earlier studies of floral function in a dynamic new framework and the themes it outlined remain valid today. In this volume, the papers by Endress (2010), Schönenberger *et al.* (2010) and Renner & Schaefer (2010) show that those themes apply across a broad range of flowering plants, and they also demonstrate how ideas on the evolution of floral biology are informed by modern phylogenetic analyses.

Endress explores the differences in the timing of maturation of reproductive parts in flowers of lineages

of living plants that diverged very early from the main line of angiosperm evolution. Various forms of dichogamy are among the subtle, but most important, mechanisms that promote 'intercrossing', rather than selfing, in bisexual flowers. Some of these mechanisms were probably established very early in angiosperm evolution. Schönenberger *et al.* show how floral features correlate with the new understanding of phylogenetic relationships among certain groups of Ericales. Their paper illuminates an important current difficulty. In many large and important groups of angiosperms, there is still a large gap between well-supported patterns of phylogenetic relationships based on analyses of molecular sequence data on the one hand and a detailed knowledge of structure on the other. Schönenberger *et al.* show how much still remains to be learnt about floral structure in many groups of angiosperms. Renner & Schaefer examine the evolution of oil-offering flowers across the full sweep of extant flowering plant diversity and consider patterns of coevolution. They demonstrate the repeated evolution and loss of this specialized, coevolutionary relationship with certain groups of bees in different parts of the world. From analyses of 'molecular clocks' they also infer that oil flowers arose shortly after the close of the Cretaceous, in a number of distinct clades of flowering plants, but other new oil flower groups continued to evolve, the latest only a few million years ago.

Floral diversity of the kind discussed by Endress, Schönenberger *et al.* and Renner & Schaefer has its basis in differences of floral development. Evolutionary change occurs through modification of developmental processes, and increasingly these processes can be studied at the molecular level. The papers by Venail *et al.* (2010), Kramer & Hodges (2010) and Jasinski *et al.* (2010) take up this challenge in different ways. Jasinski *et al.* make a general point regarding the importance of micro-RNA-mediated gene expression in controlling floral development and how this important aspect of floral evolution might be investigated. Both Venail *et al.* and Kramer & Hodges focus on new insights from integrated studies of model systems.

Venail *et al.* investigate the developmental genetics underlying the different kinds of flowers that occur in the genus *Petunia*, and the different kinds of pollinators that correspond to them. Building on earlier work that initiated/adopted the development of *Petunia* as a model system, they link the classical and quantitative genetics of variation in floral traits with studies of pollinator behaviour. Such studies at the micro-evolutionary level hint at the mechanisms that lie behind the great diversity of floral form seen in other Solanaceae, which is elaborated in this volume by Knapp (2010). Against the background of species level differences in a single genus, the diversity of flower form and pollination in the large and economically important family Solanaceae illustrates the potential creativity of the kinds of developmental processes seen in the *Petunia* system. Integration of current large-scale syntheses of diversity in Solanaceae, including a 'planetary biodiversity inventory' now underway, with genetic studies of *Petunia*, various

species of *Solanum* and other genera, will ultimately provide a new basis for understanding floral evolution in this large and important family.

Kramer & Hodges examine patterns of rapid floral evolution in *Aquilegia* from developmental and micro-evolutionary perspectives. *Aquilegia* has emerged recently as the preeminent model system in which studies of floral development have been integrated with field investigations to illuminate patterns of floral evolution and their consequences. Kramer & Hodges focus specifically on the evolution of petals, key structures in *Aquilegia* that mediate the interaction with different kinds of pollinators.

The theme of plant/pollinator interactions and its role in creating and sustaining plant diversity is taken up in three papers by Tremblay *et al.* (2010), Johnson (2010) and Phillips *et al.* (2010). Tremblay *et al.* emphasize the complexity of coevolutionary relationships involving flowers and pollinators under conditions where floral traits vary in size among different reproductive bouts. The papers by Johnson and by Phillips *et al.* examine the diversity of floral biology at the biome scale in the species-rich plant communities of Southern Africa and southwestern Australia. These papers illuminate the ecological dimensions of reproductive and floral diversification and provide clues as to how these systems may be impacted by disturbance or other kinds of environmental change.

Finally, returning to Darwin, the principles that he established and the attendant theory that he began to develop remain important. In his second book on the biology of flowers '*The effects of cross and self fertilization in the vegetable kingdom*' (Darwin 1876), he established the basis for all subsequent studies of plant breeding systems by documenting inbreeding depression and by highlighting the importance of out-crossing. These themes are taken up here by Harder & Aizen (2010). They present a new model to account for floral diversification under pollen limitation. They show that pollen limitation and the mechanisms to assure out-crossing or reproductive assurance have the potential to be major drivers in the evolutionary diversification of floral form.

The papers in this volume show that the field of evolutionary plant reproductive biology, which Darwin created more than a century and half ago, remains a vital one. New discoveries are still being made and new perspectives continue to emerge, including through the purposeful application of relatively simple structural techniques that have been part of scientific work in this area for many decades. Careful observation of floral structure and function still has an important role to play in developing a more complete understanding of the evolution of flowers. It is also encouraging to see how much new and highly informative palaeobotanical information continues to come to light, which provides not only new insights into floral form among early lineages of flowering plants, but also initial indications of the extent of extinction in the early phases of angiosperm evolution. It seems very likely that the palaeobotanical record still has some surprises in store as we learn more about these extinct plants and how they relate to diversity among extant angiosperms.

In the area of theory, the fundamental principles worked out by Darwin still have great explanatory power. In most cases, they have stood the test the time. But there has also been rich elaboration of Darwin's ideas. The theory through which we think about the evolution of floral form continues to be developed in ever more sophisticated ways. In addition, the precision and depth with which the many dimensions of floral evolution can now be studied has increased in ways that Darwin would surely find astonishing. Advances made possible by developments in phylogenetic theory and its fusion with increasingly large quantities of cheap, easy to obtain, molecular sequence data have provided a new framework for evolutionary studies of all kinds. At the same time, the molecular revolution is facilitating new ways to study plant development and to probe the molecular genetics behind the variety of angiosperm floral form. The possibilities for future research are exciting. The rich vein of research on the evolution of plant reproductive biology and how it is manifested in the forms of flowers, which Darwin initiated, is far from exhausted.

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REFERENCES

- Barrett, S. C. H. 2010 Darwin's legacy: the forms, function and sexual diversity of flowers. *Phil. Trans. R. Soc. B* **365**, 351–368. (doi:10.1098/rstb.2009.0212)
- Darwin, C. 1859 *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. London, UK: John Murray.
- Darwin, C. 1862 *On the various contrivances by which British and foreign orchids are fertilised by insects, and on the good effects of intercrossing*. London, UK: John Murray.
- Darwin, C. 1868 *The variation of animals and plants under domestication*. London, UK: John Murray.
- Darwin, C. 1875 *Insectivorous plants*. London, UK: John Murray.
- Darwin, C. 1876 *The effects of cross and self fertilisation in the vegetable kingdom*. London, UK: John Murray.
- Darwin, C. 1877 *The different forms of flowers on plants of the same species*. London, UK: John Murray.
- Endress, P. K. 2010 The evolution of floral biology in basal angiosperms. *Phil. Trans. R. Soc. B* **365**, 411–421. (doi:10.1098/rstb.2009.0228)

- Friedman, W. E. 2009 The meaning of Darwin's 'abominable mystery'. *Am. J. Bot.* **96**, 5–21. (doi:10.3732/ajb.0800150)
- Friis, E. M., Pedersen, K. R. & Crane, P. R. 2010 Diversity in obscurity: fossil flowers and the early history of angiosperms. *Phil. Trans. R. Soc. B* **365**, 369–382. (doi:10.1098/rstb.2009.0227)
- Harder, L. D. & Aizen, M. A. 2010 Floral adaptation and diversification under pollen limitation. *Phil. Trans. R. Soc. B* **365**, 529–543. (doi:10.1098/rstb.2009.0226)
- Jasinski, S., Vialette-Guiraud, A. C. M. & Scutt, C. P. 2010 The evolutionary-developmental analysis of plant micro-RNAs. *Phil. Trans. R. Soc. B* **365**, 469–476. (doi:10.1098/rstb.2009.0246)
- Johnson, S. D. 2010 The pollination niche and its role in the diversification and maintenance of the southern African flora. *Phil. Trans. R. Soc. B* **365**, 499–515. (doi:10.1098/rstb.2009.0243)
- Knapp, S. 2010 On 'various contrivances': pollination, phylogeny and flower form in the Solanaceae. *Phil. Trans. R. Soc. B* **365**, 449–460. (doi:10.1098/rstb.2009.0236)
- Kramer, E. M. & Hodges, S. A. 2010 *Aquilegia* as a model system for the evolution and ecology of petals. *Phil. Trans. R. Soc. B* **365**, 477–490. (doi:10.1098/rstb.2009.0230)
- Mathews, S., Clements, M. D. & Beilstein, M. A. 2010 A duplicate gene rooting of seed plants and the phylogenetic position of flowering plants. *Phil. Trans. R. Soc. B* **365**, 383–395. (doi:10.1098/rstb.2009.0233)
- Phillips, R. D., Hopper, S. D. & Dixon, K. W. 2010 Pollination ecology and the possible impacts of environmental change in the Southwest Australian Biodiversity Hotspot. *Phil. Trans. R. Soc. B* **365**, 517–528. (doi:10.1098/rstb.2009.0238)
- Renner, S. S. & Schaefer, H. 2010 The evolution and loss of oil-offering flowers: new insights from dated phylogenies for angiosperms and bees. *Phil. Trans. R. Soc. B* **365**, 423–435. (doi:10.1098/rstb.2009.0229)
- Rudall, P. J. & Bateman, R. M. 2010 Defining the limits of flowers: the challenge of distinguishing between the evolutionary products of simple versus compound strobili. *Phil. Trans. R. Soc. B* **365**, 397–409. (doi:10.1098/rstb.2009.0234)
- Schönenberger, J., von Balthazar, M. & Sytsma, K. J. 2010 Diversity and evolution of floral structure among early diverging lineages in the Ericales. *Phil. Trans. R. Soc. B* **365**, 437–448. (doi:10.1098/rstb.2009.0247)
- Tremblay, R. L., Ackerman, J. D. & Pérez, M.-E. 2010 Riding across the selection landscape: fitness consequences of annual variation in reproductive characteristics. *Phil. Trans. R. Soc. B* **365**, 491–498. (doi:10.1098/rstb.2009.0239)
- Venail, J., Dell'Olio, A. & Kuhlemeier, C. 2010 Speciation genes in the genus *Petunia*. *Phil. Trans. R. Soc. B* **365**, 461–467. (doi:10.1098/rstb.2009.0242)