Preface

> Amongst the most characteristic features of modern science are: first, a variety of contradictory views on the same problems, secondly, the conflict of these with views recently accepted, and thirdly, the extravagance of the new conceptions.
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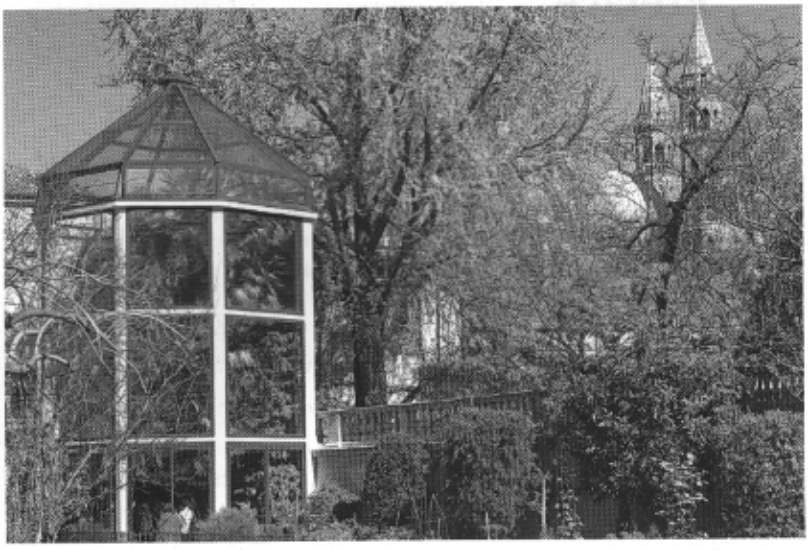
> B. Kozo Poljanski, 1936, p. 479

In the late 1960s I was a student in natural sciences at the University of Padova. I learned then from my botany professor, Carlo Cappelletti, that the leaves of a palm growing in our botanical garden had been a major source of inspiration for a German traveller who saw it in 1786. Eventually, this man, whose name was Johann Wolfgang von Goethe, encapsulated the core idea of his theory of plant morphology in the well-known aphorism, *alles ist Blatt* (all is leaf). Goethe's palm, as it is universally known today, is currently the oldest inhabitant of the Padova botanical garden, where it was planted in 1586.

In my student days, I was fascinated by the modularity of the plant body, by the geometrical and arithmetical relationships among its parts. I dreamed of finding something comparable in animals, in arthropods in particular, which represented anyway my favourites among living beings. Eventually, I became a zoologist and continued studying arthropods – although, for many years, addressing questions other than the development and evolution of their modular, segmented organization. It was a comparative study of segment number in centipedes, and the vague hope of eventually explaining the idiosyncrasies of their distribution (for example, all adult centipedes have an odd number of leg-bearing segments) in the light of the then recent discoveries on *Drosophila* segmentation genes, that fuelled my quick transfer to the discipline that was soon to get its



Goethe's palm, Padova botanical garden.

name (and the corresponding nickname) of evolutionary developmental biology (or evo-devo). That was indeed the title of a slim (in its first edition) but stimulating book published by Brian K. Hall in 1992. Of course, a number of facts and ideas eventually pertaining to the new discipline had been published before, even long before, if we accept the popular idea that Etienne Geoffroy Saint-Hilaire (1772–1844) should be regarded as a precursor of evo-devo; of more recent authors, I mention here Gavin de Beer and Stephen Jay Gould, for their pages on embryos and ancestors (see Chapter 1), and Rudy Raff and Thom Kaufman, whose book on *Embryos, Genes, and Evolution* (1983) was really, for many researchers of my generation, the most important source of inspiration to decide that the study of the relationships between development and evolution was worthy of becoming one's life research field.

Since it took its first steps, the new discipline of evo-devo has manifested two characteristic traits: a strong zoological bias and the dominant impact of comparative developmental genetics. This is not to say that plant evo-devo has been totally neglected, or that

evolutionary biology and comparative morphology have failed to provide their contribution. However, animals and forms of genetic control still dominate the field – witness books, articles and talks at the congresses of the two societies born since then, the European Society for Evolutionary Developmental Biology, founded in 2006, and the Pan-American Society for Evolutionary Developmental Biology, founded in 2015.

With my book on *The Development of Animal Form*, published in 2003, I tried to offer a view of animal evo-devo complementary to the (at the time, and still today, although not to the same degree) dominant molecular perspective. Already at that time it was clear to me that plants deserved a parallel effort. Thus, when eventually, in July 2011, Dominic Lewis asked me if I was ready to write another book for Cambridge University Press, I asked him, in turn, if he was ready to support the metamorphosis of an evo-devoist trained in zoology to something like a plant evo-devoist. The fact that six years later I am finally delivering this work to the publisher demonstrates two important points: first, that commissioning editors can be much more flexible, and supportive, than the academic world usually is; second, that moving from animals to plants as a professional in evo-devo is a long process that generates its first fruits only after several years. Those I am offering here are quite probably unripe, but at any rate they will fill a previously empty slot on the (book) shelves, and will hopefully stimulate new research and eventually the production of a better synthesis of the field.

Here and there, I have allowed my familiarity with animals to intrude, at a very moderate level, but I have avoided attempting the systematic comparison between animals and plants that some readers might have expected to find here. For this decision, I owe the readers some justification (provided in Section 1.2), and this will explain why I do not offer any apology for this intentional omission.

The plants this book is about are only the angiosperms, the flowering plants. The main reason for this somewhat narrow circumscription is that an adventure into further groups, both extinct

and extant, would have required an additional effort that I am not ready to undertake. In the following pages, I will mention mosses, lycophytes, ferns and gymnosperms in very few places.

The way the book is articulated into chapters is easily explained, except perhaps for Chapter 9.

In the first three chapters I give a conceptual introduction to plant evo-devo, providing definitions for concepts to some extent specific to this discipline (e.g. modularity, evolvability) and redefinitions of others. A few tools are provided too, including a refreshed outline of angiosperm classification and a list of model plant species, with some comments on problems with generalizing from results obtained on them.

Chapter 4, devoted to genes and genomes in so far as they are relevant to evo-devo, includes a section on the histories of duplication of a number of important gene families and remarks on subsequent functional specializations.

Chapters 5 to 7 deal with three main architectural components of the plant body: in Chapter 5, the shoot, its meristems, its branching patterns, and the positioning and differentiation of the lateral organs; in Chapter 6, the leaves; in Chapter 7, the flowers. Only short paragraphs are devoted to roots (at the end of Chapter 5) and fruits (at the end of Chapter 7), mirroring both my meagre familiarity with these subjects and the comparatively negligible attention these plant parts have received till now in evo-devo.

General aspects of plant body architecture are discussed in Chapter 8. These include some intriguing patterns such as paramorphism (strictly similar patterning expressed along body axes of different order) and the development and evolution of unconventional structures that defy classification into one of the standard categories of plant morphology.

Chapter 9 is devoted to pheno-evo-devo, i.e. to the evolutionary developmental biology of temporal phenotypes. In my view, indeed, temporal properties such as the order of inception of floral organs or the temporal patterns of abscission of leaves or flower parts must be

regarded as phenotypes generated by development and subject to evolution, on a par with morphological phenotypes.

Evolutionary trends in body complexity, convergence and parallelism, evolutionary reversal and, more controversially, saltational evolution are the subject of Chapter 10.

The very short Chapter 11 summarizes a few key ideas presented in the book and suggests a few items for a future plant evo-devo agenda.

Acknowledgements, as usual, fill the last lines of this preface, but are the first in importance. My warmest thanks are for my wife, Maria Pia Mannucci, not only for her moral support over the years (especially in the crazy months in which I was struggling to digest a huge and poorly structured amount of information extracted from the literature) but also for offering her beautiful photographs to illustrate an otherwise arid text. All illustrations in this book are by her, except for the flower of *Passiflora incarnata* (Fig. 10.3) kindly provided by our friend and excellent nature photographer Ioannis Schinezos.

Most sincere thanks to Dominic Lewis, who quietly but firmly supported this book project from its inception, and to Jenny van der Meijden, also at Cambridge University Press, who provided sensible and timely advice on how to solve the many problems of which I became aware only when I wrongly thought I was at last ready to deliver my long-overdue manuscript within a couple of weeks. Equally worthy of the warmest thanks is Hugh Brazier, my excellent copy-editor, who smoothly but firmly rescued the text from hundreds of linguistic barbarisms and other unpleasant defects.

Other people are probably not aware of their contribution to this book and must therefore not be blamed for their indirect support of a project for which I retain fully responsibility: I mean the plant scientists with whom I have enjoyed exchanges of views on matters of development and evolution, without ever mentioning this book; in strict alphabetical order, Richard Bateman, Peter Endress, Angela

Hay, Rainer Melzer, Paula Rudall, Rolf Rutishauser, Günter Theißen and Miltos Tsiantis. Their real contribution to my project is in their precious books and articles, on which, together with those of many other scientists, I have heavily (and gratefully) relied, as documented by the bulky list of references.