

Evolution and systematics of plants (*Archaeplastida*) – Ordering without orders

Summary

This book, a greatly expanded version of the third edition (2015), breaks again with the tradition of standard plant systematics texts in two major aspects:

- Plants are understood as members of one of the most natural groups of the living world, the *Archaeplastida*, containing all organisms (except *Paulinella*) that are known to possess plastids of primary endosymbiotic origin. That is, glaucophytes, red algae and green plants are treated such that
- Linnaean ranks are almost completely rejected, only genera and species and therefore binomial names are retained for practical, rather than theoretical reasons. The PhyloCode is followed for clades with published names and contents, for extinct and extant plants alike. Clades for which no proper PhyloCode names and definitions have been established are considered node-based, with names and contents corresponding to Linnaean taxa as revised by molecular phylogenetic methods.

In addition, the text provides a relatively balanced treatment of clades independently of geographic origin and species number, especially for embryophytes. Circa 3000 species are mentioned, most of them illustrated, representing a little less than 1% of the world flora. Further novelty is the inclusion of coral diagrams and condensed cladograms (see below) to depict phylogeny of various groups. The book is divided into 10 major chapters; each concluded with an imaginary discussion between a student of plant systematics and her/his professor. This offers the possibility of relaxation and better digestion of what has been said in each chapter.

Chapter 1, **Introduction**, establishes the underlying theory of systematics. First, possibilities for selecting basic units of biological classification, ranging from cells through individuals to species, are examined. These units are represented by nodes (or vertices) in spatio-temporal graph theory models of evolution, such as networks and trees. Fundamental terms of cladistics are presented, with emphasis on the meaning of monophyletic and monochadistic groups which are interpreted with reference to *phylogenetic trees* and *cladograms*,

respectively. The use of graphs is somewhat limited, however, because nodes and links are not always appropriate, especially if past and present are to be shown simultaneously. Therefore, Darwinian *corals* (a form of branching silhouettes) are also introduced; these graphical vehicles are useful tools to demonstrate cladistic relationships and the temporal change of species diversity along different lineages. Examples are the corals of embryophytes (p. 171) and angiosperms (p. 315). Figure 1.37 (p. 42) provides a comparison of different types of trees and branching silhouettes. If interest lies only in the present, *condensed cladograms* provide a simple solution. In these, dichotomies within large clades are compressed into isosceles triangles such that the length of their third side becomes proportional to the species diversity of the given group. Examples are on pages 312-313 and 450. Pages 134 and 135 offer the possibility of comparing the two types of diagrams for the same group, namely bryophytes. Sometimes, both extinct and extant organisms appear at the same time in a cladogram, these trees are called asynchronous cladograms in which sister group relationships are uncertain because extinct plant can be ancestors of recent plants. This uncertainty is expressed by dashed edges (as in Fig. 8.1). It is repeatedly emphasized that the Linnaean inclusive hierarchy of ranked categories is not compatible with evolution for several reasons. If organisms of the past and present are classified in the same system, boundaries between groups become paradoxical (Fig. 1.10): differences that we see between higher ranks of extant organisms diminish when we go back to their ancestors. Furthermore, the requirement of monophyly cannot be applied to all Linnaean groups in a diachronous system. Nestedness of groups is different in a cladistic, rank free classification, providing a hierarchy which is compatible with both the tokogenetic network and the Darwinian evolutionary tree of life. Consequently, hybrids between the Linnaean and the cladistic systems appear to be illogical constructs, such as the APG systems of angiosperms. Due to the interdependence of nomenclature and classification at the genus level, this ambiguity cannot be resolved completely, however. It is noted that a Linnaean nested system may still work well (with arbitrary ranks, of course) if adapt-

ed to a set of contemporary organisms only. Throughout the book, the cladogram for extant taxa is the basis for showing the phylogeny of a group (synchronous cladogram) and fossils – when applicable – are inserted within it to form asynchronous cladograms.

The origin of the plant life form is the starting subject of Chapter 2, **What is considered a plant?** First, a short overview examines how the concept of plant has changed in the history of systematics. Then, some fundamental aspects of the plastid and its cyanobacterial origin, and its relevance to the photosynthetic life of Earth are discussed. Chapter 3, **Red algae and glaucophytes**, discusses two groups of photosynthetic organisms in which the plastids are not green. One of them, the glaucophytes still have the bacterial cell wall around their plastids. Red algae, a much larger natural group of plants have lost the bacterial wall around the plastids and developed a high variety of plastid types and multicellularity. Chapter 5, **Green plants (*Viridiplantae*) – the algal grade**, is devoted to the deepest parts of the clade of green plants. These are characterized by the appearance of chlorophyll-b – one of the most significant evolutionary novelties in the history of plant life on Earth. The simplest green plants are algae, with a very early evolutionary split into chlorophytes and streptophytes. In the first group several kinds of multicellularity or multinuclearity evolved, but none of these forms allowed the plants to conquer the land. The latter group developed several cytological features which develop fully in embryophytes – eventually allowing them to tolerate the terrestrial habitat. Embedded into *Streptophyta*, plants starting their diploid stage of life as embryos on the mother individual constitute the next clade – *Embryophyta*. Considerable space is devoted to the abiotic and biotic conditions of switching to the terrestrial environment from the aquatic one. Extant bryophyte groups, liverworts, hornworts and mosses are the closest morphologically to the pioneering organisms (Chapter 5: **Protecting the young: Embryophytes**). Although some time ago the bryophytes were considered paraphyletic, the most recent understanding is that they are monophyletic. They share several fundamental features, such as the fairly balanced size of their gametophyte and sporophyte phases. Since each sporophyte bears a single sporangium, I suggest the clade name *Monosporangiophyta* to cover liverworts, mosses and hornworts. The next chapter – *Polysporangiophyta* – describes the early success of the rapidly evolving sporophyte – which produces more sporangia per plant than bryophytes. Which is equally if not more important, the sporophyte appears to adapt vegetatively to the harsh terrestrial environment more efficiently than any other preexisting organisms: vascularization – to mention only the most crucial aspect. A separate – now species poor – clade is the *Lycopodiophyta* discussed here. They are a good example for the transition from

homospory to heterospory and, eventually, to the ovule or some analogous reproductive structure. Chapter 7 – *Pan-Euphyllophyta* – introduces the reader to ferns and fern allies, and some of their immediate ancestors. In these groups developed several times the macrophyll, a most efficient photosynthetic organ of plants. Extant representatives of this clade form two sister clades - one of them, *Monilophyta* is discussed in detail here. In this, horsetails, whisk ferns, adder's tongues and moonworts, marattioid and leptosporangiate ferns are included. Although the ovule and – possibly – the seed or some equivalent reproductive structures have already evolved independently several times, only one lineage proved successful – the one leading to the gymnosperms. These, together with their hypothesized ancestors or extinct sister groups („stem relatives”) are discussed in Chapter 8 – *Pan-Spermatophyta*. Much emphasis is laid on progymnosperms and various extinct groups of the so-called „seed ferns”. Three clades of extant gymnosperms (*Acrogymnospermae*) have been recognized, these are cycads, ginkgos and conifers. Within the latter is embedded the all-time troublemaker in plant systematics, the *Gnetales* – as unanimously suggested by molecular phylogenetic analyses.

No doubt that the most successful group of plants is in every respect that of the angiosperms. Together with their extinct relatives, they form the *Pan-Angiospermae* clade. Their major morphological novelty is the flower and the fruit. Extant angiosperm clades are illustrated by the condensed cladogram on pages 312-313 and are treated in two chapters. The basalmost groups such as the ANITA grade plus *Ceratophyllum*, the chloranthoid group and the magnolids are discussed first, and then the monocots conclude Chapter 9. In this, I propose the clade name *Lilianaes* for *Liliales*+*Asparagales*, recently recognized sister groups. Finally, the phylogeny and systematics of the *Eudicotyledoneae* clade are summarized in Chapter 10. The last figure of this book, Fig. 10.156 (p. 654) gives a summary of the cladistic relationships among crown clades of extant plants, with some gray edges added arbitrarily as symbols of extinct plant lineages. The classical gradist view of plant evolution, namely the transitional sequence given by „algae – bryophytes – pteridophytes – gymnosperms – angiosperms” is superimposed as a “ladder” upon the cladogram. This illustrates the simultaneity of two basic views on evolution – such that both of them can be perfectly explained by the six most important transitions: 1) the appearance of plastids as a result of endosymbiosis with cyanobacteria, 2) the development of chlorophyll-b, giving rise to green plants, 3) evolution of the embryo, 4) dominance of the sporophyte, 5) the occurrence of the ovule and the seed and, finally, 6) the evolution of the fruit of flowering plants.

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The book is richly illustrated by photographs of several thousand species. Approximately 40% of pictures are the author's own work. For these photos, in the figure captions the species names are followed by the location in parentheses. If no location is given at all, the photo was taken in Hungary in the wild or on plants cultivated in botanical gardens. The majority of the remaining photographs were taken from the worldwide biodiversity web site, iNaturalist.org, for which reference is made to the location, the photographer and the license type. I am grateful to all people who made their work accessible to the wide audience by allowing reproduction under different license agreements. I can only reciprocate their kindness by uploading my own photos to https://www.inaturalist.org/observations?place_id=any&user_id=podani&verifiable=any which is continuously expanded. In the bryological chapter, I used

many photos from the website of the British Bryological Society (<https://www.britishbryologicalsociety.org.uk/>), by courtesy of C. Halpin and S. Pilkington. I also acknowledge Des Callaghan (Bryophyte Surveys Ltd, England) for generously allowing to use his photographs from <https://bryophytes.myportfolio.com/>. Further photos were obtained directly from their authors upon my request. My sincerest thanks are due to T. Pócs (Eszterházy Károly Catholic University, Eger), L. Mucina (Murdoch University, Western Australia), T. Kalapos, B. Oborny, T. Standovár, T. Tóth (Eötvös Loránd University, Budapest), L. Papp, Sr. (Botanical Garden, University of Debrecen), L. Papp, Jr. (Botanical Garden, Eötvös Loránd University, Budapest), A. V. Molnár, G. Sramkó (University of Debrecen), the late G. Kósa (Vácrátót Botanical Garden), V.S.F.T. Merckx (University of Amsterdam), M. Melkonian (Max Planck Institute for Plant Breeding Research, Cologne), J. Veselá and colleagues (Charles University, Prague, <https://botany.natur.cuni.cz/algo/database/>), R.H.G. Ranil (University of Peradeniya, Sri Lanka), Zs. Debreczy and I. Rácz (Budakeszi Herbarium, International Dendrological Foundation), C. Shirley (Auckland, New Zealand, <http://www.hiddenforest.co.nz/>), I. Vanha-Majamaa (Natural Resources Institute Finland, Helsinki), A. Wilson (Department of Geography, University at Buffalo), B. Csányi (Göd), and B. Páll-Gergely (Centre for Agricultural Research, Martonvásár). I suppose that they maintain the license conditions for their work, which are not specified here. A few photos were derived from the Tropicos database (<https://www.tropicos.org/>) and my thanks are extended to their authors.

