

# 11.

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

### Summary

This book breaks 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 abandoned, 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 as node-based with names and contents corresponding to Linnaean taxa as revised by molecular phylogenetic methods.

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 previously. Included is a supplementary CD containing ca. 5000 plant photographs whose arrangement into folders follows the discussion of clades throughout chapters 3–10.

Chapter 1 is a theoretical and methodological introduction. Since classification has to do with sets, and phylogenetics involves various types of trees, it is important to be familiar with the elements of set theory, relations, and graphs. The author is convinced that without clear theoretical foundations, correct interpretation of any type of phylogenetic trees and cladograms, and meaningful discussions on problems of monophyly and paraphyly are not possible. After giving a mathematical introduction to graph theoretical trees, many examples are given to illustrate their various uses in systematics and evolutionary biology. Two basic types of cladograms are considered (Podani 2013), one for organisms living at the same time (synchronous cladograms) and another for extinct and extant organisms taken together (asynchronous cladograms). Only the first one can provide hypotheses on the backbone of Darwinian trees, i.e., the true phylogenies. Thanks to our limited knowledge of past evolutionary events, these are used only as models of evolution (diachronous trees). Trees in which highly ranked groups are connected directly illustrate gradual aspects of evolution (achronous trees). Figure 1.11 (p. 32) is of central importance by showing how these trees, plus dendrograms and romerograms are derived for some taxa sampled from the very same

tokogenetic network imitating true genealogical history. 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. 1.16, p. 50): 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 (see Fig. 1.19, page 53, for comparison). Consequently, hybrids between the Linnaean and the cladistic systems appear to be illogical constructs, such as the APG III system of angiosperms. Due to the interdependence of nomenclature and classification at the genus level, this ambiguity cannot be resolved completely, however. It is emphasized that a Linnaean nested system may still work well if restricted to a set of contemporary organisms. Throughout the book, the cladogram for extant taxa is the basis for showing the hypothetical phylogeny of a group (synchronous cladogram) and fossils – when applicable – are inserted within it to form asynchronous cladograms. Edges connecting fossils to the tree are dotted lines, emphasizing our uncertainty whether fossil taxa are ancestors or sisters to extant plant groups.

The next chapter summarizes the history of biological classification, starting with some examples of ethnic classifications and continuing with pre-Linnaean systems. Linnaeus remains one of the greatest figures in this history because he was able to summarize knowledge of his times by standardizing nomenclatural issues in an efficient way. His rank-based system represented significant deviation from the concept of *scala naturae*, which was an important step from an exclusive hierarchy to an inclusive one. After the breakthrough of evolutionary theory, the usual goal of botanists had long been to explain their classifications *a posteriori* in evolutionary terms. This attitude towards classification first changed in the works of Hennig, who suggested to begin with phylogeny reconstruction upon which a classification may be built. Yet, even in the age of molecular phylogenetics, with large sequence data bases and sophisticated tree generating algorithms, most studies still attempt to improve the Linnaean classification. Apparently, ideas about phyla, orders and families are deeply carved into our brain – making difficult any significant change to adjust the classifications to the process that created biological diversity, i.e., evolution. The author feels that abandonment of Linnaean ranks and a switch to cladograms may facilitate this change.

The origin of the plant life form is the starting subject of Chapter 3 – *Archaeplastida* – which is the most inclusive crown clade of plants as defined above. After discussing some fundamental aspects of the plastid and its cyanobacterial origin, as well as its relevance to the photosynthetic life on Earth, the basal clade of plants, glaucophytes are introduced. These organisms still have the bacterial 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 4 – *Viridiplantae* – 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. The simplest green plants are algae, with a very early evolutionary split into chlorophytes and streptophytes. In the first group evolved several kinds of multicellularity or multinuclearity, 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 that allowed switching to the terrestrial environment from the aquatic one. Extant bryophyte groups, liverworts, mosses and hornworts are morphologically the closest to the pioneering organisms (Chapter 5). These do not form a monochlaestic group, while sharing several fundamental features, such as the fairly balanced size of their gametophyte and sporophyte phases. 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. This is achieved through vascularization – to mention only the most crucial aspect. A separate – now species poor – clade is the *Lycopodiophyta*, which is a good example for the transition from homospority to heterospority 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, a single 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 clade of *Gnetales* – as unanimously suggested by molecular phylogenetic analyses.

No doubt that the most successful group of plants in every respect is that of the angiosperms. Together with their extinct relatives, they form the *Pan-Angiospermae* clade. Their major morphological novelties are the flower and the fruit. Extant angiosperm clades 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 the chapter. Finally, the phylogeny and systematics of the *Eudicotyledoneae* clade are summarized in Chapter 10. The last figure of this book, Fig. 10.14 (p. 361) 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.

### List of figures showing cladograms of plant groups

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Fig. 3.1. – p. 117. Synchronous cladogram of *Archaeplastida*.

- Fig. 4.1. – p. 138. Synchronous cladogram of *Viridiplantae*.
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- Fig. 10.8. – p. 338. Synchronous cladogram of *Caryophyllales* (modified after Stevens 2002 onwards).
- Fig. 10.12. – p. 347. Synchronous cladogram of *Lamiales* (modified after Stevens 2002 onwards).
- Fig. 10.14. – p. 361. Cladogram summarizing relationships among crown clades of plants, with major evolutionary grades superimposed.