Phylogenetic relationships in Rosaceae inferred from chloroplast \textit{mat}K and \textit{trnL-trnF} nucleotide sequence data

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\textbf{Abstract.} Phylogenetic relationships in Rosaceae were studied using parsimony analysis of nucleotide sequence data from two regions of the chloroplast genome, the \textit{mat}K gene and the \textit{trnL-trnF} region. As in a previously published phylogeny of Rosaceae based upon \textit{rbcL} sequences, monophyletic groups were resolved that correspond, with some modifications, to subfamilies Maloideae and Rosoideae, but Spiraeoideae were polyphyletic. Three main lineages appear to have diverged early in the evolution of the family: 1) Rosoideae \textit{sensu stricto}, including taxa with a base chromosome number of 7 (occasionally 8); 2) actinorhizal Rosaceae, a group of taxa that engage in symbiotic nitrogen fixation; and 3) the rest of the family. The spiraeoid genus \textit{Gillenia}, not included in the \textit{rbcL} study, was strongly supported as the sister taxon to Maloideae \textit{sensu lato}. A New World origin of Maloideae is suggested. The position of the economically important genus \textit{Prunus} and the status of subfamily Amygdaloideae remain unresolved.

\textbf{Key words:} Rosaceae, \textit{Gillenia}, Maloideae, Amygdaloideae, Spiraeoideae, phylogeny, \textit{mat}K, \textit{trnL-trnF}.

The large and economically important angiosperm family Rosaceae has a worldwide distribution and includes over 3000 species in 122 genera (Heywood 1993). The vast majority of economically important fruits of temperate regions is produced by members of this family, including species of \textit{Malus} (apples), \textit{Pyrus} (pears), \textit{Prunus} (plums, peaches, cherries, almonds, and apricots), \textit{Rubus} (raspberries), and \textit{Fragaria} (strawberries). The family also includes many ornamentals, e.g., species of \textit{Rosa} (roses), \textit{Potentilla} (cinquefoil), and \textit{Sorbus} (mountain ash). A variety of growth habits, fruit types, and chromosome numbers is found within the family (Robertson 1974), which is traditionally divided into four subfamilies on the basis of fruit type (e.g., Schulze-Menz 1964). Spiraeoideae are characterized by follicles or capsules, Rosoideae by achenes, Amygdaloideae (Prunoideae) by drupes, and Maloideae by pomes. In the traditionally circumscribed Rosoideae, the base chromosome number is \(x = 7, 8,\) or 9; in Amygdaloideae, \(x = 8;\) in Spiraeoideae, \(x = 9\) (15, 17); and in Maloideae, \(x = 17.\) The division of the family into four subfamilies has not been followed universally. For example, Hutchinson (1964) recognized 20 tribes and did not group these into subfamilies.

Because of their economic importance and diversity, the Rosaceae have been the subject of numerous taxonomic and evolutionary studies. The family is generally considered to
form a natural group united by floral characteristics (Robertson 1974, Dickson et al. 1992). Kalkman (1988) suggested that the presence of a hypanthium may be the only morphological synapomorphy for the group, but the uncertainty of the relationship of Rosaceae to other families casts some doubt on this conclusion. This, as well as the relationships among subfamilies, genera, and species, are subjects of considerable discussion and investigation (summarized in Morgan et al. 1994, Pipps et al. 1991). Recent phylogenetic analyses have employed a variety of data, including vegetative, floral, and fruit morphology (Kalkman 1988; Pipps et al. 1991; Rohrer et al. 1991, 1994), floral ontology (Evans and Dickinson 1999a, b), wood anatomy (Zhang 1992), pollen morphology (Hebda and Chinnappa 1994), chloroplast DNA sequences (Morgan et al. 1994), nuclear gene sequences (Potter 1997, Evans et al. 2000), and combined data from multiple sources (Evans and Dickinson 1997, 1999c), to address questions about the placement of problematic genera and the relationships of the subfamilies. Sequences of the internal transcribed spacer (ITS) regions of nuclear ribosomal DNA have been used in phylogenetic studies of two of the subfamilies (Maloiidae, Campbell et al. 1995, Rosoideae, Eriksson et al. 1998). These studies have done much to improve our understanding of the affinities of particular taxa and the evolution of specific characters in Rosaceae, but a variety of questions remain, and all of the cited papers point out areas in which further resolution is needed.

In a phylogenetic study of rbcL gene sequence variation across the family (Morgan et al. 1994), monophyletic groups of genera were identified that corresponded, with some modifications, to all of the subfamilies except Spiraeoideae, which was shown to be grossly polyphyletic. The data strongly supported recognition of Rosoideae sensu stricto, excluding several taxa with \( x = 9 \), and of Maloideae sensu lato, including several spiraeoid taxa with \( x = 15 \) or 17. Weak support was found for Amygdaloideae sensu lato, including Prunus, Prunsepia, Oemleria, and Exochorda. The results suggested that, since some fruit types have evolved several times within the family, they are not as reliable as indicators of relationship as chromosome numbers.

Takhtajan (1997) incorporated some results from recent phylogenetic studies, such as that of Morgan et al. (1994), into his classification of the family, in which he recognized twelve subfamilies. Exochorda, previously classified in Spiraeoideae, was included in Amygdaloideae, Maloideae were expanded to include the traditionally spiraeoid genera Kagenekia, Vauquelinia, and Lindleya, and both Rosoideae and Spiraeoideae were subdivided.

A long-standing question concerns the origin of Maloideae. Because of a base chromosome number of 17, it is generally accepted that the subfamily originated either via polyploidization of a spiraeoid ancestor with \( x = 9 \) (e.g. Gladkova 1972) or by hybridization between two lineages, most likely a spiraeoid with \( x = 9 \) and an amygdaloid with \( x = 8 \), followed by polyploidization (e.g. Sax 1933). The exact identity of the putative parental lineage(s) remains controversial, however. The rbcL analysis by Morgan et al. (1994) indicated that members of the spiraeoid tribe Sorbarieae (plus the traditionally rosoid genus Adenostoma) are sister to Maloideae sensu lato, a relationship consistent with data from carpel anatomy (Sterling 1966), but this relationship was weakly supported. Morgan et al. (1994) pointed out that, since rbcL is a chloroplast-encoded gene, phylogenetic hypotheses based upon it represent phylogenies of maternal lineages only. Thus, the results are not inconsistent with an ancestral member of Amygdaloideae with \( x = 8 \) having been one of the parents involved in an ancient hybridization that led to the origin of Maloideae (Sax 1933, Pipps et al. 1991). Recent phylogenetic studies of the nuclear gene waxy by Evans et al. (2000), however, have not provided any evidence for an amygdaloid ancestor having been involved in the origin of Maloideae; nor have phylogenetic studies of several nuclear genes in our laboratory (e.g. Potter et al. 1999).