1. Rosaceae: Taxonomy, Economic Importance, Genomics

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A rose by any other name would smell as sweet.
Shakespeare

A rose is a rose is a rose.
Gertrude Stein

The Rose Family
The rose is a rose
And was always a rose;
But the theory now goes
That the apple's a rose,
And the pear is, and so's
The plum, I suppose.
The dear only knows
What will next prove a rose.
You, of course, are a rose,
But were always a rose.
Robert Frost

1 Nomenclature and Taxonomy

1.1 Origins

The magnificent simplicity, or to some, the monotonous consistency, of the actiniomorphic flowers of the rose family has been recognized for millennia. The origin of the name rose is summarized in the American Heritage Dictionary (2000):

> The English word rose comes from Latin and Old French. Latin rosa may be an Etruscan form of Greek Rhodia, "Rhodian, originating from Rhodes." The Attic Greek word for rose

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is rhodon, and in Sappho's Aeolic dialect of Greek it is wrodon. In Avestan, the language of the Persian prophet Zoroaster, "rose" is varda and in Armenian vard, words both related to the Aeolic form. The Modern Persian word for "rose" is gul.

Soon after Linnaeus published his *Systema Naturae* (1735), botanists worked to improve systematic classification. Michel Adanson (1763, 1963) was first to publish "Rosaceae" as the name for the rose family, although the International Code of Botanical Nomenclature (ICBN) (2006) now accepts Antoine Laurent de Jussieu (1789) as the author. The ICBN conserved Jussieu's names for 76 plant families, because he combined the Linnaean concept of binominal nomenclature with Adanson's methodology for defining groups based on multiple characteristics.

Recently, controversies and deficiencies in angiosperm classifications (Cronquist, 1981; Dahlgren, 1980; Thorne, 1992, 2000; Takhtajan, 1997) are being resolved by phylogenetic approaches based on analysis by the angiosperm phylogeny group (APG I, 1998; APG II, 2003). The APG system is based on the analysis of chloroplast and ribosomal coding genes in association with morphological charateristics.

Fossil record shows that Rosaceae is cogent with ancient dicotyledons (Heywood, 2007). Turonian fossils from 90 million years before the present (mybp) are attributed to this family (Crepet et al., 2004). Wikström et al. (2001) estimates that the stem rosaceous group dates to ca. 76 mybp, and crown group divergence (Rosoideae not included) from 47 to 46 mybp. Rosaceous physiological structure and anthecology also suggest that it is primitive. Hutchinson (1964) states that Rosaceae is an offshoot of the ancient woody magnolias, and on a common evolutionary line leading to orders such as Leguminales (Fabales), Araliales (Umbellales), Fagales, and Juglandales, that have more specialized inflorescences.

The APG phylogeny has separated plant orders and families on a linear time scale into basal angiosperms, eudicots, early diverging dicots, and core dicots. Research supporting APG (Soltis and et al., 2005) considers the rosids, of which rosales and its typical family, Rosaceae to be of the core eudicot group. Although the Rosaceae has great morphological diversity, to the point of being "indefinable" (Dickinson et al., 2002), the family is robust as along with morphological and chemical assessments (Challice, 1974), analyses of rbcL sequences strongly support the monophyly of Rosaceae (Fig. 1) (Morgan et al., 1994).

1.2 Morphology

Judd et al. (1999) describe Rosaceae to include herbs, shrubs, or trees, which are sometimes rhizomatous, climbing, or thorny. Plant hairs are simple or stellate, and can be present with prickles. Leaves are usually alternate, and are simple to palmately or pinnately compound. Stipules are usually present and flowers are often showy, bisexual or infrequently unisexual. The hypanthium ranges from flat to cup-shaped or cylindrical and either free from or adnate to the carpels, often enlarging in fruit. Sepals are usually pentamerous, sometimes alternating with epicalyx lobes.

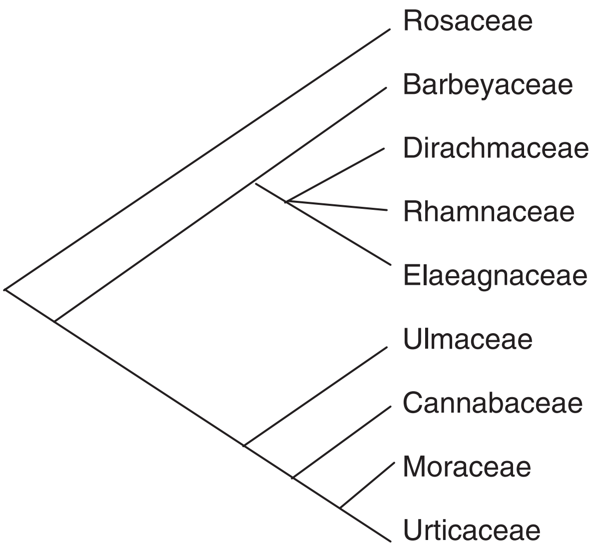

Fig. 1 Cladogram based on the *rbcL* of the Rosaceae within Rosales (tree phylogeny from APG II, APW, 2007, based on Morgan et al., 1994)

Petals are usually pentamerous, while stamens are usually 15 or more, sometimes 10 or fewer. Filaments are distinct or basally fused to the nectar disk. Pollen grains are tricolpate. Carpels are 1 to many, and are distinct or connate, though sometimes adnate to the hypanthium. The ovary varies from superior to inferior depending on the genus. The styles are present in the same number as carpels. The fruit can be a follicle, achene, pome, drupe, aggregate or accessory with drupelets or achenes, or rarely a capsule. Endosperm is usually absent from the seed. The occurrence of numerous stamens and the absence of endosperm have been key structural apomorphies for systematic classification.

1.3 Distribution and Ecology

Rose family distribution is cosmopolitan (Judd et al., 1999) to sub-cosmopolitan, but is diversified, particularly in the Northern hemisphere. The herbaceous species grow in temperate forests as understory plants, in salt or freshwater marshes, in arctic tundra, in old fields, and along roadsides. Woody members are pioneer species, and are prominent in the early stages of forest succession. Rosaceous trees may also be minor components of mature mixed deciduous forests.

The Rosaceae is the 19th largest family of plants (APW, 2007). It includes from 95 to more than 100 genera and 2830−3100 species (Judd et al., 1999; Mabberley, 1987). Familial synonyms include: Agrimoniaceae Gray, Alchemillaceae Martinov, Amygdalaceae (Juss.) D. Don, Cercocarpaceae J. Agardh, Cliffortiaceae Mart., nom. nud., Coleogynaceae J. Agardh, Dryadaceae Gray, Fragariaceae Rich. ex Nestl., Lindleyaceae J. Agardh, Malaceae Small ex Britton, Neilliaceae

Miq., Potentillaceae (Juss.) Wilbr., Prunaceae Bercht. & J. Presl, Quillajaceae D. Don, Rhodotypaceae J. Agardh, Sanguisorbaceae Durande, Spiraeaceae Bertuch, Ulmariaceae Gray. The ICBN accepted genera for the family are listed (Table 1).

Table 1 International code of botanical nomenclature (ICBN) accepted genus names within Rosaceae

Acaena Mutis ex L.	*Osteomeles* Lindl.
Adenostoma Hook. & Arn.	*Pentactina* Nakai
Agrimonia L.	*Peraphyllum* Nutt. 60
Alchemilla L.	*Petrophytum* (Nutt. ex Torr. & A. Gray) Rydb.
Amelanchier Medik.	*Photinia* Lindl.
Aphanes L.,	*Physocarpus* (Cambess.) Raf., nom. cons.
Aremonia Neck. Ex Nestl., nom. cons.	*Polylepis* Ruiz & Pav.
Aria (Pers.) Host, *Aronia* Medik., nom. cons.	*Potaninia* Maxim.
Aruncus L.	*Potentilla* L.
Bencomia Webb & Berthel.	*Prinsepia* Royle
Brachycaulos R. D. Dixit & Panigrahi	*Prunus* L.
Cercocarpus Kunth	*Pseudocydonia* (C. K. Schneid.) C. K. Schneid.
Chaenomeles Lindl., nom. cons.	*Purshia* DC. ex Poir. 70
Chamaebatia Benth.	*Pyracantha* M. Roem.
Chamaebatiaria (Porter ex W. H. Brewer & S. Watson) Maxim.	*Pyrus* L.
Chamaemeles Lindl.	*Quillaja* Molina
Chamaemespilus Medik.	*Rhaphiolepis* Lindl., nom. cons.
Chamaerhodos Bunge	*Rhodotypos* Siebold & Zucc.
Cliffortia L.	*Rosa* L., nom. cons. prop.
Coleogyne Torr.	*Rubus* L., nom. cons. prop.
Coluria R. Br.	*Sanguisorba* L.
Cormus Spach	*Sarcopoterium* Spach
Cotoneaster Medik.	*Sibbaldia* L.
Cowania D. Don	*Petrophytum* (Nutt. ex Torr. & A. Gray) Rydb.
Crataegus L.	*Photinia* Lindl.
Cydonia Mill.	*Physocarpus* (Cambess.) Raf., nom. cons.
Dalibarda L.	*Polylepis* Ruiz & Pav.
Dichotomanthes Kurz	*Potaninia* Maxim.
Docynia Decne.	*Potentilla* L.
Docyniopsis (C. K. Schneid.) Koidz.	*Prinsepia* Royle
Dryas L.	*Prunus* L.
Duchesnea Sm.	*Pseudocydonia* (C. K. Schneid.) C. K. Schneid.
Eriobotrya Lindl.	*Purshia* DC. ex Poir.
Eriolobus (DC.) M. Roem.	*Pyracantha* M. Roem.
Exochorda Lindl.	*Pyrus* L.
Fallugia Endl.	*Quillaja* Molina
Filipendula Mill.	*Rhaphiolepis* Lindl., nom. cons.
Fragaria L.	*Rhodotypos* Siebold & Zucc.
Geum L.	*Rosa* L., nom. cons. prop.
Gillenia Moench	*Rubus* L., nom. Cons. prop.
Guamatela Donn. Sm.	*Sanguisorba* L.

Table 1 (continued)

Hagenia J. F. Gmel.	*Sarcopoterium* Spach
Hesperomeles Lindl.	*Sibbaldia* L.
Heteromeles M. Roem.	*Sibiraea* Maxim.
Holodiscus (K. Koch) Maxim., nom. cons.	*Sieversia* Willd.
Horkelia Cham. & Schltdl.	*Sorbaria* (Ser. ex DC.) A. Braun, nom. cons.
Horkeliella (Rydb.) Rydb.	*Sorbus* L.
Ivesia Torr. & A. Gray	*Spenceria* Trimen
Kageneckia Ruiz & Pav.	*Spiraea* L.
Kelseya (S. Watson) Rydb.	*Spiraeanthus* (Fisch. & C. A. Mey.) Maxim.
Kerria DC.	*Stephanandra* Siebold & Zucc.
Leucosidea Eckl. & Zeyh.	*Taihangia* T. T. Yu & C. L. Li
Lindleya Kunth, nom. cons.	*Tetraglochin* Poepp.
Luetkea Bong.	*Torminalis* Medik.,
Neviusia A. Gray	*Vauquelinia* Corrêa ex Bonpl.
Oemleria Rchb.	*Waldsteinia* Willd.
Orthurus Juz.	*Xerospiraea* Henr.

As the gynoecium varies greatly among species of this family, this variation has been utilized for classification within the family to subfamilies Takhtajan (1997):

Rosoideae – many apocarpous pistils mature into achenes; Amygdaloideae (prunoideae) – a single monocarpellate pistil matures into a drupe; Spiraeoideae – the gynoecium consists of two or more apocarpous pistils that mature into follicles; Maloideae (Pomoideae) – the ovary is compound and inferior, and an epigynous zone may occur.

1.4 Conventional Taxonomy

In addition to the subgenera, tribes have been described to accommodate outlying genera. The composition of genera within subfamilies and tribes has been problematic. Intergeneric hybridization occurs within these groups. Species definitions are extended to account for apomixis or hybridization. Some treatments have suggested that some of the subfamilies have familial status (Hutchinson, 1964); others overlook subfamilies and worked solely with tribes (GRIN, 2007).

Although molecular analysis agrees with traditional determinations that the Rosaceae family is robustly monophyletic, it has added to the debate on the subfamily and tribal groupings. Genetic analysis has been performed to examine phylogenies for the family, individual subfamilies, tribes, and the larger genera.

Dickinson et al. (2002) has produced a parsimonious tree derived from the cladistic analysis of 125 combined morphological and molecular characters from members of the Rosaceae (Fig. 2) and added several genera to Maloideae. Spiraeoideae, no longer monophyletic, is split by Amygdaloideae (Prunoideae). The Rosoideae have been subdivided into individual tribes. Thus, Dickinson et al. recircumscribes Maloideae and Rosoideae, the two largest subfamilies. They

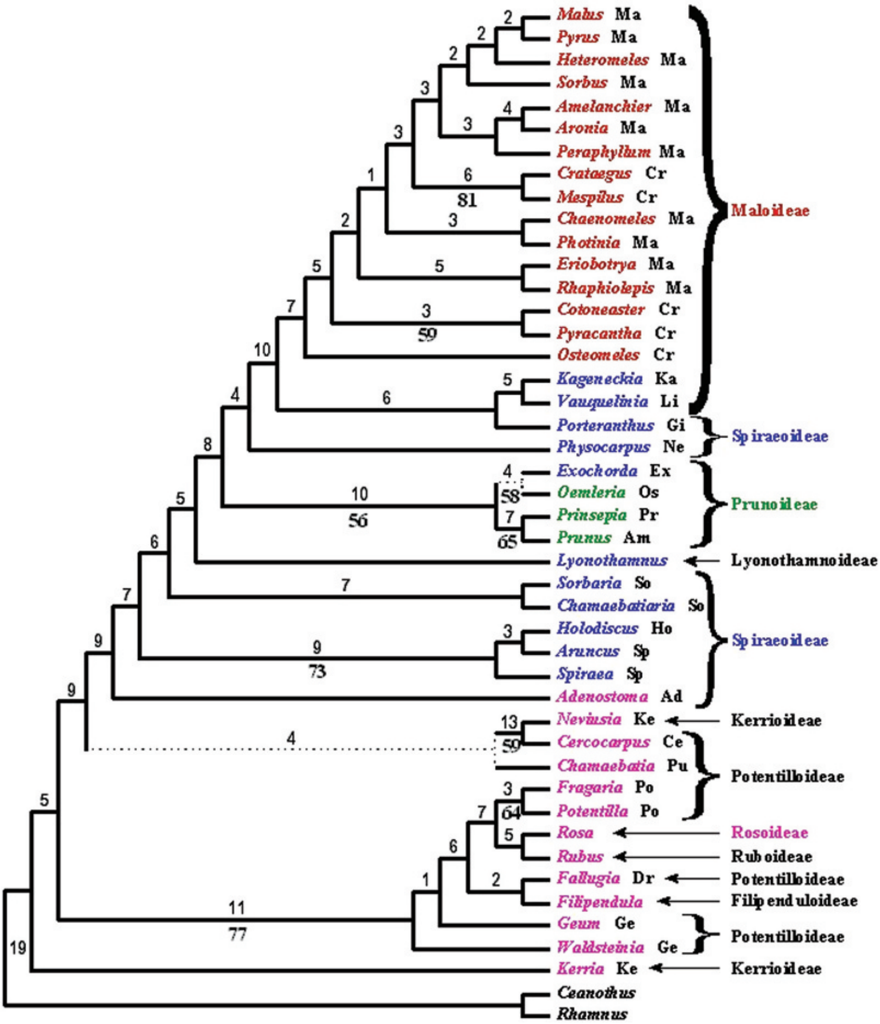

Fig. 2 Parsimonious tree derived from the cladistic analysis of 125 combined characters (61 non-molecular + 64 from molecular tree branches (ndhF, rbcL, nrITS). Adapted from: Dickinson et al. (2002). The colors represent traditional subfamilies (red = maloideae; blue = spiraeoideae; green = amygdaloideae; pink = rosoideae). *Ceanothus* and *Rhamnus* are outgroup taxa. The classification to tribes are as proposed by Takhtajan (1997): (**Ad**enostomateae, **Am**ygdaleae, **Ce**rcocarpeae, **Dr**yadeae, **Ex**ochordeae, **Ge**eae, **Cr**ataegeae, **Gi**llenieae, **Ho**lodisceae, **Ka**geneckieae, **Ke**rrieae, **Li**ndleyieae, **Ma**leae, **Ne**illieae, **Os**maronieae, **Po**tentilleae, **Pr**insepieae, **Pu**rshieae, **So**rbarieae, **Sp**iraeeae). Colored names outside of brackets correspond to traditional subfamilies, black names to subfamilies proposed by Takhtajan (1997)

rejected Amygdaloideae and Spiraeoideae, neither of which proved to be monophyletic. Lastly, they redefined old tribes and suggested new ones.

Not only does this study offer insights on monophyly and relationship between the groups, but it can be interpreted to provide commentary concerning the origin of subfamilies.

The traditional hypothesis suggests that the origin of the Maloideae (Pomoideae) occurred in an ancient polyploidization event, because the maloid base chromosome number is $x = 17$, whereas other Rosaceae are $x = 7$, 8, or 9. For the hybridization, Challice (1974; 1981) suggested that the Maloideae were created by an allotetraploidization event following an ancient hybridization between Amygdaloideae ($x = 8$) and "Spiraeoideae" ($x = 9$) ancestors. A second theory suggests an allo- or auto-polyploidization event occurred solely within the "Spiraeoideae." If the Maloideae originated within the "Spiraoideae," then the fleshy "pome" fruit, e.g., apple, must have been derived from the expansion of the hypanthium (floral cup). Incorporation of the ovaries by the enlarged hypanthium resulted in the inferior ovaries present in the majority of Maloideae genera (Dickinson, 2007). Molecular analysis is continuing and has not yet eliminated the possibility of an allotetraploidization event. The uniting of formerly "Spiraeoid" genera to the Maloideae, however, gives credence to the solely "Spiraeoid" event hypothesis.

Although definition of the four major rosaceous subfamilies may be collapsing from a taxonomic view, these grouping still have great utility from an economic and horticultural standpoint. The ultimate decision on subfamilies may depend on future development in genomics, the subject of this volume.

2 Economic Importance

The Rosaceae include many well known and beloved species of economic importance particularly edible temperate zone fruits (Janick, 2005) and ornamentals, but also some timber crops and medicinals or neutriceuticals. Some economically important taxa of the Rosaceae are summarized in (Table 2). The more important species are briefly reviewed below by subfamilies. The total world production of the edible rosaceous fruits in 2005 based on FAO statistics is about 113 million tonnes. At a very conservative farm gate value of US$400 per tonne this translates to $45 billion. Adding in the world value of almonds, cut roses, rose plants, and other products suggests that that rosaceous plants could be worth at least $60 billion annually at the farm gate, with a consumer value of triple this amount, $180 billion.

2.1 Amygdyloideae

The stone fruits, i.e. species of *Prunus*, include delicious gifts of summer (peach, cherry, plum, and apricot), as well as almond, the most important nut worldwide.

Table 2 Some economically important species of Rosaceae by subfamily

Subfamily	Genus	Species	Common name	Uses
Amygyloideae	*Prunus*	*armeniaca*	Apricot	Fresh and processed fruit
		avium	Sweet cherry	Fresh and processed fruit
		cerasus	Tart (sour) cherry	Fresh and processed fruit
		domestica	European plum	Fresh and processed fruit
		dulcis	Almond	Fresh and processed nut
		mume	Mume	Ornamental
		persica	Peach, nectarine	Fresh and processed fruit
		serotina	Black cherry	Timber species
Maloideae	*Amelanchier*	*alnifolia*	Saskatoon, serviceberry; shadbush	Landscape ornamental
	Aronia	*melanocarpa*	Black chokeberry	Processed fruit for juice, nutriceutical
	Chaenomales	*japonica*	Japanese quince	Landscape ornamental, processed fruit
	Cotoneaster	*spp.*	Cotoneaster	Landscape ornamental
	Crataegus	*spp.*	Hawthorn, thornapple	Landscape ornamental, craft uses for wood
	Cydonia	*oblonga*	European quince	Fresh and processed fruit, dwarfing rootstock for pear and loquat
	Eriobotrya	*mespilus*	Loquat	Fresh and processed fruit
	Malus	*×domestica (M. pumila)*	Apple	
		spp.	Crabapples	Landscape ornamentals
	Pyrus	*calleryana*	Callery pear	Landscape ornamental
		communis	European pear	Fresh and processed fruit
		serotina	Japanese pear (nashi)	Fresh fruit
		ussurienses	Chinese pear	Fresh fruit
	Mespilus	*germanica*	Medlar	Fresh fruit (bletted)
	Photinia	*spp.*	Photinia	Landscape ornamental
	Pyracantha	*spp.*	Firethorn	Landscape ornamental
	Sorbus	*spp.*	Mountain ah, rowan	Landscape ornamental
Rosoideae	*Fragaria*	*×ananassa*	Strawberry	Fresh and processed fruit
	Geum	*spp.*	Avens	Herbaceous perennial
	Kerria	*japonica*	Kerria	Landscape ornamental
	Potentilla	*spp.*	Cinquefoil	Landscape ornamental
	Rosa	*spp.*	Rose	Cut flowers, landscape ornamental, perfume oil, medicinal
	Rubus	*spp. and hybrids*	Blackberry, raspberry, hybrid berry	Fresh and processed fruit
Spiraeoideae	*Spirea*	*prunifolia*	Bridal wreath	Landscape ornamental
	Exochorda	*racemosa*	Exochorda	Landscape ornamental
	Physocarpus	*opulitolius*	Ninebark	Landscape ornamental

The stone fruits are less hardy than the pome fruits; they tend to flower earlier, making them very susceptible to spring frosts. The fruits tend to be soft at maturity and have much poorer storage life than the pome fruits, however their exquisite flavors have made them much admired. Many are consumed dried, especially plum and apricot. Black cherry, *P. serotina*, is an important timber species. A number of interspecfic crosses within *Prunus,* such as plum with apricot, have led to new fruits such as plumcot, pluot®, and aprium®.

Almond. *Prunus dulcis* (synonym = *Amydalis*) originates in Asia and is an ancient central Asian crop cultivated in the Mideast since antiquity and apparently re-introduced to Spain during the incursions of Arabs into Europe in the 8^{th} century. The domesticated almond with "sweet," in contrast to "bitter" (high amygdalin) seeds have made almond a popular nut for both fresh and processed products for millennia. World production of this nut (2005) was 1.7 million tonnes (Mt). A favorite confection made from almond paste mixed with sugar, molded, and painted to resemble other fruits and products was introduced by Arabs to Sicily where it has become a unique culinary art form. Immature almonds are also eaten in the Mideast. Almond has been transformed into a large scale,industry in California, that now produces over 70% of the world crop, and ranks as seventh largest US food export.

Apricots. The delectable apricot, *Prunus armeniaca*, is consumed fresh and canned, but is principally known in the form of semi-dried fruit, usually sulfured to maintain color and longevity. World production exceeds 3 Mt. The major dried industry is located in southwest Turkey (Malatya). Some seeds are also consumed, similarly to almonds. The beautiful flowers of the Japanese apricot, *P. mume*, make them popular ornamentals in Asia.

Cherries. Cherry is the common name of several *Prunus* species that include sweet cherry (*P. avium)*, tart or sour cherry (*P. cerasus*), Duke cherries (hybrids between *P. avium* and *P. cerasus*). World cherry production is about 3 Mt. Black cherry (*P. serotina*) an important timber species and there are a number of flowering species, principally *P. serrulata* that are included in a group called ornamental cherries, however their taxonomy is confused.

Sweet cherry is native to the Caucuses and has become a much beloved fruit but is restricted to cooler climates. Cherry is consumed fresh as a gourmet fruit, and also consumed in soups, tarts, pies, and candied, often covered with chocolate and as an almost artificial product called *maraschino*. Cherry is used for liqueurs and wines. Cherry wood is used for furniture and veneers, as well as decorative paneling and is cultivated for this purpose in plantations in Europe.

Tart or sour cherry is hardier than sweet cherry and requires a longer season to mature. Its use is restricted to processing, mainly as a filling for pies and pastries, however is now becoming popular as a dried fruit and as a source of syrup that is promoted as having health properties. Tetraploid natural hybrids between the diploid sweet cherries and the tetraploid sour cherries, known as Duke cherries, are a distinct minor crop.

Black cherry*, P. serotina* is a prized timber species used for veneer, furniture, and paneling due to its beautiful red color. It is usually the highest or second highest valued fine hardwood. Black cherry is cultivated in plantations and breeding programs are underway in Indiana and Pennsylvania. The bark has been used medicinally.

Ornamental cherries are favorite landscape species of Asia. The flowering cherry known as *Sakura* were donated to the United States as a gift in 1912, promoted by the wife of President Taft. Flowering cherry has become a landmark and important symbol for Washington, D.C.

Peach and Nectarine. *Prunus persica*, despite its name, is native to warm areas of China. The peach and its smooth skin mutation, the nectarine, are the most important contributors to stone fruit production. In 2005 this production reached almost 16 Mt. Peach thrives in hot summer climates, however, many low chill cultivars have enabled expansion of peach production to the subtropics. The nectarine or fuzzless peach has been increasing in popularity. Peaches occur in a wide variety of fruit and flesh color from yellow to red and shape. There are basically two types of flesh texture, melting and rubbery. The rubbery flesh types are clingstone and are used for processing principally, however their use is now being promoted for fresh consumption because they can be shipped in a riper state. Peaches are processed into juice and sliced or diced products, while some are dried. Peaches have been beloved in Asia as a symbol of longevity. Major problems of peaches have been quality problems, especially cottony flesh texture, associated with long distance shipping and chilling injury. Peach and nectarine tend to be susceptible to summer diseases such as peach leaf curl and brown rot.

Plums. Plums represent a diverse group of fruits that include European, Asian, and American species. The cultivated European plum, *P. domestica* is a hexaploid ($2n = 6x = 42$) that probably originated as a hybrid between *P. cerasifera* (diploid) and *P. spinosa* (a tetraploid). Asian species include *P. salicina* (Japanese plum) and *P. simonii* (Simon or apricot plum). There are at least five American species: *P. americana* (common wild plum), *P. nigra* (Canada plum), *P. angustifolia* (chickasaw), *P. horulana* (hortulna plum) and P. *munsoniana* (wild goose plum). The principal economically important plum species are *P. domestica* and *P. salicina* with world production in 2005 exceeding 9 Mt.

While plums are mostly consumed as a fresh or processed fruit, the prune-type plums (French prune or "Agen") produce a well known product called prunes or dried plums. Principally produced in California, prunes have long been a health product promoting digestive regularity among seniors, although the industry has developed moist types as a snack food.

2.2 Maloideae

This subfamily includes important edible temperate fruit species (known collectively as pome fruits) and a great number of landscape plants (Table 2). The most economically important members are apple and pear, in addition there are a number of minor fruits such as medlar, loquat, and quince.

Apples. *Malus ×domestica= M. pumila* is the most economically important rosaceous species with annual world fruit production (2005) in excess of 62 Mt, the fourth most important fruit after citrus, grapes, and banana. Apples are produced in all temperate and subtropical countries of the world, with minor production in high altitudes of tropical countries. The popularity of apple derives from the fact that the fruit has multiple uses. It can be consumed fresh and some cultivars can be stored for an entire year, while a considerable proportion of the crop is processed into sauces, juice, and slices which are a favored ingredient for pastries, cakes, pies, and tarts. Some of the juice is sold as a fermented product called cider (often special apples, many of which are may be hybrids with native species such as *M. sylvestris*) and a small portion is distilled as apple brandy (calvados). Much vinegar production derives from apple cider.

Various species of *Malus*, usually small fruited species referred to crabapples, are very popular as ornamentals for their spring flowers and fall fruit. Crabapples are particularly popular in the US nursery trade. Apple wood (*M. sylvestris*) has been used in furniture and has specialized uses for turning, mallet heads, croquet and skittle balls, umbrella handles, toys, cog wheels, wood screws, canes, pianos, tool handles, drawing instruments, and bookbinder screws. The wood is widely used for smoking meats and for barbecues and is especially valued for fireplace burning.

Aronia. *Aronia melonicarpa* (black chokeberry), native to North America, is grown in Europe for its juice which has high antioxidant properties. Fruit extract has been used as a component of nutrient supplements.

Hawthorn. There are about 1000 *Crataegus* species that are used in landscape plantings. A number have edible fruit and a few species such *as C. monygna* (English hawthorn) are used for timber. *Crataegus pinnatifida*, Chinese hawthorn, is processed for juice in China.

Loquat. *Eriobotrya japonica*, despite its name is native to China, where it is a favorite since it is the first fruit that appears in the summer. Production is now increasing rapidly in China and production is also advancing in Mediterranean countries. Spain is the principal exporter of loquat. Development of seedless triploids could transform this fruit into a very popular crop worldwide.

Medlar. *Mespilus germanica*, a monotypic genus, is an ancient fruit that must be consumed after it undergoes a fermentation called bletting, where the fruit softens and develops a spicy flavor. Medlar is still marketed in Northern Italy and Germany, but is now considered a minor fruit elsewhere.

Mountain Ash. There are about 80 *Sorbus* species in North America, Europe and Asia that are widely used as ornamentals or as windbreaks. Most species have bitter fruits, but some are sweet and have been suggested as a possible new fruit. There are intergeneric hybrids between *Sorbus* with *Amelanchier* and *Pyrus*.

Pears. Species of *Pyrus* are the second most important rosaceous fruit species, with world pear production of about 10 Mt (2005). There are three economically important species, *P. communis* (European pear), *P. pyrifolia*, (Japanese pear or

Nashi), and *P. usuriensis* (Chinese pear). Japanese and Korean cultivars are complex hybrids of *P. pyrifolia* and *P. ussuriensis*. Pear has similar uses to apple, although its popularity may be somewhat lower because the best quality is ephemeral in European pear. In European winter pears this eating quality is achieved by ripening after harvest. Pear cider is usually made from cultivars of *P. nivalis* and is called perry. The pear tree is also an important ornamental and is beloved in Asia where pear is considered a sign of good luck. In the United States, the most popular ornamental pear trees were selections of *Pyrus calleryana,* the Callery pear. These street trees can be found from Oregon to Ohio to New York, and south to Alabama and Georgia. *Pyrus koehnii*, an evergreen species native to Taiwan, is planted in California and Florida.

Quinces. Two closely related genera, *Cydonia* and *Chaenomeles* are referred to as quince. The genus *Cydonia* consists of a single species *Cydonia oblonga*, native to southwest Asia. Quince is now a minor crop used principally for processing into preserves, although there is considerable production in Argentina. Most cultivars are too astringent to consume fresh, however there are non-astringent types grown in Iran, India, Afghanistan, and Central Asia, suggesting this fruit has developmental possibilities. Quince is used as a dwarfing rootstock for pear and loquat. Intergeneric hybrids have been reported between quince and pear (Trabut, 1917).

Asian flowering quinces, *Chaenomeles,* are closely related to *Cydonia*, *Pyrus*, and *Malus*. The Japanese quince (*C. japonica*) is a shrubby plant with attractive red flowers and aromatic hard fruit that resemble loquat in appearance. It is a popular landscape ornamental. Japanese quince fruit are a minor crop in the Baltic countries, and efforts are underway to commercialize this species for processing

Serviceberry. *Amelanchier* species known by various local names including Serviceberry, Juneberry, or Saskatoons are hardy plants used as landscape plants. Various attempts have been made at domestication for uses as a new fruit crops, but it appears that these species crops will be best used as edible landscape species.

2.3 Rosoideae

This subfamily is the home of the rose, the species that has provided the name for Rosaceae, and includes a number of other ornamentals such as *Potentilla* and small fruits including strawberry (*Fragaria)* and the brambles blackberry, raspberry, and various hybridberries (*Rubus*).

Brambles. Bramble is a collective term for various prickly shrubs sometimes classified horticulturally as small, bush, or berry fruits. All brambles are species of *Rubus*, a taxonomically complex group that includes blackberry (European and American species), raspberries (*R. ideaus*) and various hybrids. Hybrid combinations include upright and trailing types such as eastern dewberry (*R. trivialis*) and blackberry × raspberry crosses such as youngberry, marionberry, loganberry, and tayberry. Raspberries include red raspberry, black raspberry (*R. occidentalis* and *R. leucodermis*), and purple raspberry (black raspberry × black raspberry). World production of brambles is now increasing with the development of new cultivars and air transport and in 2005 was 0.6 Mt (154 thousand t of blackberry and 498 thousand t of raspberry.

Roses: *Rosa* is one of the major economically important genera of ornamental horticulture and the area under cultivation continues to expand. The rose, admired since antiquity for its beauty and fragrance has multiple uses: cut flowers, landscape plant, oils (attar of rose) for perfume as well as culinary use (rose water), and hips (fruits) as a source of Vitamin C. *Rosa* species are found throughout the colder and temperate regions of the Northern hemisphere form the Artic to the subtropics with more than 100 species but modern cultivars are mostly interspecific hybrids deriving from only 10 of these: *R. canina*, *R. chinensis*, *H. foetida*, *R. gallica*, *R. gigantea*, *R. moschata*, *R. multiflora*, *R. phoenicea* and *R. rugosa*, and *R. wichuraina.* The multiflora rose *(R. multiflora*) is considered a noxious weed. The cut flower industry is becoming globalized with production moving to South and Central America and Africa, however plant production for landscape use is usually local because of the problems of transporting soil.

Strawberry. The domesticated strawberry *F.* ×*ananassa* is a hybrid between *F. chiloensis* and *F. virginiana* that was first found in France in the 18^{th} century. Subsequent breeding efforts have produced large size, high quality fruits produced by in field cultivation or in protected culture. Most of the crop is grown for fresh fruit, but a small portion of the crop is frozen or used to make preserves. Total 2005 world production has been estimated at 3.6 Mt.

3 Rosaceae Genomics

The Rosaceae is an ancient plant family containing many genera and a plethora of systematic challenges that are beyond the scope of morphological determination. A coordinated effort in developing crop genomics in the Rosaceae will unravel complex relationships within the cultivated genera, provide insights into basic physiological understanding of species within the family, and assist in genetic improvement of individual crop species. With these goals in view, members of the scientific community who are devoted to species of the Rosaceae have been studying the genomics of individual crops, and the time is ripe to coordinate this effort to resolve overarching issues within the family.

3.1 Systematic Challenges

Each of the crops within Rosaceae has nomenclatural challenges. Traditional descriptions of certain genera, such as those in the Maloideae, seem unrestricted by the boundaries of botanical species or generic definitions. In this group cross- and graft-compatibilities are known to occur not only between species but between genera as well.

Widely disjunct populations of species and genera abound in the Rosaceae, a globally distributed family. New populations of some genera, such as *Mespilus canescens*, an Arkansan distribution of an otherwise European genus, have been found. In other cases, such as *Rubus*, species have been defined in unprecedented numbers and species aggregates are used as a taxonomic reference.

The breakdown of the present taxonomy of the Rosaceae has been an issue among taxonomists and the family is presently under revision. Crop specific genomics and studies of synteny within the family are needed to clarify these relationships.

3.2 Physiological Development

Model plants such as *Arabidopsis* have been extensively studied to provide a basis for understanding gene structure and function, in such important processes as flowering, morphology, and development. However, this species has limitations for extrapolation to the Rosaceae (Aŕus et al., 2006). The Rosaceae offers genera with small genomes, such as that of *Fragaria vesca* with 164 Mbp (Aŕus et al., 2006), which could become model systems with direct, economically important application to the many cultivated species within the family. The genomics of rosaceous species offers special opportunities to clarify problems in fruit development and ripening, incompatibility systems, hardiness, apomixis, and, given the unique system of gamete formation in *Rosa canina*, meiosis. Further, the complex ploidy systems and interspecific hybrids within Rosaceous genera also offer opportunity to look beyond simple diploids.

3.3 Genetic Improvement

Advances in Rosaceaous genomics and synteny will provide new ways to obtain genetic improvement within economically important rosaceous species. Genes that control fruit quality including flavor and texture are of immediate interest. The development of saturated maps with codominant and transferable markers within *Prunus*, *Malus*, and *Fragaria* will foster genetic research and should lead to immediate practical results through marker-assisted selection. In *Prunus*, 28 major genes affecting morphological and agronomic characters can be located on a reference map (Table 3).

Identification of genes producing desirable quality traits within the family could provide a means of crop improvement by shifting genes within the family. For example, the genes for hardiness in *Malus* might be transferred to *Prunus* while resistance genes for black spot caused by *Diplocarpon rosae* in apple could be transferred to rose. We suggest that the transfer of genes within the Rosaceae, if properly explained, will be less likely to engender consumer resistance to genetic transgenesis, than would the movement of genes from more phenologically disparate plants.

Table 3 Description of 28 major genes affecting characters in different *Prunus* crops that have been placed on a reference map (After Dirlewanger et al., 2004)

Linkage group	Character	Crop	Population
	Sharka resistance	Apricot	Lito × Lito
	Evergrowing	Peach	Empress op dwarf × P1442380
	Flower color	Almond × peach	Garfi × Nemared
G2	Root-knot nematode resistance	Peach	P.2175 × Felinem, Akame × Juseitou, Lowell × Nemared Garfi × Nemared; Padre × 54P455
	Shell Hardness	Almond	Ferragnes × Tuono
	Broomy (pillar) growth habit	Peach	Various progenies
	Double flower	Peach	NC174RL × P1
G3	Flesh color around stone	Peach	Akame × Jusetou
	Anther color (yellow/anthocyanic)	Almond × peach	Texas × Earlygold
	Polycarpel	Peach	Padre × 54P455
	Flower color	Peach	Akame ×Jusetou
G4	Blooming time	Almond	D.3.5 × Bertina
	Flesh adhesion	Peach	(*P. ferganesis* × IF310828) BC1; Akeme × Jusetou
G5	Non-acid fruit	Peach	Ferjalou Jalousia × Fantasia
	Kernel taste (bitter/sweet)	Almond	Padre × 54P455
	Skin hairiness (nectarine/peach)	Peach	Ferjalou Jalousia × Fantasia
G6	Leaf shape (narrow/wide)	Peach	Akame × Juseitou
	Plant height (normal/dwarf)	Peach	Akame × Juseitou
	Male sterility	Peach	Ferjalou jalousie × Fantasia
	Fruit shape (flat/round)	Peach	Ferjalou jalousie × Fantasia
	Self-incompatibility	Almond	Ferragnes × Tuono;D.3.5 × Bertina Padre ×54P455
		Apricot	Lito × Lito
G6–G8	Fruit skin color	Peach	Akame × Juseitou
	Leaf color (red/green)	Peach	Garfi × Nemared; P.2175 × Felinem, Akeme × Juseitou
G7	Root-knot nematode resistance	Myrobalan plum	P.2175 × Felinem
	Resistance to powdery mildew	Peach	(*P. ferganensis* IF310828)NC1
	Leaf gland (reniform/globose)	Peach	(*P. ferganensis* × IF310828)NC1

4 The Future

Full genomic sequencing, as has been achieved in human and a number of agronomic crops, is now possible for specialty horticultural crops, such as those in the Rosaceae. Representative crops within the Rosaceae are indeed currently being sequenced. Genomic libraries and physical maps for genera within Rosaceae are also forthcoming. Expressed sequence tags (ESTs), unigene sets, microarrays, proteomic and metabolomic tools are on available for analysis of significant Rosaceous crop and will be presented in later chapters. Study of Rosaceae synteny is only now beginning (Aŕus et al., 2006). Gene function validation, including high throughput plant transformation systems with cross validation are also being developed.

Bioinformatics software and databases must be developed for Rosaceous crops. Ontology must be consistent within the global community for the broadest communication of data and information. Phenotype databases that include origin and pedigree information as well as observational descriptive data should be developed to promote linkages of data and maximum use. Inventories of genebanks of wild and commercial germplasm in current gene banks, which are fortunately available, and biological resource centers that store mutants, libraries and clones are available for research use through international consortia.

Challenges do lie ahead for the Rosaceous genomics community. Traditional breeding practices have produced a standard of excellence for yesterday and today's finest cultivars for fruit and ornamentals. Though recent advances in genome-level analyses have proven a valuable route to deriving an understanding of the molecular events that govern plant responses in model systems, these new technologies must prove that they can do as well in producing useable crop products for future generations.

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