Chapter

The North American Plums (Prunus Spp.): A Review of the Taxonomic and Phylogenetic Relationships

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Abstract

North America is a center of diversity for Prunus species. Tree architecture, chilling requirement, heat requirement, fruit development period, fruit size, fruit texture, disease resistance, and adaptive changes to multiple environmental conditions are a few examples of the traits of which tremendous genetic variability is available in the native plum species. Wild native Prunus species constitute an important potential source of genetic diversity for stone fruit breeding and selection. A review of the North American plum taxonomic treatment and phylogenetic studies is described. Various studies have been done with three major groups being identified: Americana series, Chickasaw series, and Beach series.

Keywords: plums, phylogeny, taxonomy, Prunus, Prunocerasus

1. Introduction

The genus Prunus L. belongs to the subfamily Amygdaloideae (=Prunoideae) of the Rosaceae. It has a worldwide distribution with approximately 200 species. Edible species are mostly distributed in the northern hemisphere [1–5]. The genus contains species that are important in the production of fruit, nuts, and lumber. Plums, cherries, almonds, apricots, and peaches are the most commonly known fruit and nuts in this genus. The world’s net production of almonds, apricots, cherries, peaches, nectarines, plums, and sloes in 2010 was approximately 40.8 million tons. Peach and nectarine production was the largest in the world with 20.5 million tons. US peach and nectarine production was approximately 1.3 million tons, with a farm gate value of ~683 million dollars [6].

North America is an important center of diversity for plum species adapted (native) to widely divergent climates and soils representing an important potential source of genes for plant breeding. In [7], Layne and Bassi reported high levels of variation in the Prunus germplasm for tree size, growth habit, flower size and color, chill hour requirement, fruit size, flesh texture, flesh color, resistance to diseases, and adaptability to diverse climatic and geographic regions. Plums are the stone fruit with the greatest diversity of flavor, aroma, texture, color, form, and size [2, 8].

Stone fruit breeders have used this tremendous genetic variability through interspecific hybridizations (in particular with species in the subgenus Prunus or...
Prunophora) for the improvement of Prunus scion and rootstock cultivars [9]. Among those, native North American plum species have been identified as a source of resistance to blossom blight and brown rot (Monilinia fructicola), bacterial spot (Xanthomonas campestris pv. pruni), bacterial canker (Pseudomonas syringae pv. syringae), plum leaf scald (Xylella fastidiosa), peach tree short life (PTSL), root-knot nematode (Meloidogyne spp.), lesion nematode (Pratylenchus spp.), clitocybe root rot (Armillaria tabescens), and others [9–12].

Resistance to bacterial leaf spot and bacterial canker was identified in a cultivar derived from P. salicina Lindl., P. cerasifera Ehrh., P. angustifolia Marshall, P. americana Marshall, and P. munsoniana W. Wight & Hedrick. Prunus hortulana L.H. Bailey was found resistant to root-knot nematode and has been recommended as a rootstock for European plums. Improved tolerance for PTSL was found in hybrids from P. americana, P. hortulana, P. angustifolia, and/or P. umbellata Elliot. Potential uses of the native North American plum species as breeding parents, scions, and/or rootstocks were summarized by [10, 12].

2. Taxonomic treatment

In [8], Waugh described the genus Prunus as trees or shrubs, mostly with edible fruit and flowers, white or pink, with spreading petals. Stamens 15–30, distinct, with filiform filaments. Style, terminal; stigma, usually truncate. The fruit has a fleshy exterior, is glabrous, and contains a hard bony pit, which contains the seed.

Inconsistencies in the taxonomy of Prunus were recognized by Waugh [8] and Hedrick [2]. Bortiri et al. [1] summarized the classification discrepancies in Prunus as follows: (1) four different genera (Amygdalus, Cerasus, Prunus, and Padus [13]) and later two (Amygdalus and Prunus) [14]; (2) five genera (Amygdalus, Persica, Prunus, Armeniaca, and Cerasus (including Padus and Laurocerasus)) [15]; (3) Prunus as a single genus divided in seven sections (Amygdalus, Armeniaca, Prunus, Cerasus, Laurocerasus, Ceraseidos, and Amygdalopsis) [16]; (4) Prunus with previous seven sections as subgenera [17]; (5) Prunus classified into five subgenera (Prunophora (Prunus), Amygdalus, Cerasus, Padus, and Laurocerasus) and with subgenus Prunus divided in three sections (Euprunus, Prunocerasus, and Armeniaca) [3]; and (6) Prunus divided into three genera (Padus, Laurocerasus, and Prunus) [18].

Recently, the concept of Prunus as single genus has become widely accepted, but subgenera classification is still undistinguished as new phylogenetic relationships within Prunus come to light. The USDA-GRIN [19] germplasm collection organizes the genus Prunus into subgenus Amygdalus, Cerasus, Emplectocladus, and Prunus. Subgenus Cerasus was divided into sections Cerasus and Laurocerasus and subgenus Prunus into sections Armeniaca, Microcerasus (including some plums), Penarmeniaca, Prunocerasus (the North American plums), and Prunus.

Waugh [8] recognized the difficulty in classifying the North American plums and stated “plums grow pretty much as they please, and the botanist has to take them as he finds them.” The distribution, cultivation, hybridization, and breeding value of native plums have been extensively studied [2, 4, 5, 8, 20, 21].

Waugh [8] classified the cultivated and indigenous Prunus of North America into groups. These groups were clustered into seven series: Americana, Chickasaw, Hortulana, Maritima, Sand Cherry, Choke Cherry, and Black Cherry [22] (Table 1). The Americana series included the Americana group (including P. americana var. lanata) and the Nigra group (Prunus nigra Aiton). The Chickasaw series included the Chickasaw and the Sand plum groups. The Hortulana series, categorized as “hybrids,” included the Wildgoose group, the Wayland group, and the Miner.
| Group          | Species                  | Origin                                                                 | Cultivation                                                                                                      |
|---------------|--------------------------|------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------|
| Cultivated    | Prunus domestica         | Eastern Europe and west-central Asia                                   | Nova Scotia, central New England, New York, southern Ontario and Michigan, and the Pacific coast states          |
| Damsons       | Prunus domestica         | Europe                                                                 | Europe and US used as rootstock                                                                                   |
| Myrobalan     | Prunus cerasifera        | Europe                                                                 | New York, California                                                                                             |
| Simon         | Prunus simonii           | China                                                                  | New York, California                                                                                             |
| Japanese      | Prunus triflora          | China, Japan                                                           | Maine, Vermont, Ontario, and southern Iowa                                                                         |
| Indigenous    | Prunus americana         | USA (Ohio, Texas, northward to Minnesota and Montana)                  | Prince Edward Island, Manitoba, and Vancouver, to Florida, Louisiana, and Texas                                    |
| Americana     | Prunus americana nigra   | CAN (Newfoundland west to Rainy and Assiniboine rivers), USA           | Prince Edward Island, Manitoba, and Vancouver, to Florida, Louisiana, and Texas                                    |
| Nigra group   | Prunus americana nigra   | CAN (Newfoundland west to Rainy and Assiniboine rivers), USA           | Prince Edward Island, Manitoba, and Vancouver, to Florida, Louisiana, and Texas                                    |
| Miner Group   | Prunus hortulana mineri  | USA (standing between P. americana and the Wildgoose group)            | Not cultivated                                                                                                     |
| Wayland group | Prunus rivularis Prunus  | USA (Colorado, Guadalupe, and the Leona)                               | North of Burlington, Vermont, and Iowa                                                                            |
| Wildgoose     | hortulana                | USA (the Mississippi valley)                                           | From Texas to Massachusetts                                                                                        |
| Chickasaws    | Prunus angustifolia      | USA (Southern range to Delaware and Kentucky, including southern Atlantic and Gulf states) | Iowa, Vermont, New York, and Massachusetts                                                                       |
| Sand plum     | Prunus angustifolia watsonii | USA (South and southeast Nebraska and central and western Kansas) | Cultivated by settlers in Kansas and Maryland                                                                     |
| Beach plum    | Prunus maritima          | USA (sea beaches, New Brunswick to Virginia, Georgia, Alabama, and Connecticut) | Not cultivated                                                                                                     |
| Pacific plum  | Prunus subcordata        | USA (Pacific coast)                                                    | Sierra regions of California and southern Oregon                                                                   |
group. The Maritima series the Beach plum group, the Southern sloe group including *P. umbellata* Elliot var. *injuncunda* (Small) Sarg., the Oklahoma plum group, and *P. glandulosa* Thunb. (ungrouped). The Sand Cherry series were equivalent to the Dwarf cherries group. The Choke Cherry and the Black Cherry series conserved their name as groups [8, 22] (Table 1).

Wight’s [5] separated the genus *Prunus* in plums, cherries, and dwarf cherries. Waugh’s [8, 22] taxonomic treatment included cherries as part of plums. Wight’s [5] groups/series were Americana, Subcordata, Hortulana, Angustifolia, Maritima, and Gracilis. The Angustifolia group agreed with Waugh’s [22] Chickasaw series. Waugh [22] did not include *P. mexicana S. Watson* (Americana group), *P. munsoniana* (Angustifolia group), *P. subcordata* Benth. (Subcordata group), *P. alleghaniensis* Porter (Maritima group), and *P. umbellata* (Maritima group), as part of his groups/series.

### 3. *Prunus* phylogenetic studies

Phylogeny and systematics in the genus *Prunus* was reported by [23]. They employed isozymes to study the phylogenetic relationships in *Prunus*. Section *Prunocerasus* was found to be polyphyletic, with a clade formed by *P. americana*, *P. munsoniana*, *P. hortulana*, *P. subcordata*, and *P. angustifolia*, and a clade formed by *P. maritima* Marshall and *P. umbellata*.

Chloroplast DNA is an alternative source of genetic variation and is maternally inherited in *Prunus*. Chloroplast DNA is highly conserved and in relative abundance in the cell as compared with the nuclear DNA. Kaneko et al. [24] and Uematsu et al. [25] used cpDNA to classify cherries, apricots, and wild and cultivated peaches in Japan. In [26], Badenes and Parfitt reported a phylogeny similar to Mowrey and Werner [23]. All the *Prunus* species were grouped as in conventional subgenus

| Group          | Species                      | Origin                                                                 | Cultivation       |
|----------------|------------------------------|------------------------------------------------------------------------|-------------------|
| Oklahoma plum  | *Prunus gracilis*            | USA (Southern Kansas to Texas and Tennessee)                           | Not cultivated    |
| Alleghany plum | *Prunus alleghaniensis*      | USA (Alleghany mountains in Pennsylvania)                              | Not cultivated    |
| Southern sloe  | *Prunus umbellata*           | USA (seashore from South Carolina to Florida and westward to Mississippi, Louisiana, and Arkansas) | Not cultivated    |
| Dwarf cherries | *Prunus pumila*              | *P. pumila* in USA (coasts of northern states), *P. pumila besseyi* (from Manitoba to Kansas, westward to California and Utah), and *P. cuneata* in USA (New Hampshire to Minnesota and southward to North Carolina) | Nebraska eastward |
| Choke Cherry   | *Prunus virginiana*          | CAN (Newfoundland to Manitoba and British Columbia) to USA (Georgia, Texas, and Colorado) | Not cultivated    |
| Black Cherry   | *Prunus serotina*            | CAN (Quebec) to USA (Kansas and southward, New Mexico, and Mexico)     | Not cultivated    |

*Classified as Prunus rivularis but with doubts.*

*Prunus hortulana consider as part of the Wayland and the Wildgoose group.*

Table 1. Cultivated and indigenous plums in North America by group, area of origin, and cultivation [8].
classifications [3]. *Prunus persica* L.-*P. dulcis* (Mill.) D.A. Webb, *P. domestica* L.-*P. salicina* Lindl., and *P. cerasus* L.-*P. fruticosa* Pall were monophyletic.

Lee and Wen’s [27] phylogenetic analysis of the genus *Prunus* using ITS sequences recognized two major groups: the *Amygdalus-Prunus* group, and the *Cerasus-Laurocerasus-Prunus* group. The results were not congruent with Rehder’s [3] taxonomic treatment.

In Bortiri et al. [1] the phylogeny and systematics of *Prunus* based on ITS and chloroplast *trnL-trnF* spacer DNA sequences identified two major clades: subgenera *Padus-Laurocerasus-Cerasus* and subgenera *Prunus-Amygdalus-Emplectocladus-Cerasus* (sect. *Microcerasus*)-sect. *Penarmeniaca* (similar to Mowrey and Werner [23], Lee and Wen [27], and Bortiri et al. [1]). Their results indicated that plums of northeastern North America were closely related and that *P. mexicana* belonged to a sister clade.

Bortiri et al. [28] used the nuclear gene *6pdh*, which encodes NADP⁺-dependent sorbitol-6-phosphate dehydrogenase, to assess the lack of support for deep nodes in the clade subgenera *Prunus-Amygdalus-Emplectocladus* (as reported in previous data). The phylogenies based on ITS, cpDNA *trnL-trnF*, and *6pdh* sequences were compared and combined. Phylogenetic analysis of the combined data supported two major clades: subgenera *Cerasus-Laurocerasus-Prunus* and subgenera *Amygdalus-Emplectocladus-Prunus*. Section *Microcerasus* (subgenera *Cerasus*) was reported nested within subgenus *Prunus*.

*Prunus* subg. *Prunus* sect. *Prunocerasus* was reported to be monophyletic by Shaw and Small [29]. The phylogenetic analysis was based on seven cpDNA regions: *rpS16, rpL16, trnL, trnG, trnL-trnF, trnS-trnG*, and *trnH-psbA*. Three clades were strongly supported in sect. *Prunocerasus*: the “American Clade,” the “Chickasaw Clade,” and the “Beach Clade” (names based on Waugh’s (1901) classification). The American clade included *P. americana* Marshall var. *americanana* Sudw., *P. americana* Marshall var. *lanata*, *P. mexicana*, *P. rivularis* Scheele, *P. hortulana*, and *P. umbellata* var. *injucunda*; the Chickasaw clade included *P. angustifolia*, *P. munsoniana*, *P. gracilis* Engelm. & A. Gray, *P. nigra*, *P. umbellata* Elliot var. *umbellata*, *P. alleghaniensis* Porter var. *alleghaniensis*, and *P. alleghaniensis* Porter var. *davisi* (W. Wight) Sarg.; and the Beach clade included *P. geniculata* Harper, *P. maritima* Marshall var. *maritima*, and *P. maritima* Marshall var. *gravesii* (Small) G.J. Anderson.

Similarly, a survey of cpDNA haplotypes available within section *Prunocerasus* was reported by Shaw and Small [30]. The cpDNA *rpL16* region was sequenced for 207 accession representatives of 17 North American plums, including *P. texana* D. Dietr. (as described before). More than one of the three primary cpDNA haplotypes was found in many of the taxa.

Bortiri et al. [31] studied the evolution of vegetative and morphological characters of 37 species of *Prunus* and other genera of Rosaceae. Morphological characters were combined with ITS, *trnL-trnF*, and *trnS-trnG* data from previous studies [1, 28]. The addition of the morphological data with *trnS-trnG* supported some nodes that were found in ITS and *trnL-trnF* studies. Three clades were reported: “Clade A” with subgenera *Padus* and *Laurocerasus*; “Clade B” with subgenera *Amygdalus, Emplectocladus, and Prunus*; and “Clade C” with subgenera *Cerasus*. “Clade B” was characterized by the production of three axillary buds. *Padus* and *Laurocerasus* were not supported as monophyletic (high homoplasy).

Genetic diversity within *Prunus cerasifera* (cherry plum) was studied using morphological characters, cytometry, cpDNA, and SSR markers [32]. Morphological characters showed differences between clones. Analysis of cpDNA reported 15 haplotypes clustered in 3 groups. Considerable diversity among accessions was reported based on these studies.
|         | Paper*          | Kaneko et al. [24] | Mowrey and Werner [23] |
|---------|----------------|---------------------|------------------------|
| Phylogenetic analysis | Molecular       | Molecular           |
| Analytical methods | Phenetics—percent differential restriction fragments and Engel's genetic distance | Phenetics—principal components |
| Metrics (analysis) | cpDNA using BamHI, HindIII, and SmaI | Isozyme |
| Taxa (no.)/subgenus (sect.) genus | 11 species/3 subgenus: Cerasus, Padus, Armeniaca [3]/genus Prunus | 34 species/4 subgenus: Prunus (sect.: Prunus, Prunocerasus, Armeniaca), Amygdalus, Cerasus (sect.: Sargentella, Microcalymma, Magniculpula), Phyllomahaleb), and Lithocerasus (sect.: Microcerasus, Armeniacocerasus) [35] |
| Outgroups | | |
| Trees (no.) | 2 | 2 (average 30 principal components) |
| Characters or bp (no.) | | |
| Informative characters (no.) | | |
| Indels (no.) | | |
| Substitutions (no.) | | |
| Inversions (no.) | | |
| PIC | | |
| Percent variability | | |
| Phylogeny in classification | Support for subgenus Prunus. Subgenus Lithocerasus was identified as an artificial grouping of species |
| Notes | Lithocerasus formed part of Cerasus in Rehder's [3] classification |
|         | Paper | Badenes and Parfitt [26] | Lee and Wen [27] |
| Phylogenetic analysis | Molecular | Molecular |
| Analytical methods | MP | MP, NJ, ML |
| Metrics (analysis) | cpDNA cutting with 21 3.2 kb and 10 2.1 kb endonucleases | ITS nuclear ribosomal DNA |
| Taxa (no.)/subgenus (sect.) genus | 9 species/5 subgenus: Prunus, Amygdalus, and Cerasus. | 40 species (represented by 52 accessions)/5 subgenus: Prunus (sect.: Prunus, Prunocerasus, Armeniaca), Amygdalus, Cerasus (sect.: Microcerasus, Pseudocerasus, Mahaleb, Phyllomahaleb), Padus, and Laurocerasus [3] |
| Outgroups | Fragaria vesca | Exochorda giraldii, Maddenia hypoleuca, Oemleria cerasiformis, Prinsepia sinensis, Prinsepia uniflora, Lyonothamnus floribundus |
### Badenes and Parfit [26]

| Tree (no.) | MP = 15,000 MPT (L = 630, CI = 0.632, RC = 0.510). Consensus tree 16,383 MPTs (L = 630, CI = 0.632, RI = 0.808). ML tree log likelihood = −3641.3155 |
|------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Characters (no.) | 23/662 bp aligned (ITS1 = 223–242 bp, 5.8 s = 154 bp, and ITS2 = 201–219 bp) |
| Informative characters (no.) | 218 bp aligned (ITS1 = 114 bp, 5.8 s = 12 bp, and ITS2 = 92 bp) |
| Indels (no.) | 29 indels (>3 bp) aligned (ITS1 = 13 bp, ITS2 = 16 bp) |

### Lee and Wen [27]

| Substitutions (no.) |  |
|---------------------|---|
| PIC | 218 bp aligned (ITS1 = 114 bp, 5.8 s = 12 bp, ITS2 = 92 bp) (not including indels) |
| Percent variability | 32.9% aligned (ITS1 = 47.1%, 5.8 s = 7.79%, ITS2 = 42.0%) |

### Phylogeny in classification

Support for subgenus Prunus, Cerasus, and Amygdalus. Relative small number of taxa used in the study. Subgenus Cerasus suggested to be more extensively evolved than either Prunus or Amygdalus.

Genus Prunus was monophyletic. Support for Maddenia nested within genus Prunus. Within genus Prunus, two major groups were recognizable: Amygdalus-Prunus group and Cerasus-Laurocerasus-Padus group.

### Notes

Number of parsimony informative characters included outgroups. The % variability cannot be directly compared with studies that excluded the outgroups for the number of PICs.

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### Bortiri et al. [1]

| Paper | Phylogenetic analysis | Analytical methods | Metrics (analysis) | Taxa (no.)/subgenus/sect. |
|-------|-----------------------|--------------------|--------------------|--------------------------|
|       | Molecular             | MP, ML             | ITS nuclear ribosomal DNA and chloroplast **trnL-trnF** spacer DNA | 48 species/5 subgenus: Prunus (sect.: Prunus, Prunocerasus, Armeniaca), Amygdalus, Cerasus (sect.: Microcerasus, Pseudocerasus, Mahaleb, PhylloMahaleb), Padus, and Laurocerasus [3] |
|       |                       |                    | Nuclear gene sorbitol 6-phosphate dehydrogenase (**s6pdh**) and data from previous study ITS and **trnL-trnF** [1] | 22 species (representing all the major clades found in previous study)/5 subgenus: Prunus (sect.: Prunus, Prunocerasus, Armeniaca), Amygdalus, Cerasus (sect.: Microcerasus, Pseudocerasus, Mahaleb, PhylloMahaleb), Padus, and Laurocerasus [3] |

### Outgroups

Exochorda racemosa, Oemleria cerasiformis, Prunus spinosa, Physocarpus capitatus, Sorbaria sorbifolia, and Spiraea cantoniensis.
### Phylogeny in classification

Genus *Prunus* was monophyletic. *Exochorda*, *Oemleria*, and *Prinsepia* were not supported as sister groups with *Prunus*. Genus *Prunus* was divided in two clades: subgenera *Amygdalus-Prunus-Cerasus* (sect. *Microcerasus*)- *Emplectocladus* group and subgenera *Cerasus-Laurocerasus-Padus* group. Subgenus *Prunus* sect. *Prunus* was monophyletic.

### Notes

First time that *P. fasciculata* (sect. *Emplectocladus*) was used in a study. Includes *P. fasciculata* sect. *Emplectocladus*.

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| Paper | Bortiri et al. [1] | Bortiri et al. [28] |
|-------|-------------------|---------------------|
| Trees (no.) | trnL-trnF sequence—MP = 76 MPT (L = 187, CI = 0.733, RI = 0.834). ITS sequence—MP = stopped at 30000 MPT (L = 678, CI = 0.567, RI = 0.714). Combined data set—consensus tree 8318 MPT (L = 676, CI = 0.695, RI = 0.727). | s6pdh sequence—MP = 273 MPT (L = 1198, CI = 0.58, RI = 0.81). s6pdh sequence—ML tree log likelihood = −7720.96. For combined data set—MP = 9 MPT (L = 1592, CI = 0.58, RI = 0.61). For combined data set—ML tree log likelihood = −12056.56 |
| Characters (no.) | trnL-trnF = 563 bp, ITS = 759 bp | s6pdh = 1387 bp. Combined data set = 2760 bp (s6pdh, trnL-trnF, and ITS) |
| Informative characters (no.) | trnL-trnF = 26 bp (excluding outgroups), ITS = 76 bp (excluding outgroups = among *Prunus* species) | s6pdh = 234 bp (excluding outgroups = among *Prunus* species). Combined data set = 226 bp (s6pdh = 148, trnL-trnF = 18, and ITS = 60) |
| Indels (no.) | trnL-trnF = 9 indels (>2 bp), ITS = 2 indels (>2 bp) |
| Substitutions (no.) |
| Inversions (no.) |
| PIC | trnL-trnF = 26 bp (excluding outgroups), ITS = 76 bp (excluding outgroups = among *Prunus* species) (not including indels) | s6pdh = 234 bp (excluding outgroups = among *Prunus* species). Combined data set = 226 bp (s6pdh = 148, trnL-trnF = 18, and ITS = 60) |
| Percent variability | trnL-trnF = 4.62%, ITS = 10.01% | s6pdh = 16.87%. For combined data set = 8.18% (s6pdh = 10.67%, trnL-trnF = 3.19%, and ITS = 7.9% = calculated with characters from Bortiri et al. [1]) |

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| Paper | Shaw and Small [29] |
|-------|---------------------|
| Phylogenetic analysis | Molecular |
| Analytical methods | MP, BI |
| Metrics (analysis) | Seven noncoding chloroplast DNA regions: *trnL*<sup>UAA</sup>, *rps16*, *rpL16*, and *trnG*<sup>UUC</sup> introns; *trnS*<sup>GCU</sup>-*trnG*<sup>UUC</sup>; *trnL*<sup>UAA</sup>-*trnF*<sup>GAA</sup>; and *trnH*<sup>U3</sup>-*psbA* intergenic spacers |
| Taxa (no.)/subgenus (sect.) | 43 species/5 subgenus: *Prunus* [sect.: *Prunus, Prunocerasus* (17 taxa), *Armeniaca*], *Amygdalus, Cerasus* (sect.: *Microcerasus, Pseudocerasus, Mahaleb, Phyllomahaleb*), *Padus*, and *Laurocerasus* [3] |
| Outgroups | *Physocarpus opulifolius* |
| Trees (no.) | Combined data set—MP = 25,171 MPT (L = 422, CI = 0.92, RI = 0.94) |
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### Characters or bp (no.)

*Prunocerasus* analysis introns: *trnL*\(^{UAU}\) = 522 bp, *rps16* = 683 bp, *rpl16* = 996 bp, and *trnG*\(^{UGC}\) = 711 bp. Intergeneric spacers: *trnS*\(^{GCC}\)-*trnL*\(^{UAU}\), *trnL*\(^{GAA}\) = 397 bp, and *trnH*\(^{UGU}\)-*psbA* = 363 bp. Combined data = 4375 bp. *Prunus* analysis *trnH*\(^{UGC}\)-*psbA* = 516 bp, *rpl16* = 1105 bp, *trnS*\(^{GCC}\)-*trnL*\(^{UAU}\) = 903 bp, and *trnG*\(^{UGC}\) = 746 bp. Combined data = 3270 bp.

### Indels (no.)

*Prunocerasus* analysis introns: *trnL*\(^{UAU}\) = 0 bp, *rps16* = 2 bp, *rpl16* = 7 bp, and *trnG*\(^{UGC}\) = 0 bp. Intergeneric spacers: *trnS*\(^{GCC}\)-*trnG*\(^{UAC}\) = 2 bp, *trnL*\(^{UAU}\), *trnL*\(^{GAA}\) = 3 bp, and *trnH*\(^{UGU}\)-*psbA* = 3 bp. Combined data = 14 bp. *Prunus* analysis *trnH*\(^{UGC}\)-*psbA* = 13 bp, *rpl16* = 10 bp, *trnS*\(^{GCC}\)-*trnG*\(^{UAC}\) = 14 bp, and *trnG*\(^{UAC}\) = 4 bp. Combined data = 41 bp.

### Substitutions (no.)

*Prunocerasus* analysis introns: *trnL*\(^{UAU}\) = 1 bp, *rps16* = 4 bp, *rpl16* = 6 bp, and *trnG*\(^{UGC}\) = 4 bp. Intergeneric spacers: *trnS*\(^{GCC}\)-*trnG*\(^{UAC}\) = 4 bp, *trnL*\(^{UAU}\), *trnL*\(^{GAA}\) = 3 bp, and *trnH*\(^{GUC}\)-*psbA* = 1 bp. Combined data = 23 bp. *Prunus* analysis *trnH*\(^{UGC}\)-*psbA* = 11 bp, *rpl16* = 21 bp, *trnS*\(^{GCC}\)-*trnG*\(^{UAC}\) = 28 bp, and *trnG*\(^{UAC}\) = 32 bp. Combined data = 92 bp.

### Inversions (no.)

*Prunocerasus* analysis introns: *trnL*\(^{UAU}\) = 0 bp, *rps16* = 0 bp, *rpl16* = 0 bp, and *trnG*\(^{UGC}\) = 0 bp. Intergeneric spacers: *trnS*\(^{GCC}\)-*trnG*\(^{UAC}\) = 0 bp, *trnL*\(^{UAU}\), *trnL*\(^{GAA}\) = 0 bp, and *trnH*\(^{UGU}\)-*psbA* = 0 bp. Combined data = 0 bp. *Prunus* analysis *trnH*\(^{UGC}\)-*psbA* = 0 bp, *rpl16* = 0 bp, *trnS*\(^{GCC}\)-*trnG*\(^{UAC}\) = 1 bp, and *trnG*\(^{UAC}\) = 0 bp. Combined data = 1 bp.

### Percent variability

*Prunocerasus* analysis introns: *trnL*\(^{UAU}\) = 0.19%, *rps16* = 0.88%, *rpl16* = 1.31%, and *trnG*\(^{UGC}\) = 0.56%. Intergeneric spacers: *trnS*\(^{GCC}\)-*trnG*\(^{UAC}\) = 0.85%, *trnL*\(^{UAU}\), *trnL*\(^{GAA}\) = 0.76%, and *trnH*\(^{UGU}\)-*psbA* = 1.10%. Combined data = 37 bp. *Prunus* analysis *trnH*\(^{UGC}\)-*psbA* = 4.65%, *rpl16* = 2.80%, *trnS*\(^{GCC}\)-*trnG*\(^{UAC}\) = 4.76%, and *trnG*\(^{UAC}\) = 4.80%. Combined data = 4.09%.

### Phylogeny in classification

Genus *Prunus* was monophyletic. Subgenus *Prunus* sect. *Prunocerasus* and sect. *Prunus* were monophyletic. The genus *Prunus* was formed by two groups: subgenera *Laurocerasus-Prunus* and subgenera *Amygdalus-Emplectocladus-Prunus-Cerasus* (sect. *Microcerasus*). *Prunus texana* and *P. subcordata* were included in sect. *Prunocerasus*. Within sect. *Prunocerasus* three groups were identified: the American, the Chickasaw, and the Beach clades.

### Notes

*Prunus texana* was first used in this study. *Prunus texana* and *P. fasciculata* were not recognized by Waugh [8], Wight [5], and Rehder [3].

### Paper

| Shaw and Small [29] | Rohrer et al. [36] | Katayama and Uematsu [37] |
|--------------------|-------------------|---------------------------|
| **Phylogenetic analysis** | Molecular | Molecular | Molecular |
| **Analytical methods** | UPGMA | MP | UPGMA |
| **Metrics (analysis)** | Fifteen microsatellites primer pairs | *rpL16* intron | CpDNA analysis based on five restriction enzymes (SalI, XhoI, BamHI, SacI, and PstI) by RFLP |
| **Taxa (no.)/subgenus (sect.)/genus** | 18 species/subgenus *Prunus* sect. *Prunocerasus* (13 and 3 undetermined hybrids), subgenus *Prunus* (*P. cerasifera*), and | A total of 207 accessions = 18 species (subgenera *Prunus* sect. *Prunocerasus*) | A total of 18 accessions = 14 *Prunus* species and 1 interspecific hybrid |
### Prunus

| Paper                  | Rohrer et al. [36] | Shaw and Small [30] | Katayama and Uematsu [37] |
|------------------------|--------------------|---------------------|---------------------------|
| **Outgroups**          | subgenus Armeniaca (P. armeniaca). | | Pyrus ussuriensis var. hondoensis |
| **Trees (no.)**        | Strict consensus = 3 MPT (L = 34, CI = 0.97, RI = 0.99) | Strict consensus = 8 MPT (L = 68, CI = 0.93, RI = 0.64) | |
| **Characters or bp (no.)** | A total of 186 putative alleles with a mean value of 12.4 per locus | rpL16 intron = 797 bp | |
| **Informative characters (no.)** | rpL16 intron = 23 bp | | |
| **Indels (no.)**       | | | |
| **Substitutions (no.)** | | | |
| **Inversions (no.)**   | | | |
| **PIC**                | | | |
| **Percent variability** | rpL16 intron = 2.88% | | |

**Phylogeny in classification**
- No clear phylogenetic relationships were determined. The microsatellites are evolving too rapidly in North American plums to be truly useful at resolving species relationships.
- Twenty-two unique haplotypes were identified in sect. Prunocerasus. Ten different haplotypes were associated with the American clade, two haplotypes with the Beach clade, and seven haplotypes with the Chickasaw clade. Additionally, one Texana haplotype, one Subcordata haplotype, and one peculiar Umbellata haplotype.
- Eleven genome types. The UPGMA tree consisted of two major groups: genome types A-I (subgenus Amygdalus, Prunus, and Cerasus sect. Microcerasus) and other with genomes J-K (subgenus Laurocerasus and Padus).

**Notes**
- The congeneric relationship of plums to peach and cherry allowed the successful use of these primers in section Prunocerasus. Microsatellites are evolving too rapidly to be truly useful at resolving species phylogeny.
- The common practice of choosing one specimen to represent a taxon can be misleading in closely related groups. Choosing different genotypes could have resulted in a different result than previous studies.
- The 9.1 kb region between psbA and atpA genes would be useful tool to study the cpDNA evolution in Prunus.

| Paper              | Bortiri et al. [31] | Wen et al. [38] |
|--------------------|---------------------|----------------|
| **Phylogenetic analysis** | Morphology and molecular | Molecular |
| **Analytical methods** | MP, ML, and BI | MP and BI |
Chloroplast *ndhF* region and ITS nuclear ribosomal gene.

A total of 59 (*ndhF*) or 51 (ITS) accessions of Prunus/5 subgenus: Prunus (sect.: Prunus, Prunocerasus, Armeniaca), Amygdalus, Cerasus (sect.: Microcerasus, Pseudocerasus, Mahaleb, Phyllomahaleb), Padus, and Laurocerasus [3].

Outgroups Oemleria cerasiformis, Sorbaria sorbifolia, Spiraea cantoniensi, Gillenia stipulata, Lyonothamnus floribundus, Maddenia hypoleuca, Physocarpus capitatus, Physocarpus opulifolius, and Rhodotypos scandens.

Trees (no.) Morphological data set—MP = 50,000 MPT (L = 110, CI = 0.36, RI = 0.73).

Molecular data results from Bortiri et al. [1] and Bortiri et al. [28]. Combined data set—MP = 20 MPT (L = 1741, CI = 0.49, RI = 0.65). Combined data set—ML tree log likelihood = 12499.63.

MPT (L = 815, CI = 0.71, COI = 0.56, RI = 0.86).

Combined data set—ML tree log likelihood = 12499.63.

Characters or bp (no.) Combined data set = 771 bp.

Informative characters (no.) ITS = 178 bp, *trnL-trnF* = 50 bp, and *trnS-trnG* = 142 bp.

Indels (no.) Combined data set = 3.

Substitutions (no.)

Inversions (no.)

PIC ITS = 178 bp, *trnL-trnF* = 50 bp, and *trnS-trnG* = 142 bp.

Percent variability

Phylogeny in classification Three clades were reported: “Clade A” with subgenera Padus and Laurocerasus; “Clade B” with subgenera Amygdalus, Emplectocladus, and Prunus; and “Clade C” with subgenera Cerasus. “Clade B” was characterized by the production of three axillary buds. Padus and Laurocerasus were not supported as monophyletic (highly homoplasie).

Both data set identified genus *Prunus* as a monophyletic group. Both data sets were incongruent at the species level in *Prunus*. The *ndhF* data supported two major groups: subgenera *Laurocerasus* (including *Pygeum*) and Padus, and subgenera Amygdalus, Cerasus, and *Prunus*. The ITS data supported a clade composed of subgenera Amygdalus, *Prunus*, and Cerasus sect. *Microcerasus*, and the paraphyletic clade of *Padus* and *Laurocerasus*.
Endocarp and leaf morphometrics combined with AFLP markers were used to study the morphological and genetic variation of five European members of section \textit{Prunus}: \textit{P. cerasifera}, \textit{P. cocomilia} Ten., \textit{P. domestica}, \textit{P. insititia} L., \textit{P. spinosa} L., and \textit{P. × fruticans} [33]. Three clusters were reported: a first cluster \textit{P. cerasifera}–\textit{P. cocomilia}, a second \textit{P. domestica}–\textit{P. insititia}, and a third \textit{P. spinosa} and \textit{P. × fruticans}. 

\begin{table}[h]
\centering
\begin{tabular}{|l|l|l|}
\hline
\textbf{Paper} & \textbf{Depypere et al. [33]} & \textbf{Chavez et al. [39]} \\
\hline
Metrics (analysis) & Leaf and endocarp morphometrics and AFLP primers & SSRs (41), cpDNA (seven regions), nuclear genes (33 vernalization response genes, 16 tree architecture, and 3 isozymes), and ITS \\
\hline
Taxa (no.)/subgenus (sect.)/genus & A total of 82 accessions/5 species: \textit{P. cerasifera}, \textit{P. domestica}, \textit{P. insititia}, \textit{P. spinosa}, and \textit{P. × fruticans}, & A total of 8 species: \textit{P. americana}, \textit{P. angustifolia}, \textit{P. hortulana}, \textit{P. mexicana}, \textit{P. munsoniana}, \textit{P. geniculata}, \textit{P. maritima}, \textit{P. umbellata} \\
\hline
Outgroups & & \textit{P. fasciculata}, \textit{P. persica}, and \textit{P. pumila} \\
\hline
Trees (no.) & cpDNA sequences—MP = 13 MPT (L = 623, CI = 0.92, RI = 0.81, RC = 0.74) – ML = −lnL = 5414.74. Nuclear genes – MP = 1 MPT (L = 2535, CI = 0.88, RI = 0.88, RC = 0.78) – ML = −lnL = 41509.34. Combined nuclear + cpDNA + ITS – MP = 2 MPT (L = 2732, CI = 0.88, RI = 0.88, RC = 0.77) – ML = −lnL = 48496.34. & \\
\hline
Characters or bp (no.) & Combined data set = 27,623 bp & \\
\hline
Informative characters (no.) & 1594 & \\
\hline
Indels (no.) & & \\
\hline
Substitutions (no.) & & \\
\hline
Inversions (no.) & & \\
\hline
PIC & & \\
\hline
Percent variability & & \\
\hline
Phylogeny in classification & PCoA and AFLP of three distinct clusters. A first cluster consists of all \textit{P. cerasifera} samples and the sole \textit{P. cocomilia}. A second cluster includes all individuals of \textit{P. domestica} and \textit{P. insititia}. A third cluster comprises all \textit{P. spinosa} and \textit{P. × fruticans} samples & The American and the Chickasaw clades were identified. An outgroup clade was comprised by \textit{P. persica} and \textit{P. fasciculata} \\
\hline
Notes & Low number of \textit{Prunus} species for sampling & Identified multiple gene regions that provided the greatest number of characters, variability, and improved phylogenetic signal at the species level in \textit{Prunus} section \textit{Prunocerasus} \\
\hline
\end{tabular}
\caption{Summary of \textit{Prunus} phylogenetic studies.}
\end{table}
Phylogenetic analysis based on four single-copy cpDNA regions (atpB-rbcL, matK, rpl16, and trnL-trnF) of Eurasian plums, *Prunus section Prunus*, confirmed this section to be monophyletic. Four well supported clades were reported: “Clade A” with *P. salicina*, *P. sogdiana*, and *P. ussuriensis*; “Clade B” with *P. cocomilia*; “Clade C” with *P. brigantina*, *P. ramburii*, and *P. spinosa*; and “Clade D” with subclade D1 *P. domestica-P. insititia-P. divaricata-P. ursine* and subclade D2 *P. cerasifera* [34].

Chavez et al. [39] identified genomic regions that provided the greatest number of characters and variability and improved the phylogenetic signal at the low level in *Prunus section Prunocerasus* relationships. The American and the Chickasaw clades were identified. An outgroup clade was comprised by *P. persica* and *P. fasciculata*. The results reported were similar to those reported by Mowrey and Werner [23].

Previous studies demonstrated the value of morphology, cytometry, nuclear DNA, and cpDNA as data for phylogenetic studies in *Prunus*. Most of the previous phylogenetic research used Mason’s [21] and Rehder’s [3] taxonomic classification. A complete summary of *Prunus* phylogenetic research is summarized in Table 2.

4. Final remark

The subgenus *Prunus section Prunocerasus* (the North American plums) constitutes important genetic resources (gene pool) of unique traits such as tree architecture, chilling requirement, heat requirement, fruit development period, fruit size, fruit texture, disease and insect resistance, and adaptive changes to multiple environmental conditions, among others. These species could be used in the breeding of improved stone fruit cultivars in the future. The summary of the taxonomic and phylogenetic relationships presented in this chapter provides a base to understand the species relationships. In addition, it will help for the conservation and maintenance of a broader germplasm base within *Prunus*.

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