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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*, *Ceriseidos*, 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), *Penarmeriaca*, *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	Domestica plums	<i>Prunus domestica</i>	Eastern Europe and west-central Asia	Nova Scotia, central New England, New York, southern Ontario and Michigan, and the Pacific coast states
	Damsons	<i>Prunus domestica</i>	Europe	
	Myrobalan plums	<i>Prunus cerasifera</i>		Europe and US used as rootstock
	Simon plums	<i>Prunus simonii</i>	China	New York, California
Indigenous	Japanese plums	<i>Prunus triflora</i>	China, Japan	Maine, Vermont, Ontario, and southern Iowa
	Americana group	<i>Prunus americana</i>	USA (Ohio, Texas, northward to Minnesota and Montana)	Prince Edward Island, Manitoba, and Vancouver, to Florida, Louisiana, and Texas
	Nigra group	<i>Prunus americana nigra</i>	CAN (Newfoundland west to Rainy and Assiniboine rivers), USA (New England states)	Prince Edward Island, Manitoba, and Vancouver, to Florida, Louisiana, and Texas
	Miner Group	<i>Prunus hortulana mineri</i>	USA (standing between <i>P. americana</i> and the Wildgoose group)	Not cultivated
	Wayland group	<i>Prunus rivularis</i> ^z <i>Prunus hortulana</i> ^y	USA (Colorado, Guadalupe, and the Leona)	North of Burlington, Vermont, and Iowa
	Wildgoose group	<i>Prunus hortulana</i>	USA (the Mississippi valley)	From Texas to Massachusetts
	Chickasaws	<i>Prunus angustifolia</i>	USA (Southern range to Delaware and Kentucky, including southern Atlantic and Gulf states)	Iowa, Vermont, New York, and Massachusetts
	Sand plum	<i>Prunus angustifolia watsonii</i>	USA (South and southeast Nebraska and central and western Kansas)	Cultivated by settlers in Kansas and Maryland
	Beach plum	<i>Prunus maritima</i>	USA (sea beaches, New Brunswick to Virginia, Georgia, Alabama, and Connecticut)	Not cultivated
	Pacific plum	<i>Prunus subcordata</i>	USA (Pacific coast)	Sierra regions of California and southern Oregon

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

^zClassified as *Prunus rivularis* but with doubts.
^y*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].

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 [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

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-Padus* 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 *s6pdh*, 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 *s6pdh* sequences were compared and combined. Phylogenetic analysis of the combined data supported two major clades: subgenera *Cerasus-Laurocerasus-Padus* 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. *americana* 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. *davisii* (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 ^z	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 <i>Bam</i> HI, <i>Hind</i> III, and <i>Sma</i> I	Isozyme
Taxa (no.)/subgenus (sect.) genus	11 species/3 subgenus: <i>Cerasus</i> , <i>Padus</i> , <i>Armeniaca</i> [3]/genus <i>Prunus</i>	34 species/4 subgenus: <i>Prunus</i> (sect.: <i>Prunus</i> , <i>Prunocerasus</i> , <i>Armeniaca</i>), <i>Amygdalus</i> , <i>Cerasus</i> (sect.: <i>Sargentiella</i> , <i>Microcalymma</i> , <i>Magniculpula</i> , <i>Phyllomahaleb</i>), and <i>Lithocerasus</i> (sect.: <i>Microcerasus</i> , <i>Armeniacocerasus</i>) [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 <i>Prunus</i> . Subgenus <i>Lithocerasus</i> was identified as an artificial grouping of species
Notes		<i>Lithocerasus</i> formed part of <i>Cerasus</i> 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.)	9 species/5 subgenus: <i>Prunus</i> , <i>Amygdalus</i> , and <i>Cerasus</i> .	40 species (represented by 52 accessions)/5 subgenus: <i>Prunus</i> (sect.: <i>Prunus</i> , <i>Prunocerasus</i> , <i>Armeniaca</i>), <i>Amygdalus</i> , <i>Cerasus</i> (sect.: <i>Microcerasus</i> , <i>Pseudocerasus</i> , <i>Mahaleb</i> , <i>Phyllomahaleb</i>), <i>Padus</i> , and <i>Laurocerasus</i> [3]
Outgroups	<i>Fragaria vesca</i>	<i>Exochorda giraldii</i> , <i>Maddenia hypoleuca</i> , <i>Oemleria cerasiformis</i> , <i>Prinsepia sinensis</i> , <i>Prinsepia uniflora</i> , <i>Lyonothamnus floribundus</i>

Paper	Badenes and Parfitt [26]	Lee and Wen [27]
Trees (no.)	10	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)
Substitutions (no.)		
Inversions (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 <i>Prunus</i> , <i>Cerasus</i> , and <i>Amygdalus</i> . Relative small number of taxa used in the study. Subgenus <i>Cerasus</i> suggested to be more extensively evolved than either <i>Prunus</i> or <i>Amygdalus</i>	Genus <i>Prunus</i> was monophyletic. Support for <i>Maddenia</i> nested within genus <i>Prunus</i> . Within genus <i>Prunus</i> , two major groups were recognizable: <i>Amygdalus-Prunus</i> group and <i>Cerasus-Laurocerasus-Padus</i> 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
Paper	Bortiri et al. [1]	Bortiri et al. [28]
Phylogenetic analysis	Molecular	Molecular
Analytical methods	MP	MP, ML
Metrics (analysis)	ITS nuclear ribosomal DNA and chloroplast <i>trnL-trnF</i> spacer DNA	Nuclear gene sorbitol 6-phosphate dehydrogenase (<i>s6pdh</i>) and data from previous study ITS and <i>trnL-trnF</i> [1]
Taxa (no.)/subgenus (sect.)	48 species/5 subgenus: <i>Prunus</i> (sect.: <i>Prunus</i> , <i>Prunocerasus</i> , <i>Armeniaca</i>), <i>Amygdalus</i> , <i>Cerasus</i> (sect.: <i>Microcerasus</i> , <i>Pseudocerasus</i> , <i>Mahaleb</i> , <i>Phyllomahaleb</i>), <i>Padus</i> , and <i>Laurocerasus</i> [3]	22 species (representing all the major clades found in previous study)/5 subgenus: <i>Prunus</i> (sect.: <i>Prunus</i> , <i>Prunocerasus</i> , <i>Armeniaca</i>), <i>Amygdalus</i> , <i>Cerasus</i> (sect.: <i>Microcerasus</i> , <i>Pseudocerasus</i> , <i>Mahaleb</i> , <i>Phyllomahaleb</i>), <i>Padus</i> , and <i>Laurocerasus</i> [3]
Outgroups	<i>Exochorda racemosa</i> , <i>Oemleria cerasiformis</i> , <i>Prinsepia sinensis</i> , <i>Physocarpus capitatus</i> , <i>Sorbaria sorbifolia</i> , and <i>Spiraea cantoniensis</i>	<i>Exochorda racemosa</i> , <i>Oemleria cerasiformis</i> , <i>Sorbaria sorbifolia</i> , <i>Spiraea cantoniensis</i> , <i>Holodiscus microphyllus</i> , <i>Chamaebatiaria millefolium</i> , <i>Kageneckia oblonga</i> , <i>Vauquelinia californica</i> , <i>Gillenia stipulata</i> , <i>Pyrus caucasica</i> , <i>Sorbus</i> sp., <i>Amelanchier alnifolia</i> , <i>Aruncus dioicus</i> , <i>Neillia sinensis</i> , and <i>Spiraea betulifolia</i>

Paper	Bortiri et al. [1]	Bortiri et al. [28]
Trees (no.)	<i>trnL-trnF</i> 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 = 876, CI = 0.695, RI = 0.727)	<i>s6pdh</i> sequence—MP = 273 MPT (L = 1198, CI = 0.58, RI = 0.81). <i>s6pdh</i> 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.)	<i>trnL-trnF</i> = 563 bp, ITS = 759 bp	<i>s6pdh</i> = 1387 bp. Combined data set = 2760 bp (<i>s6pdh</i> , <i>trnL-trnF</i> , and ITS)
Informative characters (no.)	<i>trnL-trnF</i> = 26 bp (excluding outgroups), ITS = 76 bp (excluding outgroups = among <i>Prunus</i> species)	<i>s6pdh</i> = 234 bp (excluding outgroups = among <i>Prunus</i> species). Combined data set = 226 bp (<i>s6pdh</i> = 148, <i>trnL-trnF</i> = 18, and ITS = 60)
Indels (no.)	<i>trnL-trnF</i> = 9 indels (>2 bp), ITS = 2 indels (>2 bp)	
Substitutions (no.)		
Inversions (no.)		
PIC	<i>trnL-trnF</i> = 26 bp (excluding outgroups), ITS = 76 bp (excluding outgroups = among <i>Prunus</i> species) (not including indels)	<i>s6pdh</i> = 234 bp (excluding outgroups = among <i>Prunus</i> species). Combined data set = 226 bp (<i>s6pdh</i> = 148, <i>trnL-trnF</i> = 18, and ITS = 60)
Percent variability	<i>trnL-trnF</i> = 4.62%, ITS = 10.01%	<i>s6pdh</i> = 16.87%. For combined data set = 8.18% (<i>s6pdh</i> = 10.67%, <i>trnL-trnF</i> = 3.19%, and ITS = 7.9% = calculated with characters from Bortiri et al. [1])
Phylogeny in classification	Genus <i>Prunus</i> was monophyletic. <i>Exochorda</i> , <i>Oemleria</i> , and <i>Prinsepia</i> were not supported as sister groups with <i>Prunus</i> . Genus <i>Prunus</i> was divided in two clades: subgenera <i>Amygdalus-Prunus-Cerasus</i> (sect. <i>Microcerasus</i>)- <i>Emplectocladus</i> group and subgenera <i>Cerasus-Laurocerasus-Padus</i> group. Subgenus <i>Prunus</i> sect. <i>Prunus</i> was monophyletic	Genus <i>Prunus</i> was monophyletic. In the combined data set, the genus <i>Prunus</i> was formed by two groups: subgenera <i>Cerasus-Laurocerasus-Padus</i> and subgenera <i>Amygdalus-Emplectocladus-Prunus-Cerasus</i> (sect. <i>Microcerasus</i>)
Notes	First time that <i>P. fasciculata</i> (sect. <i>Emplectocladus</i>) was used in a study	Includes <i>P. fasciculata</i> sect. <i>Emplectocladus</i>
Paper	Shaw and Small [29]	
Phylogenetic analysis	Molecular	
Analytical methods	MP, BI	
Metrics (analysis)	Seven noncoding chloroplast DNA regions: <i>trnL</i> ^{UAA} , <i>rpS16</i> , <i>rpL16</i> , and <i>trnG</i> ^{UUC} introns; <i>trnS</i> ^{GCU} - <i>trnG</i> ^{UUC} ; <i>trnL</i> ^{UUA} - <i>trnF</i> ^{GAA} ; and <i>trnH</i> ^{GUG} - <i>psbA</i> intergeneric spacers	
Taxa (no.)/subgenus (sect.)	43 species/5 subgenus: <i>Prunus</i> [sect.: <i>Prunus</i> , <i>Prunocerasus</i> (17 taxa), <i>Armeniaca</i>], <i>Amygdalus</i> , <i>Cerasus</i> (sect.: <i>Microcerasus</i> , <i>Pseudocerasus</i> , <i>Mahaleb</i> , <i>Phyllomahaleb</i>), <i>Padus</i> , and <i>Laurocerasus</i> [3]	
Outgroups	<i>Physocarpus opulifolius</i>	
Trees (no.)	Combined data set—MP = 25,171 MPT (L = 422, CI = 0.92, RI = 0.94)	

Paper	Shaw and Small [29]		
Characters or bp (no.)	<i>Prunocerasus</i> analysis introns: $trnL^{UAA}$ = 522 bp, $rpS16$ = 683 bp, $rpL16$ = 996 bp, and $trnG^{UUC}$ = 711 bp. Intergeneric spacers: $trnS^{GCU}$ - $trnG^{UUC}$ = 703 bp, $trnL^{UUA}$ - $trnF^{GAA}$ = 397 bp, and $trnH^{GUG}$ - $psbA$ = 363 bp. Combined data = 4375 bp. <i>Prunus</i> analysis $trnH^{GUG}$ - $psbA$ = 516 bp, $rpL16$ = 1105 bp, $trnS^{GCU}$ - $trnG^{UUC}$ = 903 bp, and $trnG^{UUC}$ = 746 bp. Combined data = 3270 bp		
Informative characters (no.)			
Indels (no.)	<i>Prunocerasus</i> analysis introns: $trnL^{UAA}$ = 0 bp, $rpS16$ = 2 bp, $rpL16$ = 7 bp, and $trnG^{UUC}$ = 0 bp. Intergeneric spacers: $trnS^{GCU}$ - $trnG^{UUC}$ = 2 bp, $trnL^{UUA}$ - $trnF^{GAA}$ = 0 bp, and $trnH^{GUG}$ - $psbA$ = 3 bp. Combined data = 14 bp. <i>Prunus</i> analysis $trnH^{GUG}$ - $psbA$ = 13 bp, $rpL16$ = 10 bp, $trnS^{GCU}$ - $trnG^{UUC}$ = 14 bp, $trnG^{UUC}$ = 4 bp. Combined data = 41 bp		
Substitutions (no.)	<i>Prunocerasus</i> analysis introns: $trnL^{UAA}$ = 1 bp, $rpS16$ = 4 bp, $rpL16$ = 6 bp, and $trnG^{UUC}$ = 4 bp. Intergeneric spacers: $trnS^{GCU}$ - $trnG^{UUC}$ = 4 bp, $trnL^{UUA}$ - $trnF^{GAA}$ = 3 bp, and $trnH^{GUG}$ - $psbA$ = 1 bp. Combined data = 23 bp. <i>Prunus</i> analysis $trnH^{GUG}$ - $psbA$ = 11 bp, $rpL16$ = 21 bp, $trnS^{GCU}$ - $trnG^{UUC}$ = 28 bp, and $trnG^{UUC}$ = 32 bp. Combined data = 92 bp		
Inversions (no.)	<i>Prunocerasus</i> analysis introns: $trnL^{UAA}$ = 0 bp, $rpS16$ = 0 bp, $rpL16$ = 0 bp, and $trnG^{UUC}$ = 0 bp. Intergeneric spacers: $trnS^{GCU}$ - $trnG^{UUC}$ = 0 bp, $trnL^{UUA}$ - $trnF^{GAA}$ = 0 bp, and $trnH^{GUG}$ - $psbA$ = 0 bp. Combined data = 0 bp. <i>Prunus</i> analysis $trnH^{GUG}$ - $psbA$ = 0 bp, $rpL16$ = 0 bp, $trnS^{GCU}$ - $trnG^{UUC}$ = 1 bp, and $trnG^{UUC}$ = 0 bp. Combined data = 1 bp		
PIC	<i>Prunocerasus</i> analysis introns: $trnL^{UAA}$ = 1 bp, $rpS16$ = 6 bp, $rpL16$ = 13 bp, and $trnG^{UUC}$ = 4 bp. Intergeneric spacers: $trnS^{GCU}$ - $trnG^{UUC}$ = 6 bp, $trnL^{UUA}$ - $trnF^{GAA}$ = 3 bp, and $trnH^{GUG}$ - $psbA$ = 4 bp. Combined data = 37 bp. <i>Prunus</i> analysis $trnH^{GUG}$ - $psbA$ = 24 bp, $rpL16$ = 31 bp, $trnS^{GCU}$ - $trnG^{UUC}$ = 43 bp, and $trnG^{UUC}$ = 36 bp. Combined data = 134 bp		
Percent variability	<i>Prunocerasus</i> analysis introns: $trnL^{UAA}$ = 0.19%, $rpS16$ = 0.88%, $rpL16$ = 1.31%, and $trnG^{UUC}$ = 0.56%. Intergeneric spacers: $trnS^{GCU}$ - $trnG^{UUC}$ = 0.85%, $trnL^{UUA}$ - $trnF^{GAA}$ = 0.76%, and $trnH^{GUG}$ - $psbA$ = 1.10%. Combined data = 37 bp. <i>Prunus</i> analysis $trnH^{GUG}$ - $psbA$ = 4.65%, $rpL16$ = 2.80%, $trnS^{GCU}$ - $trnG^{UUC}$ = 4.76%, and $trnG^{UUC}$ = 4.80%. Combined data = 4.09%.		
Phylogeny in classification	Genus <i>Prunus</i> was monophyletic. Subgenus <i>Prunus</i> sect. <i>Prunocerasus</i> and sect. <i>Prunus</i> were monophyletic. The genus <i>Prunus</i> was formed by two groups: subgenera <i>Laurocerasus</i> - <i>Padus</i> and subgenera <i>Amygdalus</i> - <i>Emplectocladus</i> - <i>Prunus</i> - <i>Cerasus</i> (sect. <i>Microcerasus</i>). <i>Prunus texana</i> and <i>P. subcordata</i> were included in sect. <i>Prunocerasus</i> . Within sect. <i>Prunocerasus</i> three groups were identified: the American, the Chickasaw, and the Beach clades		
Notes	<i>Prunus texana</i> was first used in this study. <i>Prunus texana</i> and <i>P. fasciculata</i> were not recognized by Waugh [8], Wight [5], and Rehder [3]		
Paper	Rohrer et al. [36]	Shaw and Small [30]	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 (<i>Sal</i> I, <i>Xho</i> I, <i>Bam</i> HI, <i>Sac</i> I, and <i>Pst</i> I) by RFLP
Taxa (no.)/subgenus (sect.)/genus	18 species/subgenus <i>Prunus</i> sect. <i>Prunocerasus</i> (13 and 3 undetermined hybrids), subgenus <i>Prunus</i> (<i>P. cerasifera</i>), and	A total of 207 accessions = 18 species (subgenus <i>Prunus</i> sect. <i>Prunocerasus</i>)	A total of 18 accessions = 14 <i>Prunus</i> species and 1 interspecific hybrid

Paper	Rohrer et al. [36]	Shaw and Small [30]	Katayama and Uematsu [37]
	subgenus <i>Armeniaca</i> (<i>P. armeniaca</i>).		
Outgroups			<i>Pyrus ussuriensis</i> var. <i>hondoensis</i>
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	<i>rpL16</i> intron = 797 bp	
Informative characters (no.)		<i>rpL16</i> intron = 23 bp	
Indels (no.)			
Substitutions (no.)			
Inversions (no.)			
PIC		<i>rpL16</i> intron = 23 bp	
Percent variability		<i>rpL16</i> 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. <i>Prunocerasus</i> . 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 <i>Umbellata</i> haplotype	Eleven genome types. The UPGMA tree consisted of two major groups: genome types A-I (subgenus <i>Amygdalus</i> , <i>Prunus</i> , and <i>Cerasus</i> sect. <i>Microcerasus</i>) and other with genomes J-K (subgenus <i>Laurocerasus</i> and <i>Padus</i>).
Notes	The congeneric relationship of plums to peach and cherry allowed the successful use of these primers in section <i>Prunocerasus</i> . 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 <i>psbA</i> and <i>atpA</i> genes would be useful tool to study the cpDNA evolution in <i>Prunus</i>
Paper	Bortiri et al. [31]	Wen et al. [38]	
Phylogenetic analysis	Morphology and molecular	Molecular	
Analytical methods	MP, ML, and BI	MP and BI	

Paper	Bortiri et al. [31]	Wen et al. [38]
Metrics (analysis)	ITS nuclear ribosomal gene, <i>trnL-trnF</i> spacer, <i>trnS-trnG</i> spacer, <i>trnG</i> intron, and 25 morphological characters.	Chloroplast <i>ndhF</i> region and ITS nuclear ribosomal gene.
Taxa (no.)/subgenus (sect.)/genus	37 species/5 subgenus: <i>Prunus</i> (sect.: <i>Prunus</i> , <i>Prunocerasus</i> , <i>Armeniaca</i>), <i>Amygdalus</i> , <i>Cerasus</i> (sect.: <i>Microcerasus</i> , <i>Pseudocerasus</i> , <i>Mahaleb</i> , <i>Phyllomahaleb</i>), <i>Padus</i> , and <i>Laurocerasus</i> [3]	A total of 59 (<i>ndhF</i>) or 51 (ITS) accessions of <i>Prunus</i> /5 subgenus: <i>Prunus</i> (sect.: <i>Prunus</i> , <i>Prunocerasus</i> , <i>Armeniaca</i>), <i>Amygdalus</i> , <i>Cerasus</i> (sect.: <i>Microcerasus</i> , <i>Pseudocerasus</i> , <i>Mahaleb</i> , <i>Phyllomahaleb</i>), <i>Padus</i> , and <i>Laurocerasus</i> [3]. In addition, <i>Madenia hypoleuca</i> and the <i>Pygeum</i> group
Outgroups	<i>Oemleria cerasiformis</i> , <i>Sorbaria sorbifolia</i> , <i>Spiraea cantoniensis</i> , <i>Gillenia stipulata</i> , <i>Lyonothamnus floribundus</i> , <i>Maddenia hypoleuca</i> , <i>Physocarpus capitatus</i> , <i>Physocarpus opulifolius</i> , and <i>Rhodotypos scandens</i>	<i>Oemleria cerasiformis</i> , <i>Prinsepia uniflora</i> , <i>Physocarpus monogynus</i> , <i>Lyonothamnus floribundus</i> , and <i>Holodiscus discolor</i>
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	<i>ndhF</i> sequence—MP = 196,200 MPT (L = 815, CI = 0.71, COI = 056, RI = 0.86). ITS sequence—MP = 49,200 MPT (L = 791, CI = 0.56, COI = 0.45, RI = 0.70)
Characters or bp (no.)	Combined data set = 771 bp	
Informative characters (no.)	ITS = 178 bp, <i>trnL-trnF</i> = 50 bp, and <i>trnS-trnG</i> = 142 bp	
Indels (no.)	Combined data set = 3	
Substitutions (no.)		
Inversions (no.)		
PIC	ITS = 178 bp, <i>trnL-trnF</i> = 50 bp, and <i>trnS-trnG</i> = 142 bp	
Percent variability		
Phylogeny in classification	Three clades were reported: “Clade A” with subgenera <i>Padus</i> and <i>Laurocerasus</i> ; “Clade B” with subgenera <i>Amygdalus</i> , <i>Emplectocladus</i> , and <i>Prunus</i> ; and “Clade C” with subgenera <i>Cerasus</i> . “Clade B” was characterized by the production of three axillary buds. <i>Padus</i> and <i>Laurocerasus</i> were not supported as monophyletic (highly homoplasy)	Both data set identified genus <i>Prunus</i> as a monophyletic group. Both data sets were incongruent at the species level in <i>Prunus</i> . The <i>ndhF</i> data supported two major groups: subgenera <i>Laurocerasus</i> (including <i>Pygeum</i>) and <i>Padus</i> , and subgenera <i>Amygdalus</i> , <i>Cerasus</i> , and <i>Prunus</i> . The ITS data supported a clade composed of subgenera <i>Amygdalus</i> , <i>Prunus</i> , and <i>Cerasus</i> sect. <i>Microcerasus</i> , and the paraphyletic clade of <i>Padus</i> and <i>Laurocerasus</i>
Paper	Depypere et al. [33]	Chavez et al. [39]
Phylogenetic analysis	Morphology and molecular	Molecular
Analytical methods	UPGMA, PCo, and BI	MP and ML

Paper	Depypere et al. [33]	Chavez et al. [39]
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
Taxa (no.)/subgenus (sect.)/genus	A total of 82 accessions/5 species: <i>P. cerasifera</i> , <i>P. domestica</i> , <i>P. insititia</i> , <i>P. spinosa</i> , and <i>P. × fruticans</i> ,	A total of 8 species: <i>P. americana</i> , <i>P. angustifolia</i> , <i>P. hortulana</i> , <i>P. mexicana</i> , <i>P. munsoniana</i> , <i>P. geniculata</i> , <i>P. maritima</i> , <i>P. umbellata</i>
Outgroups		<i>P. fasciculata</i> , <i>P. persica</i> , and <i>P. pumila</i>
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.
Characters or bp (no.)		Combined data set = 27,623 bp
Informative characters (no.)		1594
Indels (no.)		
Substitutions (no.)		
Inversions (no.)		
PIC		
Percent variability		
Phylogeny in classification	PCoA and AFLP of three distinct clusters. A first cluster consists of all <i>P. cerasifera</i> samples and the sole <i>P. cocomilia</i> . A second cluster includes all individuals of <i>P. domestica</i> and <i>P. insititia</i> . A third cluster comprises all <i>P. spinosa</i> and <i>P. × fruticans</i> samples	The American and the Chickasaw clades were identified. An outgroup clade was comprised by <i>P. persica</i> and <i>P. fasciculata</i>
Notes	Low number of <i>Prunus</i> species for sampling	Identified multiple gene regions that provided the greatest number of characters, variability, and improved phylogenetic signal at the species level in <i>Prunus</i> section <i>Prunocerasus</i>

^aPIC = total indels + nucleotide substitutions + inversions. Percent variability = PIC/characters or bp.
PIC = potentially informative character.

Table 2.
Summary of *Prunus* phylogenetic studies.

Endocarp and leaf morphometrics combined with AFLP markers were used to study the morphological and genetic variation of five European members of section *Prunus*: *P. cerasifera*, *P. cocomilia* Ten., *P. domestica*, *P. insititia* L., *P. spinosa* L., and *P. × fruticans* [33]. Three clusters were reported: a first cluster *P. cerasifera*-*P. cocomilia*, a second *P. domestica*-*P. insititia*, and a third *P. spinosa* and *P. × fruticans*.

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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