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Capsicum—An Abbreviated Compendium

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Abstract. Pepper (*Capsicum* L.) is a major vegetable and spice crop worldwide. Global production of both fresh and dried fruit continues to increase steadily in terms of area harvested and yield. Various topics are addressed in this review, including recent additions to and clarification of *Capsicum* taxonomy, genetic resources of *Capsicum*, cytogenetic studies, the current status of our understanding of the mechanisms affecting the biosynthesis of capsaicinoids, the use of gene mutations to elucidate carotenoid biosynthetic pathways and their regulation, and recent advances in whole-genome sequencing and assembly.

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Archaeological data allude to the use of *Capsicum* species (pepper, chilies) as a spice as early as 5500 BCE (Basu and De, 2003; Davenport, 1970). The crop was first introduced into Europe by Christopher Columbus during his travels in the 15th century. It later spread to countries in Africa and Asia by way of the trade routes operating at that time (Andrews, 1992). The fruit was traded initially as black pepper (*Piper nigrum* L.), a species with its own unique form of pungency but otherwise dissimilar in appearance and taxonomically unrelated to *Capsicum* (Gordo et al., 2012). For this reason, cultivated *Capsicum* acquired the common name "pepper." Early imported cultivars were likely forms of *C. chinense* Jacq. (Scotch Bonnet, Habanero, etc.), which were favored for consumption at that time (Walsh and Hoot, 2001). The flourishing trade routes of Spain and Portugal facilitated the spread of pepper around the globe, where it was quickly adopted (Davenport, 1970) and served as a spice for those parts of the population that could not afford to purchase cinnamon (*Cinnamomum verum* J. Presl), nutmeg (*Myristica fragrans* Houtt.), or other spices that were used for seasoning and/or preserving food (Lauden, 2013).

Asia currently contributes ≈65% of the global production of pepper, whereas the Americas, Europe, Africa, and Oceania each contribute 13.3%, 11.9%, 10.1%, and 0.2%, respectively. The increasing value of the pepper crop coincides with its role in international trade [Table 1 (FAO, 2017)]. However, the genetic variability within the genus *Capsicum* manifests itself in its ability to acclimate and produce a crop in a wide range of environments (Pickersgill, 1997). This is reflected in the number of countries in which it is produced. Fresh pepper is cultivated in ≈126 countries and dried pepper in ≈70 countries [Figs. 1 and 2 (FAO, 2017)]. Although developed countries continue to be the main producers of the pepper crop, its cultivation provides an important source of income for small producers in many developing countries where production is increasing (FAO, 2017). The estimated (global) value of the fresh and dried pepper crops in 2016 was ≈$30 billion and ≈$3.8 billion, respectively (FAO, 2017).

Taxonomy

In the last few years, our understanding of the genus *Capsicum* and its member species has increased considerably as a result of the many published studies on the genus' systematics, karyology, reproductive biology, and phylogeny. In the phylogenetic reconstructions of Solanaceae by Olmstead et al. (2008) and Särkinen et al. (2013), *Capsicum* and its sister taxon *Lycianthes* (Dunal) Hassl. have been recognized as the only members of the tribe Capsiceae (Solanoideae).

Progress has been made in the delimitation of some species, the addition of new species (Baral and Bosland, 2004; Barboza, 2011; Barboza and Bianchetti, 2005; Barboza et al., 2011; Bosland and González, 2000; Carrizo García et al., 2013; Nee et al., 2006), and the clarification of some nomenclatural problems (Barboza, 2011; Knapp et al., 2015). Molecular phylogenetic analyses have contributed to the understanding of species relationships (Jarret and Dang, 2004; Walsh and Hoot, 2001). However, the most comprehensive phylogeny that includes the majority of the currently recognized *Capsicum* species (based on the molecular markers *matK*, *psbA-trnH*, and

Fig. 1. Paprika drying in the sun at Cerro Prieto, Peru, in 2006 (upper). Paprika drying in the sun at Urumqi, China, in 2014 (middle). Dried chilies for sale in an open market in Hyderabad, India, in 2015 (lower).

Table 1. The 10 largest exporters of sweet and chili pepper, crop value, and production, in 2017.[z]

Exporting country	Value (million $)	Production (% world total)
Spain	1140	22.4
Netherlands	1100	21.6
Mexico	985	19.4
Canada	353	6.9
USA	232	4.6
Morocco	155	3.0
Israel	106	2.1
Turkey	96	1.9
South Korea	91	1.8
China	82	1.6

[z]Workman (2018).

Fig. 2. Half-long bell pepper harvest in Culiacan, Sinaloa, Mexico in 2014 (upper). Red bell peppers being sorted on a packing line in Hermosillo, Mexico, in 2016 (middle). Aerial view of 40,000 acres of plastic houses in the Almeria province (lower left); Almeria pepper greenhouse Almeria, Spain, in 2011 (lower right).

waxy), is that presented by Carrizo García et al. (2016), in which *Capsicum* forms a monophyletic clade with *Lycianthes* as a sister group. Eleven well-supported clades (four of them monospecific) are recognized: Andean, Caatinga, Flexuosum, Bolivian, Longidentatum, Atlantic Forest, Purple Corolla, Pubescens, Tovarii, Baccatum, and Annuum (Fig. 3). The Andean and the Atlantic Forest clades display the greatest species richness and therefore deserve special comments.

Andean clade. This clade consists of at least six species native to the Andes of northwestern South America and Central America. These species (Table 2) include *C. rhomboideum* (Dunal) Kuntze, *C. lanceolatum* (Greenm.) Morton & Standl., *C. geminifolium* (Dammer) Hunz. (incl. *C. scolnikianum* Hunz.), *C. dimorphum* (Miers) Kuntze, *C. lycianthoides* Bitter, *C. hookerianum* (Miers) Kuntze, and another two to three as-yet undescribed species from Peru and Ecuador. Species in this clade are characterized by leaves strongly anisophyllous (Fig. 4A, C, and D), nongeniculate pendent flowering pedicels (Fig. 4B), rotate (Fig. 4B) to campanulate (Fig. 4G) or funnel-shaped, yellow to ochre corollas (except in *C. lanceolatum*), orange–red or red nonpungent fruit (Fig. 4B, E, F, and G), a smooth pericarp (giant cells absent in the innermost pericarp), the presence of stone cells, mostly blackish brown seeds (G.E. Barboza, unpublished data), and by a base chromosome number $n = x = 13$ (Moscone et al., 2007; M.A. Scaldaferro, unpublished data). *Capsicum lanceolatum* is easily recognized by having only one to two axillary flowers, corollas that are white or yellowish–white with purple lines, and found growing only in Mexico and Central America (Table 2). *Capsicum rhomboideum* (Fig. 4B) has one of the most extensive distributions in the genus (Mexico to Peru) and is morphologically variable in its indumentum (abundance and type of hairs) but with a consistently yellow campanulate corolla and generally more than 10 axillary flowers. *Capsicum dimorphum* has toothless (or with two to three tiny teeth) calyx (Fig. 4F) in comparison with the three to five long subulate calyx teeth of *C. geminifolium* and *C. lycianthoides* (Fig. 4G). These latter three species have a more restrictive distribution (Colombia, Ecuador, and Peru) inhabiting the montane moist forests. Finally, *C. hookerianum* (Fig. 4E) is very peculiar for its calyx with 10 unequal linear teeth and is the only extra-Andean species in the clade growing in low altitudes and in drier environments. The Andean clade is strongly divergent from the rest of the genus, as evident in the most recent phylogenetic reconstruction (Carrizo García et al., 2016; G.E. Barboza, unpublished data).

The Atlantic Forest clade. This clade includes 10 to 11 species endemic to the Brazilian Atlantic Forest, particularly to the coastal rainforests (Table 2): *C. campylopodium* Sendtn., *C. cornutum* (Hiern) Hunz., *C. friburgense* Bianch. & Barboza, *C. hunzikerianum* Barboza & Bianch., *C. mirabile* Mart. ex. Sendtn., *C. pereirae* Barboza & Bianch., *C. recurvatum* Witasek, *C. schottianum* Sendtn., *C. villosum* Sendtn., and one to two undescribed species (G.E. Barboza, unpublished data). These species are shrubs or small trees, characterized mostly by their plagiotropic habitat (Fig. 5A), geniculate erect pedicels at anthesis (Fig. 5B, D, and E), stellate white corollas with different color spot patterns (Fig. 5D and E), with the exception of *C. friburgense* (Fig. 5B) greenish–golden or yellow scarcely pungent or nonpungent fruit at maturity (Fig. 5C), alveolate pericarp (giant cells in the innermost pericarp), absence of stone cells, blackish brown seeds (G.E. Barboza, unpublished data), and a base chromosome number of $n = x = 13$ (Moscone et al., 2007; Pozzobon et al., 2006; M.A. Scaldaferro, unpublished data). *Capsicum friburgense* (Fig. 5B) is unique in the group for its campanulate entirely pink or lilac corolla and is confined to a small area in Nova Friburgo (Rio de Janeiro), Brazil. Other species in this group peculiar for their morphology or habitat are *C. pereirae*, which is the only species with coriaceous leaves and nongeniculate pendent pedicels at anthesis. It inhabits shady areas with high environmental humidity in southeastern Brazil [Carrizo García et al., 2013 (Table 2)]. *Capsicum cornutum*, *C. villosum*, and some populations of *C. recurvatum* (Fig. 5F) share a dense pubescence of long nonglandular trichomes on leaves, pedicels, and calyces, all of them restricted primarily to southeastern Brazil (Table 2). *Capscium recurvatum* has 5 to 10 unequal, mainly recurved calyx teeth and stellate corollas with interior greenish

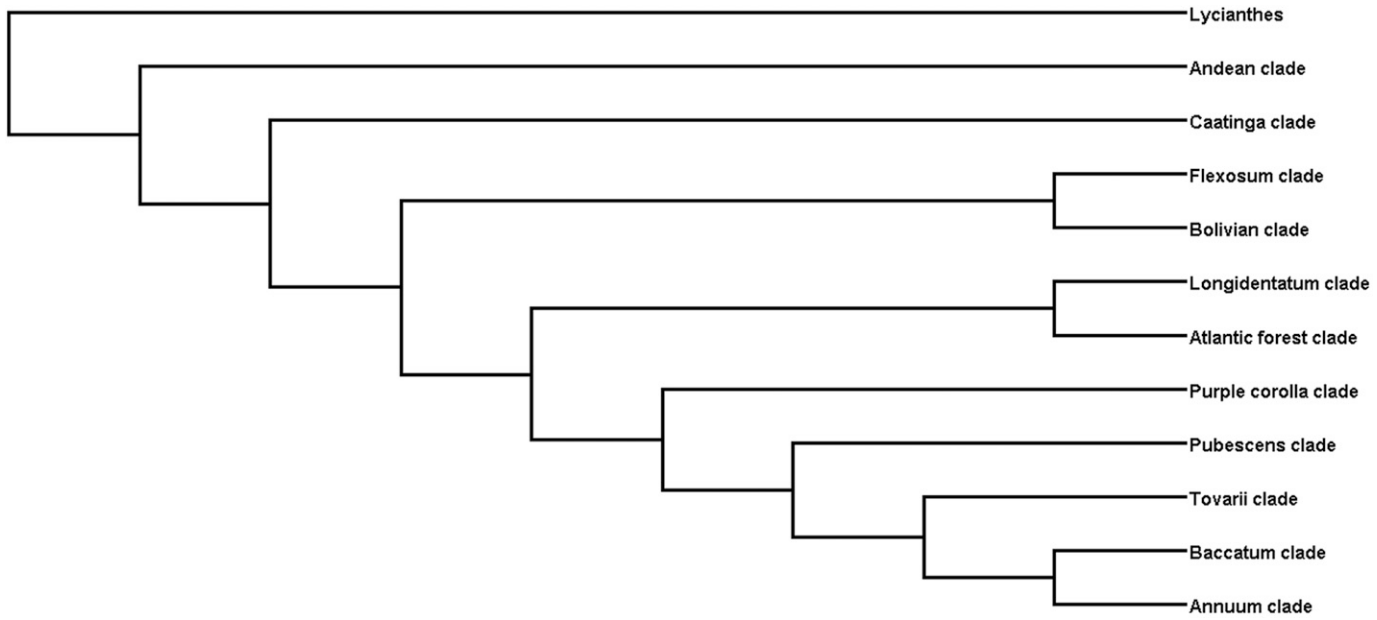

Fig. 3. Dendrogram adapted from Carrizo García et al. (2016) and Spalink et al. (2018) showing proposed taxonomic relationships among *Capsicum* species and *Lycianthes*.

yellow spots, whereas *C. cornutum* has up to 10 long but not recurved calyx teeth, rotate-stellate white corollas with purple or maroon interior spots. *Capsicum villosum* has only five shorter calyx teeth and white corollas with purple pigmentation inside. *Capsicum mirabile* and *C. hunzikerianum* (Fig. 5D and E) are not sympatric species (Table 2) and are characterized by the glabrate indument and the purple spots in the corolla. *Capsicum mirabile* has narrow elliptic leaves and calyces with five teeth, in comparison with *C. hunzikerianum*, where the leaves are ovate and the calyx teeth vary from 6 to 10. *Capsicum campylopodium* and *C. schottianum* have toothless calyces and differ in the corolla pigmentation—the first species with yellow or golden spots in the lobes and limbs and *C. schottianum* with noticeable purple spots to absent.

In regard to the recognized monospecific clades Flexuosum (Fig. 5G and H), Longidentatum, Pubescens, and Tovarii, their placement within the genus is not yet strongly resolved (Carrizo García et al., 2016). The case of *C. pubescens* Ruiz & Pav. is particularly interesting. This species is known only as a cultigen (grown mainly in Bolivia, Peru, and northwestern Argentina) whose origin remains unclear. This and many other issues are subjects to be addressed using recent advances in DNA sequencing and data analysis that permit a broader examination of polymorphic markers across the entire genome (C. Carrizo García, unpublished data).

Genetic Resources of *Capsicum*

Genebanks are viewed as the providers of the raw materials upon which crop improvement activities often depend. Collections of pepper germplasm are available to provide seed of various fruit and plant types and taxa for crop improvement and related research activities. Two of the largest collections of *Capsicum* germplasm are those of the World Vegetable Center (WVC, Tainan, Taiwan) and the U.S. Department of Agriculture (USDA) in Griffin, GA. In addition to the WVC and the USDA, other notable collections are maintained in Costa Rica, Mexico, Brazil, The Netherlands, and Germany (Berke and Engle, 1997; Bettencourt and Kopoka, 1990).

The Asian Vegetable Development and Research Center [AVRDC (now WVC)] recognized *Capsicum* species as one of the center's principal crop groups in 1986. At the time, the AVRDC collection held 286 accessions of *Capsicum*. In the years following, the collection rapidly expanded in size. *Capsicum* was first introduced into the U.S. National Plant Germplasm System as early as the mid-1930s, and the collection was ultimately assigned to the USDA genebank in Griffin, GA, which became operational in 1949. Maintenance activities at both locations are similar and involve regeneration in the field and greenhouse using pollination control measures. Facilities for cryopreservation are available at the WVC. Backup samples (98%) of accessions in Griffin are stored off-site at the National Laboratory for Genetic Resource Preservation in Fort Collins, CO, where cryopreservation facilities are also available.

The WVC and the USDA currently maintain active collections of 8264 and 4953 accessions, respectively (Table 3). These numbers include those accessions that are currently unclassified. In both instances, more than 99% of the classified materials are domesticated taxa that include *C. annuum* L., *C. baccatum* L., *C. chinense*, *C. frutescens* L., and *C. pubescens.* *Capsicum annuum* is the dominant taxon in both collections. *Capsicum pubescens* is only marginally represented, and crop wild relatives constitute only a fraction of a percent of the total holdings in either collection. Accessions in the WVC and the USDA collections represent materials acquired from more than 100 countries.

Characterization and evaluation data, passport data, and digital images of genebank holdings are available in the Genetic Resources Information Network (GRIN, 2018), and the WVC Genetic Resources Information System (WVC, 2018) databases. Data typically include information such as fruit and plant morphological characteristics, disease and pest resistance/susceptibility characteristics, fruit quality attributes,

Table 2. Wild relatives of the cultivated *Capsicum* species, recognized and/or proposed.

Taxon	Geographic range[z]	Chromosomes (no.)[y]	Clade[x]	Description reference
C. buforum Hunz.	Br	13[2]		Hunziker, 1969
C. caballeroi M. Nee	Bo	?	Bolivian	Nee et al., 2006
C. campylopodium Sendtn.	Br	13	Atlantic Forest	Sendtner, 1846
C. cardenasii Heiser & Smith	Bo	12	Purple Corolla	Heiser and Smith, 1958
C. caatingae Barboza & Agra	Br	12	Caatinga	Barboza et al., 2011
C. ceratocalyx M. Nee	Bo	?	Bolivian	Nee et al., 2006
C. chacoense Hunz.	Ar, Bo, Ch, Pa	12	Baccatum	Hunziker, 1950
C. coccineum (Rusby) Hunz.	Bo, Pe	?	Bolivian	Hunziker, 1956
C. cornutum (Hiern) Hunz.	Br	13	Atlantic Forest	Hunziker, 1961
C. dimorphum (Miers) Kuntze	Co, Ec. Pe	?	Andean	Kuntze, 1891
C. eshbaughii Barboza	Bo	?	Purple Corolla	Barboza, 2011
C. eximium Hunz.	Ar, Bo	12	Purple Corolla	Hunziker, 1950
C. flexuosum Sendtn.	Ar, Br, Pa	12	Flexuosum	Sendtner, 1846
C. friburgense Bianch. & Barboza	Br	?	Atlantic Forest	Barboza and Bianchetti, 2005
C. galapagoense Hunz.	Ec	12	Andean	Hunziker, 1956
C. geminifolium (Dammer) Hunz.	Co, Ec, Pe	13	Andean	Hunziker, 1956
C. hookerianum (Miers) Kuntze	Ec, Pe	?		Kuntze, 1891
C. hunzikerianum Barboza & Bianch.	Br	?	Atlantic Forest	Barboza and Bianchetti, 2005
C. lanceolatum (Greenm.) Morton & Standl.	Gu, Me	13	Andean	Morton and Standley, 1940
C. longidentatum Agra & Barboza	Br	12	Longidentatum	Barboza et al., 2011
C. lycianthoides Bitter	Col, Ec, Pe	?		Bitter, 1921
C. minutiflorum (Rusby) Hunz.	Br	?	Bolivian	Hunziker, 1956
C. mirabile Mart. ex. Sendtn.	Br	13	Atlantic Forest	Sendtner, 1846
C. parvifolium Sendtn.	Br, Co, Ve	12	Caatinga	Sendtner, 1846
C. pereirae Barboza & Bianch.	Br	13	Atlantic Forest	Barboza and Bianchetti, 2005
C. praetermissum Heiser & P.G. Sm.	Br, Pa	12		Heiser and Smith, 1958
C. recurvatum Witasek	Br	13	Atlantic Forest	Witasek JA, 1910
C. rhomboideum (Dunal) Kuntze	Co, Ec, Me, Gu, Pe, Ho, Ve	13	Andean	Kuntze, 1891
C. schottianum Sendtn.	Br	13	Atlantic Forest	Sendtner, 1846
C. scolnikianum Hunz.	Ec, Pe	13	Andean	Hunziker, 1961
C. tovarii Eshbaugh, P.G.Sm. & Nickrent	P	12	Tovarii	Eshbaugh et al., 1983
C. villosum Sendtn.	Br	13	Atlantic Forest	Sendtner, 1846

[z]Argentina (Ar), Brazil (Br), Bolivia (Bo), Chile (Ch), Colombia (Co), Cuba (Cu), Ecuador (Ec), Guatemala (Gu), Honduras (Ho), Mexico (Me), Paraguay (Pa), Peru (Pe), Venezuela (Ve).
[y]Carrizo García et al., 2016; Pozzobon et al., 2006.
[x]Carrizo García et al., 2016.

photographs of plants or plant parts, etc. The diversity within *Capsicum* germplasm also has been examined using molecular markers and other approaches (Table 4). Many published studies of these types examined a relatively small number of the accessions/populations available from the existing genebank collections, indicating that much remains to be done in terms of fully evaluating/characterizing *Capsicum* genetic resources. An accurate estimate of the global genetic diversity of *Capsicum*, or that within individual taxa, remains to be determined.

Capsicum Cytogenetics

Polyploidy can be induced in *Capsicum* (Kulkarni and Borse, 2010; Kumar and Raja Rao, 2003; Pal and Ramanujam, 1939; Panda et al., 1984) but is otherwise rare. Pickersgill (1977) and Jha et al. (2012) both described what they believed to be natural tetraploids. Molecular characterization of the cultivar Dalle Khursani, a perennial shrub from West Bengal, India, confirmed it as an allotetraploid rich in GC heterochromatin (Jha et al., 2017). This cultivar differed at the cytomolecular and morphological levels from the diploid species of the *C. annuum* complex (*C. annuum*, *C. chinense*, and *C. frutescens*), leading the authors to hypothesize that it is a natural interspecific hybrid. Further analysis using fluorescent in situ hybridization (FISH) and genomic in situ hybridization is expected to facilitate the identification of the parental species (Jha et al., 2017).

The most common use of FISH in *Capsicum* has been in efforts to identify and characterize 5S and 18S-5.8S-26S (45S) rDNA sites, although the location and copy number of other DNA sequences also can be identified using this methodology. Earlier physical mapping of the rDNA sequences in *Capsicum* species (Kwon and Kim, 2009; Park et al., 1999, 2000; Scaldaferro et al., 2006, 2016) detected chromosome homeologies and indicated a common ancestor of the species in the *C. annuum* complex, validating the species–complex proposed by Pickersgill (1991) and Zijlstra et al. (1991). FISH also was performed to verify a reciprocal translocation between chromosomes 1 and 8 in *C. frutescens* and *C. annuum* (Park et al., 2014). The number and localization of rDNA sites of some *Capsicum* species are presented in Table 5. This table also presents genome sizes of 14 *Capsicum* species as estimated by flow cytometry. Small differences in DNA content were found

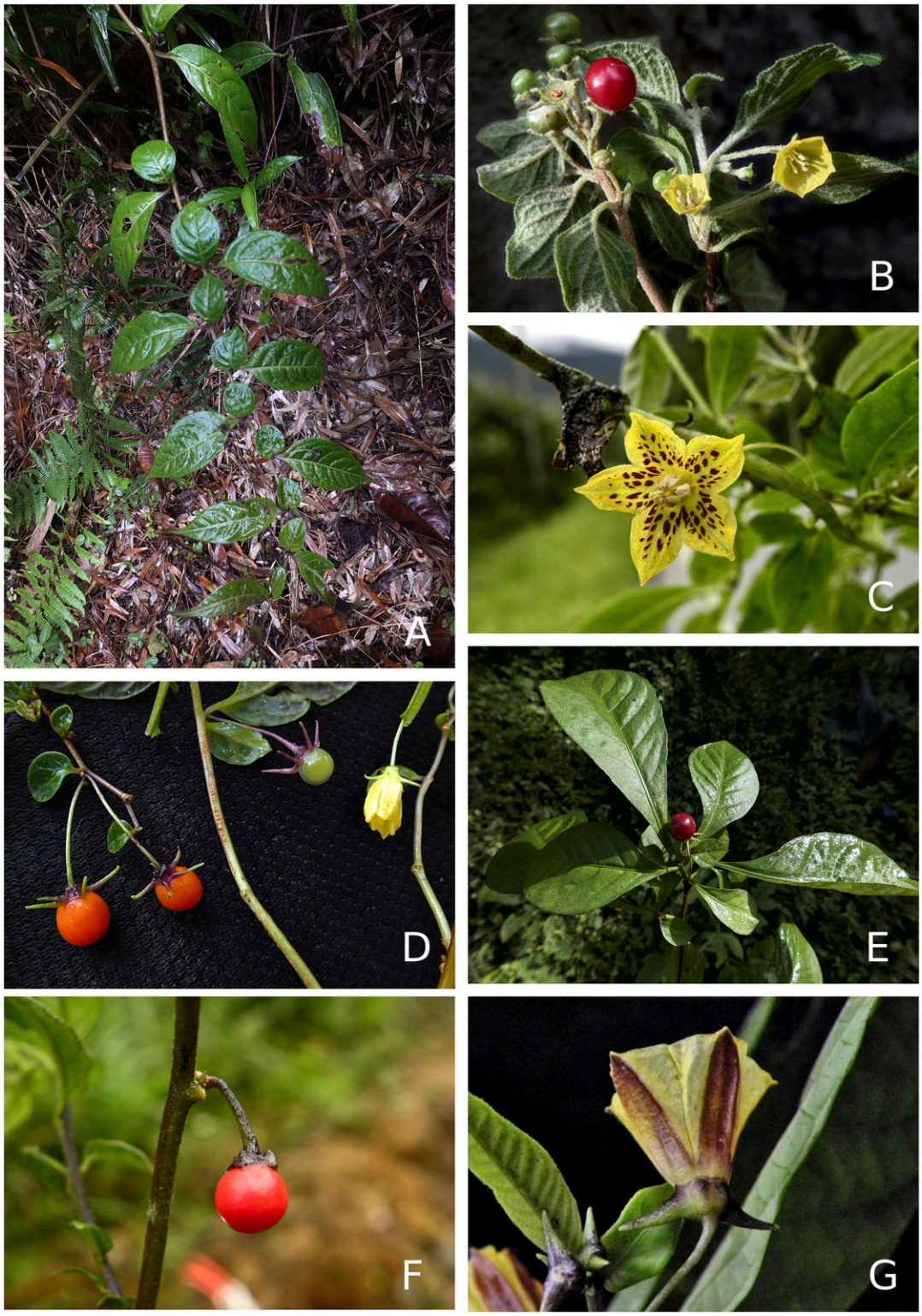

Fig. 4. Andean Clade species. (**A**, **C**, **D**) *Capsicum geminifolium*. (**B**) *C. rhomboideum*. (**E**) *C. hookerianum*. (**F**) *C. dimorphum*. (**G**) *C. lycianthoides*.

between analyses (within species). DNA content (2C) values varied from ≈3.91 pg in *C. rhomboideum* to 9.72 pg in *C. pubescens* (Belletti et al., 1998; Moscone et al., 2003). Analysis of DNA content and characterization of 5S and 18S-5.8S-26S (45S) rDNA sites has yet to be conducted with many *Capsicum* species.

Capsicum disploidy (i.e., the presence of two basic chromosome numbers in the genus *Capsicum*) is an interesting feature to be more closely examined in relation to genome size evolution and species diversification. Rates of genome size evolution (not strictly genome size) have been found to be positively correlated with diversification rates in angiosperms

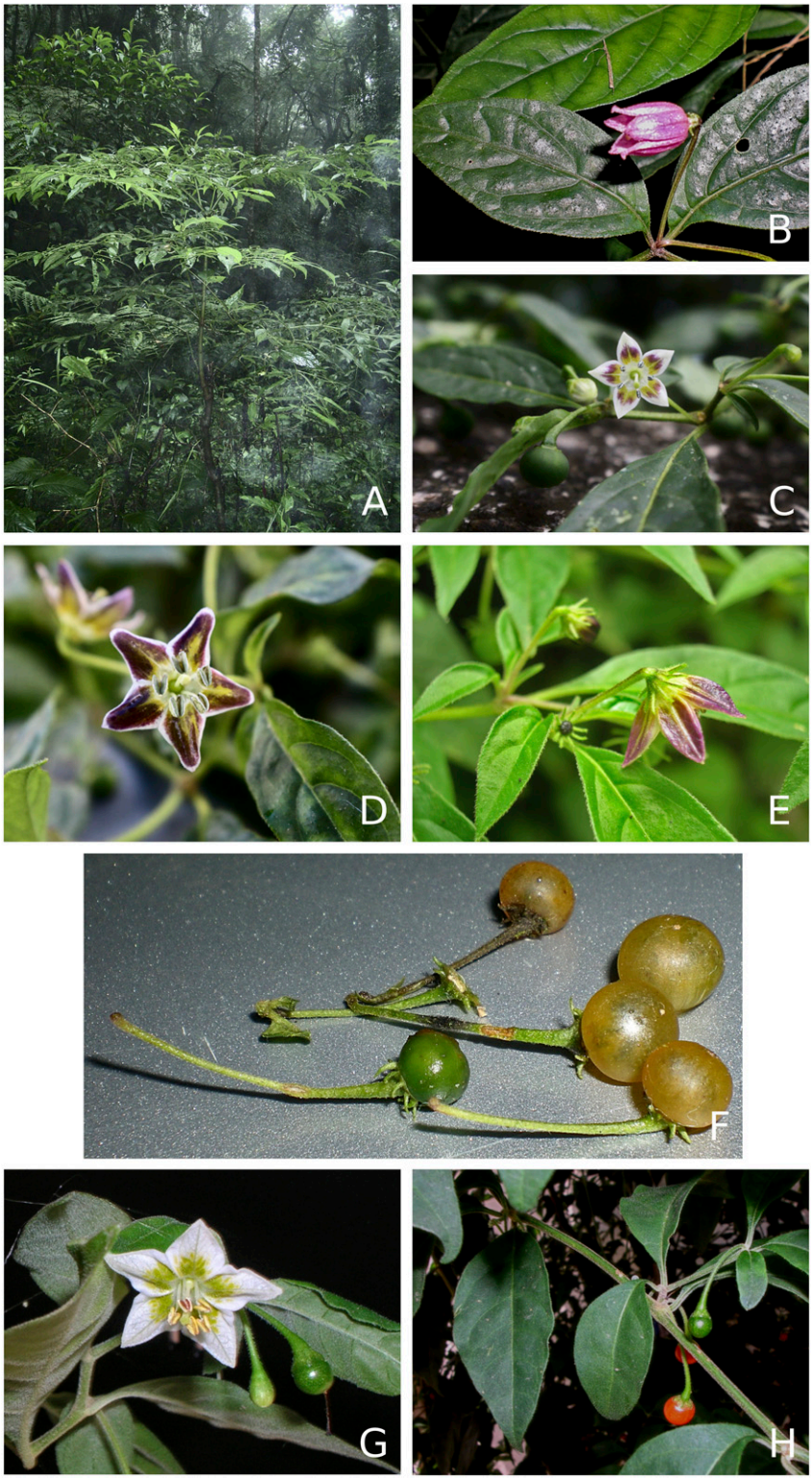

Fig. 5. Atlantic Forest and Flexuosum Clade species. (**A**) *Capsicum campylopodium*. (**B**) *C. friburgense*, (**C**) *C. schottianum*. (**D**, **E**) *C. hunzikerianum*. (**F**) *C. recurvatum*. (**G, H**) *C. flexuosum*.

(Puttick et al., 2015). The chromosome number x = 12 is dominant across all the *Capsicum* clades recognized, whereas the x = 13 taxa are restricted to two clades (Andean and Atlantic Forest). However, the latter two clades are the more speciose and include almost one-half of *Capsicum* wild species. Genome size is highly variable between *Capsicum* species (Moscone et al., 2003), although information is still lacking for many species/clades (e.g., Andean clade). Qin et al. (2014) determined that more than 81% of the *C. annuum* genome was composed of transposable elements. The activation of transposable elements can generate significant changes in the genome upon which evolutionary forces can work. This is particularly of interest in regard to these elements as promoters of genome size changes in the genus.

Species with 12 chromosome pairs have more symmetrical karyotypes than those with 13 pairs. Some data indicate that the latter group is derived from the former (Moscone et al., 1993, 1995, 1996, 2007; Pickersgill, 1991; Scaldaferro et al., 2013; Tong and Bosland, 2003). However, the opposite scenario has also been proposed by Pozzobon et al. (2006), who hypothesized that $x = 13$ is the basic ancestral chromosome number of the genus and that the reduction in chromosome number is the result of the loss of the small 13th chromosome pair. The origin and fate of the 13th chromosome pair is not known. However, the occurrence of $2n = 13$ taxa in clades separated by $2n = 12$ taxa (Carrizo García et al., 2016) suggests that the extra chromosome(s) arose and/or was lost on more than a single occasion.

It is conceivable that two $2n = 26$ subgroups with asymmetrical karyotypes have arisen via centric fission. The first of these $2n = 26$ groups is composed of *C. lanceolatum* and *C. rhomboideum*, which have smaller genomes (Table 5), single heterochromatic banding patterns, and one nucleolar organizer region (NOR) per haploid complement. The second group contains *C. mirabile* as the core species and also includes *C. campylopodium*, *C. cornutum*, *C. friburgense*, *C. pereirae*, *C. recurvatum*, *C. schottianum*, and *C. villosum*. These taxa have larger genomes and rich heterochromatic regions with complex banding patterns. They also contain AT-rich, GC-rich, and moderately GC-rich satellite DNA in addition to one or two NORs. The 13th chromosome pair shows distinctive characteristics among the subgroups. Previous morphological characterization and geographical distribution data of some wild Brazilian species (Barboza and Bianchetti, 2005; Bianchetti, 1996; Bianchetti et al., 1999) support this theory.

Capsaicinoids: The "Heat"

Capsaicinoids are compounds unique to the genus *Capsicum* and are responsible for the pungency of pepper fruit (Nelson, 1919). Aside from their value as a spice (Bosland and Votava, 1999), capsaicinoids have well-established medicinal and antimicrobial properties (Emanuela et al., 2015; Khan et al., 2014; Surh

and Lee, 1995) and affect seed dispersal and survival (Nabhan and Tewksbury 2001; Tewksbury et al., 2008). Capsacinoids are normally synthesized and accumulated in the epidermal cells of the placental tissue of the fruit (Arce-Rodríguez and Ochoa-Alejo, 2015, 2017) but also have been detected in other tissues or organs in some cultivars (Bosland et al., 2015; Noichinda et al., 2016; Tanaka et al., 2017). Advances in the understanding of the molecular biology of the capsaicinoid biosynthetic pathway often have focused on the identification of new candidate genes, the characterization of some key previously identified genes, and the exploration of possible mechanisms of regulation.

In most pungent pepper fruit, capsaicinoids follow a characteristic accumulation pattern in which pungency is detectable at 20 d post-anthesis (DPA), reaches a peak at 30 to 40 DPA, followed by a decrease in fully mature fruit (Arce-Rodríguez and Ochoa-Alejo, 2015, 2017; Barbero et al., 2014). This is also true for genotypes that accumulate nonpungent analogs (Jarret et al., 2014). However, not all genotypes follow this pattern (Barbero et al., 2016; Nagy et al., 2015; Noichinda et al., 2016). The characteristic decrease of capsaicinoids in mature fruit has been attributed to their colocalization with peroxidases, which have a known capacity for degrading capsaicin and dihydrocapsaicin (Ruiz-Lau et al., 2011; Zamudio-Moreno et al., 2014). Alternatively, it has been attributed to the diversion of precursors and intermediaries in the phenylpropanoid pathway that are shared between capsaicinoids and lignins in the fruit (Arce-Rodríguez and Ochoa-Alejo, 2017; Díaz et al., 2004; Estrada et al., 2000). Zhang et al. (2016b) have proposed the most current model of the capsaicinoid biosynthetic pathway that identified intermediary metabolites and enzymatic steps based on both new and previously reported data (Aza-González et al., 2011; Mazourek et al., 2009; Stewart et al., 2005).

RT-qPCR and RNA-seq have revealed the differential expression of many structural genes in *Capsicum* fruit. The expression patterns (transcript levels) of some genes positively correlated with capsaicinoid content have been reported by Arce-Rodríguez and Ochoa-Alejo (2017), Keyhaninejad et al. (2014), Martínez-López et al. (2014), and Tanaka et al. (2017). The analysis of quantitative trait loci (QTL) also has been useful in identifying candidate genes that participate in the capsaicinoid biosynthetic pathway (Han et al., 2016, 2018). For example, Yarnes et al. (2013) identified 12 QTLs associated with capsaicinoids, six of which had been reported previously (Ben-Chaim et al., 2006). However, none of these studies found the QTL *cap*, which was proposed to be a regulatory or structural gene in the pathway (Blum et al., 2003). Liu et al. (2013) predicted three new structural enzymes, dihydroxyacid dehydratase, threonine deaminase, and prephenate aminotransferase, based on their RNA-seq analysis of *C. frutescens* fruit that compared gene expression in pericarp and placental tissues. More recently, Zhang et al. (2016b) identified 20 candidate genes involved in the capsaicinoid biosynthetic pathway using RNA-seq and digital gene expression analysis.

Transcriptome analysis in *Capsicum* has been used to examine gene expression during plant and fruit development (Li et al., 2016; Martinez-Lopez et al., 2014) as well as

Table 3. Genetic resources of *Capsicum* species (domesticated, wild, and unclassified) maintained by the World Vegetable Center (WVC, Tainan, Taiwan) and the U.S. Department of Agriculture (USDA, Washington, DC).

		Accessions (no.)	
Category	Taxon	WVC	USDA
Domesticated			
	C. annuum L.	5489	3417
	C. baccatum L.	388	383
	C. chinense Jacq.	505	483
	C. frutescens L.	741	280
	C. pubescens Ruiz & Pav.	30	78
	Subtotal	7153	4641
Wild	*C. chacoense* Hunz.	25	20
	C. praetermissum Heiser & P.G. Sm.	9	3
	Miscellaneous	10	12
	Subtotal	1111	312
Unclassified		1067	277
	Total	8264	4953

Table 4. Reports on the characterization and/or evaluation of *Capsicum* germplasm.

Principle objective/result	Reference
Evaluation of chemical profile and antioxidant activity in *C. annuum* cultivars	Loizzo et al., 2015
Phenotyping of *Capsicum* species from Bolivia and Peru	van Zonneveld et al., 2015
Orthologous analysis of *C. annuum* cultivars	Ahn et al., 2016
AFLP analysis of 71 Brazilian *C. chinense* accessions	Baba et al., 2016
Variation in vitamin content in *Capsicum* species	Kantar et al., 2016
Profiling of carotenoids in 27 paprika (*C. annuum*) lines	Kim et al., 2016a
Selection of a *Capsicum* core collection	Lee et al., 2016
Genetic diversity and population structure in *C. annuum*	Naegele et al., 2016
Genome-wide divergence in *C. baccatum*	Nimmakayala et al., 2016
Vitamin C content and reducing sugars in 123 *C. baccatum* genotypes	Perla et al., 2016
SSR analysis of 26 landrace-derived inbred lines	Rivera et al., 2016
Diversity and population structure of Eritrean pepper	Saleh et al., 2016
Screening *Capsicum* species for pharmacological properties	Shaimaa et al., 2016
Variation in chemical composition of oleoresin from different cultivars	Sricharoen et al., 2017
SNP discovery and population structure analysis in *C. annuum*	Taranto et al., 2016
SSR analysis of 372 *C. chinese* cultivars and landraces of *C. annuum*	Zhang et al., 2016a
Variation in chemical composition of *C. annuum* from Tunisia	Lahbib et al., 2017
Genetic diversity and population structure in *C. chinense*	Moreira et al., 2018

AFLP = amplified fragment length polymorphism; SSR = simple sequence repeat; SNP = single-nucleotide polymorphism.

Table 5. Published values of nuclear DNA content in picograms as determined by flow cytometry, and rDNA sites (as determined by fluorescent in situ hybridization, in *Capsicum* species).

Taxon[z]	2C DNA content	rDNA sites[y]	
		5S[x]	45S
C. annuum L.	6.76[w]–7.65[v]	1 (6p)	3–4 (1–2 major)
C. annuum var. *glabriusculum* (Dunal) Heiser & Pickersgill)	7.32[u]	1 (2, 4, 5, or 6p)	1–6 (1–4 major)
C. baccatum L.	7.42[w]–8.43[v]	1 (5p[#])	15 (4 major)
C. baccatum var. *pendulum* (Willd.) Eshbaugh	7.36[w]–8.39[v]	1 (5p[#])	14 (4 major)
C. baccatum var. *umbilicatum* (Vell.) Hunz. & Barboza	7.52[w]	1 (5p[#])	13 (4 major)
C. caatingae Barboza & Agra (*C. parvifolium* Sendtn.)		11.54[w]	
C. campylopodium Sendtn.	9.06[w]–11.48[w]		
C. cardenasii Heiser & Smith	8.97[v]	1 (9p[#])	8–18 (4–6 major)
C. chacoense Hunz.	6.7[w]–7.66[v]	1 (6p)	4 (2 major)
C. chinense Jacq.	6.84[w]–8.04[v]	1 (6p)	5 (2 major)
C. eximium Hunz.	8.12[w]–8.7[v]	1 (9p)	6 (2 major)
C. flexuosum Sendtn.	14.4[u]	1 (9p[#])	14–15 (2 major)
C. frutescens L.	6.8[w]–7.94[v]	1 (5p[#])	9 (2 major)
C. praetermissum Heiser & P.G. Sm.	9.13[w]	1 (7p[#])	11–13 (2 major)
C. pubescens Ruiz & Pav.	8.94[w]–9.72[v]	1 (3p[#])	14 (12 major)
C. recurvatum Witasek		1 (3q)	4 (2 major)
C. rhomboideum (Dunal) Kuntze	4.15[u]	1 (3p)	1 (9p)
C. tovarii Eshbaugh, P.G.Sm. & Nickrent	7.93[v]	1 (9q)	8 (3 major)
C. villosum Sendtn.		1 (1p[#])	30 (2 major)

[z]Adapted from: Barboza, 2011; Barboza and Bianchetti, 2005; Barboza et al., 2011; Bianchetti 1996; Bianchetti et al., 1999; Moscone et al., 2007; Nee et al., 2006; Pozzobon et al., 2006.
[y]Scaldaferro et al., 2006, 2016.
[x]# = synteny of 5S and 45S sites; *p* = short arm, *q* = long arm.
[w]Moscone et al., 2003.
[v]Belletti et al., 1998.
[u]This publication.

capsaicinoid biosynthesis. Kim et al. (2014) and Qin et al. (2014) studied the orthologous genes of the capsaicinoid pathway via transcriptomic analyses to detect differential gene expression in pepper and tomato (*Solanum lycopersicum* L.). Significant differences in the expression levels of *BCAT*, *Kas*, and *AT3* were found, indicating that these are key genes in the pathway (Kim et al., 2014). Qin et al. (2014) analyzed the genome of pungent pepper and proposed that as many as 51 gene families were involved in the capsaicinoid biosynthetic pathway. Orthologous genes in tomato, potato (*Solanum tuberosum* L.), and arabidopsis [*Arabidopsis thaliana* (L.) Heynh.] also were described (Qin et al., (2014).

Few of the many genes reported to be involved in capsaicinoid biosynthesis have been characterized. Virus-induced gene silencing (VIGS) was used to demonstrate the participation of *Kas*, *Comt*, p*Amt*, and *AT3* in the pathway (Abraham-Juárez et al., 2008; Arce-Rodríguez and Ochoa-Alejo, 2015; Stewart et al., 2005). The silencing of these genes decreased capsaicinoid production. Gururaj et al. (2012) transformed *Nicotiana tabacum* L. callus cultures with the p*Amt* gene and generated transgenic callus lines with the capacity to produce vanillylamine. They also obtained transformed callus cultures of *C. frutescens* containing a p*Amt*-antisense binary vector and observed a significant reduction in vanillylamine. The purified pAmt enzyme exhibited the biochemical activity of vanillin transaminase (Weber et al., 2014). Ogawa et al. (2015) generated anti*Pun*1 antibodies and used them to antagonize endogenous AT3 activity. The addition of anti*Pun*1 antibodies to the in vitro assay of de novo capsaicinoid synthesis (using protoplasts from placental tissue of a pungent pepper line) inhibited the synthesis of capsaicin.

A variety of studies have proposed *AT3* as a key regulator of the capsaicinoid biosynthetic pathway. Nonfunctional *AT3* alleles are responsible for the nonpungency of some pepper cultivars (Stellari et al., 2010; Stewart et al., 2005, 2007). The association mapping of 94 accessions of *C. annuum* revealed the presence of six single-nucleotide polymorphisms (SNPs) in *AT3* that were associated with principle metabolites in the capsaicin pathway (Reddy et al., 2014). In addition, *AT3* silencing not only decreased the capsaicinoid content in pungent pepper fruit, it also reduced the expression of other capsaicinoid structural genes (*BCAT*, *Kas*, *Acl*, and p*Amt*), possibly through a negative regulatory mechanism at the transcriptional level via the accumulation of intermediates or precursors (Arce-Rodríguez and Ochoa-Alejo, 2015). The final product of the capsaicinoid biosynthetic pathway, capsaicin, suppresses the expression of *AT3*, *Pal*, *Kas*, and p*Amt* genes, indicating negative feedback regulation (Kim et al., 2009).

The loss of function of p*Amt* is associated with a loss of pungency in pungent pepper fruit. Lang et al. (2009) reported a T insertion in the p*Amt* gene that produced a stop codon (TGA) that prevents its normal translation in the cultivar CH-19 Sweet. A different p*Amt* allele, important for its enzymatic activity, was identified in the cultivar Himo, which has a SNP (T→C) substitution in the coding region of the protein that results in one amino acid substitution of cysteine by arginine in the pyrodoxal 5-phosphate binding domain (Tanaka et al., 2010a). Similarly, in the cultivar Belize Sweet, the presence of a 5-bp insertion (TGGGC) in the p*Amt* gene led to a frameshift mutation that inhibited capsaicinoid biosynthesis (Tanaka et al., 2010b). Park et al. (2015) reported a 12-bp deletion (TCTGCTGGTCTC) in exon seven, and a SNP in exon 14

(T→C substitution) in a p*Amt* allele of the nonpungent genotype S3212 of *C. frutescens*.

The expression patterns of the transcription factor genes *Erf*, *Jerf*, and *CaMYB31* were positively correlated with the capsaicinoid content and proposed as candidate genes regulating the capsaicinoid biosynthetic pathway (Arce-Rodríguez and Ochoa-Alejo, 2017; Keyhaninejad et al., 2014). In addition, a function study of *CaMYB31* by VIGS showed strong evidence of its participation as a regulator of capsaicinoid biosynthesis. Silencing it caused a reduction in capsaicin and dihydrocapsaicin contents and diminished expression levels of most of the capsaicinoid structural genes in fruit of the cultivar Tampiqueño 74 (Arce-Rodríguez and Ochoa-Alejo, 2017). QTL and genome-wide association studies recently revealed several SNPs in the structural genes *Fat* (acyl-ACP thiosterase), *4CL* (4-coumaroyl-CoA ligase), *CSE* (caffeoyl shikimate esterase), *Ca4H*, and p*Amt*, indicating that they also participate in the regulation of capsaicinoid content (Han et al., 2018).

Capsicum genotypes respond differentially to environmental and cultural factors in regard to capsaicinoid biosynthesis (Gurung et al., 2011, 2012; Meckelmann et al., 2015; Wahyuni et al., 2011). Examples are noted in Table 6 and include temperature, light, water stress, nitrogen, and phytohormones. However, some genotypes do appear to show less of a response than others to environmental influences (Gurung et al., 2012).

Carotenoids and Fruit Color

Fruit color is an extremely important characteristic in *Capsicum* (Lang et al., 2004; Paran and Fallik, 2011). The main determinants of pepper fruit color are chlorophyll, carotenoids, and anthocyanins (Aza-González et al., 2011), whereas the main determinants of the typical red color of mature fruit are the carotenoids capsanthin and capsorubin (Kumar et al., 2011). Many other types of carotenoids accumulate in the fruit during the ripening process, for example, β-carotene, violaxanthin, lutein, and zeaxanthin (Ha et al., 2007).

Hurtado-Hernandez and Smith (1985) proposed that the color of mature pepper fruit is governed by the action of the *C1*, *C2*, and *Y* loci (Hurtado-Hernandez and Smith, 1985). If dominant alleles are present at all three loci, then the ripe fruit color will be red. The *C2* locus, associated with phytoene synthase (*Psy*), is considered a major locus for orange fruit color. However, mutations in capsanthin capsorubin synthase (*Ccs*) also can lead to orange coloration. The red fruit color phenotype was found to cosegregate with the *Y* locus, and with *Ccs*, which converts antheraxanthin and violaxanthin into the red pigments capsanthin and capsorubin, respectively. The gene corresponding to the *C1* locus has not yet been identified. Rather than altering the carotenoid composition, it has been suggested that *Cl* affects the concentrations of carotenoids (Lang et al., 2004; Lefebvre et al., 1998; Li et al., 2013; Thorup et al., 2000; Wahyuni et al., 2013).

Studies using monogenic mutations (Table 7), VIGS, and mapped QTLs have been useful in efforts to decipher the genetic mechanisms that govern fruit coloration. The enzyme *Ccs* catalyzes the first step in the subpathway that synthesizes capsanthin and capsorubin from antheraxanthin and violaxanthin, respectively (Lefebre et al., 1998). Promoter analysis of *Ccs* in different orange-fruited genotypes revealed three SNPs, none of which were linked to the differing *Ccs* transcription levels. Hence, in addition to structural genes such as *Ccs* or *Psy*, other complex mechanisms contribute to the carotenoid accumulation in the fruit (Rodriguez-Uribe et al., 2011). A variant of *Ccs*, termed *ccs*, was described in a yellow-fruited cultivar by Li et al. (2013). Two mutations were detected. The first was a bp change in the coding region that resulted in a premature stop codon. The second was determined to occur in the same position as that found previously in an orange-fruited cultivar. The expression of *Ccs* was detected in both the yellow- and the orange-fruited genotypes, although its expression was lower than in red-fruited genotypes. The promoter sequence was analyzed and a 176-bp-long tandem repeat sequence was detected. Three copies of this repeat were present in *C. annuum* cultivars, and four copies were present in *C. chinense* cultivars (Li et al., 2013).

Fruit color is not associated with *Ccs* alone (Tian et al., 2015). Although red fruit coloration is dependent on a functional

Table 6. Environmental factors effecting capsaicinoid biosynthesis/accumulation in *Capsicum* fruit.

Effector	Result	Reference
Temperature	Positive correlation between elevated temperature and capsaicin content	Rahman and Inden, 2012
	Negative correlation between temperature and capsaicin content	Gurung et al., 2012
	Kas and p*Amt* display negative response to high temperature	Arce-Rodríguez and Ochoa-Alejo, 2017
Light	LED enhances capsaicin content when compared with fluorescent	Gangadhar et al., 2012
	Expression of *Kas*, p*Amt*, and *CaMYB3*1 greater in light (vs. dark)	Arce-Rodríguez and Ochoa-Alejo, 2017
Water stress	Negative effect larger on mildly pungent vs. pungent cultivars	Phimchan et al., 2012, 2014
	Water stress increased capsaicinoids in fruit of *C. chinense*	Ruiz-Lau et al., 2011; Zamudio-Moreno et al., 2014
	Activities of enzymes PAL, Ca4H, and AT3 increase under drought conditions	Phimchan et al., 2014
	Peroxidase enzyme activity decreased under drought conditions	Zamudio-Moreno et al., 2014
	Differential effect of water stress on *C. chinense* cultivars	Jeeatid et al., 2018
Nitrogen	Nitrate accumulation in fruit positively correlated with increased capsaicinoids	Monforte-González et al., 2010; Rahman and Inden, 2012
	Capsaicinoid induction (in vitro) requires primary ammonia assimilation	del Ancona-Escalante et al., 2013
Phytohormones	Positive effect of salicylic acid, and positive or negative effect of jasmonic acid on the capsaicinoid biosynthetic pathway	Gutiérrez-Carbajal et al., 2010; Altúzar-Molina et al., 2011; Rodas-Junco et al., 2013
	GA_3 and IAA effect expression of *Kas*, p*Amt* and *CaMYB31*	Arce-Rodríguez and Ochoa-Alejo, 2017

LED = light-emitting diode; PAL = phenylalanine ammonia lyase; GA_3 = gibberellic acid; IAA = idole-3-acetic acid.

Table 7. Examples of mutations affecting fruit color in *Capsicum.*

Gene	Coloration/cause	Reference
Capsanthin capsorubin synthase[z]	Yellow ripe fruit color/two-point mutations and a tandem repeat.	Li et al., 2013
	Orange ripe fruit color/*ccs-3* allele due to premature stop codon.	Rodriguez-Uribe et al., 2011
	Orange ripe fruit color/three different SNPs.	Kim et al., 2017b
Phytoene synthase[y]	Orange ripe fruit color/point mutation in *Psy* that generates a frame shift and premature translation in the recessive allele *c2*.	Kim et al., 2010
B-carotene hydroxylase[x]	Orange fruit from X-ray–induced mutant (red progenitor)/impaired gene activity due to 3′ terminal region mutation.	Petrov et al., 2013
B-carotene hydroxylase 2[w]	Orange fruit from EMS-induced mutant (red progenitor)/point mutation leads to *B*-carotene accumulation.	Borovsky et al., 2013
Arabidopsis pseudo response Regulator2-like[v]	Immature fruit color and color intensity/base change results in a stop codon in white-fruited lines.	Pan et al., 2013
Golden2 ortholog[u]	Immature fruit chlorophyll content altered/alternation of chloroplast compartment size.	Brand et al., 2014

[z]Catalyzes conversion of antheraxanthin and violaxanthin into capsanthin and capsorubin, respectively.
[y]Catalyzes the formation of phytoene from prephytoene diphosphate.
[x]Involved in xanthophyll biosynthesis.
[w]Produces *B*-cryptoxanthin and zeaxanthin.
[v]Involved in xanthophyll biosynthesis.
[u]Transcriptional activator; regulates chloroplast development.
SNP = single-nucleotide polymorphism; EMS = ethyl methane sulfate.

Ccs, other factors, such as normal expression levels of this gene during fruit color development and the existence and normal expression of additional genes such as *Psy*, lycopene-β-cyclase (*Lycb*), and β-carotene hydroxylase (*CrtZ*), are necessary for red coloration (Tian et al., 2015). Kim et al. (2017b) described a *Ccs* mutant with a nonsense mutation due resulting in a single-base insertion in the coding region. Fruit of this mutant lacked the major carotenoid capsanthin but accumulated β-carotene, lutein, and zeaxanthin in greater concentrations than the normal red-fruited cultivar. Orange peppers carrying the *Ccs* mutation can be nutritionally superior to other orange-fruited cultivars due to elevated levels of carotenoids (Kim et al., 2017b). Now, only the *Ccs*' promoter region has been examined (Gómez-García and Ochoa-Alejo, 2013; Li et al., 2013).

The gene *C2* encodes *Psy*. *Psy* is a rate-limiting enzyme in the carotenoid biosynthetic pathway (Kim et al., 2010). A point mutation was identified in a recessive allele (*c2*) in a *C. annuum* ×*C. chinenese* recombinant inbred line that resulted in both a frame shift and a premature translation termination. This indicated that the orange coloration of the fruit was due to the impaired activity of *Psy* (Kim et al., 2010).

Orange coloration also can occur as the result of induced mutation. An ethyl methane sulfate–induced, orange-fruited mutant was identified using a red-fruited cultivar as the progenitor. The mutant had a unique pattern of carotenoid accumulation when compared with the wild type in that it accumulated β-carotene. A point mutation was identified in *crtZ* in the orange-fruited mutants. Thus, this gene was considered to be responsible for the orange mutation (Borovsky et al., 2013). An additional orange-fruited induced mutant (*of*) with elevated levels of β-carotene accumulation was developed via X-ray mutagenesis of dry seeds of a red-fruited genotype. This mutation was later termed the ''orange-fruited'' trait and was found to be in the 3′-terminal region of CrtZ (Daskalov, 1986; Daskalov and Poulos, 1994; Petrov et al., 2013). This *of* mutation was transferred into several cultivars that subsequently displayed enhanced β-carotene levels at maturity. The elevated levels of β-carotene in the fruit had no detrimental effect on the concentrations of essential minerals (Tomlekova et al., 2017).

Evidence indicates that the pepper ortholog of the tomato *APRR2-like* gene acts as a regulator of fruit color and intensity. Upon sequencing genes derived from a wild-type and from a white parental line, a single-nucleotide base change resulting in a stop codon was detected. This SNP was associated with both immature fruit color and intensity (Pan et al., 2013).

Multiple gene interactions, in relation to changes in fruit color, were studied in detached fruit using VIGS. The silencing of a single or multiple genes differentially affected fruit color. When *Ccs* was silenced, the fruit color was yellow due to decreased capsanthin synthesis. Capsanthin synthesis also was reduced in the *Psy*-silenced fruit, although it was greater when compared with the *Ccs*-silenced fruit, and the resulting fruit color was orange. Fruit-carrying constructs of TRV-*Lycb* or TRV-*CrtZ* showed yellow coloration. When applied together, the resulting fruit phenotype was yellow in all silencing combinations, indicating that yellow and orange coloration are not the result of a single *Ccs* gene but are also dependent on the interactions of other genes (Tian et al., 2014). All these studies indicated that the regulation of the pathways is more complex than previously proposed.

A VIGS approach was successfully employed in the silencing of the R2R3-*MYB* transcription factor in *Capsicum* species (Kim et al., 2017a). Silencing of the *MYB* also altered *MYC* and *WD40* transcript levels in the *CaMYB*-silenced leaves. The expression of flavonoid pathway-related genes also was altered in the silenced plants (Zhang et al., 2015). Similar results were found when *Tobacco rattle virus* constructs were used for VIGS in *Capsicum eximium* Hunz. When plants were agro-infected

with TRV2-*MYB* and TRV2-*WD40* constructs, the accumulation of anthocyanins was reduced when compared with the control. This reduction included both the structural and the transcription factor genes. Plants transformed with TVR2-*MYB* constructs exhibited decreased expression of the structural genes *CHS*, *CHI*, *F3′5′H*, *DFR*, and *3GT*, whereas there was no decrease in the level of *F3H.* Those infected with the TRV2-*WD40* construct displayed reductions in *CHS*, *F3H*, *F3′5′H*, *DFR*, and *3GT* (but not in *CHI*) in their fruit (Aguilar-Barragán and Ochoa-Alejo, 2014).

Brand et al. (2014) reported two QTLs associated with variations in fruit pigmentation. QTL pc8.1 and pc10.1 both acted to regulate immature fruit chlorophyll content. QTL pc8.1 also affected the carotenoid content of the mature fruit, although its effect was not consistent in subsequent generations. QTL pc8.1 affected the color intensity via an increase in chloroplast compartment size. In addition to chlorophyll, the level of chlorophyll-associated tocopherols and carotenoids also were elevated (Brand et al., 2012). In a later study, the pepper ortholog of the tomato *GOLDEN2* gene was found to govern QTL pc10.1, which also affects the natural variation of the immature fruit chlorophyll content by altering chloroplast compartment size (Brand et al., 2014; Kilcrease et al., 2013).

Capsicum Genomics

Adoption of advanced technologies in crops that command large funding pools and have small, less-complicated genomes such as maize (*Zea mays* L.), soybean [*Glycine max* (L.) Merr.], and rice (*Oryza sativa* L.) has largely been rapid and straightforward. The rice genome was sequenced to a high quality in 2002 (Goff et al., 2002; Yu et al., 2002), maize in 2009 (Schnable et al., 2009), and soybean in 2010 (Schmutz et al., 2010). In contrast, for small-market specialty crops, particularly those with larger complex genomes such as *Capsicum*, advances in genomics have lagged behind. Pepper has the largest estimated genome size within the Solanaceae group at 3.25 to 3.48 Gbp (Fig. 6), depending on genotype (Bombarely et al., 2016; Hirakawa et al., 2014; Moscone et al., 2003), although this value is likely to change as the genomes of additional taxa are analyzed.

Over the past few decades, sequencing technologies have both decreased in price as well as increased in sophistication. This allowed for multiple sequencing efforts in pepper to be accomplished, with the first draft genome sequences becoming available in 2014 (Kim et al., 2014; Qin et al., 2014). Two efforts led to the availability of multiple cultivated *C. annuum* draft genomes for the cultivars CM334, Zunla-1, and a wild progenitor [*C. annuum* var. *glabriusculum* (Dunal) Heiser & Pickersgill], as well as resequencing of the cultivars Perennial and Dempsey. A draft genome for *C. chinense* also was produced (Kim et al., 2017c). These initial draft genomes used short-read sequencing technologies with multiple insert libraries and generated assemblies with similar statistics (Tables 8 and 9) such as the N50. Initial studies also determined that 76% to 81% of the pepper genome was composed of transposable elements, primarily long terminal repeat elements, and that *Gypsy* elements were the main cause of genome expansion (Kim et al., 2014). Comparing annotations, all assemblies showed *C. annuum* to have ≈35,000 genes, which is consistent with the findings in other members of the Solanaceae.

Initial efforts spurred a rapid proliferation of genome-wide analyses to characterize gene families, including some of the efforts described previously (Guo et al., 2015), development of markers for mapping disease resistance and other traits (Cheng et al., 2016; Devran et al., 2015; Han et al., 2018; Hill et al., 2013, 2015; Hulse-Kemp et al., 2016; Kang et al., 2016), and experiments with technologies for reducing the costs associated with the integration of genomics into breeding programs (Taranto et al., 2016). The draft sequences also allowed for the structuring of reference data sets such as the identification of a reference gene set for normalization of future qPCR studies (Cheng et al., 2017). Genes that were identified and implicated in important phenotypes can be validated and targeted for additional studies through genetic transformation and genetic engineering (Cardi et al., 2017). The full application of these studies and their integration moving forward into breeding programs are dependent on the quality of the genome sequences. The studies highlighted the different advantages and shortcomings of the currently available draft sequences (Gapper et al., 2014).

Additional efforts recently have been undertaken to provide a greater-quality version of the *C. annuum* cultivar CM334 genome (Kim et al., 2014), the development of an additional *C. chinense* draft sequence, and a genome of an additional species (*C. baccatum*) using traditional Illumina short-read sequencing

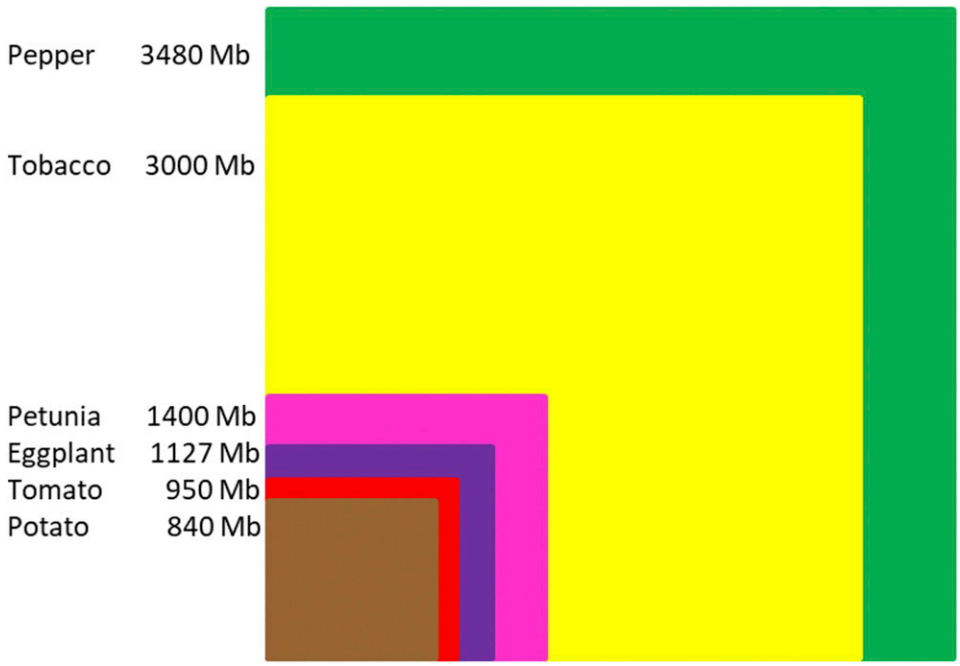

Fig. 6. Variation in published genome sizes in the Solanaceae. All genomes are diploid except for tobacco and potato, which are tetraploid. All genome sizes are listed in megabases (Mb).

Table 8. Statistics for the available *Capsicum* draft and reference genomes.

Species	Line/cultivar	N50 size		Total size (Gb)	Assembled (%)	Version	Reference
		Scaffold (Mb)	Contig (Kb)				
C. annuum	CM 334	2.47	30	3.06	88	1.0	Kim et al., 2014
C. annuum	CM334	2.08	30	3.06	88	1.6	Kim et al., 2017c
C. annuum	CM 334		30	3.06	88	2.0	Kim et al., 2017c
C. chinense	PI 159236	3.3	50	3.00	94	1.2	Kim et al., 2017c
C. baccatum	PBC81	2	39	3.20	82	1.2	Kim et al., 2017c
C. annuum	Zunla	1.23	55	3.35	103	2.0	Qin et al., 2014
C. annuum	var. *glabriusculum*	0.45	52	3.48	113	2.0	Qin et al., 2014
C. annuum	F_1 – CM 334 × Bell	3.69	123	3.21	92	1.0	Hulse-Kemp et al., 2018

technology (Kim et al., 2017c). These second-generation short-read genomes attempted to fill gaps and decrease the number of contigs and the amount of missing sequence in the genomes, as well as providing a more accurate ordering of the contigs into pseudomolecules.

Improved disease resistance is one of the primary goals of plant breeders. Kim et al. (2017c) investigated the importance of the process of retroduplication and subsequent neofunctionalization of disease resistance genes in the Solanaceae using the greater-quality genome sequences. The authors (Kim et al., 2017c) found that a large portion of the overall genes (≈4% to 10%) appeared to have originated from long terminal repeat retrotransposons. This emphasizes the importance of resolving the large complex repetitive regions of the genome, as important genes for disease resistance are typically found in highly repetitive regions (Ellis et al., 2000). Due to the nature of traditional short-read sequencing technologies, these regions can sometimes be misordered or completely unresolved. Xu et al. (2011) found this to be the case with the known resistance gene *R3a* of potato.

To overcome some of the shortfalls associated with traditional short-read sequencing technologies, third-generation sequencing technologies have focused on sequencing longer fragments to attempt to ameliorate difficulties associated with genome assembly and the inherently repetitive regions present in most genomes (Chin et al., 2016). One example is the Chromium Linked-Read technology by 10× genomics (Weisenfeld et al., 2017). This technology produces linked reads that are fundamentally similar to bacterial artificial chromosome end sequencing, which retains inherent physical information. This approach was used to test the technology on a complex plant genome using a *C. annuum* F_1 hybrid (cultivar CM 334 × Bell) (Hulse-Kemp et al., 2018). This approach provided an improvement in contig and scaffold sizes in the assembly when compared with previous efforts using only short-read technologies (Table 8). Although completely phased molecules were not obtained, the technology was able to successfully generate representatives of each of the two parental haplotypes containing important genes with structural differences. This was demonstrated with the *PUN1* gene, which is responsible for pungency as discussed previously, where both the serrano-type (cultivar CM 334) and the bell-type representatives of the sequence were obtained.

The recent efforts by Kim et al. (2017c) and Hulse-Kemp et al. (2018) emphasize the need for the continued improvement of the currently available genome resources, as there are inherent shortcomings in each of the used technologies. To move *Capsicum* genomics forward, a special effort must be directed toward integrating these resources and improving them to ensure that regions of particular interest to breeders, such as disease resistance loci, which are likely to be located in particularly problematic regions of the genome assemblies, are improved and are not omitted from the reference genomes. Breeder use of the reference genomes and associated forthcoming technologies are dependent on the quality of the references available and applicability will only continue to improve with improvement of the resources.

Table 9. Sequenced organelle genomes of *Capsicum* species with corresponding reference.

Organelle	Taxon	Reference
Chloroplast		
	C. annuum	Jo et al., 2011
	C. annuum var. *glabriusculum*	Raveendar et al., 2015
	C. annuum var. *glabriusculum*	Zeng et al., 2014
	C. baccatum	Kim et al., 2016b
	C. frutescens	Shim et al., 2016
	C. chinense	Park et al., 2016
	C. chinense	Raveendar et al., 2017
Mitochondria		
	C. annuum (CMS + normal)	Jo et al., 2014

CMS = cytoplasmic male sterile.

One such resource that has been developed to allow validation across the Solanaceae is the SOL Genomics Network database (Fernandez-Pozo et al., 2015). Although this database provides broad applicability to evolutionary studies, a more thorough and targeted database specifically for pepper has recently been developed, the PepperHub (Liu et al., 2017). This effort is the first step in centralizing *Capsicum* data with the goal of empowering ''omics''-level studies and incorporating multilevel experiments. As multiple genomes and improved versions of genomes are now becoming available in pepper, breeders can start to use genomics-based methods to identify traits of interest. Now and in the future, adequate reference genomes will enable the study of complex biological questions associated with crop improvement and move breeding and related research programs forward.

Conclusion

Progress has been made in conserving and characterizing genetic diversity in *Capsicum*, although many taxa remain unrepresented or underrepresented in the available genebanks. No taxon-wide assessment of diversity has yet been undertaken. Field studies supported by molecular and cytological/karyological analyses continue to provide new information that

advances the understanding of broad taxonomic and genetic relationships. Mechanisms governing the genetic regulation of the pathways involved in capsaicinoid and pigment synthesis remain unclear. Further research targeting regulatory elements and post-transcriptional regulation is needed. Advances in technology have resulted in the current availability of sequenced *Capsicum* genomes. The potential of this information to augment crop improvement activities is substantial, given adequate resources to employ this information and to improve and expand upon it.

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