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Review Article

Family Solanaceae: Taxonomy and modern trends

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Abstract: Solanaceae belongs to that group of families, which are included in almost all angiosperm classifications indicating naturalness of the family. The family being one of the most evolutionarily successful and advanced taxa shows astonishing level of diversity reflected in the form of various types of adaptations. The high level of diversity within the family in addition to other unusual features have reflected in poor understanding of its phylogenetics. Fossil record of angiosperms particularly of Solanaceae) is very meager and relatively recent, so use of morphology and other conventional characters is not convincing in revealing true phylogeny of the family. This all has necessitated using alternative marker types in phylogenetic analysis of the family. Since advent of molecular biology molecular markers have been constantly refined to serve the purpose. Solanaceous species, such as tomato, potato, chilli pepper, tobacco, and petunia serve as model systems for the investigation of molecular and agronomic questions, and the family is the subject of intensive phylogenetic studies that are providing new insights into species boundaries and generic relationships. Results from recent morphological, molecular, and biosystematic research have shed new light on the systematic relationships in the family at virtually all taxonomic levels from subfamily to variety.

Key words: Solanaceae, petunia, phylogenetic studies, biosystematic research

Introduction

Family Solanaceae is one the largest and economically most important families of angiosperms, including important food, spice, and drug plants (D'Arcy, 1979). There has been much change in recent years regarding generic circumscription in the family. In 1979, D'Arcy estimated it to contain 83 genera and 2671 species, but the most recent estimate is that the family includes more than 3000 species. Approximately half the species in the family are included in the widespread, morphologically diverse, and economically important genus *Solanum*. The family is nearly cosmopolitan in distribution, found throughout tropical and temperate regions, but with a concentration of diversity in Australia and Latin America.

Diversity within this family is also indicated by the variety of life forms of the taxa included in this family, ranging from ephemeral herbs (*Leptoglossis* spp. and *Schizanthus* spp.) to large trees (*Duckeodendron* spp.). Characteristic morphological attributes of the family include presence of exstipulate, alternate or rarely opposite leaves and with hypogynous, regular or nearly regular cymose flowers. Five-lobed calyx and sympetalous corolla, which is also 5-lobed, with lobes being induplicate-valvate or plicate in the bud, are also found in the family. Epipetalous stamens, mostly equal in number to petals (in certain cases fewer) and arranged alternately with them, are equal in length and perfect except in certain genera. Gynoecium consists of two united carpels and very rarely three or five carpels fuse to form the gynoecium. Ovules and seeds are numerous, a feature differentiating Solanaceae from Convolvulaceae. Fruit is a berry or capsule and most of the solanaceous members have a basic set of twelve chromosomes.

Perusal of the literature reveals that one of the earliest references to the Solanaceae is in the *Dioscorides Codex* of 815 A.D., and it is here that many of the present day Solanaceous members have been described (D'Arcy, 1979). While Casper Bauhin's (1623) concept of Solanaceae as a group was gaining general acceptance, Linnaeus (1753) recognized two groups, which loosely encompassed the present day Solanaceae. However, his grouping on the basis of number of stamens led to many unnatural assemblages. It was ultimately Antoine Laurent de Jussieu (1789) who established the family Solanaceae and since then this family has been reviewed and re-examined by many taxonomists. Like other large angiosperm families, such as Scrophulariaceae (Olmstead and Reeves, 1995), Solanaceae is also represented by several core genera, which have been assigned to this family in all the classificatory treatments (D'Arcy 1979, 1991). While some workers have included a number of allied genera or groups of genera in this family others have placed them in related families and still others have even segregated them into separate

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families (Bentham and Hooker, 1862-1883; Engler and Prantl, 1887-1915; Hutchinson, 1973; Cronquist, 1981; Takhtajan, 1997 and APG, 2009). This inconsistent systematic treatment is largely due to the presence of unusual character combinations in these allied genera. Either they lack the characters typical of the family or have attributes characteristic of another family. It is because of this inconsistent systematic position of several genera within this family. The uncertain taxonomic status of taxa, briefly presented above, is a result of factors, such as the origin of the family in an area (tropical America) which is still largely unexplored (D'Arcy, 1979), certain important morphological trends within the family that are contrary to those prevalent in other angiosperms (Stebbins, 1974), occurrence of annual habit and strongly zygomorphic flowers in species belonging to basal clades of Solanaceae and this also is exactly opposite to what is prevalent in other angiosperms (Stebbins, 1974), and unusual hyperdiversity of genus *Solanum* which makes Solanaceae interesting from an evolutionary standpoint (Knapp *et al.*, 2004) as well. It is for these reasons that Solanaceae is called as 'paradoxical family' (Heiser, 1969 and Knapp *et al.*, 2004).

Molecular markers vs systematic position

To resolve the taxonomic riddles within Solanaceae, recourse has been taken to modern and revolutionary molecular markers, which, since their development and use, have revolutionized the entire scenario of biological sciences. These markers have acted as versatile tools for taxonomy and their application in Solanaceae is expected to result in a classification that is more predictive with respect to interpreting evolution. Morphological markers, though indispensable both to taxonomy as well as phylogeny have the universal disadvantage of not lending themselves to meaningful statistical comparisons and also are less used because of the controversies about character homologies (Scotland *et al.*, 2003). These anomalies have curtailed the role of morphology in taxonomic and phylogenetic description of the family Solanaceae (Knapp, 2001) and invoked use of other types of markers, particularly, molecular markers. Molecular markers present diverse applications to efficiently obtain useful genetic information (Karp *et al.*, 1997) and so have been utilized for the analysis of the genetic diversity in a number of plant species like *Solanum tuberosum*, *S. melonogena*, *Petunia* spp, *Nicotiana* spp etc. It is here emphasis that results of molecular markers are not in general antagonistic to that by other conventional markers (Spooner *et al.*, 2006) but in most of the instances they provide complementary evidences. However, use of a particular molecular marker type depends upon the nature of the study and the extent of taxonomic resolution desired (Junli *et al.*, 2000; Zhang *et al.*, 2000 and Sylvain *et al.*, 2000). Since it is extremely difficult to find an ideal DNA marker that meets all the necessary criteria, a set of markers is commonly used to unravel a significant proportion of genetic diversity (Weising *et al.*, 1995). Various types of DNA-based molecular techniques (Botstein *et al.*, 1980; Joshi *et al.*, 1999) are utilized to evaluate DNA polymorphism and the available DNA markers are categorized as: DNA band-based, hybridization-based and sequence -based markers. Band based molecular markers include randomly amplified polymorphic DNA (RAPD), inter-simple sequence repeats (ISSR), simple sequence repeats (SSR), polymerase chain reaction restriction fragment length polymorphism (PCR-RFLP) and amplified fragment length polymorphism (AFLP) etc.

RAPD and ISSR Markers

Being efficient, simple and inexpensive, RAPD has been employed in many taxonomic and phylogenetic studies of Solanaceae (Spooner *et al.*, 1995; Rio and Bamberg *et al.*, 2000 and 2004; Singh *et al.*, 2006). Study of Spooner *et al.,* (1995) showed the applicability of RAPDs for both intra-and inter-specific studies in section *Etuberosum* of *Solanum.* Singh *et al.,* (2006) used RAPD technique as a tool for assessing genetic diversity and species relationships among 28 accessions of *Solanum* species. It discriminated all the accessions of eggplants and the resulting dendrogram showed that *Solanum incanum* was closest to *S. melonogena* and then to *S. nigrum*. Also RAPD markers efficiently distinguished heterogeneous populations of wild potato from closely related tetraploid species, *S. oplocense*, *S. gourlayi* and *S. tuberosum* ssp. *andigena*, suggesting that it is not a duplicate of these species (Rio and Bamberg, 2004). Besides, RAPD profiles clearly differentiated populations within highly heterogeneous tetraploid of *S. sucrense* and were useful for determining germplasm organization within the potato species (Rio and Bamberg, 2004). Similar conclusion was obtained by Demeke *et al.,* (1993), Xu *et al.,* (1993) for *Solanum tuberosum* and other related species. Applicability of RAPD and semi-arbitrary primers (targeting intron-exon boundaries) was advocated by Przetakiewicz *et al.,* (2002) in *Solanum tuberosum*. Suganda *et al.*, (2006) successfully applied RAPD to distinguish three Indonesian species *Brugmansia*, which, otherwise, were indistinguishable by morphological or metabolite analysis. This study revealed that each species had different DNA fragment patterns, thus allowing each species to be individually identified. Based on RAPD analysis of 53 species and cultivars of the genus *Lycopersicon* (*sensu lato*), Kochieva *et al.,* (2002a) reported more divergence among cross-pollinating tomato species than self-pollinating species. Karihaloo *et al.,* (1995) used RAPD for studying variations in *Solanum melongena*. Notwithstanding these useful systematic applications, RAPD analysis did not support assumption of *Solanum aethiopicum* and *S. anguivi* as two separate species (Stedje and Bukenya-Ziraba 2003). Egashira *et al.,* (2000) also found RAPD markers helpful in assessing genetic diversity within *Lycopersicon peruvianum* and *L. chilense*. However, it needs to be emphasized that it is essential to set up a negative control reaction as RAPD primers potentially find their way during amplification in any prokaryotic and eukaryotic DNA, which may produce false positive results. Besides, RAPD and its modified versions (Caetano-Anolles *et al*., 1991; Sivolap and Kalendar, 1995; Aagaard *et al*., 1998 and Atienzar *et al*., 2000) have reproducibility problems and due to non-stringent conditions a certain band may not show fidelity for a given sample at different times or in different laboratories.

Another band based molecular marker, named as ISSR (Zietkiewicz *et al*., 1994), is amplified by PCR in presence of a primer complementary to a target microsatellite. Here target of the amplification is the region between two simple sequence repeat (SSRs) regions, which are inverted in orientation and within amplifiable range. It is generally assumed that there are many SSR motifs in a eukaryotic genome (Li and Ge, 2000) and copies of many of them are in opposite orientation in vicinity. Such amplification does not require genome sequence information and leads to multilocus and highly polymorphic patterns (Zietkiewicz *et al*., 1994; Tsumura *et al*., 1996. But one has to screen a genome for presence of different SSR motifs with above stated characteristics. Each band corresponds to a DNA sequence delimited by two inverted microsatellites. Like RAPDs, ISSR markers are quick and easy to handle, but they have higher reproducibility because of longer length of their primers. There are two types of ISSR markers: one is anchored and another is non-anchored. In the former, one or more extra nucleotides are at 3' end of the primer, which allows it to anneal specifically at the junction of SSR and ISSR regions. Further, such extension of a nucleotide leads to more specification of the primer. In non-anchored version there is no extension in primer at 3´ end giving it more freedom in amplification of unknown ISSR sequence. Absence of a particular band or variation of band length could also signify that an SSR site (ISSR primer binding site) might have been lost or a chromosomal structure rearrangement may have taken place. Because ISSRs are a variant of the RAPD technique, they have inherited many of the problems that beset RAPD (band scoring and homology). Bornet and Branchard (2001) in an attempt to cope with these difficulties modified their PCR protocol raising annealing temperature till constant amplification pattern is obtained and found this version more effective. Polymorphisms are mostly of the dominant type because of changes in the anchoring nucleotide, but codominant types occur if length of the intervening space between the microsatellites has changed (Andersen, 2000). In Solanaceae, ISSR markers have been mainly used for cultivar identification (Prevost and Wilkinson, 1999). Pérez de la Torre and Escandón (2006) used anchored ISSR primers for the fingerprint generation in *Nierembergia linariaefolia* and found that six out of the seven primers used, discriminated all the individuals involved in the study. Kumar *et al.,* (2001) used ISSR markers successfully for infra-specific identification in *Capsicum annuum*. Using non-anchored ISSR primers, Kochieva *et al*., (2002b) found species-specific ISSR fragments for each tomato species.

RFLP, AFLP and other Markers

In addition to these markers, RFLP has also been used for elucidation of systematic position of taxa within Solanaceae (Prince *et al*., 1992). This technique involves cutting up the DNA into a number of fragments using a variety of restriction enzymes, separating the resultant fragments of variable size using electrophoresis, followed by visualization of the banding profile of fragments using ethidium bromide. Presence or absence of bands can be scored as in other band-based techniques and the banding profile directly reflects the position and frequency of restriction sites within the DNA (Sylvain *et al*., 2000). In case of complex genome where there are more chances of band overlapping, labelled probes are used through hybridization to determine the presence of particular type of DNA fragment. Because of being ubiquitous throughout the plant, highly heritable and relatively highly polymorphic, RFLPs are superior genetic markers and have been used in polymorphism studies, cultivar identification and for phylogenetic studies. However, a major drawback of hybridization based RFLP is that its application is technically difficult, relatively slow, labour intensive and may involve expensive and sometimes radioactive / toxic reagents. A modified version of RFLP called as PCR-RFLP or cleaved amplified polymorphic sequences **(**CAPS) have been developed where a PCR locus is first amplified with PCR and then it is subjected to restriction enzyme digestion. Such digests are compared for their differential migration during electrophoresis (Koniecyzn and Ausubel, 1993 and Jarvis *et al*., 1994). PCR primer for this process can be synthesized based on the sequence information available in databank of genomic or cDNA sequences or cloned RAPD bands. Like other marker types, RFLP has been used in taxonomic studies of various taxa of Solanaceae.

Simple sequence repeat (short tandem repeats or simple sequence length polymorphisms or simply microsatellites) markers are based on difference in tandem repeats of sequence units generally 2-8 bp in length (Godwin *et al*., 2001). SSR loci are particularly ubiquitous in plant genome (Kubis *et al*., 1998; Li and Ge, 2001 and Rakoczy-Trojanowska and Bolibok, 2004). The principle of SSR polymorphism is the presence of variability either in number of repeats within SSR or in priming sites. SSRs can be amplified by using primers that flank these regions and the same are designed by searching the DNA sequence banks for SSR loci of related species or by screening genomic libraries. In certain cases SSR primers from one-species have been used in phylogenetically distant species and have fulfilled the purpose of exploring the intra and inter-specific diversity (Smelcerovic *et al.*, 2006). In spite of many practical difficulties (Kelly and Willis, 1998), SSR markers are ideal for genome mapping as well as for population genetic and diversity studies. Hence Marcucci-Poltri *et al.,* (1998) used SSR markers for analysing genetic relationship in the genus *Solanum* sub-section *Potatoe*. Bindler *et al.,* (2007) used them for genome evaluation of tobacco with satisfactory results. Guzmán *et al.,* (2005), while faced difficulty to distinguish accessions of *Capsicum* spp. with AFLP markers, recommended use of microsatellite markers for such study and considered them more powerful for intra-specific discrimination. In view of the limitations of the molecular markers discussed above, continuous refinements have resulted in more sophisticated markers, like randomly amplified microsatellite polymorphisms (RAMPO) in which genomic DNA is first amplified using arbitrary (RAPD) primers and the amplified products are then electrophoretically separated and dried gel is hybridized with microsatellite oligonucleotide probes. Several advantages of oligonucleotide fingerprinting (Jarvis *et al.*, 1994), RAPD and microsatellite-primed PCR (Weising *et al.*, 1995) are thus combined in this technique. It is fast with high sensitivity, and reveals high level of variability and does not need prior DNA sequence information as is required in RAPD (Richardson *et al.*, 1995). This technique has been successfully employed in the genetic fingerprinting of tomato and other related genotypes (Richardson *et al.*, 1995).

Cytochrome P450 mono-oxygenases are widely found in plants, animals and micro-organisms (Shalk *et al.*, 1999). In higher plants, cytochrome P450s play important role in oxidative detoxification and biosynthesis of secondary metabolites (Ohkawa *et al.*, 1998) and many P450 gene families have been reported in various plant species. Furthermore, P450 genes that have so far been characterized are very diverse and very variable in their gene alignments (Ohkawa *et al.*, 1998). This marker represents a valuable new tool and with only a relatively small number of primers, it is able to analyse both diversity and conservation in plant genomes. Because of significantly high reproducibility of results, these markers have enormous advantages over RAPD and ISSRs and are particularly useful in cases where good sequence information is not available. Similarly, amplified fragment length polymorphism (AFLP) technique developed by Vos *et al.,* (1995) and its modified versions named as SAMPL (selectively amplified microsatellite polymorphic loci) are used to visualize hundreds of amplified DNA restriction fragments simultaneously which are produced by restriction digestion and amplified using PCR, followed fragments by their analysis through autoradiography or use of special fluorescently labelled primers. AFLP enables to estimate diversity at multiple loci within DNA, particularly of species with low genetic base (Campbell *et al.*, 2003 and Després *et al.*, 2003) and without any obligate sequence knowledge (Ridout and Donini, 1999 and Hodkinson *et al.*, 2000) and with high reproducibility (Money *et al.*, 1996). Since its introduction, AFLP and its modified versions (Ranamukhaarachchi *et al.*, 2000) has become prime choice of polymorphism detection and has helped to resolve intra and inter-generic level of polymorphism in many plant species. It has been used in inter-populational studies (Amsellem *et al.,* 2000) and also to establish relationship between different species or sub-species (Kardolus *et al.*, 1998; Koopman *et al.*, 2001; Zhang *et al.*, 2001 and). Studies of Mace *et al.,* (1999) indicated that the AFLP technique is an efficient and effective tool for determining genetic relationships among taxa in Solanaceae. On the basis of AFLP data they proposed a new classification for the tribe Datureae, and placed the arborescent species in a separate genus *Brugmansia*, and within *Datura* recognised three sections, namely *Stramonium*, *Dutra* and *Ceratocaulis*. Besides, *Datura discolor*, previously placed in section *Dutra*, and was reported to be intermediate between sections *Dutra* and *Stramonium* (Mace *et al.*, 1999). Furthermore, AFLP primers were four times more efficient than RAPD primers in their ability to detect polymorphism in *Capsicum annuum* (Paran *et al.*, 1998). While Marcucci-Poltri *et al.,* (1998) used this marker for infra-generic taxonomic studies in *Potatoe* sub-section of *Solanum*, Thomas *et al.,* (1995) used it for similar study in tomato. Mace *et al.,* (1999) used AFLP analysis for genetic relationships among cultivated eggplant, *Solanum melongena* and its wild relatives. Julio *et al.,* (2005) developed AFLP markers linked to three disease resistant varieties in *Nicotiana tabacum*. Ren and Timko (2001) used AFLP markers for polymorphism analysis and evolutionary relationships among cultivated and wild *Nicotiana* species. The AFLP data placed all members of series *Longipedicellata* of genus *Solanum* into a single clade, sister to *S. verrucosum* and *S. brachycarpum* series *Demissa* (Kardolus 1998). Spooner *et al.,* (2000) developed AFLP markers for series *Longipedicellata* which is otherwise difficult to distinguish from members of other series of *Solanum*. Even AFLP of selected organelles in certain cases has helped to resolve taxonomic riddles. For instance, Komarnyts'kyi and Komarnyts'kyi (2004) using AFLP data of chloroplast DNA, recorded three major clusters within *Solanum-Lycopersicon* complex and observed that *Lycopersicon* (sensu lato) species and *Solanum lycopersicoides* fall in one group. The second cluster included *S. verrucosum* a polyploid species of series *Longipedicellata*, and all diploid and polyploid species native to South America. Two diploid series *Pinnatisecta* and *Bulbocastana* were grouped together in another cluster (Komarnyts'kyi and Komarnyts'kyi, 2004). This phylogenetic treatment is strongly supported by morphological and other molecular marker data (Komarnyts'kyi and Komarnyts'kyi, 2004). Negi *et al.,* (2000), on the basis of AFLP data identified two varieties of *Withania somnifera* in India and also estimated the level of diversity between *W. somnifera* and *W. coagulans*. In recent years, advances in DNA sequencing have contributed significantly to the understanding of the relationships of flowering plants which together with computerized cladistics (Hennig, 1966 and Kitching *et al.*, 1998) has led to the large scale use of a variety of regions of the genome, both from the nucleus and the chloroplast for sequencing. The molecular data so generated have enabled taxonomists to put forth certain audacious taxonomic conclusions. Systematic studies in the Solanaceae have benefited greatly from these advances, with phylogenetic studies having been published for a variety of genera and species groups (Mione *et al.*, 1994; Axelius, 1996; Bohs, 2001) and the resolution of the relationships of several enigmatic genera, like *Duckeodendron*, whose inclusion in the family has been the subject of much debate (D'Arcy, 1991). For example, tomatoes previously recognized as a separate genus called *Lycopersicon* and tree tomatoes (ex *Cyphomandra*) are deeply nested in the genus *Solanum* (Bohs, 2005; Bohs and Olmstead). Molecular data have resolved enigma of kinship of Solanaceae, and now it is established that its closest sister taxon is Convolvulaceae (Olmstead *et al.*, 1992). The disagreement that still exists about the utility of classifications largely based on DNA sequence data would disappear as more gene sequences from both chloroplast and nucleus become available. In tune with this requirement, ribosomal DNA sequence has been extensively used for diversity analysis, species identification and phylogenetic analysis. In fact, phylogenetic analysis based on 5S ribosomal RNA (rRNA) genes (about 120 bp in length) have long been used to elucidate the origin and evolution of a number of organisms. Matyášek *et al.,* (2003) demonstrated the role of 5S ribosomal DNA (rDNA) in the taxonomy of *Nicotiana* and phylogenetic reconstruction of species and relationships, particularly, in section *Tomentosae*. This study also indicated that *Nicotiana glutinosa* diverged early from the section *Tomentosae*. Likewise, 18S ribosomal RNA genes, about 2 kb in size, have been widely sequenced for reconstruction of phylogeny at higher taxonomic levels in plants, including species of Solanaceae (Kiss *et al.*, 1989 and Chaw *et al.*, 1997). In several instances, 18S rDNA sequence data have provided a critical test of phylogenetic inferences obtained from other data (Kron, 1996). In certain cases 18S rDNA sequence data sufficiently resolved infra-familial and infra-generic taxonomic puzzles. Harding and Millam (1999) exploited ribosomal RNA genes as markers to identify somatic hybrids between *Solanum tuberosum* cv. Brodick and wild diploid species, like *S. megistacrolobum*, *S. sanctae-rosae* and *S. sparsipilum*. The markers revealed some intermediate ribosomal RNA gene profiles indicative of hybrid nature of certain species whereas others were characteristic of *S. tuberosum* cv. Brodick. This evidence is suggestive of somatic exchange / re-arrangement between the nucleolar organizer region (NOR) region of *S. sanctae-rosae* and *S. tuberosum* cv. Brodick. Ribosomal RNA gene copy number analysis of the somatic hybrids did not reveal hexaploid values suggesting that these products are not symmetric hybrids derived from the parental diploid and tetraploid plants of *S. sparsipilum* (Harding and Millam, 1999). Komarova *et al.,* (2004) studied organization of rDNA in allopolyploids of *Solanum* for taxonomic elucidation. Similarly, Borisjuk *et al.,* (1997) analysed rDNA including intergenic spacer of *Nicotiana* for taxonomic studies. Levin *et al.,* (2005) used sequence of four genes for studying evolutionary relationships in *Solanum* section *Acanthophora*. The spacers, particularly, flanking the 5.8S ribosomal gene find their use for such purposes within and among closely related genera (Baldwin, 1992; McBreen *et al.*, 2003; Ahmad *et al.*, 2006 and Verma *et al.*, 2005). Ryzhova *et al.,* (2002) reported that two types of rDNA internal transcribed spacers (ITSs) in *Capsicum* were helpful in resolving infra-generic relationships within the genus. Molecular data from the nuclear ITS region established that *Normania* and *Triguera* are nested within the large genus *Solanum*, where they together form a well-supported clade (Bohs and Olmstead, 2001). However, the relationship of this clade to other *Solanum* sub-groups is not clear. The study necessitated transfer of *Normania* and *Triguera* epithets to *Solanum*. The molecular data also confirmed that the species of *Solanum* endemic to Micronesia belonged to two distinct clades, each showing an independent evolution of heteromorphic anthers. Anderson and Jansen *et al.,* (1998) evaluated relationships of *Solanum muricatum* based on ITS sequence data.

Intergenic spacer (IGS) i.e. the spacer between 18S and 28S ribosomal genes particularly its external transcribed spacer (ETS) region is another suitable marker for diversity analysis. Borisjuk *et al.,* (1997) found unique sequence in the central part of the IGS in the genus *Nicotiana tabacum*, which distinguished it from *Solanum tuberosum* and *Solanum lycopersicon* (syn. *Lycopersicon esculentum*). The IGS rDNA, in latter two species, exhibited similar length and general architecture with high level of similarity (86% and 86.5%, respectively) in the AT-rich domain containing the transcription initiation site (TIS) and the region approximately 800 bp upstream of the 18S rRNA gene (Borisjuk and Hemleben, 1993). However, as compared to tomato (Perry and Palukaitis, 1990) repeated elements down-stream of the putative TIS are absent in potato, which is compensated by sub-repeats upstream of the TIS (Borisjuk and Hemleben, 1993). Santiago-Valentini and Olmstead (2003) used DNA sequences of the intergenic spacer along with ITS for phylogenetic analysis and elucidation of the evolutionary relationships of *Coeloneurum*, *Espadaea* and *Henoonia* with *Goetzea* and other major lineages of the Solanaceae. The results inferred that these genera comprise a group together with *Metternichia* and *Duckeodendron* in a clade within the Solanaceae, pointing towards a broader circumscription of the sub-family Goetzeoideae. Matyášek *et al.,* (2003) demonstrated the presence of the GC-rich sub-region in non-transcribed spacer of IGS rDNA in a range of *Nicotiana* species, which was absent in *N. sylvestris*, *N. longiflora* and two closely related genera, *Petunia* and *Solanum*. The sequence data suggested that this sub-region of the non-transcribed spacers (NTS) is likely to have evolved within the genus *Nicotiana*. The absence of the sub-region in *N. sylvestris* and *N. longiflora* is likely to have arisen by a deletion event in the evolution of section *Alatae*. Volkov *et al.,* (1996) compared external transcribed spacer (ETS) of two close diploid relatives of the allotetraploid *Nicotiana tabacum*, *N. sylvestris* (subg. *Petunioides*) and *N. tomentosiformis* (subg. *Nicotiana*) and other species of Solanaceae and obtained sequence differences in ETS region between these different species. Characteristically there were 5 sub-repeats in *N. sylvestris* and 10 sub-repeats in *N. tomentosiformis* in the ETS region. The portion of ETS adjacent to 18S rRNA gene, exhibited much higher similarities between species, not only among *N. sylvestris* and *N. tomentosiformis* but also within more distantly related Solanaceae. At the 5´end of the ETS in the two *Nicotiana* species studied, were three copies of highly divergent sub-repeats (Volkov *et al.*, 1996). At lower taxonomic levels, 3´ end of ETS (3´-ETS) has been used as a useful locus (King *et al.*, 1993 and Volkov *et al.*, 1996) and has been successfully used for phylogenetic reconstruction of several genera of Solanaceae (Bena *et al.*, 1998; Baldwin and Markos, 1998 and Linder *et al.*, 2000).Volkov *et al.,* (1996) studied molecular organization and evolution of the ETS region in two diploid relatives of *Nicotiana tabacum*. Volkov *et al.,* (2003) estimated evolutionary relationships of section *Petota* of genus *Solanum* from the sequence data of 5´ of external transcribed spacer region of rDNA. They resolved nature of ancestral organization of ETS in non-tuber bearing species of series *Eutuberosa*, *Bulbocastana*, *Pinnatisecta* and *Poladenia* and in *Solanum dulcamera*. The study maintained that species of *S. commersonii* represents a sister taxon for all species with rotate corolla within the section *Petota* and series *Circaeifolia* diverged very earlier within the section.

DNA sequence data of organelles other than nucleus, particularly of chloroplast genes, has proved of immense value in phylogenetic studies (Ritland and Clegg, 1987; Clegg, 1993 and Sakata and Lester, 1997). Though large but of manageable size relative to animal mitochondrial DNA, lack of independently evolving duplicated genes (Olmstead and Palmer, 1994) and intron free genes have made cpDNA ideal for phylogenetic study. This potential is borne out by extensive use of cpDNA-encoded genes to study plant phylogeny. Besides, there are other reasons for this focus on a single organelle that by itself accounts for less than 0.1% of the genetic complement of plants. One important reason for extensive use of cpDNA in systematic studies is a conservative rate of nucleotide substitution (Palmer, 1991), which makes it ideal for the study of plant phylogeny and for elucidating relationships at or beyond family level (Olmstead and Palmer, 1994). Besides, plastid sequences are less plagued by problems of among-site and among-lineage rate heterogeneity, which have often compromised the accuracy of phylogenetic inference in animals. Comparative study of cpDNA is particularly relevant to Solanaceae because chloroplast genome of *Nicotiana tabacum* is completely sequenced which could serve as a reference genome within the family. Many of the systematic advances made on the basis of extensive cpDNA studies have been reviewed by several workers (Palmer *et al.*, 1988; Clegg, 1993; Doyle, 1993; Systma and Hahn, 1994). A perusal of this information in the context of Solanaceae (Bradford and Barnes, 2001) reveals that the DNA sequence data of cpDNA have helped to resolve some long-standing problems in Solanaceae systematics, like phylogenetic relationships in *Solanum* (Palmer and Zamir, 1982; Spooner *et al.*, 1993), *Nicotiana* (Kung *et al.,* 1982 and Olmstead and Palmer, 1991), *Jaltomata* (Mione *et al.*, 1994), *Physalis* and related genera (Mione *et al.*, 1994). On the basis of molecular phylogeny of chloroplast and mitochondrial genes, Kulcheski *et al.,* (2006) separated the genus *Petunia* into two complexes while Livingstone *et al.*, (1999) showed that *Capsicum* species differed by at least one reciprocal translocation. Rodriguez and Spooner (1997) and Bohs and Olmstead (1998) used chloroplast DNA study for taxonomic analysis of *Solanum*. Mione *et al.,* (1994) and Olmstead and Palmer (1997) explored systematic implications of chloroplast DNA variations in taxonomy of *Jaltomata* and *Solanum,* respectively. Similarly Spooner *et al.,* (1993) used sequence data of chloroplast DNA as an evidence for interpreting interrelationships of tomatoes and potatoes. Sequence data of two chloroplast genes viz. *rbcL* (ribulose 1, 5-bisphosphate carboxylase / oxygenase large subunit) and *atpB* (ATP synthase as β-subunit) have been most extensively used for taxonomic resolution of plant species (Chase and Cox, 1998; Hoot and Douglas, 1998). Both the genes are located in the plastid genome separated by a small spacer region (Savolainen *et al.*, 1997). Though different evolutionary constraints are likely to be involved because the two genes code for distinct enzymatic functions but at the same time being part of the same non-recombining piece of DNA, they are believed to share the same evolutionary history. Although the gene sequence data of *rbcL* and *atpB* is more suitable to infer relationships at family level but in certain cases it has served the purpose at generic or infra-generic level. Fukuda *et al.,* (2001) examined evolutionary relationships within species of *Lycium* using chloroplast DNA sequence data from *mat*K and *trn*T-*trn*F loci. Olmstead and Sweere (1994) found molecular data of *ndh*F (a chloroplast gene) and *rbcL* congruent with perceived phylogeny of Solanaceae but found it conflicting upon its extension to sub-family level. On the basis of sequence data of chloroplast genome, *Bouchetia*, *Hunzikeria*, and *Nierembergia* were found to be of monophyletic origin. The *rbcL* and *ndhF* sequence data suggested that Solanoideae and Nicotianoideae (including *Nicotiana* and the Anthocercideae) represent a monophyletic group and together form the "x = 12" complex (Olmstead *et al.*, 1998). Within the later, tribe Nicotianeae is sister to tribe Anthocercideae. Within Solanoideae, basal branch consists of tribes Hyoscyameae, Lycieae, Nolaneae and Jaborosae; with Hyoscyameae as a sister group to the clade composed of other three tribes. The second basal branch in the Solanoideae consists of Mandragoreae and Solandreae. The data also supported weak unification of *Nicandra and Exodeconus* as suggested by D'Arcy (1991). The chloroplast sequence data of *ndh*F and *rbcL* supported opinion of Hunziker (1979) and D'Arcy (1991) that Datureae form a sister group to a large clade comprising most of the traditional Solaneae. The cpDNA results provided the first evidence for dividing the traditional Solaneae along phylogenetic lines. Olmstead *et al.,* (1998) suggested a classification that included a much reduced Solaneae, including *Solanum* (with *Lycopersicon* and *Cyphomandra*) and *Jaltomata*, a new tribe Capsiceae and a new large tribe Physaleae. While the cpDNA study showed that *Solanum etuberosum* and *S. palustre* are more similar to each other than to *S. fernandezianum* (Spooner *et al.*, 1996). On the basis of sequence data of *ndh*F, Bohs and Olmstead (1997) and Bohs (2005) identified major clades within *Solanum*. Santiago-Valentini and Olmstead (2003) used DNA sequences of the chloroplast genes *ndh*F, *rbcL* and *trnL-trnF* intron, in addition to IGS and ITS for phylogenetic analysis among solanaceous genera, including *Coeloneurum*, *Espadaea*, *Henoonia, Goetzea* and other major lineages of Solanaceae. The DNA sequences pointed out that these genera group together with *Metternichia* and *Duckeodendron* in a clade within the Solanaceae, pointing towards a broader circumscription of sub-family Goetzeoideae. Combined data of *rbcL* and *ndh*F yielded a more fully resolved tree of Solanaceae (Olmstead and Sweare, 1994). The "x = 12" complex forming a single clade was also well supported by the study of Olmstead and Sweare (1994). Levin and Miller (2005) using DNA sequence data from nuclear granule-bound starch synthase gene (GBSSI, *waxy*) and the chloroplast region *trnL-trnF*, inferred phylogenetic relationships among *Lycium*, *Grabowskia*, and the monotypic genus *Phrodus microphyllus.* Tribe Lycieae was strongly supported as of monophyletic origin, but *Lycium* likely included both *Grabowskia* and *Phrodus*. The results also suggested a single dispersal event from the Americas to the Old World, and frequent dispersal between North and South America (Levin and Miller, 2005). Walsh and Hoot (2001) found sequence data of *atpB-rbcL* spacer region and nuclear *waxy* introns helpful in resolving phylogenetic relationships of *Capsicum.* Similar was the corollary of Bohs and Olmstead (1997) for *Solanum* based on *ndh*F and other chloroplast sequence data. With molecular data from the nuclear granule-bound starch synthase gene (GBSSI or *waxy*) and the chloroplast *trn*T-F region, (Anderson *et al.*, 2006) confirmed the hypothesis that *Solanum vespertilio* and *S. lidii* are phylogenetically associated with *Solanum* lineages from Africa, rather than with previously suggested Mexican species. In recent years, molecular marker technology in higher plants has witnessed a shift from the so-called random DNA markers (RDMs), developed in the past arbitrarily from genomic DNA and cDNA, to the molecular markers representing the transcriptome and the other coding sequences (Gupta and Rustgi, 2004). These markers have been described as gene targeted markers (GTMs). Another specific class of markers includes the so-called functional markers (FMs), which are supposed to have a cause and effect relationship with the traits of interest. Markers of different classes are derived from cDNA clones, expressed sequence tags (ESTs), gene sequences and the unique (coding) sequences obtained through methyl filtration or genome normalization (high C_0t fraction) from genomic DNA libraries. Similarly RFLPs, SSRs, AFLPs, SNPs and many more novel markers are being developed from the transcriptome (cDNA clones and EST databases) and specific genes (Gupta and Rustgi, 2004). These novel markers include expressed sequence tag polymorphisms (ESTPs), conserved orthologue set (COS) markers, amplified consensus genetic markers (ACGMs), gene specific tags (GSTs), resistance gene analogues (RGAs) and exon-retrotransposon amplification polymorphism (ERAP). Use of these markers is being extended to Solanaceae also (Gupta and Rustgi, 2004). Sequence data of β -tubulin, salicylic acid methyltransferase, SNPs etc is being included with this purpose. Using cDNA sequences of SAMT (salicylic acid methyltransferase) gene in Solanaceae, Martins and Barkman (2005) obtained results mostly congruent with previous cpDNA estimates. The relationships observed with SAMT data included *Schizanthus* as a sister taxon to the rest of the family. The second branch was Schwenckioideae + Cestroideae. The final two lineages were Petunioideae, sister to the 'X = 12' complex, which included Nicotianoideae plus Solanoideae. However, clades of *Nicandra* and *Exodeconus* were not treated as sister taxa; rather, *Exodeconus* was near the base of Solanoideae while *Nicandra* appeared to belong to a lineage that included *Physalis*, *Capsicum*, *Solanum*, and *Datura*.

The use of sequence data in phylogenetic elucidation is restricted not only to coding regions and their spacers but some scientists advocated utilizing alignable sequence tracts from other regions. Kress *et al.,* (2005) used DNA bar coding as a marker. They have recommended using sequence data of various loci, particularly, nuclear rDNA for such purposes in flowering plants. Such 'DNA barcodes' showed promise in providing a practical, standardized, species-level identification tool that can be used for biodiversity assessment and analysis. Despite the controversy over the value of DNA bar coding, largely because of the perception that this new identification method would diminish rather than enhance traditional morphology-based taxonomy, there is a support of bar coding as a species identification process from various corners (Besansky *et al.*, 2003; Hebert *et al.*, 2003 and Janzen, 2004), who stressed on its utility as a powerful tool for identifying specimens.

Conclusion and future prospects

Solanaceae belongs to that group of families, which are included in almost all angiosperm classifications indicating naturalness of the family. The family being one of the most evolutionarily successful and advanced taxa shows astonishing level of diversity reflected in the form of various types of adaptations (Cocucci, 1999; Raguso *et al.*, 2003; Sazima *et al.*, 2003 and Kaczorowski *et al.*, 2005). The high level of diversity within the family in addition to other unusual features have reflected in poor understanding of its phylogenetics. Fossil record of angiosperms particularly of Solanaceae (Collinson *et al.*, 1993) is very meager and relatively recent, so use of morphology and other conventional characters (Scotland *et al.*, 2003) is not convincing in revealing true phylogeny of the family. This all has necessitated using alternative marker types in phylogenetic analysis of the family. Since advent of molecular biology molecular markers have been constantly refined to serve the purpose. Genetic diversity studies through molecular markers will help to solve the taxonomic ambiguities of several genera further the study will unfold the diversity at genetic level which will be helpful in crop genetic studies and breeding programmes.

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