Review

Inclusion of Tomato in the Genus *Solanum* as “*Solanum lycopersicum*” is Evident from Phylogenetic Studies

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As DNA sequence data were rapidly accumulated in the last decade, the intense debate on the position of the genus “*Lycopersicon*” with respect to “*Solanum*” was recently settled. In this review, we focus on chloroplast DNA restriction fragment length polymorphism (cpRFLP) analysis and molecular phylogenetic study of the chloroplast-encoded NADH dehydrogenase (*ndhF*) gene of numerous Solanaceae family members including tomato, *Solanum lycopersicum* (formerly *Lycopersicon esculentum*). Both studies revealed that *S. lycopersicum* is clearly included in the large genus *Solanum*, which includes potato (*S. tuberosum*) and eggplant (*S. melongena*). All cpRFLP and different algorithms in *ndhF* phylogenetic analysis classified *S. lycopersicum* into the same clade as *S. tuberosum*. Comparative genome analysis using a high-density genetic linkage map of *S. lycopersicum* and *S. tuberosum* indicated that the chromosome structure is highly conserved between the two species. These recent studies indicated that tomato and potato are phylogenetically close and share a recent common ancestor.

Key Words: genus *Solanum*, phylogeny, scientific name, *Solanum lycopersicum*, tomato.

Introduction

The first Solanaceae family species introduced in Japan was eggplant, more than 800 years ago in the Heian period. Since then, numerous original eggplant cultivars have been bred in various parts of the country and are a popular vegetable in Japanese food. Because of the popularity of eggplant, “nasuka”, which means “family related to eggplant”, is the Japanese word for the Solanaceae family. On the other hand, tomato has become a popular Japanese food relatively recently. Although it was introduced in Japan about 300 years ago in the Edo period, it was esteemed as an ornamental plant until generally adapted as food in the last century.

In the academic world, tomato has long been distinguished from the genus *Solanum*, which includes eggplant (*Solanum melongena*) and potato (*Solanum tuberosum*) as well as 1400 other species, and classified in an original genus *Lycopersicon*. The scientific name *Lycopersicon esculentum* was given to tomato in the 1760s by a Scottish botanist Philip Miller, and the name has been widely accepted since then. Readers should refer to a well-summarized historical debate on the Solanaceae phylogenetic relationship by Spooner et al. (1993).

As a fruit of rapid progress in DNA sequencing technology in the 1990s, a large amount of DNA sequence data has been produced and accumulated in public databases. In the last decade, molecular phylogenetic analyses were accelerated using sequence data. The obtained results suggested that it is necessary to reclassify the plant kingdom. In this article, we review the reclassification of the genus *Solanum* with special emphasis on molecular phylogenetic studies at the DNA level, and conclude that the inclusion of tomato “*Solanum lycopersicum*” is quite persuasive.

Phylogenetic analysis of chloroplast DNA restriction sites

Olmstead and Palmer (1992) investigated the phylogeny of Solanaceae based on chloroplast DNA restriction site mapping. They took 42 species of Solanaceae and digested the chloroplast DNA with each of 10 restriction enzymes. Among the 1,000 fragments generated, 447 gave phylogenetically informative data. They performed restriction fragment length polymorphism (RFLP) analysis using 40 hybridization probes developed from *Nicotiana tabacum* chloroplast DNA, which had been completely sequenced (Shinozaki et al., 1986). They then mapped 14 restriction-fragment length variants representing insertions and deletions ranging in size from 150 to 700 base pairs. According to the result,

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Solaneae including *Capsicum*, *Solanum candidum*, *S. carolinense*, *S. luteoalbum*, *S. americanum*, and *Lycopersicon*, was monophyletic and was derived from an ancestral paraphyletic Cestroideae which includes *Nicotiana* and *Petunia*. The tree indicated that *Lycopersicon* was grouped into the same clade as other Solanums.

Spooner et al. (1993) also performed chloroplast RFLP analysis to test hypothetical relationships among *Solanum* subgenus *Potatoe*, *Cyphomandra* (tree-tomato), and *Lycopersicon*. As a result of analysis using 17 accessions of *Solanum* subgenus *Potatoe*, four other *Solanum*, three *Lycopersicon*, one *Cyphomandra*, and one each for *Capsicum* and *Datura* as the outgroup, they concluded that *Lycopersicon* should be treated as a member of the genus *Solanum*, subgenus *Potatoe*. They also provided supportive results for the inclusion of *Cyphomandra* in *Solanum*.

Olmstead and Palmer (1997) refined their work using the same methodology to investigate the detailed infrageneric phylogeny of subgenera, including *Lycopersicon* and *Cyphomandra* (tree-tomato). They took 49 species, of which 36 were *Solanum* and 13 were outgroup species. They showed that *Solanum*, including *Lycopersicon* and *Cyphomandra* formerly designated as

distinctive genera, are monophyletic. The result indicated that *Solanum* could be divided into 3 clades: Clade I, consisting of *S. aviculare*, *S. ptychanthum* (revised from *S. americanum* in the previous work of Olmstead and Palmer, 1992), *S. crispum*, *S. dulcamara* and *S. jasminoides*; Clade II, consisting of *S. lycopersicum*, *S. tuberosum* and *S. muricatum*; Clade III, consisting of the remaining sampled members of the genus including *S. luteoalbum* (*Cyphomandra*) (Fig. 1). The result suggested that *Lycopersicon* and *Cyphomandra* should be treated as a clade within the genus *Solanum* rather than as a distinctive genus.

Phylogenetic analysis based on *ndhF* sequences

It was previously demonstrated that NADH dehydrogenase (*ndhF*) encoded in the chloroplast genome is suitable for inferring the phylogenetic relationship at intra-familial level because of the elevated rate of base substitution in its nucleotide sequence compared to the ribulose biphosphate carboxylase (*rbcL*) gene accepted widely in large-scale phylogenetic analyses at the inter-familial level (Olmstead and Palmer, 1994; Savolainen and Chase, 2003). Bohs and Olmstead (1997) used 2000 base pairs of the *ndhF* sequence to analyze the phylogenetic relationship of *Solanum*. They sequenced

Fig. 1. Schematic view of the *Solanum* tree modified from Olmstead and Palmer (1997). *Solanum* was divided into 3 clades. *S. lycopersicum* was grouped into clade II with *S. tuberosum* and *S. muricatum*. Clade III included tree-tomato species e.g. *S. luteoalbum* and *S. betaceum*, as well as 19 spiny solanums such as *S. melongena*, which were classified into the subgenus *Leptostemonum*.

the *ndhF* gene for 18 species of *Solanum* for which the sampled species were generally common with those used in the chloroplast DNA RFLP (cpRFLP) study (Olmstead and Palmer, 1997). Results of two different algorithms, parsimony and maximum likelihood analyses, indicated that the genera *Lycopersicon* (as *S. lycopersicum*) and *Cyphomandra* (as *S. betaceum*) are nested within *Solanum* and inclusion of these two species supported the monophyletic feature of *Solanum*. *Solanum* was distinguished by 4 clades in this analysis, where *S. lycopersicum* and *S. tuberosum* were classified in the same clade, which included no other species. Readers are encouraged to see the phylogenetic tree produced by grafting cpRFLP (Olmstead and Palmer, 1997) and *ndhF* (Bohs and Olmstead, 1997) histories in a review article by Kellogg (1998).

Conclusion

The position of the genus formerly known as *Lycopersicon* relative to *Solanum* has been a long-standing question, which was solved only recently by utilizing DNA structural information since it may provide direct evidence of molecular evolution. This review focused on phylogenetic studies based on cpRFLP (Olmstead and Palmer, 1992; Olmstead and Palmer, 1997) and *ndhF* sequence (Bohs and Olmstead, 1997). Alternative researches also support the idea that *Solanum* is monophyletic. High-density genetic linkage maps of tomato (*S. lycopersicum*), potato (*S. tuberosum*), and eggplant (*S. melongena*) were generated (Doganlar et al., 2002; Tanksley et al., 1992) and comparison of the chromosome structure based on a common set of DNA markers was made. The result indicated that the chromosome organization of tomato and potato could be distinguished by only 5 rearrangements resulting in chromosome arm inversions. This strikingly similar chromosome organization indicates that they share a recent common ancestor. In the case of comparison between tomato/eggplant and potato/eggplant, 28 and 24 rearrangements were observed, respectively. It was also indicated that these 3 *Solanum* genomes were largely collinear.

Tomato is recognized as a model organism of Solanaceae and its entire euchromatic genome is being sequenced (http://www.sgn.cornell.edu/about/tomato_sequencing.pl, October 2, 2008). In the near future, an interesting challenge to elucidate evolutionary history of *Solanum* on a genome-wide scale should become a reality.

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