Eggplant origins: Out of Africa, into the Orient

Terri L. Weese[1,2] & Lynn Bohs[1]

1 *Department of Biology, University of Utah, Salt Lake City, Utah 84112, U.S.A.*
2 *Present address: Centre for Plant Biodiversity Research, CSIRO Plant Industry, Canberra, ACT 2601, Australia*
Author for correspondence: *Lynn Bohs, bohs@biology.utah.edu*

Abstract The eggplant (*Solanum melongena* L.), also known as aubergine or brinjal, has been cultivated for centuries in the Old World and is currently a crop species of global importance. Despite this, hypotheses of eggplant evolution have been fraught with controversy. Previous conclusions have relied solely on morphological characters or have been based on insufficient taxonomic sampling, leading to conflicting opinions of the number of species, phylogenetic relationships, and patterns of domestication in a group of related taxa termed the *S. melongena* complex. The *S. melongena* complex shows a series of morphological intermediates from small-fruited spiny plants to large-fruited non-spiny plants. We use DNA sequence data to show that eggplants arose in Africa and were dispersed throughout the Middle East to Asia. *Solanum linnaeanum*, a wild species not previously associated with eggplant evolution, is a member of the *S. melongena* complex. These data provide the most comprehensive evidence to date for the evolution of the cultivated eggplant.

Keywords Africa; Asia; crop domestication; eggplant; *Solanum incanum*; *Solanum melongena*

INTRODUCTION

The eggplant (*Solanum melongena* L.), also known as aubergine or brinjal, has been cultivated for centuries in Asia, Africa, Europe, and the Near East and is currently a crop species of global importance. Although commonly sold in American, European, and Australian markets, over 90 per cent of eggplant production is concentrated in seven countries, including China, India, Egypt, Turkey, and Japan (Lucier & Jerardo, 2006). It is one of a dozen or so species of the Solanaceae, or nightshade family, that have been selected and developed as human food plants; others include the New World crops tomato (*Solanum lycopersicum* L.), potato (*S. tuberosum* L.), and chili pepper (*Capsicum* spp.). The large, oblong, purple-skinned "Black Beauty"-type eggplant is a familiar item in grocery stores and home gardens. However, wild and semi-domesticated eggplant relatives usually have small, round, yellow fruits and the plants are abundantly prickly (Fig. 1).

In addition to *S. melongena*, two other Old World *Solanum* species are commonly known as "eggplants" and cultivated for their edible fruits. *Solanum aethiopicum* L., the scarlet eggplant, is native to Africa but has been introduced into the West Indies and South America, primarily Brazil (Lester & Niakan, 1986; Daunay & al., 2001a). This species differs from *S. melongena* in its small white corollas and usually bright scarlet fruits that often resemble *Capsicum* peppers. It is widely grown in Africa and South America for its edible fruits, and human selection has resulted in a variety of domesticates with differing fruit morphologies. In addition, some African forms of *S. aethiopicum* with glabrous leaves are used as cooked vegetables. *Solanum macrocarpon* L., the Gboma eggplant, is native to the humid tropics of central Africa and also grown for its edible fruits and leaves. It can be distinguished from *S. melongena* by its usually deeply lobed leaves and very large calyces. *Solanum melongena* and *S. macrocarpon* are placed into *S.* sect. *Melongena* (Mill.) Dunal, whereas *S. aethiopicum* belongs to *S.* sect. *Oliganthes* (Dunal) Bitter. Although all three domesticated eggplant species are partially interfertile (Daunay & al., 2001a), *S. aethiopicum* and *S. macrocarpon* are considered to be only distantly related to the brinjal eggplant and not directly involved in its evolution (Whalen, 1984). In the remainder of this paper, the term "eggplant" refers to *S. melongena* and its immediate relatives.

The relationships among wild, semi-domesticated, and cultivated forms of *S. melongena* have been controversial, and the origin, evolution, migration patterns, and systematics of this crop have been unclear. Taxonomists have recognized anywhere from one to dozens of species within the eggplant complex, have debated about the species most closely related to eggplants, and have developed varied hypotheses of eggplant evolution and biogeography. In this study, we investigate the phylogenetic relationships of eggplant and its close relatives using DNA sequence data and compare the results to previous studies. In particular, we test the monophyly of the eggplant complex and several specific hypotheses formulated by Lester and colleagues (Lester & Hasan, 1991; Mace & al., 1999; Daunay & al., 2001a) regarding eggplant taxonomy, evolution, and biogeography. Studies of crop plant evolution such as these can unravel interesting patterns of plant migration and domestication and identify closely related species that may contain useful genes for desirable agronomic traits as well as disease and herbivore resistance. Conclusions about eggplant evolution may also shed light on the domestication processes involved in other solanaceous crops such as tomato, potato, and chili pepper.

Wild plants, field weeds, and landraces (primitive cultivars) forming the eggplant complex are distributed from Africa throughout the Middle East into India and Asia. As a whole, the African taxa are morphologically variable and occupy ecologically diverse habitats ranging from equatorial savanna woodlands to near deserts. Individual populations likely have adapted to local environmental conditions, and numerous

taxonomists have attempted to account for this variation by recognizing as many as 27 species among the African eggplants (Bitter, 1923). Alternatively, other workers have lumped all the wild African members of the eggplant complex into a single species, *S. incanum* (Furini & Wunder, 2004; Singh & al., 2006). Asian eggplants comprise wild and weedy plants, landraces, and derived cultivars that have been recognized as separate species or lumped into a single species, *S. melongena*.

For the sake of simplicity we will use the system of Lester (Table 1) that recognizes two botanical species, *S. incanum* and *S. melongena*, each with four groups (Lester & Hasan, 1991; Daunay & al., 2001a). The *S. incanum* lineage, comprising groups A–D, is native to eastern Africa and the Middle East and includes wild plants exhibiting morphologically variable, locally adapted ecotypes. *Solanum melongena* groups E–H include wild and weedy plants as well as landraces and derived cultivars found in India and Asia and now cultivated worldwide (Fig. 2).

Lester and colleagues considered *S. incanum* groups A and B to be the most plesiomorphic forms within the *S. incanum–S. melongena* complex (Lester & Hasan, 1991). Within central east Africa (Fig. 2), group A is found in equatorial savanna woodlands and group B in temperate savanna grasslands (Mace & al., 1999). The plants are highly variable morphologically and are mainly distinguished by stature and leaf width. The fruits are small, round, and yellow and the plants are variably prickly (Fig. 1). Plants of groups A and B were thought to have expanded their original ranges to the north and into the Middle East, evolving into group C, and adapting to extreme xerophytic conditions to the south to give rise to group D (Fig. 2; Lester & Hasan, 1991; Daunay & al., 2001a).

According to Lester and colleagues (Lester & Hasan, 1991; Daunay & al., 2001a), *S. incanum* group C of the Middle East was introduced into Asia, either spontaneously or deliberately during human migrations. Within Asia, this group gave rise to a widespread, weedy form identified as *S. melongena* group F (Lester & Hasan, 1991; Mace & al., 1999; Daunay & al., 2001a). As a garden weed, *S. melongena* group F may have been gradually and repeatedly domesticated into the primitive cultivars of *S. melongena* group G. These represent the small fruited, early domesticates commonly grown in gardens of Southeast Asia. Primitive cultivars of *S. melongena* group G were postulated to have spread to India as crop plants, where they were further selected into the advanced cultivars of group H that are now cultivated worldwide (Lester & Hasan, 1991).

Fig. 1. Flowers and fruits of *Solanum incanum* groups A–D and *S. melongena* groups E–H. Scale bars = 1 cm. Note the increasing size of fruits in *S. incanum* groups A through D and *S. melongena* groups F through H.

Solanum melongena group E includes extremely prickly, low growing disordered plants that are often weeds of cultivated land. These may have persisted in fallow garden plots and were thought by Lester to represent a reversion to the feral prickly state from the primitive cultivated forms of group G (Lester & Hasan, 1991; Daunay & al., 2001a). Alternatively, some authors have postulated that *S. melongena* group E represents the wild ancestor from which the other *S. melongena* groups were derived (Lester & Hasan, 1991).

Sanskrit texts document the wide use of eggplants for food and medicine in India at least 2000 years ago (Bhaduri, 1951; Khan, 1979), and Chinese literature mentions eggplant cultivation in southwest China as early as 59 BC (Wang & al., 2008). Domestication of eggplants into *S. melongena* group H is therefore likely to have taken place subsequent to about the 1st century BC in India, China, or both. Through selection, plants of *S. melongena* group H are far less prickly than the primitive cultivars; prickles are reduced and limited to the calyx lobes or are completely absent (Fig. 1). Additionally, fruits are as much as five times as large as those observed in the primitive cultivars. According to cultural and linguistic evidence, eggplants then spread throughout Indochina and beyond along human

Table 1. Characteristics of the eggplant groups following Lester's classification (Daunay & al., 2001a). *Solanum linnaeanum* is added for comparison based on the results reported here. Alternative taxonomic designation lists scientific names commonly encountered in the literature for the groups or taxa.

Group	Alternative taxonomic designation	Distribution	Distinguishing characteristics
S. incanum group A	*S. campylacanthum* A. Rich.	Tropical and equatorial Africa	Wild; usually prickly; fruits 1–1.5 cm in diameter
S. incanum group B	*S. panduriforme* E. Mey., *S. delagoense* Dunal	Subtropical southern African savannas	Wild; usually prickly; fruits 1–1.5 cm in diameter
S. incanum group C	*S. incanum* L. sensu stricto	Central and northern Africa to Middle East and Southwest Asia	Wild; somewhat prickly; fruits 1.6–2.1 cm in diameter
S. incanum group D	*S. lichtensteinii* Willd.	Southern African semi-deserts	Wild; prickly; fruits 3.5–4.5 cm in diameter
S. melongena group E	*S. insanum* L.	India and Central Asia	Field weeds; extremely prickly; fruits ca. 2 cm in diameter
S. melongena group F	*S. cumingii* Dunal	Indochina, Indonesia	Wild plants or field weeds; moderately prickly; fruits 2.5–3 cm in diameter
S. melongena group G	*S. ovigerum* Dunal	Southeast Asia	Primitive cultivars of southeast Asia; slightly prickly; fruits 3–4 cm in diameter
S. melongena group H	*S. melongena* L.	Worldwide	Advanced cultivars grown worldwide; slightly or not prickly, prickles restricted to calyx; fruits highly variable in size and color (10–20 cm long and 7–12 cm in diameter).
S. linnaeanum Hepper & P.-M.L. Jaeger	*S. sodomeum* L., *S. hermannii* Dunal	South Africa; introduced into the Mediterranean, Macaronesia, and other areas	Wild; prickly; fruits ca. 2.5 cm in diameter

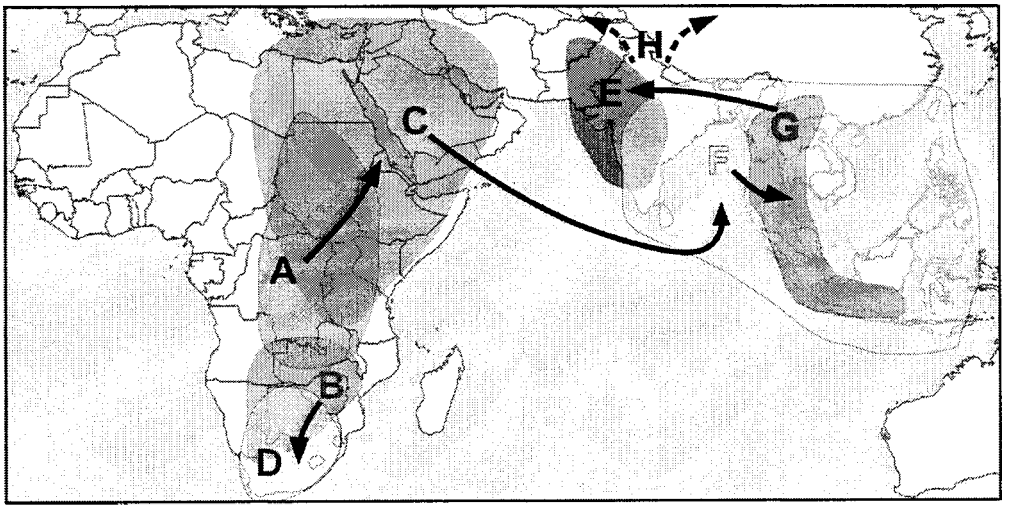

Fig. 2. Distribution of *Solanum incanum* groups A–D and *S. melongena* groups E–G. Arrows indicate the proposed migration of the wild species of *S. incanum* groups A and B into South Africa and the Middle East, the introduction of *S. incanum* group C into Asia, the domestication of *S. melongena* group G from weedy plants of group F, and the reversion of the primitive group G cultivars to the feral form *S. melongena* group E. *Solanum melongena* group H is cultivated worldwide and its specific range is not shown on the map.

migration routes (Bhaduri, 1951; Lester & Hasan, 1991; Daunay & al., 2001a,b, 2007) and were present in Japan by the 8th century. They may have moved westward along the Silk Route, were introduced into northern Africa prior to the Middle Ages, and into the Iberian Peninsula during the Moorish invasion in the 9th century. Eggplant cultivation began in Italy during the 15th and 16th centuries, expanded into other parts of Europe, and ultimately spread worldwide (Daunay & al., 2001b, 2007).

The above concepts regarding the origin, introduction, and domestication of the eggplant provide a working hypothesis that can be tested in a phylogenetic context. Previous studies have explored levels of variation among members of the *S. incanum–S. melongena* species complex using experimental crosses (Rao, 1979; Daunay & al., 1991, 1999), allozymes (Lester & Hasan 1991; Karihaloo & Gottlieb, 1995), AFLPs (Mace & al., 1999; Furini & Wunder, 2004), RAPDs (Karihaloo & al., 1995; Singh & al., 2006), and chloroplast restriction site data (Sakata & al., 1991; Sakata & Lester, 1994, 1997), but no study to date has examined these hypotheses in an explicitly phylogenetic context using DNA sequence data and complete sampling of members of each of the *S. incanum–S. melongena* species groups.

MATERIALS AND METHODS

Taxon sampling and DNA sequencing. — Previous analyses (Levin & al., 2006) were used to identify appropriate outgroups for the eggplant complex. A total of 43 individuals were included in this study, including three species previously shown to be outside the Old World clade (*S. elaeagnifolium*, *S. tridynamum*, *S. hindsianum*; Levin & al., 2006). To the extent possible, two accessions of each *S. incanum–S. melongena* species group were sampled. Alternative taxonomic designations for the *S. incanum–S. melongena* groups are given in Table 1. DNA was extracted from fresh or silica-dried leaves, or occasionally from herbarium specimens, using either a modified CTAB buffer method (Doyle & Doyle, 1987) followed by cesium chloride density gradient centrifugation or phenol chloroform purification, or using the DNEasy plant mini extraction kit (Qiagen, Inc., Valencia, California, U.S.A.).

PCR amplification was performed using methods described previously for the nuclear ribosomal internal transcribed spacer regions 1 and 2 (ITS; White & al., 1990; Baldwin & al., 1995; Bohs & Olmstead, 2001; Levin & al., 2006; Bohs, 2007) and granule bound starch synthase gene (*waxy*; Levin & al., 2006), and the chloroplast *trnT-L* and *trnL-F* intergenic spacer region (*trnT-F*; Taberlet & al., 1991; Bohs & Olmstead, 2001; Bohs, 2004). PCR products were cleaned using the QIAquick PCR purification kit (Qiagen, Inc.) and sequenced at the University of Utah DNA Sequencing Core Facility using an ABI automated sequencer. Sequences were edited in Sequencher (Gene Codes Corp., Ann Arbor, Michigan, U.S.A.), and all new sequences were submitted to GenBank (Appendix).

Data assembly and analysis. — Sequence alignment was straightforward and was performed manually in Se-Al (Rambaut, 1996). Phylogenetic analyses were performed using both parsimony and Bayesian methods for each dataset separately prior to combining the data into a total-evidence analysis. Parsimony analyses were conducted using PAUP* v.4.0b10 (Swofford, 2002). All characters were weighted equally in analyses that implemented TBR branch swapping with 1000 heuristic random addition replicates. Bootstrapping (BS; Felsenstein, 1985) was used to evaluate branch support with 1000 random addition replicates and TBR branch swapping. Parsimony strict consensus trees of the separate datasets (*waxy*, *trnT-F*, ITS) are illustrated in Figs. S1–S3 in the Electronic Supplement.

Prior to combined analyses, two methods were used to evaluate data congruence. First, bootstrap values were used to identify strongly supported clades (>90% bootstrap support, 95% posterior probabilities) in each phylogeny. Strongly supported nodes that suggest different relationships were considered to be in conflict. Second, the incongruence length difference test (ILD; Farris & al., 1995) was implemented in PAUP* (as the partition homogeneity test) using 1000 partition homogeneity replicates, TBR branch swapping, and including constant characters.

Prior to performing Bayesian analyses, a general model of nucleotide evolution was selected for each dataset using the AIC criterion identified in Modeltest v.3.7 (Posada & Crandall, 1998). The best-fit model for ITS was TIM+I+G, for *waxy* was TrN+I, and for *trnT-F* was TVM+G. MrBayes v.3.1.2 (Huelsenbeck & Ronquist, 2001) was used to analyze each dataset separately prior to combining. Two replicates of four Markov chains were run for 3,000,000 generations for each dataset, each initiated from a random tree and sampled every 1,000 generations. All parameters from each analysis were visualized graphically, and samples obtained prior to achieving stationary were discarded. Model parameters, likelihood values, and clade posterior probabilities (PP) from separate analyses of each data partition were compared before combining datasets to assess convergence in independent runs, and then summarized on a majority rule consensus tree (Huelsenbeck & al., 2002; Huelsenbeck & Imennov, 2002).

RESULTS

ITS sequences ranged in length from 586 to 639 bases, with an aligned length of 676 characters. Of these, 78 characters were parsimony informative. Parsimony analyses generated 2964 most parsimonious trees of 275 steps, consistency index (CI) = 0.633, retention index (RI) = 0.678. Trees obtained prior to generation 100,000 in Bayesian analysis were eliminated as burn-in.

The *waxy* sequences ranged from 1715 to 1731 bases in length. Aligned sequence length was 1738 characters, and the alignment contained 62 parsimony informative characters. The 1659 most parsimonious trees had a length of 226 steps, CI = 0.920, RI = 0.927. The first 10,000 trees were eliminated as burn-in from Bayesian analyses.

The length of *trnT-F* sequences varied between 1666 and 1854 bases, with an aligned length of 2050 characters, of which 42 were parsimony informative. The single most parsimonious trees had a length of 131 steps, CI = 0.969, RI = 0.978. The first 10,000 trees were eliminated as burn-in in Bayesian analyses.

Parsimony and Bayesian trees obtained from separate and combined analyses of ITS (White & al., 1990; Baldwin & al., 1995; Levin & al., 2006; Bohs, 2007), *waxy* (Levin & al., 2006), and *trnT-F* (Taberlet & al., 1991; Bohs & Olmstead, 2001; Bohs, 2004) generated topologies that were identical for the principal groupings (Figs. S1–S3 in the Electronic Supplement). However, results of the ILD test suggest that the data partitions are incongruent ($P = 0.001$). Visual examination of toplogies inferred from these three regions suggest few strongly supported differences in relationships. The toplogies differ most dramatically in the resolution of outgroup taxa (Figs. S1–S3). The incongruence could reflect variation in the substitution rates between markers (Dolphin & al., 2000; Darlu & Lecointre, 2002), or differences in the number of informative characters between data partitions. Because the toplogies vary mainly in placement of outgroup taxa, and topological comparisons indicated no well-supported differences among ingroup taxa, we proceeded to combine the data for subsequent analyses and consider the ILD results to unreliable as has frequently been noted elsewhere (e.g., Dolphin & al., 2000; Yoder & al., 2001; Barker & Lutzoni 2002; Darlu & Lecointre, 2002).

A combined analysis including each DNA sequence region for all 43 taxa included 182 parsimony informative characters and resulted in 44 most parsimonious trees of 663 steps. The strict consensus tree inferred from the combined data was more resolved at all taxonomic levels (Fig. 3) than were those based on the separate analyses. The majority rule consensus tree produced from the mixed model Bayesian analysis of the three DNA sequence regions is consistent with the parsimony strict consensus tree, although the Bayesian tree is better resolved than is the parsimony tree. These analyses confirm a close relationship among the eight species groups in the *S. incanum–S. melongena* complex, in agreement with results of other methodological approaches such as morphological studies, crossing experiments, and analyses of molecular data.

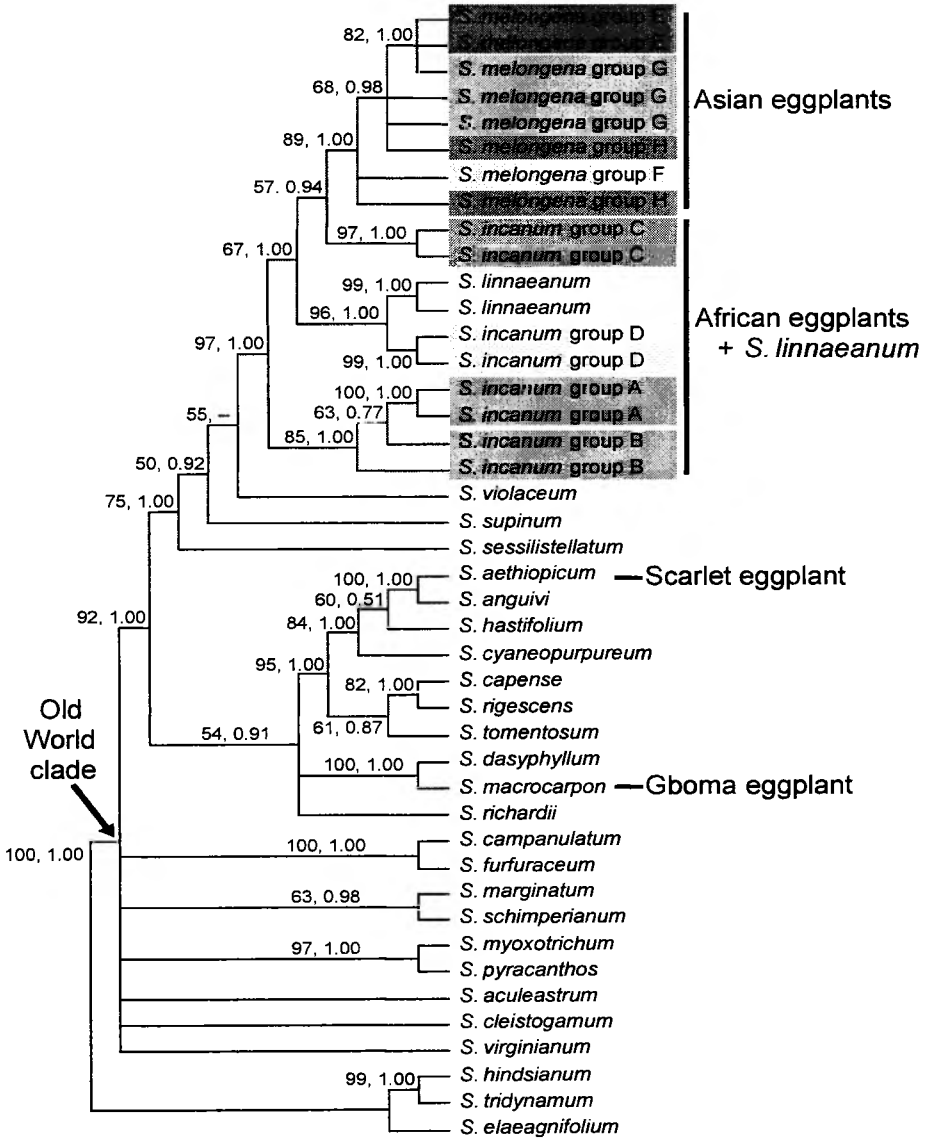

Fig. 3. Maximum parsimony strict consensus tree from combined sequence data from the nuclear internal transcribed spacer region (ITS) and granule bound starch synthase gene (*waxy*) and the chloroplast *trnT-L* and *trnL-F* intergenic spacer region. Numbers above branches indicate bootstrap values and Bayesian posterior probabilities over 50%. All taxa shown are Old World spiny Solanums except *S. hindsianum*, *S. tridynamum*, and *S. elaeagnifolium*.

■ DISCUSSION

The maximum parsimony strict consensus tree illustrates that all members of the *S. incanum–S. melongena* species complex form a clade, with the African taxa forming a paraphyletic grade with respect to the monophyletic Asian accessions. This tree implies an African origin for the Asian accessions. *Solanum linnaeanum*, a wild South African species, is nested within the *S. incanum–S. melongena* clade and sister to *S. incanum* group D (Fig. 3).

Within the African eggplants, *S. incanum* groups A and B are sister to all other *S. incanum–S. melongena* taxa and form a strongly supported clade (Fig. 3). Plants of groups A and B easily cross to form fertile offspring, although crosses between groups A and B and all other groups in *S. incanum* and *S. melongena* are far more difficult (Lester & Hasan, 1990, 1991; Daunay & al., 2001a).

Solanum incanum groups C and D, however, are not part of this clade, and the wild species *S. linnaeanum* is apparently closely related to *S. incanum* group D. *Solanum incanum* group D is adapted to the xerophytic, semi-desert conditions of southern Africa. It has been suggested that *S. incanum* group D may have adapted to these more extreme desert conditions from *S. incanum* group B since their ranges partially overlap (Fig. 2; Lester & Hasan, 1991). However, our results suggest a close relationship between *S. incanum* group D and *S. linnaeanum*. *Solanum linnaeanum* is also from South Africa, but has not been regarded as a member of the *S. incanum–S. melongena* complex (Whalen, 1984). In a broadly sampled study using AFLP data, it was noted that the *S. incanum–S. melongena* complex was more closely related to *S. linnaeanum* than to other cultivated African "eggplants" such as *S. macrocarpon* (Gboma eggplant) or *S. aethiopicum* (the scarlet eggplant), although it is difficult to discern which members of the *S. incanum–S. melongena* species complex were sampled in this analysis (Furini & Wunder, 2004). In our phylogenies, the Gboma and scarlet eggplants are not part of the *S. incanum–S. melongena* complex or clade (Fig. 3).

Morphologically, *S. incanum* group D and *S. linnaeanum* are quite different. Plants of *S. incanum* group D are somewhat prickly and densely tomentose (Lester & Hasan, 1991; Daunay & al., 2001a). The leaves are entire to slightly lobed, as in all members of the *S. incanum–S. melongena* complex, and the fruits are fairly large (3.5–4.5 cm in diameter), lack stripes, and are yellow at maturity (Fig. 1). Plants of *S. linnaeanum* are extremely prickly and nearly glabrous to sparsely hairy. The leaves are highly pinnately dissected and the fruits are small (<3 cm diameter) and initially white with green stripes, turning yellow at maturity. Although crossability between *S. incanum* group D and *S. linnaeanum* has not been documented, both taxa can form fertile hybrids with the domesticated eggplant (presumably *S. melongena* group H; Lester & Hasan, 1991; Daunay & al., 1991, 1999), and *S. linnaeanum* was used as the female parent to produce a genetic linkage map for the cultivated eggplant (Doganlar & al., 2002); this cross, however, was possible only through embryo rescue (M.-C. Daunay, pers. comm. 2007). It is possible that the observed sister-group relationship between *S. incanum* group D and *S. linnaeanum* may be the product of occasional gene flow in shared portions of their ranges. However, population-level sampling across the range of *S. linnaeanum* is necessary to draw firm conclusions regarding introgression between these two taxa. *Solanum linnaeanum* exhibits resistance to high salinity and certain pathogens and therefore may be a source of genes conferring useful traits to cultivated eggplants (Daunay & al., 1991).

As previously hypothesized (Lester & Hasan, 1991; Daunay & al., 2001a), *S. incanum* group C is sister to the Asian taxa. The range of *S. incanum* group C includes northeast Africa and the Middle East (Fig. 2), where it exists as a wild plant of undisturbed habitats. The plants are tomentose and somewhat prickly, with rather small fruits (1.6–2.1 cm in diameter; Daunay & al., 2001a) that are yellow at maturity (Fig. 1). The fruits of *S. incanum* are thought to have been used by humans during the Palaeolithic and Neolithic epochs to tan animal hides and are important today in African traditional medicine (Bitter, 1923; Lester & Hasan, 1991; Bukenya-Ziraba & Carasco, 1999; Daunay & al. 2001a), thus the plants may have been encouraged, or at least tolerated by migrating humans. Alternatively, the fruits may have dispersed without human intervention.

The Asian eggplants put into *S. melongena* groups F through H form a well-supported clade (Fig. 3). *Solanum melongena* group E is nested within this clade and is sister to one accession of *S. melongena* group G, supporting the idea proposed by Lester that the prickly plants of group E represent primitive eggplant cultivars of group G that reverted to feral weedy forms (Mace & al., 1999; Daunay & al., 2001a).

Relationships among the Asian *S. melongena* eggplant complex are poorly resolved based on these data, and the specifics of eggplant evolution and domestication in Asia remain unclear. Genetic variation within the Asian taxa sampled here is quite low, and insufficient nucleotide substitutions exist to resolve relationships in the phylogeny. Several processes that are not mutually exclusive may account for this lack of resolution. For instance, the tree suggests a single introduction of eggplants into Asia (Fig. 3), which could have produced a severe genetic bottleneck and extreme loss of variation, especially if this introduction was a relatively recent event. Further, if the early cultivars were independently domesticated in different areas, exclusive taxon lineages are not expected in the phylogeny; rather each primitive cultivar should be allied with its parent population. The low genetic diversity observed here may also be a result of sampling bias that underrepresents the complexity of the Asian *S. melongena* alliance. Finally, all members of the Asian eggplant complex are highly interfertile (Lester & Hasan, 1991; Daunay & al., 1991, 2001a), and gene flow is likely among individuals from various groups, particularly if the early domesticates, the weedy forms, and the feral forms are growing in close proximity, as in a garden plot. Therefore, relationships among these taxa are expected to be reticulate and not tree-like and may best be interpreted using population-level sampling and methodology.

Human selection has resulted in a loss of prickles and an enormous increase in fruit size and color in the cultivated eggplant (*S. melongena* group H). Selection for larger fruit size is a common theme in plant domestication, and selective processes similar to those in eggplant have operated on the tomato

(*Solanum lycopersicum* L.), which also produces fruits much larger than its wild relative, *S. pimpinellifolium* L. (Tanksley & Fulton, 2007). Through genetic linkage mapping, it has been shown that fruit size, shape, color, and plant prickliness in eggplant are controlled by a small number of genetic loci with large phenotypic effects and that a significant proportion of these loci have putative orthologs in tomato, potato, and pepper, three other domesticates from the Solanaceae (Doganlar & al., 2002). This suggests that domestication within *Solanum*, and probably within Solanaceae as a whole, is the result of changes at specific loci that have responded similarly to independent selection pressures applied through the domestication process of the tomato, potato, and pepper in the New World and the eggplant in the Old World (Doganlar & al., 2002; Tanksley & Fulton, 2007).

The eggplant has travelled far geographically and evolutionarily from its small-fruited spiny ancestors of the African savannas to the large-fruited, non-spiny "Black Beauty" cultivars usually found in American grocery stores and home gardens. Molecular results confirm many of the hypotheses for the evolution of the eggplant originally postulated from morphology and provide a phylogenetic framework from which to extend sampling both geographically and taxonomically in order to examine how and where this important crop was domesticated. Further investigations at the population level may unravel the still enigmatic relationships in the Asian eggplant complex. Cultural, archaeological, and linguistic evidence may shed light on the movement of the *S. incanum* complex from Africa to Asia and the timing of these events. Additionally, traditional breeding programs as well as genetic engineering techniques may exploit the wealth of useful characters found in wild and semi-domesticated members of the *S. incanum-melongena* complex such as *S. linnaeanum* for the improvement of the advanced eggplant cultivars.

■ ACKNOWLEDGEMENTS

We thank S. Howsden, R. Levin, N. Myers, S. Rosu, and A. van Wagenen for laboratory and greenhouse assistance, R.N. Lester, C. Daunay, and the Botanical Garden, Radboud University, Nijmegen, The Netherlands for plant materials, E. Nordman for mapping assistance, J. Sperry, S. Stern, E. Tepe, and two anonymous reviewers for manuscript comments, and NSF grants DEB-0235339 and DEB-0316614 for financial support. This paper is dedicated to the late R.N. Lester, a pioneer in the study of eggplant systematics and evolution.

■ LITERATURE CITED

Baldwin, B.G., Sanderson, M.J., Porter, J.M., Wojciechowski, M.F., Campbell, C.S. & Donoghue, M.J. 1995. The ITS region of nuclear ribosomal DNA: A valuable source of evidence on angiosperm phylogeny. *Ann. Missouri Bot. Gard.* 82: 247–277.

Barker F.K. & Lutzoni F.M. 2002. The utility of the incongruence length difference test. *Syst. Biol.* 51: 625–637.

Bhaduri, P.N. 1951. Inter-relationship of non-tuberiferous species of *Solanum* with some consideration of the origin of Brinjal (*S. melongena* L.). *Indian J. Genet. Pl. Breed.* 11: 75–82.

Bitter, G. 1923. Solana Africana, Part IV. *Repert. Spec. Nov. Regni Veg. Beih.* 16: 1–320.

Bohs, L. 2004. A chloroplast DNA phylogeny of *Solanum* section *Lasiocarpa*. *Syst. Bot.* 29: 177–187.

Bohs, L. 2007. Phylogeny of the Cyphomandra clade of the genus *Solanum* (Solanaceae) based on ITS sequence data. *Taxon* 56: 1012–1026.

Bohs, L. & Olmstead, R.G. 2001. A reassessment of *Normania* and *Triguera* (Solanaceae). *Pl. Syst. Evol.* 228: 33–48.

Bukenya-Ziraba, R. & Carasco, J.F. 1999. Ethnobotanical aspects of *Solanum* L. (Solanaceae) in Uganda. Pp. 345–360 in: Nee, M., Symon, D.E., Lester, R.N. & Jessop, J.P. (eds.). *Solanaceae IV: Advances in biology and utilization*. Kew: Royal Botanic Gardens.

Darlu, P. & Lecointre, G. 2002. When does the incongruence length difference test fail? *Molec. Biol. Evol.* 19: 432–437.

Daunay, M.-C., Dalmon, A. & Lester, R.N. 1999. Management of a collection of *Solanum* species for eggplant (*Solanum melongena*) breeding purposes. Pp. 369–383 in: Nee, M., Symon, D.E., Lester, R.N. & Jessop, J.P. (eds.), *Solanaceae IV: Advances in biology and utilization*. Kew: Royal Botanic Gardens.

Daunay, M.-C., Laterrot, H. & Janick, J. 2007. Iconography of the Solanaceae from antiquity to the XVIIth century: A rich source of information on genetic diversity and uses. Pp. 59–88 in: Spooner, D.M., Bohs, L., Giovannoni, J., Olmstead, R.G. & Shibata, D. (eds.), *Solanaceae VI: Genomics meets biodiversity*. Acta Horticulturae (ISHS), vol. 745. Leuven: International Society for Horticultural Science.

Daunay, M.-C., Lester, R.N. & Ano, G. 2001a. Eggplant. Pp. 199–222 in: Charrier, A., Jacquot, M., Hamon, S. & Nicolas, D. (eds.), *Tropical plant breeding*. Montpellier: Science Publishers.

Daunay, M.-C., Lester, R.N., Gebhardt, C.G., Hennart, J.W., Jahn, M., Frary, A. & Doganlar, S. 2001b. Genetic resources of eggplant (*Solanum melongena*) and allied species: A new challenge for molecular geneticists and eggplant breeders. Pp. 251–274 in: van den Berg, R.G., Barendse, G.W.M., van der Weerden, G.M. & Mariani, C. (eds.), *Solanaceae V: Advances in taxonomy and utilization*. Nijmegen: Nijmegen Univ. Press.

Daunay, M.-C., Lester, R.N. & Laterrot, H. 1991. The use of wild species for the genetic improvement of Brinjal eggplant (*Solanum melongena*) and tomato (*Lycopersicum esculentum*). Pp. 389–412 in: Hawkes, J.G., Lester, R.N., Nee, M. & Estrada, N. (eds.), *Solanaceae III: Taxonomy, chemistry, and evolution*. Kew: Royal Botanic Gardens.

Doganlar, S., Frary, A., Daunay, M.-C., Lester, R.N. & Tanksley, S.D. 2002. Conservation of gene function in the Solanaceae as revealed by comparative mapping of domestication traits in eggplant. *Genetics* 161: 1713–1726.

Dolphin, K., Belshaw, R., Orme, C.D.L. & Quicke, D.L.J. 2000. Noise and incongruence: Interpreting results of the incongruence length difference test. *Molec. Phylog. Evol.* 17: 401–406.

Doyle, J.J. & Doyle, J.A. 1987. A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochem. Bull.* 19: 11–15.

Farris, J.S., Källersjö, M., Kluge, A.G. & Bult, C. 1995. Constructing a significance test for incongruence. *Syst. Biol.* 44: 570–572.

Felsenstein, J. 1985. Confidence limits on phylogenies: An approach using the bootstrap. *Evolution* 39: 783–791.

Furini, A. & Wunder, J. 2004. Analysis of eggplant (*Solanum melongena*)-related germplasm: Morphological and AFLP data contribute to phylogenetic interpretations and germplasm utilization. *Theor. Appl. Genet.* 108: 197–208.

Huelsenbeck, J.P. & Imennov, N.S. 2002. Geographic origin of human mitochondrial DNA: Accommodating phylogenetic uncertainty and model comparison. *Syst. Biol.* 51: 155–165.

Huelsenbeck, J.P., Larget, B., Miller, R.E. & Ronquist, F. 2002. Potential applications and pitfalls of Bayesian inference of phylogeny. *Syst. Biol.* 51: 673–688.

Huelsenbeck, J.P. & Ronquist, F. 2001. MrBayes: Bayesian inference of phylogenetic trees. *Bioinformatics* 17: 754–755.

Karihaloo, J.L., Brauner, S. & Gottlieb, L.D. 1995. Random amplified polymorphic DNA variation in the eggplant, *Solanum melongena* L. (Solanaceae). *Theor. Appl. Genet.* 90: 767–770.

Karihaloo, J.L. & Gottlieb, L.D. 1995. Allozyme variation in the eggplant, *Solanum melongena* L. (Solanaceae). *Theor. Appl. Genet.* 90: 578–583.

Khan, R. 1979. *Solanum melongena* and its ancestral forms. Pp. 629–636 in: Hawkes, J.G., Lester, R.N. & Skelding, A.D. (eds.), *The biology and taxonomy of Solanaceae*. London: Academic Press.

Lester, R.N. & Hasan, S.M.Z. 1990. The distinction between *Solanum incanum* L. and *Solanum insanum* L. (Solanaceae). *Taxon* 39: 521–523.

Lester, R.N. & Hasan, S.M.Z. 1991. Origin and domestication of the brinjal eggplant, *Solanum melongena*, from *Solanum incanum*, in Africa and Asia. Pp. 369–387 in: Hawkes, J.G., Lester, R.N., Nee, M. & Estrada, N. (eds.), *Solanaceae III: Taxonomy, chemistry, and evolution*. Kew: Royal Botanic Gardens.

Lester, R.N. & Niakan, L. 1986. Origin and domestication of the scarlet eggplant, *Solanum aethiopicum*, from *S. anguivi* in Africa. Pp. 433–456 in: D'Arcy, W.G. (ed.), *Solanaceae: Biology and systematics*. New York: Columbia Univ. Press.

Levin, R.A., Myers, N.R. & Bohs, L. 2006. Phylogenetic relationships among the "spiny solanums" (*Solanum* subgenus *Leptostemonum*, Solanaceae). *Amer. J. Bot.* 93: 157–169.

Lucier, G. & Jerardo, A. 2006. *The vegetables and melons outlook*. Electronic Outlook Report from the Economic Research Service (USDA VGS-318). http://www.ers.usda.gov/publications/vgs/2006/12dec/vgs318.pdf.

Mace, E.S., Lester, R.N. & Gebhardt, C.G. 1999. AFLP analysis of genetic relationships among the cultivated eggplant, *Solanum melongena* L., and wild relatives (Solanaceae). *Theor. Appl. Genet.* 99: 626–633.

Posada, D. & Crandall, K.A. 1998. MODELTEST: Testing the model of DNA substitution. *Bioinformatics* 14: 817–818.

Rambaut, A. 1996. Se-Al: Sequence alignment editor. http://evolve.zoo.ox.ac.uk/.

Rao, N.N. 1979. The barriers to hybridization between *Solanum melongena* and some other species of *Solanum*. Pp. 605–614 in: Hawkes, J.G., Lester, R.N. & Skelding, A.D. (eds.), *The biology and taxonomy of Solanaceae*. London: Academic Press.

Sakata, Y. & Lester, R.N. 1994. Chloroplast DNA diversity in eggplant (*Solanum melongena*) and its related species *S. incanum* and *S. marginatum*. *Euphytica* 80: 1–4.

Sakata, Y. & Lester, R.N. 1997. Chloroplast DNA diversity in brinjal eggplant (*Solanum melongena* L.) and related species. *Euphytica* 97: 195–301.

Sakata, Y., Nishio, T. & Matthews, P.J. 1991. Chloroplast DNA analysis of eggplant (*Solanum melongena*) and related species for their taxonomic affinity. *Euphytica* 55: 21–26.

Singh, A.K., Singh, M., Singh, A.K., Singh, R., Kumar, S. & Kalloo, G. 2006. Genetic diversity within the genus *Solanum* (Solanaceae) as revealed by RAPD markers. *Curr. Sci.* 90: 711–716.

Swofford, D.L. 2002. *PAUP*: Phylogenetic analysis using parsimony (*and other methods)*, version 4.0b10. Sunderland, Massachusetts: Sinauer.

Taberlet, P., Gielly, L., Pautou, G. & Bouvet, J. 1991. Universal primers for amplification of three non-coding regions of chloroplast DNA. *Pl. Molec. Biol.* 17: 1105–1110.

Tanksley, S.D. & Fulton, T.M. 2007. Dissecting quantitative trait variation: Examples from the tomato. *Euphytica* 154: 365–370.

Wang, J.-X., Gao, T.-G. & Knapp, S. 2008. Ancient Chinese literature reveals pathways of eggplant domestication. *Ann. Bot.* 102: 891–897.

Whalen, M.D. 1984. Conspectus of species groups in *Solanum* subgenus *Leptostemonum*. *Gentes Herb.* 12: 179–282.

White, T.J., Bruns, T., Lee, S. & Taylor, J. 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. Pp. 315–322 in: Innis, M., Sninsky, D.G. & White, T.J. (eds.), *PCR protocols: A guide to methods and applications*. San Diego: Academic Press.

Yoder, A.D., Irwin, J.A. & Payseur, B.A. 2001. Failure of the ILD to determine data combinability for slow loris phylogeny. *Syst. Biol.* 50: 408–424.

Appendix. Taxa and vouchers for species sampled.

Species, source of seed or geographic region, collector and collection number (herbarium), ITS GenBank accession no. / *waxy* GenBank accession no. / *trnT-F* GenBank accession no. BIRM samples have the seed accession number of the Solanaceae collection at the University of Birmingham, UK; Nijmegen (NIJ) accession numbers refer to the Solanaceae collection at Radboud University, Nijmegen, The Netherlands.

S. aculeastrum Dunal, NIJ 924750119, *Bohs 3251* (UT), AY996481/AY996376/DQ812102; ***S. aethiopicum*** L., BIRM S.0344, *Olmstead S-74* (WTU), AY996482/AY996378/DQ180394; ***S. anguivi*** Lam., Uganda, *Bohs 3227* (UT), AY996483/AY996380/DQ812103; ***S. campanulatum*** R. Br., BIRM S.0387, *Olmstead S-78* (WTU) AY996488/AY996388/DQ180395; ***S. capense*** L., NIJ 904750116, *Bohs 2905* (UT) AY996490/AY996391/DQ392958; ***S. cleistogamum*** Symon, BIRM S.0844, *Olmstead S-80* (WTU) AY996496/AY996397/DQ180478; ***S. cyaneopurpureum*** De Wild., NIJ 874750010, *Bohs 3164* (UT) AY996503/AY996405/DQ392959; ***S. dasyphyllum*** Thonn., NIJ 944750174, *Cipollini 7* (UT) AY996504/AY996406/EU176139; ***S. elaeagnifolium*** Cav., U.S.A., *Olmstead S-82* (WTU) AF244730/AY996413/DQ180399; ***S. furfuraceum*** R. Br., BIRM S.1442, *Olmstead S-84* (WTU) AY996512/AY996417/DQ180401; ***S. hastifolium*** Hochst., NIJ 944750142, *Bohs 2906* (UT) AY996514/AY996420/DQ812106; ***S. hindsianum*** Benth., Mexico, *Bohs 2975* (UT) AY996518/AY996424/DQ180402; ***S. incanum*** L. group A, NIJ 924750118, *Martine 571* (CONN) AY996489/AY996390/EU176141; ***S. incanum*** L. group A, NIJ 954750138, *Bohs 3455* (UT) EU176108/EU176124/EU176142; ***S. incanum*** L. group B, Anderson 4440, *Martine 564* (CONN) AY996539/AY996451/EU427552; ***S. incanum*** L. group B, NIJ 954750119, *Bohs 3456* (UT) EU176109/EU176125/EU176143; ***S. incanum*** L. group C, NIJ 954750150, *Bohs 3457* (UT) EU176110/EU176126/EU176144; ***S. incanum*** L. group C, NIJ 954750123, *Bohs 3466* (UT) EU176111/EU176127/EU176145; ***S. incanum*** L. group D, NIJ 954750126, *Bohs 3482* (UT) EU176112/EU176128/EU176146; ***S. incanum*** L. group D, BIRM S.1692, *Daunay 0676* (UT) EU176113/EU176129/EU176147; ***S. linnaeanum*** Hepper & P.-M.L. Jaeger, Australia, *Cipollini 117* (UT) AY996516/AY996422/EU176140; ***S. linnaeanum*** Hepper & P.-M.L. Jaeger, France, *Bohs 3238* (UT) EU915548/EU915550/EU915549; ***S. macrocarpon*** L., BIRM S.0133, *Olmstead S-88* (WTU) AF244725/AY996436/DQ180404; ***S. marginatum*** L. f., NIJ 884750020, No voucher AY996528/AY996440/EU176148; ***S. melongena*** L. group E, NIJ 954750125, *Bohs 3459* (UT) EU176114/EU176130/EU176149; ***S. melongena*** L. group E, BIRM S.1490, *Daunay MM0669* (UT) EU176115/EU176131/EU176150; ***S. melongena*** L. group F, NIJ 944750231, *Bohs 3460* (UT) EU176116/EU176132/EU176151; ***S. melongena*** L. group G, NIJ 924750202, *Bohs 3461* (UT) EU176117/EU176133/EU176152; ***S. melongena*** L. group G, NIJ 884750026, *Bohs 3462* (UT) EU176118/EU176134/EU176153; ***S. melongena*** L. group G, NIJ 954750114, *Olmstead S-91* (WTU) AF244726/AY562959/DQ180406; ***S. melongena*** L. group H, U.S.A. (cultivated), *Bohs 3650* (UT) EU176119/EU176135/EU176154; ***S. melongena*** L. group H, U.S.A. (cultivated), *Bohs 3655* (UT) EU176120/EU176136/EU176155; ***S. myoxotrichum*** Bak., Madagascar, *Bohs 2981* (UT) AY996534/AY996445/DQ392960; ***S. pyracanthos*** Dunal, U.S.A. (cultivated), *Olmstead S-95* (WTU) AY996546/AY996459/DQ180408; ***S. richardii*** Dunal, NIJ 944750152, No voucher AY996549/AY996462/EU176156; ***S. rigescens*** Jacq., NIJ 814750065, *Bohs 3468* (UT) EU176121/EU176137/EU176157; ***S. schimperanium*** Hochst., BIRM S.1538, *Olmstead S-97* (WTU) AY996552/AY996465/DQ180410; ***S. sessilistellatum*** Bitter, Daunay 1269 INRA France, *Bohs 3242* (UT) EU427555/EU427554/EU427553; ***S. supinum*** Dunal, NIJ 944750174, *Bohs 3469* (UT) EU176122/EU176138/EU176158; ***S. tomentosum*** L., NIJ 894750127, *Bohs 3107* (UT) AY996558/AY996473/DQ392961; ***S. tridynamum*** Dunal, BIRM *S.1831*, *Olmstead S-102* (WTU) EU176123/AY996474/DQ180412; ***S. violaceum*** R. Br., NIJ 924750100, *Bohs 3093* (UT) AY996560/AY996478/EU176159; ***S. virginianum*** L., NIJ 934750032, *Cipollini 17* (UT) AY996561/AY996479/EU176160.