Tomato-like Nightshades: Affinities, Autoecology, and Breeders' Opportunities[1]

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The group of nightshades I would like to discuss consists of four species: *Solanum juglandifolium* Dun., *S. lycopersicoides* Dun., *S. ochranthum* Dun., and *S. rickii* Corr. (Solanaceae). Belonging to section *Petota,* subsection *Potatoe,* series *Juglandifolia,* they differ from other species in *Potatoe* and resemble *Lycopersicon* in respect to absence of tubers and presence of yellow corolla. Other tomato-like features that distinguish them from the great majority of *Solanum* species are articulated pedicels and pinnately segmented leaves.

In the aggregate, the association of all of these traits in the four species renders them unique amongst the myriad *Solanum* species. They nevertheless differ from *Lycopersicon* in several important features to be considered below and are reproductively isolated from them by formidable reproductive barriers, which have been circumvented only in crosses with *S. lycopersicoides,* and even in this instance, only as a consequence of experimental manipulations. All of these species are diploids (2n = 24).

My interest in this group was stimulated in the 1940s by a collection of *S. lycopersicoides* provided by Professor T. H. Goodspeed, collected by R. D. Metcalf in 1942 (his No. 30382) near Candarave, Dept. Tacna, Perú, under the auspices of the third University of California Botanical Garden Expedition to the Andes. Of the seed collected, only a few germinated at the UC-Berkeley Botanical Garden, but we were able to maintain a clone therefrom and utilize it in experiments to which I shall refer later. Since that time it has been my good fortune to visit populations of all four species in their native habitats, to make many collections of them, and to culture them for seed increase and various studies.

This group is important for several reasons. Breeders constantly probe new sources of germplasm for purposes of plant improvement. The cultivated tomato (*L. esculentum* L.) is one of a large group of crop species whose genetic variability is so greatly reduced that they lack many genes needed for breeding purposes. In the case of the tomato, this depletion evidently resulted from events that ensued prior to, during, and subsequent to domestication (Rick 1976). The generally accepted immediate ancestor of the tomato is var. *cerasiforme* of the cultivated species—a largely self-pollinated taxon that evidently migrated from its ancestral area in the north central Andes to its area of domestication in Mesoamerica. Founder events during this migration (doubtlessly often in small populations) would have tended to diminish genetic variability existing in the original source(s), a situation verified by comparisons of genetic content of monogenically determined isozymes (Rick et al. 1974; Rick and Fobes 1975). The domestication process itself in a self-pollinator would have tended to further reduce reserves as a result of selection for desired types. Finally, transport to Europe, further mi-

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gration and selection there, and the return to the New World would have probably continued the same trends.

Small wonder, therefore, that breeders in the present century experienced difficulties in achieving their goals in tomato improvement. So long as they relied entirely on genetic variation in the European sources and their derivatives, progress in improving yields, disease resistance, and other desiderata was slow. This situation is reflected in the very retarded gain in yields until about 1940, when the first use of wild species as a source of desired characters was reported. Bohn and Tucker (1940) discovered strong resistance to Fusarium wilt in *L. pimpinellifolium* (Jusl.) Mill., the first high-level disease resistance known at that time in the tomato. Thereafter, exploitation of wild sources accelerated, and the consequent progress accounted for a major share of increased yields in recent decades (Rick 1978). According to the latest survey (Rick 1986), resistance to no fewer than 30 major diseases has been discovered in exotic *Lycopersicon* sources, and 16 of these resistances have been bred into important horticultural cultivars. Significant progress has also been made in such other areas as fruit quality, and breeders have started to exploit exotic sources for insect resistance and tolerance of various environmental stresses.

In the face of this recent phenomenal progress, it might seem unnecessary to seek other sources of germplasm, yet extensive tests have revealed a dearth of sources of certain characters within *Lycopersicon.* For example, the known resources therein lack certain stress tolerances—extreme aridity, excessive moisture, and freezing temperatures—as well as resistances to certain diseases and insects. Thus, although the *Solanum* spp. under consideration may not necessarily provide all of these desiderata, they decidedly broaden the horizons. According to the following considerations, the prospects appear good for satisfactory sources of some of them.

In addition to the aforementioned objectives, other, unforseen characters are often revealed in the course of standard breeding procedures. For instance, backcrossing wild species to cultivated forms often results in the appearance of novel traits, which are notably abundant in the case of tomato relatives. Many such traits, determined by various genetic mechanisms have been uncovered in hybridizing with various wild *Lycopersicon* species (Rick 1967, 1982). Possibly, the even wider bases of intergeneric hybridization could result in a higher yield of novel variants. As explained below, the prospects are excellent for determination of this phenomenon in hybridizations of *L. esculentum* × *S. lycopersicoides* in the near future. Another potential that these nightshades might offer is useful steroidal alkaloids, so widespread in the genus. As far as I am aware, little is known about their content, either qualitatively or quantitatively.

Various objectives of a more basic nature also stimulate these investigations. An obvious aim is to ascertain as much as possible regarding the natural relationships between the species and genera concerned. Thus, similarities and differences in respect to geographic distribution, gross morphology, allozyme variability, and chromosomal features, the nature of hybridization barriers, and the cytogenetics of F_1 hybrids can be expected to elucidate the affinities among these four *Solanum* spp. and between them and *Lycopersicon.* A related goal is to analyze all such data for any clues regarding the phylogeny of the group. Thus, are the roots of *Lycopersicon* to be found in any of these nightshades or in related, extinct species? What, if anything can be determined regarding the ancestry of these four fascinating taxa?

Additionally, there is the factor of personal curiosity: after some 40 yr of association with *Lycopersicon* and these nightshades, I must be excused for an intense interest in learning everything possible about them, whether or not of immediate utility.

DISTRIBUTION AND MORPHOLOGY

Even to the casual observer, first inspection of these four species will reveal that they fall into two distinct groups—*S. lycopersicoides* and *S. rickii* vs. *S. juglandifolium* and *S. ochranthum*—within which the members are similar in many respects, yet between which a surprising diversity exists. These relationships are evident, even in respect to geographic distribution: the two species of the former group are highly restricted in their southerly areas while the latter two are found in a narrow, elongated range through the more northerly Andes (Fig. 1). Although the lack of definition in the map suggests that they are largely sympatric, *S. juglandifolium* is generally found at lower elevations than *S. ochranthum.* I know of no site that they cohabit.

Both *S. lycopersicoides* and *S. rickii* are long-lived, erect plants, the former best characterized as a woody shrub (Fig. 3), the latter as a herbaceous perennial (Fig. 4). Both have small, finely divided, highly pinnatifid leaves, highly compound, dense inflorescences of brilliant yellow flowers, white anthers, and distinctive fragrances. The fruits are small berries that remain hard to maturity, those of the former somewhat smaller and often suffused black from superficial, dense anthocyanin pigmentation. Each has pronounced foliage volatiles, which, as in the case of floral fragrance, differ with the species.

In contrast, *S. juglandifolium* and *S. ochranthum* are rampant, woody climbers, almost liana-like in forested situations. The vines of *S. ochranthum* are more robust, reaching diameters of 8–10 cm with branches as long as 30 m (Fig. 2). Its leaves are large, pinnately segmented, and, as the name of the series suggests, not unlike those of the walnut. Fruits of this group are much larger, those of *S. ochranthum,* 4–6 cm in diameter and tri- or tetralocular, by far the largest of any tomato relative. Fruits of both species require exceptionally long periods to mature, those of *S. ochranthum,* 8–9 mo, remaining hard, almost woody, until eventually softening at full maturity. The pericarps are relatively thick, and the ripe fruits emit a pleasant, apple-like fragrance. Seeds are comparatively large and winged. Flowers are considerably larger than in the other group and are more openly spaced in the inflorescences, which are well displayed on long peduncles. The same description fits *S. juglandifolium* except that it is generally more diminutive in size of plant, leaves, seeds, and fruits, which require less time (6–7 mo) to mature. The harsher feel of leaves of the latter vs. a softer aspect of the former constitutes another, consistent difference between them.

To sum up the morphological observations, it would be difficult to imagine two such contrasting groups; in fact, it seems almost paradoxical that they are all classified in the same series of the same subsection of the same section of the genus. The morphological relationships are reflected to some extent in results of hybridization (Rick 1979). None of the crosses between the four species succeeds except between *S. lycopersicoides* and *S. rickii.*

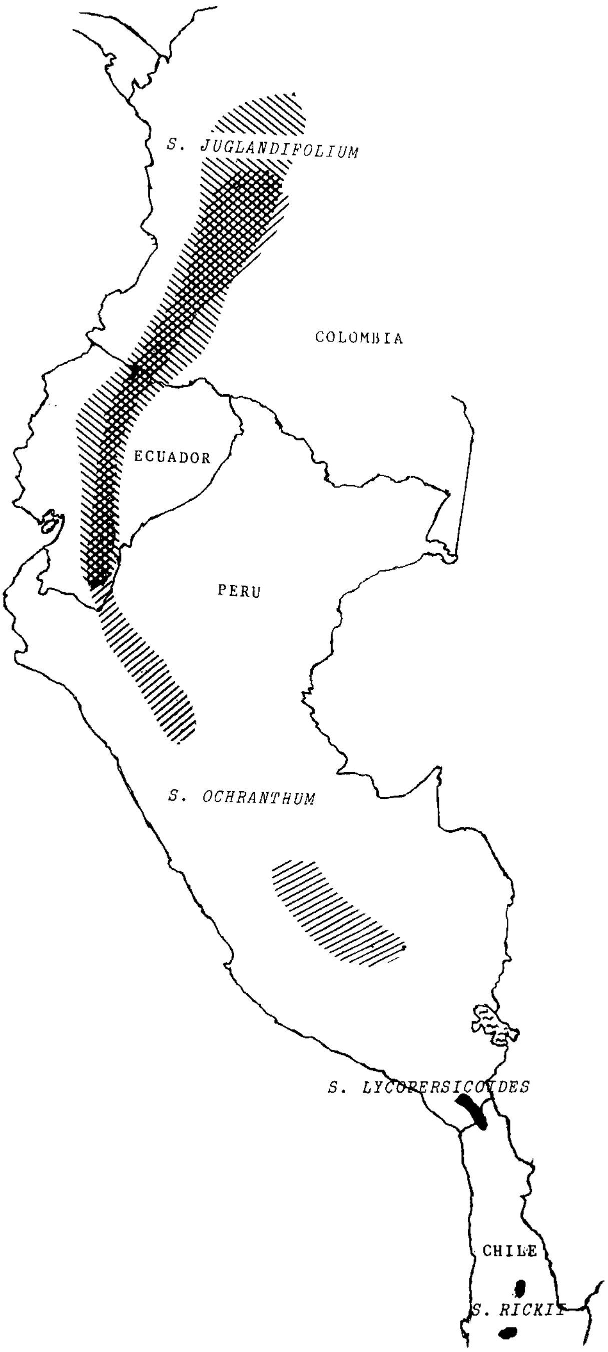

Fig. 1. Distribution of *Solanum* spp., series *Juglandifolia.*

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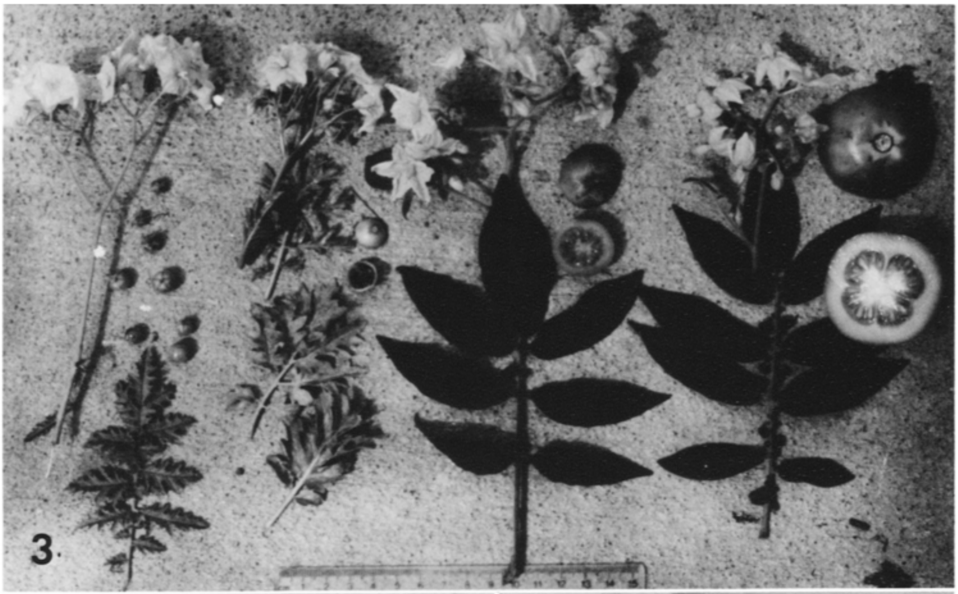
Fig. 2. Mature plant of *S. ochranthum* LA2117. Tuntún (Prov. Loja), Ecuador. Main trunk at bottom center. Vines ascending into shrubs and low trees to a height of approximately 15 m and cascading down to ground in foreground. Flowing stream at lower left.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AUTOECOLOGY

Considerations of the habitat location of these species would also classify them in the same two groups: the *lycopersicoides-rickii* pair dwells in relatively arid areas, whereas *S. juglandifolium* and *S. ochranthum* are found in wet situations. The haunts of the latter are so consistent, in fact, that wet feet are the common complaint of the collector. The two are found in regions of high rainfall, or if less pluvial, in poorly drained places or along permanent streams (Fig. 2). The only evident difference in their habitats is the higher temperature requirement of *S. juglandifolium,* as manifest in its existence at lower altitude and more equatorial latitudes.

The direct antithesis is encountered in *S. lycopersicoides* and *S. rickii*: both grow in vastly drier situations and in more southerly latitudes, and both are narrow endemics of northern Chile and southernmost Perú. Aridity is more extreme in habitats of *S. rickii.* In our first real opportunity to evaluate this inclination on a collecting experience in May 1987, every population was found in a restricted area between 2,500 and 3,000 m in a lesser cordillera between the coast range and the main Andean crest in Region 2 (Antofagasta), Chile. Similar to the Atacama desert, this area has one of the lowest of the world's recorded precipitations. The range is too distant from the coast to benefit from condensation from fogs and not sufficiently high to receive true rainfall. Here *S. rickii* is associated with a few other herbaceous xerophytes, including the highly succulent *Calandrinia crassifolia.* Yet, this nightshade was collected in sites in which *Calandrinia* had perished from drought (Fig. 7) and in others where no other flowering plant survived. Even more remarkable was the observation that nearly all surviving plants, although some severely stunted, bore remarkable quantities of fruits with good seed content. It may be of interest in this connection that in the Caracoles site in the Cordillera de Domeyko (LA2885), local silver miners were familiar with *S. rickii,* and referred to it as "uva minera" (miner's grapes), emphasizing its fruiting ability, but not implying edibility. Its value as a source of drought resistance can therefore scarcely be doubted.

Although found in arid situations, *S. lycopersicoides* grows in somewhat more mesic situations on the western slopes of the main Andean cordillera in the region of the Chile-Perú frontier (Fig. 1). The prime attribute of this species is low temperature tolerance, for it grows to higher elevations than those known for any other tomato relative. The sites at these higher levels and more southerly latitudes are known to be exposed to frosts and light freezes. Collections were made by Dr. Carlos Ochoa and us at 3,600 m in a well-exposed site in the air drainage of the

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Fig. 3-7. Fig. 3. Representative inflorescences, fruits, and leaves of *Solanum* series *Juglandifolia.* From left to right: *S. lycopersicoides, S. rickii, S. juglandifolium, S. ochranthum.* Scale in cm. **Fig. 4.** *S. lycopersicoides* LA2772, near Zapahuiri (Reg. 1, Tarapacá), Chile. Mature woody shrubs growing on dry roadbank. **Fig. 5.** *S. rickii* LA2876 at Chuquicamata (Reg. 2, Antofagasta), Chile. Typical mature plant in arid site. **Fig. 6.** *S. lycopersicoides* LA2781 at road junction above Putre (Reg. 1, Tarapacá), Chile, alt. 3,600 m in exposed site below Mt. Putre. **Fig. 7.** *S. rickii* LA2885 in arid quebrada at silver mines, Caracoles (Reg. 2, Antofagasta), Chile. Sparsely growing plant with many ripe fruits at left; dessicated plant of *Calandrinia crassifolia* at right.

glaciers and snowfields of Mt. Putre (Fig. 6). Low temperature tolerance was reported in tests by Robinson and Kowaleski (1974).

These remarkable examples of stress tolerance perceived from autoecology underscore the germplasm value of these nightshade species. In all cases they exceed all known *Lycopersicon* species for ability to withstand such stresses. Another generalization permitted by these observations is that they also emphasize the remarkable contrasts between the two subgroups of series *Juglandifolia.* These observations also exemplify the value of observations in the native habitat. As in my earlier thesis on such studies of *Lycopersicon* (Rick 1973), I could not fail to be impressed by the capacity of these species to survive in situations of extreme environmental stress. The predictions made then regarding inherited ability to survive have mostly been verified by experimental evidence accrued by various workers. And the conclusion reached in that study that survival in such harssh environments implies natural selection for tolerant genotype seems equally valid for these Solani.

Since circumstances permitted only very brief visits to the wild populations, it was impossible to evaluate them for other attributes. Other characters of possible economic importance have shown up from casual observations and experiments on field cultures of these species. In this vein, we have repeatedly observed in field cultures of *S. lycopersicoides* and *S. ochranthum* that their foliage and fruit are seldom attacked by larvae of parasitic Lepidoptera. Likewise, all four species have remained remarkably free of virus disease symptoms. The same observations apply to F_1 *L. esculentum* × *S. lycopersicoides.* The latter, in fact, proves to be the only known source of resistance to CMV (cucumber mosaic virus) known amongst tomato relatives.

PROSPECTS FOR UTILIZATION

Until 2 yr ago the outlook for exploiting germplasm in these nightshades appeared dismal. Although I had obtained F_1 hybrids between *L. esculentum* and *S. lycopersicoides* more than 35 yr ago (Rick 1951), the fertility of both 2x and 4x hybrids was so discouragingly low that efforts were diverted to hybrids with wild species of *Lycopersicon,* which, as mentioned above, greatly expedited tomato breeding. Recent intensive efforts have changed the picture, however, by breaking the crossing barriers. One development was the synthesis of sesquidiploid hybrids having two complements of the former species (LL) and one of the latter (S) (Rick et al. 1986). Chromosomes in these new hybrids pair in the expected classical fashion, the L homologs regularly forming 12 bivalents whilst the S chromosomes remain univalent and are distributed randomly at anaphase. As expected, fertility was considerably better than in 2x LS hybrids, and the progeny included the anticipated diploid and aneuploid individuals.

By means of various techniques, it was possible to identify eight of the possible 12 alien addition types amongst the trisomic progeny (DeVerna et al. 1987). Further breeding from such additional types is expected to yield transfers of genes from S to L chromosomes via recombination, the prospects for which are excellent. Noteworthy in this respect is the appearance of dominant S traits amongst the diploid progeny, unequivocally manifesting such recombination in the LLS hybrids. In our recent experience it has been possible to transfer such dominant traits to LL background by consecutive backcrosses. These investigations demonstrate that it is possible to manipulate S genes in the desired fashion via conventional methods; hence the door is now open for exploiting genes of *S. lycopersicoides.*

What about other nightshades of series *Juglandifolia*? The rather close relationship between *S. lycopersicoides* and *S. rickii* raises hopes that similar manipulations might be feasible with the latter. The many similarities between these two species have been delineated above. Attention should also be called to the success of O'Connell and Hanson (1986) in generating (necessarily polyploid) hybrids between *L. esculentum* and *S. rickii* via protoplast fusion. It therefore remains to be seen what might be feasible with these materials. As to the other species, *S. juglandifolium* and *S. ochranthum,* no progress has been reported yet; in fact, their obviously more distant relationship with *Lycopersicon* presents more of a challenge than the aforementioned pair. Protoplast fusion might also lead the way; otherwise the increasingly promising techniques of biotechnology might provide avenues for exploiting their germplasm.

All phases of this research have proved most exciting to me. It is indeed a privilege to have the opportunity to collect and observe tomato relatives in their native habitats. As many others have discovered, travel in the Andes can be fascinating. Add to this the vicissitudes of plant collecting, and every day is an adventure: countless frustrations balance delightful discoveries—old friends in new places, sometimes extending known distributions significantly, or even the discovery of new species. The satisfactions of such experiences in the native area are matched by those of experiences with progenies of the wildlings when cultured for experimental purposes. Whereas we might seldom encounter new taxa in the wild, progenies, like those derived from the *Lycopersicon-Solanum* hybrids, provide countless variants generated by segregation and recombination of parental characters. Such vicarious encounters are thrilling, partly because most of the variants have probably never been observed before by human eyes. Clearly, I have been a very lucky fellow, richly rewarded by all of these satisfactions. It is equally gratifying to be named Economic Botanist of the Year by the Society for Economic Botany.

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Notes

John V. Freudenstein of the L. H. Bailey Hortorium, Cornell University, is the recipient of the 1987 Lawrence Memorial Award. A student of Dr. Jeff J. Doyle, Mr. Freudenstein has undertaken a systematic revision of the orchid genus *Corallorhiza* and its allies. He will use the proceeds of the Award for travel to Mexico for field research. Commemorating Dr. George H. M. Lawrence, founding Director of the Hunt Institute for Botanical Documentation at Carnegie Mellon University, the annual Award of $1,000 is made to an outstanding doctoral candidate for travel in support of dissertation research in systematic botany, horticulture, or the history of the plant sciences.

Society for Economic Botany: 29th Annual Meeting. The 29th annual meeting of the Society for Economic Botany will be held at the University of California, Davis, 14–18 August 1988, in conjunction with the annual AIBS meeting. During the afternoon of 16 August and the morning of 17 August, the Society, in collaboration with the Economic Botany section, will sponsor a symposium, "New perspectives on the origin and evolution of New World domesticated plants."