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# "New" Solanums

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The nightshade family (Solanaceae) has provided many plants to humankind. The genus *Solanum* has been particularly significant for it has furnished us with one of our basic food plants, the Irish potato (*S. tuberosum*), as well as the widely used eggplant (*S. melongena*). The genus has recently become even more important with the addition of two other food plants—both because of recent changes in their names. The tomato, which has long been known as *Lycopersicon esculentum,* is now recognized as *S. lycopersicum* and the tree tomato, previously known as *Cyphomandra betacea,* has become *S. betaceum*. Three other Solanums—the pepino (*S. muricatum*) the cocona (*S. sessiliflorum*) and the naranjilla (*S. quitoense*), long valued for their fruits in South America, deserve greater attention.

## TOMATO

The tomato was originally named *Solanum lycopersicum* by Linnaeus in 1753. Philip Miller in *The Gardeners Dictionary* in 1768 used *Lycopersicon esculentum* and this became the accepted name until very recently. Various lines of evidence had suggested that the tomato belonged to the genus *Solanum* and molecular studies provided the compelling evidence that has led to the readoption of *S. lycopersicum* (Spooner et al. 1993). The other species of *Lycopersicon* have also been assigned or re-assigned to *Solanum*. More recent studies (Bohs and Olmstead 1997; Olmstead and Palmer 1997) have provided additional evidence for the inclusion of the tomato in *Solanum.* The tomatoes are placed in *Solanum* in groups very close to the tuberous and non-tuberous potatoes. This has not led to major changes in tomatoes as yet, but it does make very clear the relationship of tomatoes and potatoes, and should promote even greater efforts at interbreeding and genetic transfer among these two important groups.

## TREE TOMATO

The tree tomato, originally named *Solanum betaceum* by Cavanilles in 1799, was transferred by Sendtner in 1845 to the genus *Cyphomandra* where it remained until recently when Bohs (1995) returned it to *Solanum*. As in the tomato, molecular studies prompted the recent change in the name (Olmstead and Palmer 1992; Spooner et al. 1993; Bohs and Olmstead 1998). More recent molecular studies have furnished additional support for its inclusion in *Solanum* (Bohs and Olmstead 1997; Olmstead and Palmer 1997).

The tree tomato is hardly a new crop, for it has long been popular in the Andes, where it is native, and in many other parts of the tropics. It has been grown successfully in New Zealand and has been exported to the north temperature zone for around two decades. In New Zealand, the plant was renamed tamarillo, a made-up name. The new name does have some advantages, for although many people have claimed a resemblance of the tree tomato to the tomato it is mostly superficial. Both the aroma and taste are quite different from that of the tomato. The fruit is eaten raw as well as for the juice, preserves, jellies, and as a vegetable, either cooked or raw in salads. Some improvement of the plant has taken place in New Zealand in recent years, and on a visit to Ecuador in 1983 we were happy to learn that New Zealand had sent improved forms to South America.

Although the tree tomato now reaches the United States from New Zealand and South America, it probably first became familiar to many people here some 30 years ago through advertisements of a nursery company offering plants for sale. A few years later we saw another advertisement stating "Does 60 pounds of tomatoes from one yield sound unreasonable—not if you own the tree tomato." Other advertisements with extravagant claims have appeared from time to time, but we hadn't seen any for several years until this past spring when two companies offered it again claiming yields of 60 pounds. This time however, we saw a release from the Associated Press in a local newspaper headlined, "Gardeners should beware of catalog exaggerations" and the tree tomato was one of the plants featured.

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Several wild species of the tree tomato in South America also have edible fruits. In addition, various parts of the plants, particularly the leaves, of the tree tomato and several wild species have been used in folk medicine in Latin America. More information on the ethnobotany of the tree tomato may be found in Bohs (1989); see also National Research Council (1989). A wild ancestor of the tree tomato has not yet been identified unequivocally but recent studies indicate that it most likely had its origin in the southern Andes, perhaps Bolivia, and that the cultivated tree tomato was derived from a wild form of the same species (Bohs 1998).

**PEPINO**

The pepino (*cachum* in Quechua), *Solanum muricatum*, shows some similarities to the tree tomato in that it is also native to the Andes where it is an important fruit; it has also recently been grown in New Zealand (Hewett 1993) whence it is exported to the United States, Europe and Japan. Like the tree tomato, its future as a crop outside of the Andes is uncertain. There are many differences—the pepino is eaten raw and it was probably domesticated much earlier than the tree tomato; in addition, its origin is more complex and the two plants are very different in appearance. Pepino is the Spanish word for cucumber, and the plant was so named by the Spanish because of a slight resemblance to some cucumbers. The typical fruit of the pepino is usually broadly ovate, white or ivory colored, often with a few purple stripes, when mature. However, there are many fruit color and shape varieties among the 'indigenous' cultivars in South America e.g., see the cover of the 1993 *American Journal of Botany* 80(6). It is generally eaten out-of-hand, frequently after peeling, for its sweet pleasant taste. The plant itself somewhat resembles the Irish potato; in fact, both species are placed in the subgenus *Potatoe*. There is great variation in the pepino not only in its fruits but in vegetative features as well; the leaves may be simple or compound.

Some improvement of the plant has taken place in New Zealand, and at present it is being tried in a number of countries. The history of the plant, both ancient and modern, has been treated in some detail by Prohens et al. (1996).

Contrary to the situation in the tree tomato, and similar to the naranjilla (see following) there is no clearly defined wild ancestral form of the pepino. This highly variable cultigen is know only from cultivation. Extensive field studies have failed to indicate a wild form. However, many studies and approaches have identified three wild species that are most closely related to the pepino, and that have been treated as possible progenitors (e.g., Anderson 1979; Anderson et al. 1996; Anderson and Jansen 1998; Jansen et al. 1998): the widespread *S. caripense*, which ranges from Costa Rica to Peru, *S. tabanoense*, which is found in a few localities in Colombia, Ecuador, and Peru, and *S. basendopogon*, which has a very limited distribution in Peru. Recent molecular studies (Anderson et al. 1996; Anderson and Jansen 1998; Jansen et al. 1998) suggest *S. basendopogon* as a less likely element in the origin of the pepino. The chloroplast DNA evidence is quite strong in support of *S. tabanoense* as central to its origin; over 85% of the pepino collections from South America are linked in a cladistic study with this species (Anderson et al. 1996). The remaining pepino collections are associated with *S. caripense*, implying either a second origin, or possibly post-origin hybridization. Although multiple origins are known for a few other domesticated plants, in each of these, only one wild species is involved; none is known involving more than one species. The molecular results, however, do not rule out the possibility that the pepino evolved from a single species, most likely *S. tabanoense*, followed by hybridization with *S. caripense*, and possibly other closely related wild species (perhaps including *S. basendopogon*). Hybridization among the wild species, and with the pepino, is not obviously rampant in the wild but, is relatively easily performed in plants grown in the greenhouse. Either the unprecedented multiple origin hypothesis, or post-origin hybridization, would help explain the great variability in the fruits, flowers, and leaves of this polymorphic species. Work now in progress should help explain more about the origin of the pepino, including its place of origin. Southern Colombia and northern Ecuador, at present, would seem to be the most likely places.

**COCONA**

Although not yet grown commercially outside of Latin America, two other South American *Solanums* deserve wider cultivation. The cocona or tupiro, as it is known in Spanish speaking countries, or cubiu in Brazil (*S. sessiliflorum*) is a shrubby perennial, generally a meter or more tall with extremely large leaves (to

9.5 cm long). It bears maroon, orange-red or yellow fruits up to 10 cm in diameter with yellow flesh. The fruits are covered with small, soft readily deciduous hairs. The plant is widely cultivated, usually in very small plots, in the upper Amazon basin from sea-level to 700 m or higher. The berries have a pleasant acidulous flavor, somewhat like citrus, and are used as fruits, chiefly for the juice, and also cooked as a vegetable (Whalen et al. 1981). Parts of the plant have also been used in medicine. The species is quite variable, particularly in size, shape, and flavor of the berries, as might be expected in a species domesticated for its fruits. A wild type (*S. sessiliflorum* var. *georgicum*) with smaller (3–4 cm), globose, orange berries and prickles on the stem and leaves is the likely ancestor of the domesticate (Heiser 1972). The nutritional value, cultivation and production of the cocona have been treated by Salick (1989, 1992) who believes that its wider cultivation could significantly improve human subsistence in tropical lowlands.

**NARANJILLA**

The naranjilla or lulo (*S. quitoense*) belongs to the same section of *Solanum* (*Lasiocarpa*) as the cocona. It is a taller plant (ca. 2 m), less branched and with slightly smaller leaves (Whalen et al. 1981). The leaves, particularly younger ones, the veins and petioles are often purplish, making the plant sufficiently attractive to be grown occasionally as an indoor ornamental in the United States. The globose berries are around 5 cm in diameter, orange and covered with short stiff hairs which have usually rubbed off by the time the fruits have reached the markets. The pulp is green and gives a green juice, the form in which it is usually used. The taste is unique, but has been described by some as like that of a mixture of pineapples and strawberries. The plant was found by the Spanish in Ecuador and Colombia (Patiño 1963) where most of it is still grown. It was introduced to Panama and Costa Rica in the middle of this century where it is also grown today. Introductions to other places, including Florida, have been largely unsuccessful (Heiser 1985). Recently Bernal et al. (1998a) have postulated that the form similar to the cultivated plant that grows spontaneously as a weed in Colombia is the original wild type. We feel, however, that these plants may be nothing more than escapes from cultivation, no different from escapes in Costa Rica where the plant was introduced a half century ago. Moreover, it is difficult to imagine no change occurring in a plant that has been cultivated for several hundred years. On the other hand, no other wild ancestor has been reported and it is most unlikely that *S. quitoense* descends directly from any other species in section *Lasiocarpa*. For a domesticated plant it shows very little variability. In Colombia and Central America the plants usually have prickles on the stems and leaves whereas in Ecuador plants are unarmed. Several cultivars are recognized in Ecuador, based on slight differences in fruits.

Over 20 years ago Heiser (1969) wrote that "the fruit [of the naranjilla] yields one of the most delicious beverages known." Why then hasn't it become more widely appreciated? Many early visitors to Colombia and Ecuador spoke highly of the juice (Patiño 1963) so it is difficult to believe that the Spanish didn't carry seeds to other regions, but it was not successfully introduced elsewhere. The naranjilla grows best at between 1200 and 2300 m and it is neither a tropical plant (pollen aborts at high temperatures) nor a temperate one (it is killed by freezing and fruits need four months to mature). The juice has been canned but its unique flavor is lost in doing so. Freeze-drying techniques have shown promise in Ecuador but no attempts have been made to use them to make juice for export, probably because no certain markets are known. Fresh fruits, of course, could also be exported if produced in sufficient quantities. Root knot nematodes and various insect pests and fungal diseases limit its production in all of the countries where it is presently grown (National Research Council 1989). There are two promising recent developments toward its improvement: the use of interspecific hybrids with the cocona and the introduction of a nematode resistant variety.

In Ecuador a local farmer, Raul Viteri, crossed *S. quitoense* with the wild variety of *S. sessiliflorum* (Torre and Camacho 1981) and the resulting hybrids were vigorous and highly productive. The hybrid was propagated vegetatively. The chief disadvantage of the hybrid was that the fruits were much smaller than those of the naranjilla. This was overcome by spraying plants with dilute solutions of 2,4-D after it was learned by accident that such spraying would cause enlargement of the fruits. From the late 1980s to the present most of the naranjilla in Ecuador was from this hybrid which came to be know as the "Puyo hybrid." In the markets they could be distinguished from the pure naranjillas by the lighter green color of the pulp and the absence of filled seeds.

After learning of Viteri's hybrid, Heiser who had previously made many attempts to secure this hybrid, again attempted to do so. No fruit was ever secured with *S. quitoense* as the female parent[1]. Several fruits without seeds were secured with *S. sessiliflorum* as the maternal parent, and finally in 1989, using a large fruited cocona, a fruit was secured with two partially filled seeds. These were germinated on nutrient agar and gave rise to vigorous hybrids, differing primarily from the Puyo hybrid in the much larger berry (7 cm in diameter) having orange colored flesh (Heiser 1993)[2]. Dr. Jorge Soria carried cuttings of the hybrids to Ecuador where they were planted at the experiment station of the Instituto Nacional de Investigaciones Agropecuarias at Palora. After multiplication they were distributed to a few farmers for trial and became known as the "Palora hybrids."

The most recent reports from Ecuador (J. Soria pers. commun.) state that the cultivation of the Palora hybrid is increasing rapidly in Ecuador and has spread into southern Colombia. In addition to the larger size of the fruit the Palora hybrid has other advantages over the Puyo hybrid. It survives for three years in cultivation in contrast to one and a half years for Puyo, produces about twice as much annually and does not require spraying with 2,4-D. Moreover, the juice of Palora takes nearly 24 h to start oxidizing, whereas the juice of Puyo and that of pure naranjilla both begin oxidizing in less than an hour. Some buyers, however, are paying more for Puyo than Palora because of the color of the juice (greenish vs. orange respectively) and the thicker rinds of the latter. The thick rind, however, would be an advantage in shipping. Perhaps the cultivation of Palora will increase even more after it is formally released and its advantages become more widely known. The Palora hybrid may fare well in other countries in competition with the cocona, a fruit that is not very important in Ecuador.

One of the most serious pests—if not the most serious—of the naranjilla is root knot nematode, various species of *Meloidogyne* (National Research Council 1989). Although the naranjilla is a perennial and ought to yield for several years, because of these parasites it is often grown as an annual in many places. Resistance to nematodes was discovered in plants of *S. hirtum* grown in the greenhouse at Indiana University (Heiser 1971). Hybrid seed of *S. hirtum* × *quitoense* (for $B_1$ and $F_2$) were send to Soria at CATIE in Costa Rica who found that many of these plants were resistant to nematodes there. Subsequently seeds of hybrids were sent to plant breeders in several countries and a resistant cultivar has now been produced in Colombia from $F_2$ seeds sent to Dr. Mario Lobo in 1984 (Bernal et al. 1998a,b). The plant was backcrosssed to *S. quitoense* twice, and material from $F_2$ plants of the $BC_2$ was multiplied by tissue culture. Tests in various parts of the country showed good performance. In addition the new plant, called "lulo la selva" grows better in full sun, has fruit of better quality, outyields the traditional lulo and is also spineless. Moreover, the juice has a longer life because of delayed oxidation (M. Lobo pers. commun.). The resistant cultivar is propagated vegetatively. It was formally released in June of 1998. There are still problems to overcome but if work on the improvement of the naranjilla continues, the juice eventually may become more widely available.

## LOOKING BACKWARDS

A book on the nightshade family (Heiser 1969) appeared 30 years ago. To us, at least, it is interesting to see some of the changes that have taken place with various numbers of the family since then. Neither the tree tomato nor the pepino were available in stores in the United States at that time. In the book it was written that "several attempts have been made to make it (the tomatillo, *Physalis ixocarpa*) more popular in the United States, but it has never really caught on." It has now definitely caught on and has become a standard item in grocery stores and many gardens, not only in the Southwest but in most of the rest of the country as well. *Capsicum* peppers, of course, were widely available in 1969 but mostly the sweet kinds of *C. annuum*. The pungent sorts were seldom seen in those days and what was available belonged to a single species, *C. annuum*. Now pungent varieties are common. Furthermore, today more than one species is represented; the extremely

[1]Viteri claimed that *S. quitoense* was the female parent of his hybrid. Heiser gave material of Viteri's hybrid and the parental species to Richard Olmstead for analysis. Examination of the cpDNA indicated that *S. sessiliflorum* was the female parent of his hybrid (J.P. Whitney and R.G. Olmstead, unpubl.).

[2]Another hybrid from different parents but again with the cocona as the female was produced the following year but it had smaller fruits than either parent.

pungent *C. chinense* is now well accepted by many people. Along with this a huge increase in the number of pepper sauces has become available. Tomatoes, of course, were as popular in 1969 as they are today and then, as now, they were in demand in the winter as well as the summer. Although not mentioned in the book, we remember that some of us referred to the tomatoes then available in the winter as "little pink rocks." For several years now we have been fortunate in having more edible tomatoes in the winter. Tobacco, of course, received a lengthy chapter in the book where it was stated that "probably more has been written about tobacco than any other plant." That is still true. In fact, we can think of no other plant that has been featured in headlines recently more than tobacco. In spite of much adverse publicity over the centuries the plant still shows no signs of disappearing.

**REFERENCES**


Anderson, G. 1979. Systematic and evolutionary consideration of species of *Solanum*, section *Basarthrum*. p. 549–562. In J. Hawkes, R. Lester, and A. Shelding (eds.), The Biology and taxonomy of the Solanaceae. Linnean Society Symposium Series 7.

Anderson, G. and R. Jansen. 1998. Biosystematic and molecular systematic studies of *Solanum* section *Basarthrum* and the origin and relationship of the pepino dulce (*S. muricatum*). Ann. Missouri Bot. Gard. In Press.

Anderson, G., R. Jansen, and Y. Kim. 1996. The origin and relationships of the Pepino (Solanaceae): DNA restriction fragment evidence. Econ. Bot. 50:369–380.

Bernal E.J., M. Londoño B., G. Franco, and M. Lobo A. 1998a. Lulo la selva. Corpoica, Rionegro, Colombia.

Bernal E.J., M. Lobo A., and M. Londoño B. 1998b. Documento presentación del material "Lulo la selva." Corpoica, Rionegro, Colombia.

Bohs, L. 1989. Ethnobotany of the genus *Cyphomandra* (Solanaceae). Econ. Bot. 4:143–163.

Bohs, L. 1995. Transfer of *Cyphomandra* (Solanaceae) and its species to *Solanum*. Taxon 44:583–587.

Bohs, L. 1998. Evolutionary relationships of the tree tomato, *Solanum betaceum*, (Solanaceae) and its wild relatives. Am. J. Bot. 85:116. (Abstr.).

Bohs, L. and R. Olmstead. 1997. Phylogenetic relationships in *Solanum* (Solanaceae) based on ndhF sequences. Sys. Bot. 22:5–17.

Bohs, L. and R. Olmstead. 1998. *Solanum* phylogeny inferred from chloroplast DNA sequence data. In: Proc. Fourth International Solanaceae Conference. Adelaide, Australia (in press).

Heiser, C. 1969. Nightshades, the paradoxical plants. W.H. Freeman and Co., San Francisco.

Heiser, C. 1971. Notes on some species of *Solanum (Leptostemonum*) in Latin America. Baileya 18:59–65.

Heiser, C. 1972. The relationship of the naranjilla, *Solanum quitoense*. Biotropica 4:77–84.

Heiser, C. 1985. Of plants and people. Univ. Oklahoma Press, Norman.

Heiser, C. 1993. The naranjilla (*Solanum quitoense*), the cocona (*Solanum sessiliflorum*) and their hybrid. p. 29–34. In: J. Gustafson et al. (eds.), Gene conservation and exploitation. Plenum Press, New York.

Hewett, E. 1993. New horticultural crops in New Zealand. p. 57–64. In: J. Janick and J. Simon (eds.), New crops. Wiley, New York.

Jansen, R., G. Anderson, and S. Chen. 1998. Origin and relationships of "Pepino" (*Solanum muricatum*) based on ITS sequence data. Am. J. Bot. 85:137. (Abstr.).

National Research Council. 1989. Lost crops of the Incas: Little-known plants of the Andes with promise of the worldwide cultivation. National Academy Press, Washington, DC.

Olmstead, R. and J. Palmer. 1992. A chloroplast DNA phylogeny of the Solanaceae: subfamilial relationships and character evolution. Ann. Missouri Bot. Gard. 79:346–60.

Olmstead, R. and J. Palmer. 1997. Implications for the phylogeny, classification, and biogeography of *Solanum* from cpDNA restriction site variation. Sys. Bot. 22:19–29.

Patiño, V. 1963. Plantas cultivadas y animales domesticas en America equinoccial. Tomo I. Frutales. Imprenta Departmental. Cali, Colombia.

Prohens, J., J. Ruiz, and F. Nuez. 1996. The Pepino (*Solanum muricatum*, Solanaceae): a “new” crop with a history. Econ. Bot. 50:355–368.

Salick, J. 1989. Cocona (*Solanum sessiliflorum*): an overview of production and breeding potentials of the peach-tomato. In: G. Wickens and P. Day (eds.), New crops for food and industry. Chapman and Hall, London.

Salick, J. 1992. Crop domestication and the evolutionary ecology of cocona (*Solanum sessiliflorum* Dunal). Evol. Bio. 26:247–285.

Spooner, D., G. Anderson, and R. Jansen. 1993. Chloroplast DNA evidence for the interrelationships of tomatoes, potatoes, and pepino (Solanaceae). Am. J. Bot. 80:676–698.

Torre, R. and S. Camacho. 1981. Campesino fitomejorador de naranjilla. Carta de Frutales no. 14, Instituto Nacional de Investigaciones Agropecuarias, Quito, Ecuador.

Whalen, M., D. Costich, and C. Heiser. 1981. Taxonomy of *Solanum* section *Lasiocarpa*. Gentes Herb. 12:41–129.