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Ethnobotany of the Genus *Cyphomandra* (Solanaceae)[1]

Lynn Bohs[2]

Plants of the genus Cyphomandra *(Solanaceae) have long been utilized for their edible fruits in their native Latin America. The best-known species is the domesticated tree tomato or tamarillo,* Cyphomandra betacea. *This species, popular as a raw or cooked fruit, is widely cultivated in Andean South America and is now dispersed worldwide in subtropical areas. Its origin and wild relatives are still unknown, but there are tentative reports of wild populations of* C. betacea *in southern Bolivia and northwestern Argentina. Wild species of* Cyphomandra *such as* C. hartwegii, C. sibundoyensis, *and* C. cajanumensis *also produce edible fruits. Other species of* Cyphomandra *are used in medicinal preparations and as dyes. This group of plants is of increasing economic importance and may have considerable potential for future exploitation.*

Etnobotánica del Género *Cyphomandra* (Solanaceae). *Plantas del género* Cyphomandra *(Solanaceae) han sido utilizado por mucho tiempo por sus frutos comestibles en América Latina donde están nativas. La especie más conocida es el domesticado tomate de árbol o tamarillo,* Cyphomandra betacea. *Esta especie, que está estimada como una fruta cruda o cocinada, está extensamente cultivada en los Andes del América del Sur y ahora está crecida mundial en las regiones subtropicales. El lugar del origen y progenitores todavía están desconocidos, pero hay reportes tentativos de poblaciónes silvestres de* C. betacea *en el sur de Bolivia y el noroeste del Argentina. Especies de* Cyphomandra *no cultivadas como* C. hartwegii, C. sibundoyensis, *y* C. cajanumensis *también dan frutos comestibles. Otras especies de* Cyphomandra *se utilizan como medicinas y tinturas. Este grupo de plantas tiene mucho importancia económica y tenga gran potencial para explotación en el futuro.*

The Solanaceae is among the most economically important of all plant families, providing mankind with such familiar crop plants as potato, tomato, chili pepper, eggplant, and tobacco. Aside from these species, the family also furnishes a number of lesser-known fruit crops, such as the pepino (*Solanum muricatum* Ait.), the lulo or naranjilla (*Solanum quitoense* Lam.), the tomatillo (*Physalis philadelphica* Lam.), and the tree tomato (*Cyphomandra betacea* (Cav.) Sendtn.). These latter species, though perhaps unfamiliar to those in the North Temperate Zone, are widely grown and esteemed in tropical and subtropical regions for their juicy, edible fruits. Some of these plants are now becoming familiar in American grocery stores as specialty fruits imported from New Zealand. The tree tomato and related species in the genus *Cyphomandra* have been particularly neglected from a taxonomic and cultural standpoint and are the focus of the following account.

I will examine the economic aspects of *Cyphomandra* species with particular

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reference to their value as fruit crops. Most emphasis will be placed on *C. betacea,* the tree tomato, because of its popularity and commercial potential. In addition, because this species is known only from cultivation, it is of interest to consider its wild relatives, its place of origin, and the evolutionary events that occurred during its domestication.

In addition to *C. betacea,* several other species of *Cyphomandra* are sources of edible fruits, medicinal preparations, and dyes. Though they are often mentioned in the ethnobotanical literature, it has been difficult to assimilate this information owing to a lack of knowledge about the taxonomy of the genus. Recent systematic work on *Cyphomandra* (Bohs 1986) has made it possible to assign correct names to most of these taxa and assess their current status as useful plants. The information presented here has been taken from a survey of the literature, from my personal observations, and from herbarium specimens consulted as part of an ongoing taxonomic study of *Cyphomandra.*

DESCRIPTION OF THE GENUS

The genus *Cyphomandra* includes about 50 species found from southern Mexico through South America. All but about five species occur exclusively in South America, where there are two main centers of species diversity: one on the eastern Andean slopes in Peru and Bolivia and the other in southeastern Brazil. Most species are subtropical and inhabit moist forest at elevations of about 500–2000 m, but a few are found along the coast or in the Amazonian basin at elevations of 100 m or less. Still others prefer high elevation cloud forests at altitudes up to 3000 m. The plants are generally fast-growing trees of the forest understory. Like many other solanaceous plants, they exploit light gaps in the primary forest and also occur in secondary sites such as margins of roads, trails, and pastures.

All members of *Cyphomandra* are shrubs or small trees that reach several meters in height. The plants generally have a single trunk and a large spreading crown that bears the flowers and fruits (Fig. 1). The leaves are often large and succulent, frequently have cordate bases, and may be simple, lobed, or pinnately compound. The pentamerous, pendent flowers have corollas ranging in color from white or pinkish to lavender, violet, and green or greenish-yellow. The anthers are borne on very short filaments and dehisce by terminal pores. The enlarged anther connective is a conspicuous and diagnostic feature of all species in the genus (Bohs 1986). It is a thick, swollen area occurring on the abaxial, and occasionally on the adaxial side of the stamen and is clearly delimited from the thin-walled anther thecae. The fruit is a berry that is glabrous or variously pubescent at maturity. The fruits of most wild species are yellow when ripe, but those of *C. betacea* are orange or red; darker longitudinal stripes are often apparent on the fruit surface. In many species, sclerotic concretions are present in the mesocarp and can occasionally reach several centimeters in length.

Within the Solanaceae, *Cyphomandra* is probably most closely related to the large and complex genus *Solanum.* Both *Cyphomandra* and *Solanum* have anthers that dehisce by apical pores. *Cyphomandra,* however, is distinguished by the enlarged anther connective. Details of the architectural form and branching pattern of the shoots may also aid in distinguishing *Cyphomandra* from *Solanum* (Bohs 1986).

THE TREE TOMATO, *CYPHOMANDRA BETACEA*

Cyphomandra betacea (Cav.) Sendtn. is by far the most important member of the genus from an economic point of view. It is a common sight in dooryard gardens of Latin America, where it is found from Mexico to Central America and the West Indies, and throughout the Andes to northern Argentina, mostly at elevations between 1500 and 3000 m (Fig. 3). This species is now cultivated worldwide in subtropical or warm temperate regions. Plantations of *C. betacea* have been established at several sites in Colombia and Ecuador, in Haiti, and in New Zealand (Fletcher 1979; Heiser 1969; Morton 1982; Popenoe 1924). Despite its importance, little has been known about the biology or taxonomy of this species until recently.

Description

This species is a small tree that may become rather woody at the base, reaching a diameter of 5–10 cm. Mature individuals are usually 2–4 m tall, with occasional plants as tall as 7 or 8 m. The leaves are softly pubescent on both sides and are ovate in outline with cordate bases; they may become very large, up to 30–40 cm long and 20–35 cm wide. The flowers are pendent and very fragrant, with white or pinkish, fleshy, nearly glabrous corollas with narrow spreading lobes recurved at the tips. The mature fruit is an elliptic, smooth-skinned, many-seeded berry reaching 4–10 cm long and 3–5 cm wide (Fig. 2). The skin is usually dull red or orange, but may range from yellow to purple, sometimes with dark longitudinal stripes. The meaty mesocarp just inside the skin varies from creamy yellow to pale orange and has a bland or bitter flavor, whereas the mucilaginous watery pulp surrounding the seeds is subacid and sweet. The major commercial variety seen in the U.S. has deep red or purple fruits with a purplish or blackish layer around the seeds. In South America, however, most tree tomato fruits are orange or reddish outside with orange or yellowish mesocarp. This type, known as the yellow strain, reputedly has a milder flavor than the red type and is used in New Zealand for canning (Fletcher 1979). Several named cultivars have recently been developed, especially in New Zealand. Throughout South America, plants of *C. betacea* are notably consistent in morphological characteristics except for variability in fruit size, color, and shape; this is to be expected in plants presumably subjected to human selection for their fruits.

Uses of the fruits

Tree tomatoes are eaten by scooping out the entire inner part of the fruit, discarding the exocarp and outer layer of the mesocarp. The latter has a disagreeable bitter taste and must be removed; this is facilitated by immersing the fruits in boiling water for several minutes (Hume and Winters 1949). The seeds may be eaten or strained out. The taste is much like that of the garden tomato, *Lycopersicon esculentum* Mill., but the fruits are more acid and less juicy and have a noticeable aftertaste. Because of their resemblance to tomatoes, they may be used in similar ways: eaten raw, cut up in salads, or cooked or stewed with meat. In Bolivia, tree tomatoes are mixed with hot chili peppers to form a piquant sauce used as a condiment (Cárdenas 1969). The fruits are reputedly boiled as a

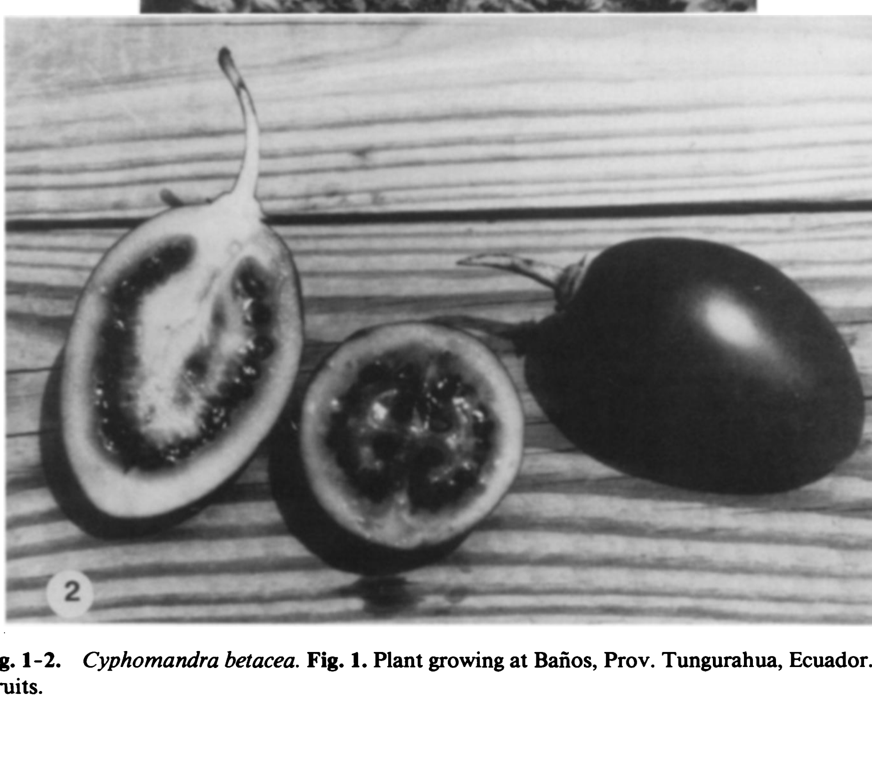

Fig. 1–2. *Cyphomandra betacea.* **Fig. 1. Plant growing at Baños, Prov. Tungurahua, Ecuador. Fig. 2. Fruits.**

soup in New Guinea (*Vink 16343,* A, L). They are usually sweetened, however, and may be made into preserves, jams, pies, and other desserts. In South America, tree tomatoes are often blended with milk and sugar to make a refreshing drink much like a North American milkshake.

The fruits of *C. betacea* are relatively nutritious because of their high vitamin content. They are very rich in β-carotene, making them good sources of provitamin A, and they also contain large amounts of ascorbic acid, or vitamin C (Dawes and Callaghan 1970). Their high pectin content makes them especially suitable for jam- and jelly-making. Levels of nitrogen and free amino acids are higher than those of most fruits except avocados and bananas; the values for potassium and phosphorus are also high among fruits, which are normally poor sources of these elements (Dawes and Callaghan 1970).

Culture

The high yield and ease of culture contribute to the popularity of the tree tomato. Each tree may bear hundreds of fruits the year round. Yields per tree average around 20 kg of fruit per year, and commercial yields are about 15–17 tons per ha (Fletcher 1979). The plants are propagated by seeds or by stem and root cuttings. Cuttings from the crown region produce lower, more bushy plants than those taken from the trunk. When grown from seed, the plants reach reproductive maturity in 1 or 2 yr and may bear fruits for 8 or 10 yr in a well-tended orchard. The tree tomato thrives best in deep, fertile, permeable soil. Though it needs abundant water, a high degree of humidity may cause the stems to rot. The plants do best in subtropical or warm temperate climates with year-round temperatures averaging about 60–70°F (15–21°C) (Choucair 1961; Morris 1884). They are apparently intolerant of constant high temperatures and often fail to mature their fruits in lowland tropical climates owing to excessive heat (Morris 1887; Ochse et al. 1961). The plants, fairly susceptible to frost damage, should be commercially grown outside only in frost-free areas; they may recover from an occasional light frost after dying back to the trunk and main branches. The brittle branches are easily broken by the wind, and plantings should be undertaken only in well-sheltered areas with adequate windbreaks. Light pruning should be done to outdoor plants to eliminate old branches and suckers, but in the greenhouse the plants should be vigorously pruned annually to prevent them from straggling. Their large size and long life cycle are the major drawbacks to their cultivation in greenhouses. For additional details pertaining to the cultivation of *C. betacea,* see the useful summaries presented by Fletcher (1979) and Morton (1982).

Cyphomandra betacea is the only member of the genus that is known to be self-compatible (Bohs 1986). Although its natural pollinators and dispersal agents are unknown, the flowers are frequently visited by bees wherever it is cultivated, and it may also set fruits in response to being shaken by the wind. This self-compatibility is interesting in light of the cultivated status of *C. betacea.* Whalen and Anderson (1981) proposed that self-incompatibility is the ancestral state in *Solanum*; the widespread occurrence of self-incompatibility in *Cyphomandra* is evidence for its primitiveness in the latter genus as well (Bohs, unpubl. data). Although self-compatibility in *C. betacea* could have arisen either before or after domestication, the enhanced fruit set occasioned by self-compatibility is advantageous to cultivation of this species and is possibly one of the reasons it has been favored over the wild species of *Cyphomandra* as a fruit crop.

Cyphomandra betacea seems to be relatively resistant to pests and diseases, though the incidence of disease depends on the density of planting and the geographical area in which it is grown. The tree tomato is resistant to several viral diseases such as tobacco mosaic and tobacco etch, which attack many members of the Solanaceae (Holmes 1946). (Only one other solanaceous species, *Physalis viscosa* L., is known to be resistant to tobacco mosaic virus [Holmes 1946].) However, a number of viral outbreaks have occurred in tree tomato plantations in New Zealand where the plants are suspected hosts of cucumber mosaic, arabis mosaic, tamarillo mosaic, and tomato aspermy viruses (Chamberlain 1948; Fletcher 1979; Mossop 1977; Procter 1975; Thomas and Procter 1972, 1977). It is probable that these diseases are spread by aphid or nematode vectors from wild hosts growing as weeds in *C. betacea* plantations. There is no evidence of transmission of these diseases in tree tomato seeds, and propagation solely by seeds may provide some measure of control. Unfortunately, this practice results in some unpredictability in the quality of fruits from individual trees (Sutton and Strachan 1971).

Principal fungal diseases of the tree tomato include anthracnose, which hardens and deforms the skin of the fruit, and powdery mildew (*Oidium* sp.), an ashy-white fungus found on the upper and lower leaf surfaces of plants in Colombia and New Zealand (Choucair 1961; Fletcher 1979). *Cyphomandra betacea* may also be susceptible to verticillium wilt, a soil-borne fungus that also infects tomato, potato, and eggplant (Bailey and Bailey 1976). Long-term storage of the fruits after harvesting has been a problem, mainly due to losses from bitter rot of fruit caused by the fungus *Colletotrichum acutatum.* A process of dipping the fruits in hot water and rewaxing has been successful in combating this problem and prolonging storage life to 12–14 wk at 3.5–4.5°C (Fletcher 1979).

The major insect pest of *C. betacea* is the tree tomato worm, the larva of the pyraustid moth *Neoleucinodes elegantalis,* which also attacks *Lycopersicon esculentum, Solanum melongena,* and *S. sisymbriifolium* (Capps 1948). Damage to tree tomato plants from this pest has been observed in the Antilles and throughout Central and South America. The larvae bore into the fruits, causing them to spoil prematurely and occasioning fruit losses of 40–80%. Chemical and possibly biological controls may be helpful in controlling or eliminating this pest (Choucair 1961; Gallego 1960).

In colloquial speech, *Cyphomandra betacea* is most often called "tree tomato," "tomate de árbol" (Spanish), or "tomate de árvore" (Portuguese). Because *C. betacea* grows readily from seed and may become naturalized around old dwellings, it is frequently called "tomate silvestre" or "tomate serrano," indicating that it is a "wild tomato." Additional vernacular names names applied to this species are given in Table 1. The name "tamarillo," chosen over "tree tomato" by New Zealanders in 1967 to avoid confusion with the garden tomato, is the designation most widely applied in commerce (Fletcher 1979).

Origin and domestication

The center of origin of *C. betacea* is most likely located in South America, where the great majority of *Cyphomandra* species are native. Beyond this, little

TABLE 1. VERNACULAR NAMES OF *CYPHOMANDRA BETACEA*.[a]

Name (language, if given)	Region	Source
Berenjena	Mexico	*Duges 393A,* GH; *Leon Arteta s.n.,* F; *Zola 469,* F
	Peru	*Ferreyra 2708,* US, USM
Caxlan pix (Quecchí)	Guatemala	Gentry and Standley 1974
Chilto	Bolivia	*Beck and Liberman 9675,* GH
Chimbal-bé (Kamsá)	Colombia	*Bohs 1599,* GH
Granadilla	Guatemala	Gentry and Standley 1974
Lima tomate	Bolivia	Cárdenas 1969; Patiño 1963
Naranjilla	Colombia	*Core 1184,* US
Pepino de árbol	Colombia	Romero-Castañeda 1961; *García-Barriga 10896,* COL
Pix (Quecchí)	Guatemala	Gentry and Standley 1974
Sima	Bolivia	Patiño 1963
Somato (Hagen-Chimbu)	New Guinea	*Vink 16343,* A, L
Terong	Java	*Hallier 17,* L, NY
Terong blanda	Java	*Balchuizen 1560,* L; *Pulle 3115,* U
Terong menen	Java	*Balchuizen 1560,* L
Terong wolanda	Java	*Hochreutiner 2602,* G
Tetamatu	New Guinea	*Dosedlie-Grotovitz 101,* W
Tomate	Mexico	*Matuda 16215,* US
	Guatemala	Gentry and Standley 1974
	Colombia	Romero-Castañeda 1961
	Ecuador	*Filskov et al. 37010,* AAU
	Peru	*Macbride 3875,* F, G, US; *West 8044,* GH, MO
Tomate chimango	Brazil	Corrêa 1975
Tomate cimarrón	Costa Rica	*Standley 35995,* US; Standley and Morton 1938
Tomate de agua	Colombia	*Lehmann 6433,* K
Tomate de Castilla	Venezuela	*Bernardi 548,* NY
Tomate de La Paz	Peru	Macbride 1962
	Chile	*Bertero 1325,* GH, MO
Tomate de Lima	Bolivia	*Weddell s.n.,* P
Tomate del monte	Argentina	*Fabris 3411,* CTES; Corrêa 1975
	Bolivia	Patiño 1963
Tomate de palo	Honduras	*Rodriguez 2270,* F; Gentry and Standley 1974
Tomate del serrano	Ecuador (Galapagos Is.)	*Wiggins and Porter 681,* GH
Tomate en arbre (French)	Martinique	*Duss 4429,* NY
Tomate extranjero	Guatemala	Gentry and Standley 1974
	Bolivia	Cárdenas 1969
Tomate francés	Venezuela	Pittier 1926, 1947
	Brazil	Hoehne 1946; Smith and Downs 1966
Tomate granadilla	Guatemala	*Standley 90903,* F; Gentry and Standley 1974
Tomate silvestre	Colombia	*Bohs 1599,* GH
Tomateiro da serra	Brazil	Corrêa 1975
Toronjo	Colombia	*Core 1184,* US
Yuncatomate	Peru	*Gade s.n.,* WIS

[a] Most commonly used names are mentioned in text.

is known of the origin or domestication of the tree tomato. Although it is widely grown throughout the Andes, truly wild populations are not yet known. The plants are nearly always associated with human habitations, and any spontaneously growing specimens could be escapes from cultivation. Fruits of *C. betacea* are said to be represented on pre-Columbian pottery vessels from Peru (Safford 1917), indicating that this species was domesticated by prehistoric inhabitants of the Andes. The general similarity of the tree tomato to many other kinds of fruits found in this area, particularly *Solanum muricatum,* the pepino, calls into question the interpretation of these pottery remains (Towle 1961; Yacovleff and Herrera 1934). Heiser (1969) and Cárdenas (1969) pointed out that most of the common names used for *C. betacea* are derived from Spanish or Portuguese rather than from native languages. According to Heiser, this may be an indication of its relatively recent domestication.

New information has been received indicating that wild populations of this species exist in undisturbed forest areas of southern Bolivia and northern Argentina (J. Solomon, pers. comm.; E. Zardini, pers. comm.; see Fig. 3). A tributary valley of the Río Zapla near the city of Jujuy in northwestern Argentina even bears the name "Los Tomates." Brücher (1977) saw *C. betacea* growing wild in the province of Salta near the Bolivian-Argentinian border in 1956. Further investigations should be carried out in this region to determine if in fact it could be the area of origin of the tree tomato.

History of dispersal

Because of its usefulness to mankind, the tree tomato has been dispersed worldwide. Figure 4 summarizes the probable routes of dispersal of this species.

The tree tomato has almost certainly been introduced into Mexico, Central America, eastern South America, and the West Indies. Its date of introduction into eastern South America is unknown, but its use by the people of Buenos Aires is mentioned by Miers in 1845. In all probability, however, it had spread to eastern South America long before this time.

Cyphomandra betacea has been used in Jamaica since the 19th century. Its arrival there is not documented, but it was well established by 1884 (Anonymous 1887; Morris 1884). *Cyphomandra betacea* was not listed in Lunan's *Hortus Jamaicensis* of 1814 and was apparently introduced there subsequent to that date. Powell's compilations of Jamaican plant introductions prior to 1806 also fail to list *C. betacea* (Powell 1972). The tree tomato is rarely seen at present in old gardens in Jamaica and is seldom used there today (G. Proctor, pers. comm.).

Roig y Mesa (1953) mentioned that the tree tomato was also cultivated in Cuba, citing Mexico as its point of origin. According to information on a herbarium specimen of *Duss 4429* (NY), it was introduced to Martinique prior to 1900, probably from Jamaica.

Cook and Collins' (1903) account of Puerto Rican plants described the successful introduction of the tree tomato into Jamaica but indicated that it was not yet grown in Puerto Rico. By 1948, *C. betacea* was successfully growing and apparently naturalized in some areas of Puerto Rico (Hume and Winters 1948).

The first mention of the tree tomato in the Old World was the original description of the species in 1799, from a plant growing at the botanical garden in Madrid

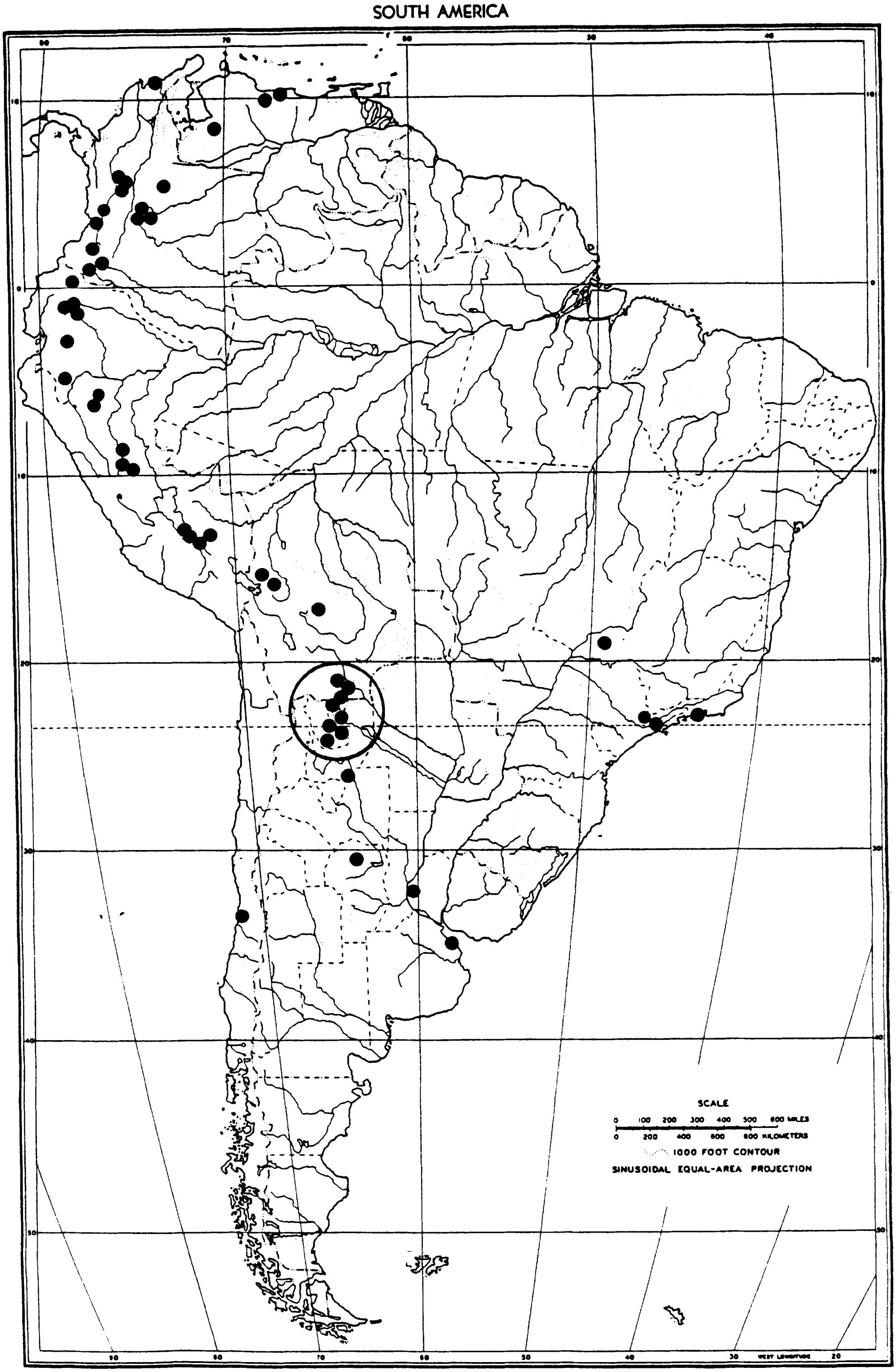

Fig. 3. Distribution of *Cyphomandra betacea* in South America. Each locality is represented by a herbarium specimen. Circle corresponds to the putative area of origin of this species. Base map copyright University of Chicago.

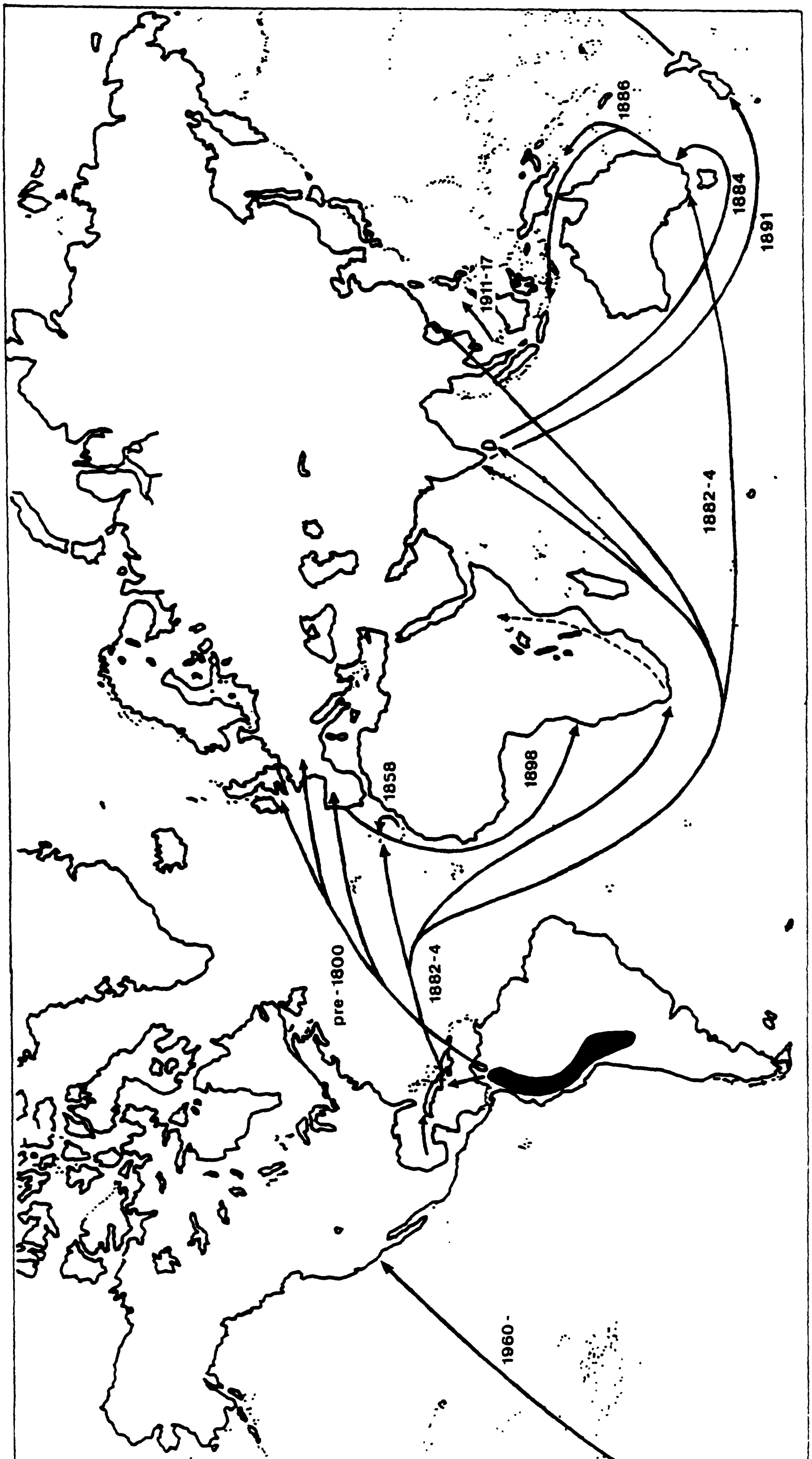

Fig. 4. Dispersal routes of *Cyphomandra betacea*. See text for details.

(Cavanilles 1799). How it reached Spain at that time is not known, but one possibility is that it was sent to Spain from the Ruiz and Pavon expedition to the New World undertaken in the late 18th century (R. E. Schultes, pers. comm.). It was next noted in 1801 in England (Andrews 1801) and in 1803 was introduced into cultivation at Kew Gardens (Aiton 1810). At about the same time it was found in France (Dunal 1813, 1814, 1816) and Berlin (Willdenow 1809) and was also dispersed through southern Europe to Egypt (Alliaume 1880; Morris 1884). It was also reported from the Canary Islands (as *Solanum insigne*) in the mid 19th century by Lowe, who introduced it into Madeira around 1858 (Lowe 1867).

In the early 1880s, one Dr. D. Morris, Director of the Botanical Gardens in Jamaica, distributed seeds to correspondents in Madeira, the Cape of Good Hope, India, Ceylon, Hong Kong, and the Australian colonies (Anonymous 1887; Morris 1884). Some of the plants from the original Jamaican stock were also brought to Australia from Ceylon by a Capt. Murray in 1884 (Maiden 1894). By 1886 *C. betacea* had been distributed to all the southeast Asian colonies, including the botanic gardens (Burkill 1966; Maiden 1894). At this time it was successful in India, especially in the southern hill regions such as the Nilgiris (Anonymous 1887; Singh et al. 1967). Hooker noted the cultivation of the tree tomato as early as 1899 in China (Hooker 1899); it is still grown there today (Lu 1986). It was introduced into the Philippines in 1911 and again in 1917 (Wester 1925). According to one account (Anonymous 1922), missionaries or settlers moving north from the Cape of Good Hope after the Boer Wars may have taken seeds of *C. betacea* with them to Kenya and Tanzania, where this plant was known as the "Cape tomato." *Cyphomandra betacea* was also brought from Oporto, Portugal, to southwestern Africa in the late 19th century (Hiern 1898; Warburg 1903).

In 1891, *C. betacea* was introduced to New Zealand from India, probably from Jamaican stock (Fletcher 1979). Today New Zealand is the largest commercial producer of tree tomatoes. At present there are some 1000–2000 acres devoted to its cultivation, and the annual harvest amounts to some 2000 tons (Sutton and Strachan 1971; A. R. Ferguson, letter to P. S. Ashton, 31 Aug 1982). Most of the plantings are small plots of about 1 ha (2.47 acres), in frost-free areas in the northern part of the country such as at Kerikeri, around Auckland, and in the Bay of Plenty (Fletcher 1979). The majority of the fruits are marketed internally, but some are exported to Australia, Japan, Canada, and the United States. Breeding and improvement work is just beginning, and the New Zealanders hope to have the same success with *Cyphomandra* as they have had with the recently popularized kiwi fruit, *Actinidia chinensis* Planch. (A. R. Ferguson, letter to P. S. Ashton, 31 Aug 1982).

The first records of *C. betacea* in the United States date from 1886–1887 in Florida and from 1890 in California (Fisch 1974). Today it is occasionally grown in southern Florida (Morton 1982) and is often advertised in seed catalogues as a horticultural curiosity. Growers in California are beginning to take an interest in the tree tomato since it has emerged as a new fruit from New Zealand (J. Riley, pers. comm.).

Commercial outlook

As yet *C. betacea* has been relatively unexplored with regard to its commercial potential. It is possible that a breeding program might be implemented to develop varieties equal or superior to the garden tomato. It may be grown at higher altitudes and in cooler climates than the garden tomato, and it is a perennial that may continue to bear fruits for 8–10 yr. Fast-maturing or cold-hardy types would be especially desirable for temperate climates, and dwarf varieties might be more suitable for cultivation in the greenhouse. Perhaps a breeding program including wild species of *Cyphomandra* would result in immunity to some of the pests and diseases that affect the tree tomato. Grafting programs have already been initiated using other species of *Cyphomandra* and species of *Solanum* and *Nicotiana* as rootstocks in order to increase yield and longevity and confer resistance to nematodes and *Phytophthora* root rot (IBPGR 1986). The fruits could be improved by breeding to increase their size and quality and reduce the number of seeds, as has been done with the garden tomato. Elimination of the stone-cell aggregates found in the mesocarp would facilitate processing. New uses must be found for the fruits before they are to gain widespread acceptance. Because the flavor of the fruits is more acceptable when they are cooked, perhaps more effort should be made to develop better processed tree tomato products, such as sauces and ketchups. A bigger market may also exist for canned fruits in syrup.

OTHER EDIBLE *CYPHOMANDRA* SPECIES

In addition to *C. betacea,* there are several wild *Cyphomandra* species yielding edible fruits. These species are not grown on a large scale, but are sporadically cultivated locally in Central and South America as curiosities or as supplements to the diet. Potentially, some of them may represent fruit crops as good as or better than *C. betacea.*

Cyphomandra hartwegii

This is the most familiar of the wild species of *Cyphomandra* eaten for their fruits. It occupies the most extensive range of any species in the genus, occurring from the state of Veracruz in Mexico south throughout Central America. In South America, it is found along the coast from Colombia to the Guianas, and in the Andean area from Colombia south to Bolivia. It inhabits areas of tropical rain forest at elevations from sea level to 2000 or 2500 m.

Cyphomandra hartwegii (Miers) Sendtn. ex Walp. is a small tree that grows from 3 to about 10 m tall. Characteristically, it has large, pinnately lobed leaves on the trunk and smaller, unlobed leaves in the crown region. The corolla is usually green with longer and narrower lobes than those of *C. betacea.* The fruits are ellipsoidal, 3–10 cm long and 3–6 cm in diameter, and yellow or orange at maturity. The flesh inside is generally creamy white. The fruits contain numerous large, flattened seeds and usually several very large stone-cell aggregates.

Because of its extensive range and morphological variability, *C. hartwegii* has been described under many botanical names. Synonyms for *C. hartwegii* encountered in ethnobotanical literature include: *C. costaricensis* J. D. Sm., *C. dendroidea* Pittier, *C. heterophylla* J. D. Sm., *C. mollicella* Standl., and *C. naranjilla* Pittier (according to taxonomic scheme of Bohs 1986). In addition to these synonyms, Romero-Castañeda (1969) gives an account of this species under the name *C. crassifolia* (Ort.) Macbr., a synonym of *C. betacea.* In other cases, the name *C.*

TABLE 2. VERNACULAR NAMES OF *CYPHOMANDRA HARTWEGII*.

Name	Country	Source
Contra gallinazo	Panama	*Duke 8283*, MO
Dwergtafrabon	Suriname	*Boerboom 9605*, U
Fruta de agua	Honduras	*Nelson et al. 3097*, MO
Kó pi (Secoya)	Ecuador	*Vickers 98, 196*, F
Monka prieto	Panama	*Cooper and Slater 181*, US
Naranjilla	Colombia	Pittier 1910
Pepinillo	Costa Rica	Allen 1956; Pittier 1908; Standley and Morton 1938
Regalgar	Colombia	*García-Barriga 12464*, COL
Reventadera	Colombia	*Romero-Castañeda 5022*, US
Sandillo	Costa Rica	*Wilbur and Stone 9804*, F, MO
Tigriston	Suriname	*Boerboom 9605*, U
Tomate de indio	Colombia	*Agudelo and Klevers 78*, US
Tomate de montaña	Ecuador	*Dodson et al. 7223*, F, MO
Tomate del monte	Colombia	*Pennell 10720*, GH
	Ecuador	*Cazalet and Pennington 5026*, US
Tomate silvestre	Ecuador	*Acosta Solís 13971*, F
Tonga	Colombia	*Archer 1759*, US
Tsutsucuru (Kamsá)	Colombia	*Bristol 1014*, ECON
Venenillo	Colombia	*Romero-Castañeda 2690*, COL
Zopilote	Costa Rica	*Allen 5241*, GH, US; Allen 1956

hartwegii has been erroneously applied to *C. betacea* (Hedrick 1919; Uphof 1968; Usher 1974). Yacovleff and Herrera (1934) and Towle (1961) also use the name *C. splendens* Dun., a synonym of *C. hartwegii,* to refer to *C. betacea.*

The vernacular names that have been applied to *C. hartwegii* are summarized in Table 2.

Cyphomandra hartwegii is not cultivated commercially, but is frequently planted locally for its yellow, mild-tasting fruits. They are used much like those of *C. betacea*: eaten raw, made into preserves, jellies, juices, or sweets, or candied in syrup (Pittier 1908, 1910; Romero-Castañeda 1961, 1969). The fruits of the typical subspecies of *C. hartwegii* in Central America and northern South America reach a length of about 3–5 cm. However, a form of this species from west central Colombia, *C. hartwegii* ssp. *ramosa* Bohs, produces very large fruits up to 8–9 cm long (Bohs, 1988b; Fig. 5). Known as the "tomate del monte" or "tomate macho," it is the source of tart fruits that reputedly make a good juice when sweetened with sugar (G. Büch, pers. comm.). On the other hand, the fruits of this same taxon have also been used to kill beetles (Bitter 1921). Although no details were given, perhaps the fruits were employed in a manner similar to those of *Solanum mammosum* L., whose fruits are used as a cockroach poison (Nee 1979). *Cyphomandra hartwegii* may have future economic potential as a fruit crop, but an obstacle to its acceptance is the presence of prominent stone-cell aggregates in the fruits.

Cyphomandra sibundoyensis

Cyphomandra sibundoyensis Bohs has been found as yet only in and around the Valley of Sibundoy in southern Colombia at elevations of about 2200 m (Bohs

1988a). Here it is known as "tomate salvaje" or "tomate silvestre." It closely resembles *C. hartwegii,* but no lobed leaves occur on the trunk and the corollas are generally violet rather than green. The fruits are yellow or orange at maturity and may grow to 6–10 cm long and 5–7 cm in diameter, making them some of the largest known in the genus (Fig. 6). Inside, the mesocarp is white, juicy, and sweet; the seeds are surrounded by a thin pinkish-purple layer. Of all wild species of *Cyphomandra* yet observed, this is the most palatable and contains the most edible pulp per fruit. The very large, sweet, and attractive fruits seem to need little improvement to be developed as a crop.

"Casana"

Growers in New Zealand have been initiating trials with a *Cyphomandra* fruit called "casana" recently collected in a high-altitude region of southern Ecuador. It was described by Child (1986) as a new species, *C. casana,* a synonym of *C. cajanumensis* (Kunth) Sendtn. ex Walp. collected in the same region of southern Ecuador. The "casana," said to be hardier than *C. betacea,* produces heavy crops of fruits in New Zealand (Child 1986). The fruits are large, 5–8 cm long and 3–4.5 cm in diameter, glabrous, somewhat pointed at the end, and yellow at maturity. Though fresh fruits are said to taste like a combination of peach and Cape gooseberry, *Physalis peruviana* L., Child (1986) reported that fruits ripened in transit have an insipid taste and an objectionable soft texture. A feature of the fruits worthy of consideration is the lack of hard stone-cell aggregates.

Cyphomandra uniloba

The Bolivian species *C. uniloba* Rusby is also reported to have a sweet, juicy fruit. It has simple, cordiform leaves, green corollas, and anthers that are shorter and thicker than the preceding species. The fruits are glabrous, pointed at the apex, and yellow with dark green stripes at maturity (Fig. 7). Although several collectors refer to their edibility and call the plant "tomate del monte" (*R. F. Steinbach 436,* GH; *Sperling & King 5500,* GH), the fruits produced from greenhouse plants in Cambridge, MA, had either a bitter or an insipid taste.

Other species

A few other species may be noted as sources of edible fruits. From personal experience, I consider the fruits of *C. diversifolia* (H. & B. ex Dun.) Bitt. to have an acidulous but refreshing taste. This species also lacks the stone-cell aggregates found in the mesocarp of many other taxa. *Cyphomandra tegore* (Aubl.) Sendtn. ex Walp. was said by Aublet (1775) to be cultivated by the natives of French

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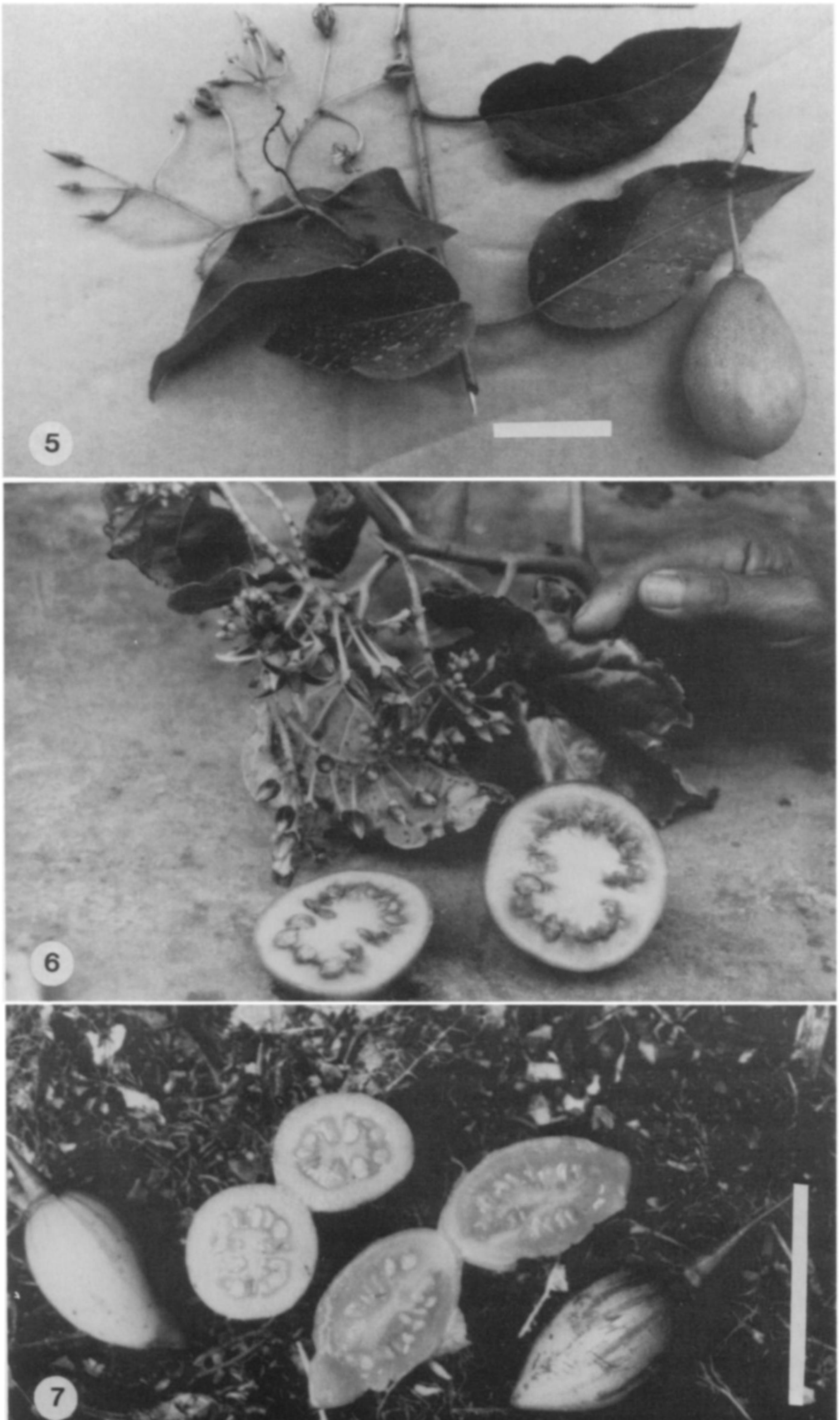
Fig. 5-7. *Cyphomandra* spp. **Fig. 5.** Crown leaves, flowers, and fruits of *C. hartwegii* spp. *ramosa* from Huila Dept., Colombia (*Bohs 1644,* GH). Scale bar = 5 cm. **Fig. 6.** Crown leaves, flowers, and fruits of *C. sibundoyensis* from Sibundoy, Putumayo, Colombia (*Bohs and Juajibioy 2222,* GH). **Fig. 7.** Fruits of *C. uniloba* from Mapiri, Prov. La Paz, Bolivia (*Sperling and King 5500,* GH). Scale bar = 5 cm. (Photo by Calvin Sperling.)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Guiana, but he gives no use for the plant. Two collectors (*Mexia 8235,* F, GH, US; *Spruce 4229,* K) reported that the fruits of *C. obliqua* (R. & P.) Sendtn. are edible and taste like a tomato, but another (*Fosberg 28993,* WIS) asserted that they are poisonous. Other *Cyphomandra* species have vernacular names such as "papaya del monte" (for *C. pendula* (R. & P.) Sendtn.; *Mexia 8245,* GH, NY, US); "wild cucumber" (for *C. chlorantha* Rusby; *Cooper 398,* F, NY, US); or "pepino del campo" (for *C. tenuisetosa* Bitter; *Mexia 8209,* F, GH, US), which indicate that they may have large, juicy fruits, but no reports exist of their utilization as foods. The seeds of *C. endopogon* Bitter are said to be eaten in the Amazon region of Peru (*King 511,* GH), but no mention is made of the fruits.

Many species of *Cyphomandra* are present in southeastern Brazil, where they are known under such vernacular names as "baga de veado" ("deer berry"), "unha de veado" ("deer hoof"), or "baga de bugre" ("indian berry") (Corrêa 1975; Smith and Downs 1966). Few reports exist, however, of their employment by humans. Hoehne (1946) observed that the indigenous species of this region produced small, yellow berries that are probably comparable in quality to *C. betacea,* but that the people were afraid to eat them. One explanation may be that the fruits of many of the species from this area are pubescent and would presumably be objectionable as foods unless the hairs easily rub off, as happens with the naranjilla, *Solanum quitoense.* Nevertheless, Smith and Downs (1966) mentioned that the pubescent-fruited *C. patrum* Sm. and Downs of southern Brazil bears edible ellipsoidal fruits about 2 cm long locally called "azeitonas brabas" ("wild olives"). *Cyphomandra divaricata* Sendtn. produces an elongated and glabrous berry that is probably also edible (Corrêa 1975). *Cyphomandra fragans* (Hook.) Sendtn. may also have potential as a fruit crop, and is currently being tried in New Zealand under the name "guava tamarillo" (L. Meadows, pers. comm.). However, the fruits have an objectionable leathery exterior and a sour taste.

MEDICINAL USES OF *CYPHOMANDRA*

The Solanaceae are well known for the abundance and diversity of their alkaloids (D'Arcy 1986). Steroidal alkaloids have been found in *Solanum* and related genera, and pyrrolidines, pyridines, and tropane alkaloids are characteristic of other Solanaceous groups. The alkaloidal constituents of *Cyphomandra* are not well known; the only species that has been investigated to date is *C. betacea.* This taxon has generally been regarded as being free of alkaloids; for this reason it has been used in grafting experiments concerned with the biogenesis of tropane alkaloids in other members of the Solanaceae (Evans et al. 1972; Hammer 1986). Recent analysis, however, has shown that various alkaloids do, in fact, exist in this species. A survey of alkaloids in fresh and dried roots of *C. betacea* revealed the presence of solamine, solacaproine, tropinone, and cuscohygrine. Tropine, ψ-tropine, hyoscyamine, and tigloidine were tentatively reported (Evans et al. 1972).

Amines and amides have also been found in *C. betacea.* Evans and his coworkers (1972) isolated the amine solamine and its amide derivative solacaproine from the roots of *C. betacea,* the first reported occurrence of these compounds in plant material. Evans and Somanabandhu (1980) later found solamine and its amides to be present in certain species of *Solanum* and in four species of *Solanum* section *Cyphomandropsis.* The related amides solapalmitene and solapalmitenine found in *Solanum tripartitum* show anti-tumor activity; solacaproine is being tested for this medicinal property (Evans et al. 1972).

Steroidal alkaloids isolated from *C. betacea* include solasodine and tomatidenol (Schreiber 1979). Solasodine is also found in *Cestrum* and *Solanum,* and tomatidenol is present in species of *Solanum* and *Lycopersicon* (Raffauf 1970). These compounds closely resemble the yam steroidal sapogenin diosgenin and may be useful as precursors for the synthesis of corticosteroids and contraceptive sex steroids (Roddick 1986).

The presence of alkaloids in species of *Cyphomandra* may account for their use as medicines in various areas. They may be prepared as an infusion that is taken internally or as a poultice applied to the affected part. In the Peruvian Oriente, the leaves and stems of *C. obliqua* (R. & P.) Sendtn., or "chupo sacha," are soaked in water and used as an analgesic and sedative for intestinal fever, rheumatism, hangovers, muscle aches, and pains in the lower back and stomach (*Bohs & Schunke 2159,* GH; *Mathias & Taylor 3979,* F; *Plowman & Schunke 7513,* F; *Plowman & Schunke 11550,* GH; *Schunke 8339,* GH; *Woytkowski 5017,* F, MO). In the region around Iquitos, Peru, the fruits and leaves of *C. endopogon,* known locally as "siuca sacha," are mixed with water and used to wash the skin to treat "siso," a skin disease (*Martin 1187,* F). A leaf poultice of *C. pilosa* Bohs, called "pungi huanduj," is used for muscle cramps in Pastaza, Ecuador (*Shemluck 319,* ECON). The Chácobo Indians of Bolivia drink a decoction of the leaves of *C. oblongifolia* Bohs to cure liver problems; this species is locally called "shía" (*Boom 4054,* GH; Boom 1987). In the province of Chiriquí, Panama, the leaves of *C. hartwegii,* there known as "monka prieto," are used to treat cuts and sores (*Cooper & Slater 181,* F, NY, US). In eastern Panama, the Chocó Indians also use the crushed leaves of this species, which they call "contra gallinazo," to treat sores and swellings around the mouth (*Duke 8283,* MO). Pittier (1908) reported that in Costa Rica the leaves of this species (under the name *C. viridiflora* Sendtn.) are used in an infusion to cure erysipelas. In southern Colombia, the bark of *C. hartwegii* is said to provide a vermifugal tea (*Schultes 3652,* ECON). Warmed leaves of *C. betacea* are wrapped around the neck as a remedy for sore throat in Ecuador (*Filskov et al. 37010,* AAU). Portilla (1951) noted that the fruit pulp of *C. betacea,* after having been cooked in embers, is used as a poultice for inflamed tonsils in Colombia. This species was known as "vegetable mercury" in Jamaica because of its presumed therapeutic value to the liver (Anonymous 1887). The placenta of the fruit of *C. sibundoyensis* is also used medicinally, and is reportedly taken internally as a cure for intestinal worms in the Sibundoy Valley of southern Colombia (*Bohs and Juajibioy 2222,* GH). Schultes (1978) reported that the leaves of this species (under the name *C. dolichorhachis* Bitt.) are employed as a vermifuge by Kamsá medicine men of the same region.

It is not known to what extent these medicinal uses actually correspond with physiologically active compounds present in these species. The only chemical test applied to wild species of *Cyphomandra* was a spot test of *C. endopogon* with Dragendorff's reagent, which resulted in a weakly positive reaction for alkaloids (*Fernández-Pérez 6863,* ECON). This finding is interesting in light of the report of Evans et al. (1972) that *C. betacea* possesses alkaloids in the roots but not in the leaves. Certainly this situation points out the need for chemical studies of additional species of *Cyphomandra.*

MISCELLANEOUS USES

In addition to their uses as edible and medicinal plants, a few species of *Cyphomandra* have been employed as dyes. The leaves of *C. betacea* and *C. sibundoyensis* were formerly used for this purpose in the Sibundoy Valley of southern Colombia (*Bohs 1599,* GH; *Bohs and Juajibioy 2222,* GH). The Siona and Secoya Indians of northeastern Ecuador use *C. hartwegii* to paint designs on pottery (Vickers and Plowman 1984). The juice of the fruit is used to paint the pottery before firing to leave a white color (*Vickers 98,* F); after firing, a stain from the leaves is painted on the inside and the pot is smoked in the fire, resulting in a black color (*Vickers 196,* F). Schultes (*3652,* ECON) also reported that this species is used to dye pots black in the Putumayo region of southern Colombia. Similarly, the lowland Quichua of northeastern Ecuador use the leaves of *C. pilosa* to smoke clay pots used for storing chicha (*Irvine 149,* F). This accounts for the Quichua names "manga caspi" ("pot tree") and "asua manga cushnichina yura" ("chicha-pot-smoking tree") applied to this species (*Irvine 149,* F). The unripe fruits of *C. betacea* are also used in the Colombian tanning industry to decolorize hides (Portilla 1951). Whether this relates to the presence of alkaloids or other chemical components such as tannins in the aerial parts is unknown.

CONCLUSIONS

The species of *Cyphomandra* have not been fully exploited as sources of useful products. *Cyphomandra betacea* is emerging as a new commercial fruit crop, and species such as *C. hartwegii, C. sibundoyensis, C. uniloba,* and *C. cajanumensis* produce edible fruits that could be commercially developed in the future. There is evidence that *Cyphomandra* contains both steroidal and tropane alkaloids that might be useful in medicine. Further investigations of the place of origin of *C. betacea* should be made, and the relationship of this species to others within the genus should be clarified. Additional ethnobotanical data gathered on wild species of this group could uncover other potential uses. This group of plants deserves more recognition and research from an economic and scientific standpoint.

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Notes

Acta Botánica Mexicana. Acta Botánica Mexicana, a publication of the Instituto de Ecología, was founded with the aim of reporting the results of scientific research in all fields of botany, with special emphasis in Mexican plants. At least four numbers are issued per year. The journal considers original and unpublished papers chiefly in Spanish, but some articles in English, French, and Portuguese are accepted; each paper includes an abstract in Spanish and English. Annual subscription $15 U.S. Additional information can be obtained from: Acta Botánica Mexicana, Instituto de Ecología, Centro Regional del Bajio, Apartado postal 386; 61600 Pátzcuaro, Michoacán, Mexico.

3rd International Symposium on Poisonous Plants. The 3rd International Symposium on Poisonous Plants will be held in Logan, Utah, 23–29 July 1989 and will be open to all persons interested in or doing research work on poisonous plants. Hotel rooms and dormitory space will be available. Inquiries may be directed to Dr. Lynn F. James, USDA-ARS Poisonous Plant Research Laboratory, 1150 East 1400 North, Logan, UT 84321; telephone (801) 752-2941.