



*Solanum allophyllum* (Miers) Standl. and the Generic Delimitation of *Cyphomandra* and *Solanum* (Solanaceae)

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*SOLANUM ALLOPHYLLUM*  
(MIERS) STANDL. AND THE  
GENERIC DELIMITATION  
OF *CYPHOMANDRA* AND  
*SOLANUM* (SOLANACEAE)<sup>1</sup>

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Lynn Bohs<sup>2</sup>

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ABSTRACT

*Solanum allophyllum* has previously been placed in *Cyphomandra* and in *Solanum*. This species has a number of morphological features not found in *Cyphomandra*, but has been included in the genus because it has a similar growth habit, three-leaved sympodial units with inflorescences in branch forks, and tapered anthers with an abaxial thickening. When each of these characters is closely examined, however, important differences are found between the taxa, indicating that the features they share may not be structurally homologous. New evidence derived from crossing studies and cytological investigations also supports the exclusion of *S. allophyllum* from *Cyphomandra*. *Solanum allophyllum* is self-compatible, whereas all but the single domesticated species of *Cyphomandra* are self-incompatible, and the chromosomes of *Cyphomandra* are about 2.5 to 5.5 times larger than those of *S. allophyllum*. The anther morphology, self-compatibility, and small chromosomes are all consistent with placement of this species in *Solanum*.

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INTRODUCTION AND TAXONOMIC HISTORY

The generic placement of the species here known as *Solanum allophyllum* (Miers) Standl. has long been a source of confusion. Various workers have placed this species in *Solanum*, *Cyphomandra*, and *Bassovia*. It was first described as *Pionandra allophylla* by Miers (1854) in Seemann's *Botany of the Voyage of the H.M.S. Herald*. *Pionandra*, erected by Miers in 1845, is synonymous with Sendtner's genus *Cyphomandra*, created a few months earlier (Sendtner, 1845). Accordingly, *P. allophylla* was transferred to *Cyphomandra* by Hemsley in 1882. Standley transferred *Cyphomandra allophylla* to *Solanum* in 1927 without explanation.

Georg Bitter, unaware of Miers's species, independently described the species as *Solanum ellipsoideibaccatum* Bitt. in 1913. He noted that the tapered anthers with small terminal pores resemble those of *Solanum* subg. *Leptostemonum* (Dun.) Bitt. but surmised that his species probably represented a new section of *Solanum*. In 1914,

Bitter received specimens illustrating the lobed leaves that often occur on the lower branches in this species. He emended his original description to include these lobed leaves and described a new variety, var. *ficilobum* Bitt., from a specimen exhibiting almost exclusively lobed leaves. Pittier (1947) later transferred *Solanum ellipsoideibaccatum* to the genus *Bassovia*, an error that Hunziker (1969) later corrected. *Solanum ellipsoideibaccatum* and its variety *ficilobum* are regarded here as synonyms of the earlier name *Solanum allophyllum* (Miers) Standley.

Standley's placement of the species in *Solanum* was followed in the older literature (Morton, 1944; Romero-Castañeda, 1965; Standley, 1928), but more recent workers have interpreted it as belonging in *Cyphomandra* (Bohs, 1986, 1988; Child, 1984; D'Arcy, 1973). All those who have included the species within *Cyphomandra* have noted its atypical anther structure, but placed it in *Cyphomandra* on the basis of other similarities. Child (1984) called attention to its anomalous features

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<sup>1</sup> I thank Alan Child for sending seeds of *S. allophyllum* and several *Cyphomandra* species and for his insightful discussions on relationships in *Solanum* and *Cyphomandra*. I also thank Dave Barrington, John Sperry, and Mel Tyree for use of their lab facilities, and Greg Anderson, Dave Barrington, W. G. D'Arcy, George Rogers, and John Sperry for reading and commenting on the manuscript.

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when he erected *Cyphomandra* sect. *Allophylla* Child to accommodate this species and the allied *Cyphomandra phytolaccoides* (Rusby) Child (= *Solanum mapiriense* Bitter).

Why has the generic placement of this species been so uncertain? Though *S. allophyllum* differs from *Cyphomandra* in a number of morphological characters, it has been considered as a *Cyphomandra* because, at least superficially, this species shares with *Cyphomandra* the very features that have been used to distinguish *Cyphomandra* from *Solanum*. Both *S. allophyllum* and *Cyphomandra* have: 1) a growth habit characterized by a single erect trunk and a spreading crown of three main lateral branches, 2) three-leaved sympodial units with the inflorescences situated mainly in branch forks, and 3) tapered anthers that are thickened on the abaxial surface. Growth habit and branching pattern have been recently proposed as new characters that distinguish *Cyphomandra* from *Solanum* (Bohs, 1986). Anther structure traditionally separates the two genera (Sendtner, 1845). Herein I reexamine the morphological features of *Cyphomandra* and *S. allophyllum* with emphasis on these three proposed generic characters. New information about the breeding system and morphology of the chromosomes, pollen, and seeds of *S. allophyllum* and *Cyphomandra* is also compared. These investigations help to ascertain the generic position of this species and shed new light upon the critical characters that separate *Solanum* and *Cyphomandra*.

#### MATERIALS AND METHODS

Morphological studies were carried out using living plants, and dried specimens from the following herbaria: A, BM, C, E, F, GH, K, M, MO, NY, P, US, and WIS. Voucher information for greenhouse material is given in the Appendix.

Growth habit is defined by reference to the architectural models of Hallé et al. (1978). This system takes into account the dynamic aspects of plant growth rather than simply considering the shape of a plant at any one time. Terminology relating to architecture and branching pattern likewise follows Hallé et al. (1978).

Compatibility studies were conducted on plants growing in pollinator-free greenhouses at Harvard University and at the University of Vermont. One to several accessions were grown of each species. Plants were either selfed or outcrossed, between accessions and between individuals of the same accession, by tapping pollen onto a clean glass slide

and rubbing it across the stigma of the female parent.

For observations of meiotic chromosomes, flower buds were fixed in Farmer's solution (3:1 absolute ethanol:glacial acetic acid) or Carnoy's fixative (6:3:1 absolute ethanol:chloroform:glacial acetic acid) shortly after sunrise. Preparations were stained with 1–2% acetocarmine and squashed in Hoyer's solution. Root tips for mitotic chromosome observations were pretreated for up to 24 hours in a saturated solution of paradichlorobenzene at approximately 4°C, then fixed in Farmer's solution for up to 24 hours. Root tips were then stored in 70% ethanol until use, hydrolyzed in 1 N HCl for 10 minutes at 60°C, and stained as above.

Histological preparations of anthers were obtained from flowers that had been fixed in FAA, dehydrated in an alcohol series, embedded in Paraplast, sectioned, and stained with safranin/fast green.

Pollen measurements were made from fresh pollen samples obtained from greenhouse plants. The grains were shaken into a mixture of 1–2% acetocarmine and Hoyer's solution and allowed to stand for exactly 10 days before measurement. Measurements of the polar and equatorial axes on 30 grains per sample were made from a 400× camera lucida projection onto a Zeiss ZIDAS digitizer. Pollen diameter was measured on stained grains only, and was taken as the distance between the innermost layers of the pollen grain wall. Pollen volume was calculated using the formula for the volume of an ellipsoid,  $V = \pi PE^2/6$ , where E is the equatorial diameter and P is the polar diameter. An analysis of variance revealed no significant difference between equatorial diameter as measured in polar and equatorial views, so P and E were measured in equatorial view only.

Pollen samples for scanning electron microscope (SEM) photos were taken from dried herbarium material. The grains were mounted on the stub with double-stick tape and coated with gold-palladium. Fresh pollen from greenhouse plants that was critical-point dried and coated appeared collapsed under the SEM.

#### RESULTS

##### DISTRIBUTION, ECOLOGY, AND MORPHOLOGY

Table 1 compares the morphological and ecological characteristics of *S. allophyllum* and *Cyphomandra* discussed below.

The ecological distribution, phenology, and generation time differ greatly in *S. allophyllum* and

TABLE 1. Comparison of morphological and other characters in *Cyphomandra* and *Solanum allophyllum* (details in text).

	<i>Cyphomandra</i>	<i>Solanum allophyllum</i>
Habitat	Mesic forest	Seasonally dry forest
Generation time	Usually > 1 yr.	< 1 yr.
Height	Up to 10 m	Up to 1.5 m
Leaf bases	Usually cordate or truncate, rarely decurrent	Subcordate to truncate, decurrent
Numer of flowers per inflorescence	> 10	4-6
Pedicle length	> 10 mm	4-6 mm
Corolla shape	Urceolate, campanulate, or stellate, not plicate	Rotate-stellate and plicate
Fruit color	Red, yellow, orange, purple, or green, never white	White to orange
Fruit shape	Not laterally compressed	Laterally compressed
Architectural model	Intermediate between Prevost's and Nozeran's models	"Fragment" of Prevost's or Nozeran's models
Sympodial units	3-4-leaved, rarely 5-leaved	3-leaved
Anthers	Tapered or not, with distinct and enlarged connective	Tapered, without enlarged connective

*Cyphomandra*. *Solanum allophyllum* has been collected from a single site in Honduras and is more abundant from Costa Rica and Panama through northwestern South America (Fig. 1). Although the plants are found in a variety of habitats, in Costa Rica and Panama the species seems to grow in drier sites than *Cyphomandra* species, which are almost always mesic-forest dwellers. No herbarium collections of this species from Costa Rica or Panama were made in the months of January-March, the dry season in these regions (Coen, 1983; Croat, 1978). This may indicate that *S. allophyllum* persists by losing its leaves during the dry season and perennating via its roots or larger shoots, but further field studies of this species are needed to ascertain its phenology. In the greenhouse the plants flower and fruit within five months from planting. This generation time is much shorter than most cultivated cyphomandras, which often take several years to reach reproductive age. *Solanum allophyllum* is a weakly woody shrub that rarely grows over 1.5 m tall (Fig. 2), in contrast to the majority of *Cyphomandra* species, which develop abundant secondary xylem and may reach heights of up to 10 m.

The subcordate to truncate leaf bases of *S. allophyllum* are decurrent along the petiole (Fig. 3). The leaves of *Cyphomandra* usually have cordate or less frequently truncate bases; decurrent leaf bases occur only in *C. fragilis* Bohs.

The inflorescences of *S. allophyllum* are un-

branched and bear 4-6 flowers on short pedicels 4-6 mm long. Those of *Cyphomandra* can be branched or unbranched, typically bear more than 10 flowers, and have pedicels longer than 10 mm. The shape of the corolla of *S. allophyllum* can best be described as rotate-stellate (sensu Correll, 1962): fairly long corolla lobes are present, but these are connected at the base by abundant interpetalar tissue that is plicate in the bud (Fig. 4). This type of corolla is often seen in *Solanum* subg. *Potatoe* (G. Don) D'Arcy. In contrast, the corolla of *Cyphomandra* has various shapes, but never rotate-stellate or plicate.

*Solanum allophyllum* produces some of the most distinctive fruits in the Solanaceae. At maturity, they are glabrous and white or occasionally orange mottled with green or purplish markings. The fruits are ellipsoidal or oblong in outline, and are laterally compressed and appear elliptic in cross section (Fig. 5). Within them are many very small flattened seeds and 3-6 small stone cell aggregates. The fruits differ from those of all species of *Cyphomandra* in color and shape, and the seeds are much smaller and more numerous than those of any species of *Cyphomandra*. In the greenhouse and presumably also in the field, the fruits fall to the ground while still hard and bitter and then ripen for several weeks before becoming soft and palatable and emitting a strong sweet odor. They are most likely dispersed by ground-dwelling animals. Those of *Cyphomandra* are held on the tree and

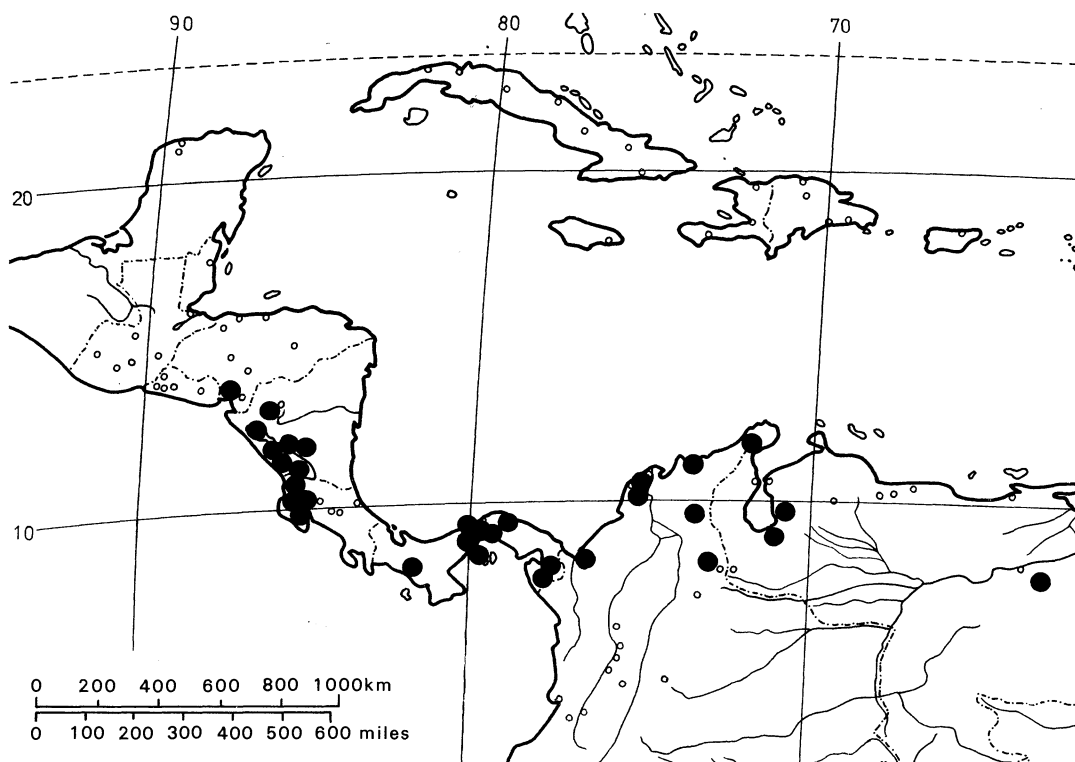


FIGURE 1. Distribution of *Solanum allophyllum*. (Base map copyright 1979 by the University of Utrecht.)

only fall after they are completely ripe. Their dispersal agents are unknown, but they may be attractive to birds or bats.

#### ARCHITECTURE

The distinctive growth habit or shape of *S. allophyllum* and many species of *Cyphomandra* is a conspicuous feature that allows the plants to be recognized easily in the field. In terms of architecture, however, *Cyphomandra* and *S. allophyllum* are similar only in the initial phase of their growth (Fig. 6). In both, the seedling axis produces a single orthotropic, or upright, trunk with the leaves spirally arranged in a 2/5 phyllotaxis. This trunk ends with the production of a terminal inflorescence. Usually three plagiotropic, or horizontal, shoots then elongate from axillary buds located just below the inflorescence to produce a spreading crown (Fig. 6A, D). Further branching within the crown occurs by sylleptic elongation of axillary shoots immediately below the successive terminal inflorescences; thus the crown is composed of a series of sympodial units where all the flowers

and fruits are borne. Beyond this, *Cyphomandra* and *S. allophyllum* diverge in their architecture.

In *Cyphomandra*, after continued sympodial growth and numerous episodes of flowering and fruiting, the plagiotropic branches begin to senesce. A new trunk then arises proleptically from an axillary bud on the old trunk below the branch tier and continues orthotropic growth until another terminal inflorescence and branch tier is produced. In this way, the main axis is composed of successive sympodial trunk modules bearing spatially and temporally separated reproductive crowns (Fig. 6B, C). I have seen this architecture in at least six species of *Cyphomandra*, and it is probably widespread in the genus. In contrast to *Cyphomandra*, *S. allophyllum* does not produce successive trunk modules. The whole plant in *S. allophyllum* is therefore equivalent to a single structural unit of the *Cyphomandra* growth form.

The architecture of *Cyphomandra* described above occupies an intermediate position between Prevost's and Nozeran's models in the scheme of Hallé et al. (1978). Both models have an orthotropic sympodial trunk and tiered plagiotropic



FIGURES 2-4. *Solanum allophyllum*.—2. Greenhouse-grown plant. Scale bar = 0.25 m.—3. Leaves from trunk. Scale bar = 2 cm.—4. Flowers. Scale bar = 1 cm.

branches. In Prevost's model both the trunk and plagiotropic branches generally have spirally arranged leaves, whereas in Nozeran's model the orthotropic and plagiotropic branches have highly contrasting leaf arrangements, usually with spiral phyllotaxis on the trunk and distichous phyllotaxy on the branches. Plagiotropy of the branches in Nozeran's model is perpetuated if a crown branch is independently propagated, whereas in Prevost's model the plagiotropy of the crown branches is usually lost when they are separated from the trunk. The leaf arrangement of the crown branches in *Cyphomandra* is affected by pronounced twisting

of the axes and differential elongation of branch internodes (see section on branching pattern below for a more detailed description of leaf arrangement, and Danert, 1958, 1967, for comparative morphology of the shoot systems in Solanaceae). Therefore, although the leaf arrangement on the plagiotropic shoots is not distichous, the crown branches show pronounced dorsiventral symmetry in contrast to the radial symmetry of the spirally arranged trunk leaves. Cuttings taken from the crown region of *C. betacea*, *C. diploconos*, and *C. diversifolia* produce lower, bushier plants than those taken from the upright axes (Fletcher, 1979; pers. obs.),

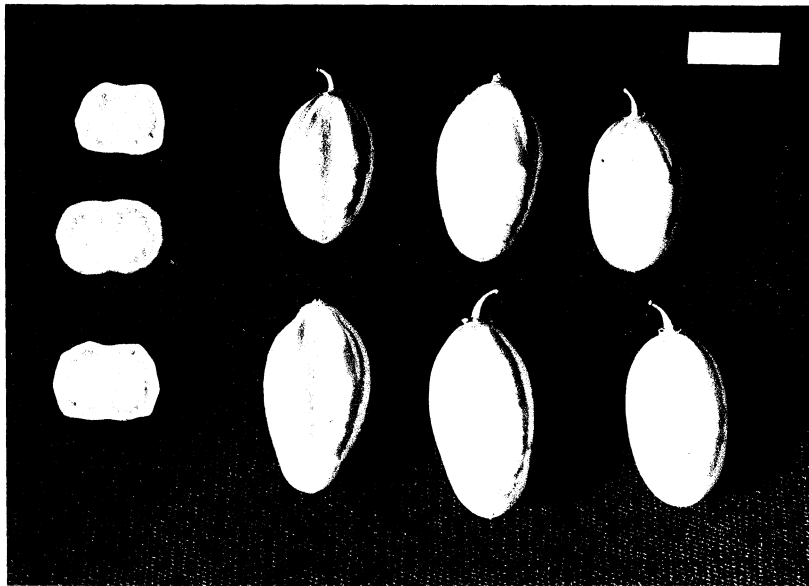


FIGURE 5. Fruits of *Solanum allophyllum*. Scale bar = 2 cm.

so these species apparently exhibit the inherent nature of plagiotropy in the crown branches characteristic of Nozeran's model. At least until an accurate interpretation of leaf arrangement on the plagiotropic shoots is available, it is probably best to consider *Cyphomandra* as being intermediate between Prevost's and Nozeran's model.

The architecture of *S. allophyllum* does not strictly conform to any of the models defined in Hallé et al. (1978). It most closely resembles Leeuwenberg's model, which is exhibited by several species of *Solanum* and *Capsicum* (Hallé et al., 1978). However, in Leeuwenberg's model, all the axes are orthotropic and equivalent, whereas in *S. allophyllum* there is evident differentiation between the trunk and crown branches. Perhaps the best way to characterize the architectural form of *S. allophyllum* is to consider that it may have been derived by "fragmentation" from more woody counterparts with multiple trunk modules, such as those seen in *Cyphomandra*. Fragmentation occurs when only a portion of the original tree model is expressed, and is commonly seen in herbaceous relatives of woody plants with more strongly developed trunk modules. Should it indeed be the case that the architectural form of *S. allophyllum* is related in this way to more extensive tree models, it may argue that this relatively herbaceous species has been derived by reduction and fragmentation from woody ancestors.

#### BRANCHING PATTERN

Three- to four-leaved sympodial units are the rule within the crown of nearly all species of *Cyphomandra* (Fig. 7); the only known exception is *C. corymbiflora*, which frequently has five-leaved sympodia. Three-leaved sympodial units are also characteristic of *S. allophyllum*. Commonly, the leaf subtending the renewal shoot is carried up to a point nearly opposite that of the first leaf produced on the axillary shoot so that the seemingly opposite leaves are actually members of successive sympodial shoot generations. In *S. allophyllum* and in many species of *Cyphomandra*, two renewal shoots grow out from below the terminal inflorescence, thus situating it in a branch fork. This shoot structure was previously thought to be peculiar to *Cyphomandra* (Bohs, 1986), and its presence in *S. allophyllum* was evidence supporting the inclusion of the species within *Cyphomandra*. Members of *Solanum* may have one- to many-leaved sympodial units, and the inflorescences may be axillary, extraaxillary, opposite a leaf or leaf cluster, or rarely in branch forks.

Subtle differences exist in leaf and shoot arrangement within the crown branches of *Cyphomandra* and *S. allophyllum* apart from the leaves and branches making up the sympodial shoot structure. In *S. allophyllum*, nearly all the axillary buds of the crown expand into short shoots, giving the

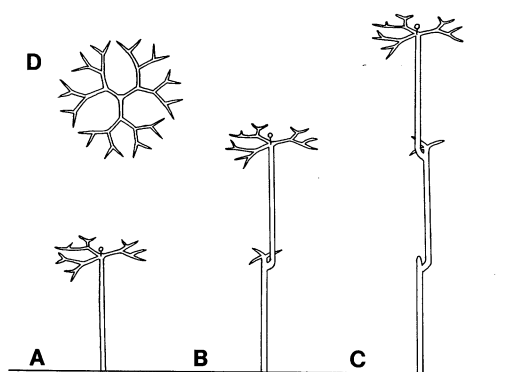


FIGURE 6. Architecture of *Cyphomandra* and *Solanum allophyllum*.—A, B, C. Successive growth stages in *Cyphomandra*, showing the sympodial nature of the trunk and the plagiotropic orientation of the crown branches. *Solanum allophyllum* does not develop beyond stage A.—D. Top view of crown, showing three main plagiotropic branches.

crown a dense leafy appearance. In *Cyphomandra*, sylleptic growth is restricted to the axillary buds immediately subtending the terminal inflorescences of the sympodial units, the rest of the buds remaining dormant unless released by pruning or breaking the tip of the branch. In the greenhouse, *S. allophyllum* also undergoes pronounced seasonal reiteration, with expansion of many buds on the trunk by prolepsis and elongation of the short shoots of the crown. It is not known whether *S. allophyllum* reiterates in this way under natural conditions; as already mentioned, it may die back to the main stem each year and produce a new plant conforming to the initial model at the beginning of the rainy season.

#### ANTHER MORPHOLOGY

Tapered anthers with an abaxial thickening occur in *Cyphomandra* and *S. allophyllum* (Figs. 8, 9). Anther shape is not a definitive characteristic of either genus, however; tapered anthers occur in other species of *Solanum* (e.g., in subg. *Leptostemonum* (Dun.) Bitt., subg. *Potatoe* (G. Don) D'Arcy, and sect. *Herposolanum* Bitt.), and although they are common in *Cyphomandra*, they are not exhibited in all of its species. There is no present evidence to indicate that tapered anthers are homologous within or among these groups. A more important criterion for distinguishing *Cyphomandra* from *Solanum* is found in the enlarged anther connective. In *Cyphomandra*, the anther connective is usually very thickened and prominent abaxially and is sharply delimited from the thin-

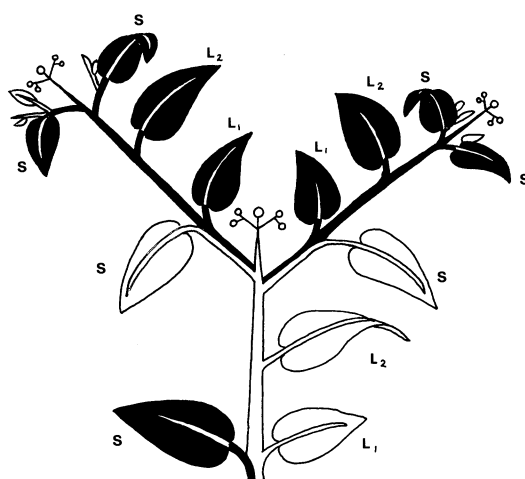


FIGURE 7. Diagram of branching pattern in the crown of *Cyphomandra* and *Solanum allophyllum*. Black and white shading denotes successive sympodial units. The subtending leaf (S) of the axillary shoot has been carried up to a level subopposite the first leaf on this shoot ( $L_1$ ). The diagram shows a species with four-leaved sympodia; in three-leaved sympodia, the leaf  $L_2$  is absent.

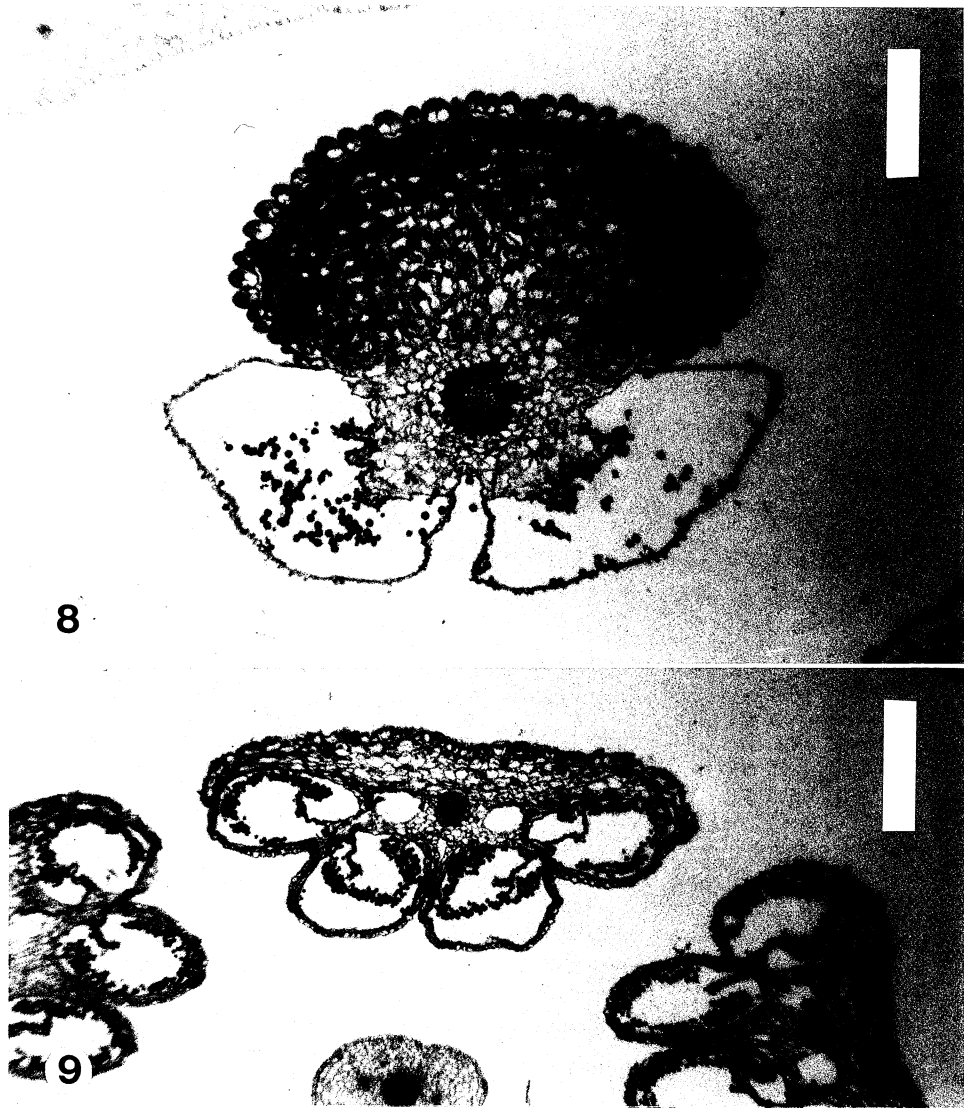
walled anther thecae. Anthers of *Solanum* can be thickened in various ways, but they never have a distinct and abaxially prominent connective.

*Solanum allophyllum* has a thickened area on the abaxial side of the anther that has been interpreted as an enlarged connective like that of *Cyphomandra*, and has led to the inclusion of *S. allophyllum* within *Cyphomandra*. Microscopic cross sections through the anther region of *S. allophyllum* and a representative of *Cyphomandra*, *C. diversifolia* (Dun.) Bitt., show that anther structure is very different in the two taxa. In *Cyphomandra* (Fig. 8), the thickened portion is expanded

TABLE 2. Compatibility studies in *Cyphomandra* and *Solanum*.

Taxon	Selfed		Outcrossed	
	N	% Successful crosses	N	% Successful crosses
<i>C. betacea</i>	20	55%	36	36%
<i>C. diversifolia</i>	77	0%	152	6%
<i>C. diploconos</i>	108	0%	117	66%
<i>C. hartwegii</i>	38	0%	19	32%
<i>C. uniloba</i>	33	0%	11	55%
<i>C. acuminata</i>	60	0%	—	—
<i>C. corymbiflora</i>	32	0%	30	93%
<i>Solanum</i>				
<i>allophyllum</i>	21	48%	52	31%





FIGURES 8, 9. Transverse sections through anthers.—8. *Cyphomandra diversifolia*.—9. *Solanum allophyllum*. Scale bars = 0.5 mm.

abaxially, the thecal walls are free and do not contribute to the thickening, and there is a sharp demarcation between the swollen connective and the thin-walled anther thecae. In contrast, the thickened area in *S. allophyllum* is not expanded abaxially and is contiguous with the walls of the anther thecae (Fig. 9). There is a gradual rather than abrupt transition from the thickened area on the abaxial surface to the thin-walled anther thecae. This type of anther structure conforms to that of many other species of *Solanum*. These differences are evident in transverse sections through fully

mature anthers; similar studies on developing stages in these species may further emphasize these differences and may also reveal the derivation of the tissue involved in the anther thickening in both taxa.

#### COMPATIBILITY

Table 2 illustrates the results of controlled pollinations in the greenhouse of flowers of *S. allophyllum* and various species of *Cyphomandra*. The results show that of the seven species of *Cy-*

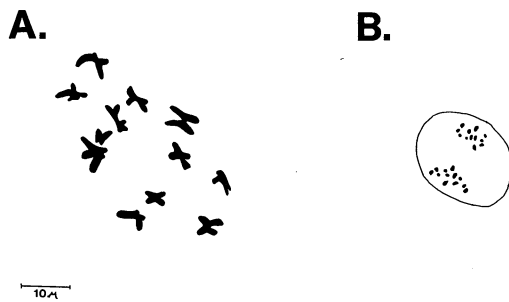


FIGURE 10. Camera lucida drawings of meiotic chromosomes in microsporangia.—A. *Cyphomandra diversifolia*.—B. *Solanum allophyllum*. A and B at same magnification.

*phomandra* tested, all are self-incompatible with the exception of the cultivated tree tomato, *C. betacea* (Cav.) Sendtn. In contrast, *S. allophyllum* appears to be self-compatible. Neither *S. allophyllum* nor *C. betacea* sets fruits in pollinator-free greenhouses without deliberate pollination. This indicates that these two species may not be autogamous and require a pollinator to transmit self pollen, or that they may be apomictic and pseudogamous. The style in *S. allophyllum* is not visible directly after anthesis, but elongates and emerges through the anther cone after the anthers dehisce. Thus, protandry may prevent selfing in this species.

CYTOLOGY

The most compelling evidence for the exclusion of *S. allophyllum* from *Cyphomandra* comes from chromosome studies. *Solanum allophyllum* and nine species of *Cyphomandra* that have been examined so far have  $n = 12$  chromosomes (Bohs, unpublished data; Pringle & Murray, in press). This chromosome number is common in *Solanum* and

the Solanaceae in general. However, chromosomes of the two taxa differ markedly in size (Figs. 10, 11). Investigations of seven species of *Cyphomandra* have revealed that the chromosomes in this genus are very large, averaging about  $8 \mu\text{m}$  in length with a range of approximately 3 to  $14 \mu\text{m}$  (Bohs, unpublished data). DNA amounts as measured by flow cytometry were among the largest yet known in the Solanaceae (Pringle & Murray, in press). In contrast, both the mitotic and meiotic chromosomes of *S. allophyllum* range between 1 and  $2.5 \mu\text{m}$  in length and are thus on the order of 2.5 to 5.5 times smaller than those of *Cyphomandra*.

POLLEN

Pollen grains of *S. allophyllum* and *Cyphomandra* were examined for potential taxonomic characters. The grains of *S. allophyllum* are tricolporate and have exine sculpturing consisting of very small rounded granules best observed with SEM (Figs. 12–14). *Cyphomandra* pollen is also tricolporate, and most species have granular exine sculpturing like that of *S. allophyllum*, although several *Cyphomandra* species (e.g., *C. pendula* (R. & P.) Sendtn. and *C. pilosa* Bohs) lack such granules and have a psilate exine.

Although the aperture type and exine sculpturing show few taxonomically useful differences, the grains of *Cyphomandra* and *S. allophyllum* do differ somewhat in size and shape. Table 3 compares the pollen dimensions and volume of *S. allophyllum* and seven species of *Cyphomandra*. In the terminology of Erdtman (1952, 1969), all species of *Cyphomandra* have spheroidal or prolate spheroidal grains, whereas those of *S. allophyllum* are more elliptic in equatorial view and fall into the subprolate shape class. All taxa ex-

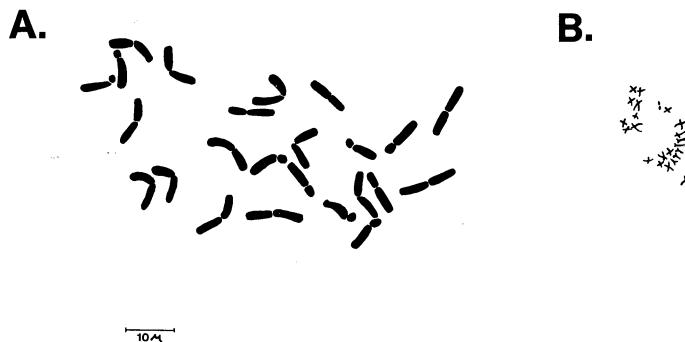
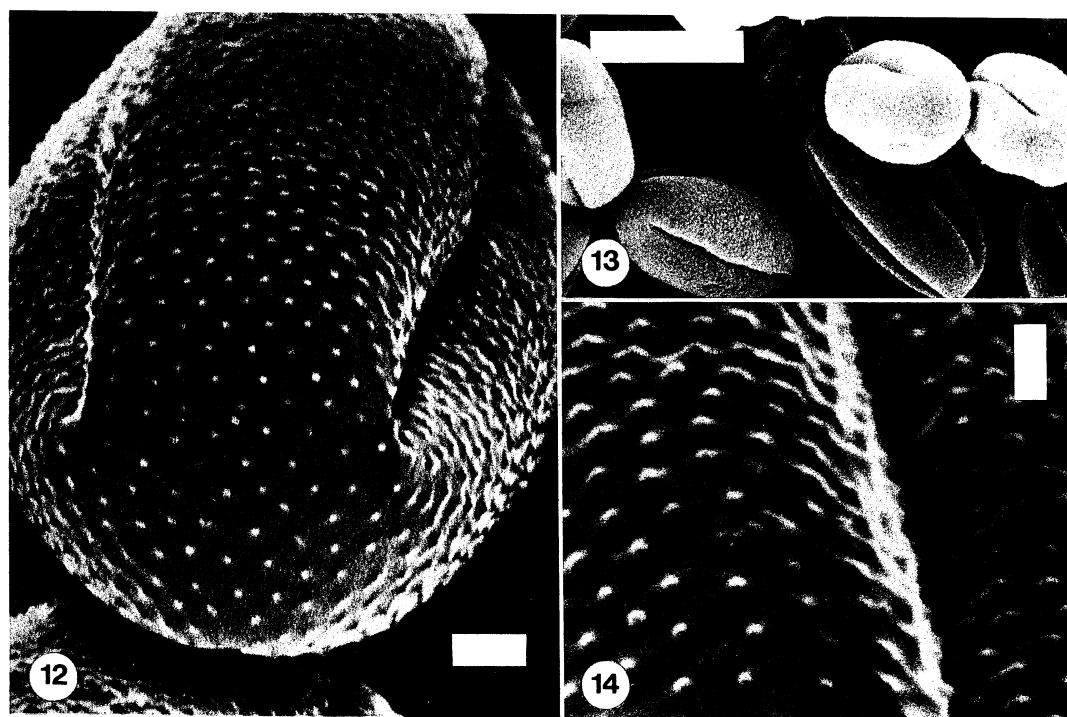


FIGURE 11. Camera lucida drawings of mitotic chromosomes in root tips.—A. *Cyphomandra acuminata*.—B. *Solanum allophyllum*. A and B at same magnification.



FIGURES 12–14. Pollen grains of *Solanum allophyllum*.—12. Scale bar = 1  $\mu\text{m}$ .—13. Scale bar = 10  $\mu\text{m}$ .—14. Scale bar = 0.5  $\mu\text{m}$ .

amined have small- to medium-sized grains (again using Erdtman's terminology), but those of *S. allophyllum* are much smaller than any species of *Cyphomandra*. *Cyphomandra* grains have volumes about 2.5 to more than 10 times larger than those of *S. allophyllum*.

#### SEED SIZE

The seeds of *S. allophyllum* are substantially smaller than those of any of the *Cyphomandra* species examined (Table 3), ranging from about  $\frac{1}{5}$  to  $\frac{2}{5}$  the size of *Cyphomandra* seeds.

#### DISCUSSION

There are numerous differences in ecology, phenology, and morphology between *S. allophyllum* and *Cyphomandra*, but these alone do not permit an unequivocal placement of the species in either *Solanum* or *Cyphomandra*. Architecture and some aspects of the branching pattern further differentiate *S. allophyllum* from *Cyphomandra*, but again not enough to place the former definitively in either genus. A problem with the use of these characters is the wide range in architecture and branching pattern seen in *Solanum*. It looks as if these two

characters cannot be as useful in distinguishing *Cyphomandra* and *Solanum* as was previously thought.

In contrast, a consideration of anther morphology shows that *S. allophyllum* does not have a distinct and enlarged anther connective like that of *Cyphomandra*. The anther structure formerly interpreted as a similarity between it and *Cyphomandra* is now revealed to be a difference that separates the two taxa. It appears that the presence of an enlarged anther connective is the most reliable morphological criterion for distinguishing *Cyphomandra* from *Solanum*.

The fact that *S. allophyllum* is self-compatible (SC), whereas the majority of *Cyphomandra* species are self-incompatible (SI), is at least an implication that *S. allophyllum* is not a *Cyphomandra*. Both SC and SI are known in *Solanum*, so the inclusion of *S. allophyllum* in *Solanum* is consistent on the basis of this character.

Self-compatibility in *C. betacea* could be an indication of its relatively recent origin. SC is considered to be a derived character in the Solanaceae (de Nettancourt, 1977; Whalen & Anderson, 1981). If this applies equally well to *Cyphomandra*, then the self-compatibility of the cultivated

TABLE 3. Pollen size and seed weight in *Cyphomandra* and *Solanum allophyllum*. Thirty grains/taxon measured for pollen size. Three measurements of 10 seeds averaged for seed weight. Standard deviations given in parentheses after measurements.

Taxon	Pollen polar diameter ( $\mu\text{m}$ )	Pollen equatorial diameter ( $\mu\text{m}$ )	Pollen volume ( $\mu\text{m}^3$ )	Seed weight (10 seeds) ( $\text{g} \times 10^{-2}$ )
<i>C. diversifolia</i>	33.66 (1.89)	31.92 (1.48)	18,068 (2,628)	3.97 (0.064)
<i>C. uniloba</i>	31.28 (1.63)	30.58 (1.42)	15,414 (2,182)	3.44 (0.276)
<i>C. diploconos</i>	29.24 (1.26)	27.73 (1.02)	12,043 (1,801)	1.84 (0.080)
<i>C. acuminata</i>	29.16 (1.09)	26.87 (0.92)	11,057 (1,108)	—
<i>C. betacea</i>	22.47 (1.21)	21.93 (0.76)	5,678 (637)	5.10 (0.127)
<i>C. hartwegii</i>	21.61 (0.96)	20.35 (0.95)	4,706 (587)	24.44 (0.706)
<i>C. corymbiflora</i>	21.45 (1.16)	19.97 (1.32)	4,520 (780)	4.03 (0.682)
<i>S. allophyllum</i>	16.54 (0.75)	14.21 (0.75)	1,756 (232)	0.70 (0.025)

*C. betacea* would be considered derived, perhaps in response to selection pressures relating to its domestication.

The small chromosomes of *S. allophyllum* conform to the size reported for species of *Solanum* from several different subgenera (Roe, 1967) and are the best indication that this species belongs in *Solanum*. The present study shows that there is a tendency toward large chromosomes in *Cyphomandra*. This appears to be a very useful character distinguishing *Cyphomandra* from *Solanum*. Further studies of chromosome size in the Solanaceae are needed to determine if this character is consistent in other species. Comparison of genome sizes between putatively primitive and derived members of many different plant groups demonstrates that changes in genome size can occur in either direction (Ohri & Khoshoo, 1986). Additional chromosome studies coupled with morphological data may eventually allow us to determine trends in the evolution of genome size in *Cyphomandra*, *Solanum*, and other solanaceous genera.

The exine sculpturing of *S. allophyllum* pollen also resembles that of *Solanum*. Anderson & Gensel (1976) and Edmonds (1984) reported similar granular exine sculpturing in *Solanum* sects. *Basarathrum* (Bitt.) Bitt. and *Solanum*, respectively. The occurrence of the same type of exine sculpturing in *Cyphomandra*, however, argues against the use of this character to distinguish *Cyphomandra* from *Solanum*. This same type of sculpturing also has been reported for other genera related to *Solanum* (Basak, 1967) and is probably the general pollen type of the tribe Solaneae.

The pollen grains and seeds of *S. allophyllum* are much smaller than those of any species of *Cyphomandra*. The pollen dimensions of *S. allophyllum* are comparable to some of the smaller

grains reported for *Solanum* (Anderson & Gensel, 1976; Basak, 1967; Murry & Eshbaugh, 1971), and the size of the seeds falls within the range for *Solanum* (pers. obs.). Pollen or seed size has not been critically examined as a taxonomic character separating *Cyphomandra* and *Solanum*.

The small pollen and seeds of *S. allophyllum* may be connected with its small chromosome size. Bennett (1972) observed that genome size was correlated with pollen volume, seed weight, and minimum generation time in various species of herbaceous plants. The association of small chromosome size with small pollen volume, seed weight, and short generation time in *S. allophyllum* may indicate that this correlation also holds in this species. Further observations are needed to ascertain whether these characteristics are correlated in other solanaceous species, and whether pollen and seed size may be used as indicators of chromosome size.

Affinities of *S. allophyllum* within *Solanum* are problematic. This species is allied with two others, *S. mapiriense* Bitter from Bolivia and an undescribed species from Amazonian Peru (Bohs, in prep.). At present I know of no existing section of *Solanum* that accommodates these three species. They are perhaps best regarded as a new section of *Solanum*, as Bitter (1913) suggested. A taxonomic treatment of these three species and a consideration of their placement within *Solanum* will appear in a later paper.

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## APPENDIX. Voucher information.

*Solanum allophyllum* (Miers) Standley

Seed from *D'Arcy 9472*, collected in Panama, Prov. San Blas, in front of Ustupo. Vouchers: *Bohs 2339* (GH, VT).

*Cyphomandra acuminata* Rusby

Seed from *Solomon & Escobar 12458*, collected in Bolivia, Prov. Nor Yungas, 8.7 km below Chuspipata on road to Yolosa. Vouchers: *Bohs 2338* (GH, VT).

*Cyphomandra betacea* (Cav.) Sendtn.

Seed collected by C. Sperling in market, Quito, Ecuador. Vouchers: *Bohs 2274* (GH), *2275* (VT).

*Cyphomandra corymbiflora* Sendtn.

Seed collected in southeastern Brazil, sent by G. Pringle, D.S.I.R., New Zealand. Vouchers: *Bohs 2343* (GH, VT).

*Cyphomandra diploconos* (Mart.) Sendtn.

Seed collected in Brazil, Prov. Paraná, city of Curitiba. Vouchers: *Bohs 2335* (GH, VT).

*Cyphomandra diversifolia* (H. & B. ex Dunal) Bitter

Seed from *Benitez de Rojas 2744*, collected in Venezuela, Estado Aragua, Parque Nacional Henri Pittier. Vouchers: *Bohs 2341* (GH, VT).

*Cyphomandra hartwegii* (Miers) Sendtn. ex Walp.

Seed collected in Colombia, Dept. Huila, Fundación Merenberg. Voucher: *Bohs 1644* (GH).

*Cyphomandra uniloba* Rusby

Seed from *Sperling & King 5500*, collected in Bolivia, Prov. La Paz, Dept. Larecaja, between Consata and Mapiri. Vouchers: *Bohs 2283* (VT), *2284* (GH).