The Relationship of Some *Elsinoë* and *Sphaceloma* Species Pathogenic on Cassava and Other Euphorbiaceae in Central and South America

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We wish to extend our appreciation to Elizabeth Alvarez and other members of the CIAT Cassava Program for their technical support and to R. P. Korf for his comments on the manuscript. The National Fungus Collection (BPI) kindly provided many of the type specimens. The first author gratefully acknowledges the financial support of CIAT, the Department of International Agriculture and Rural Development, Cornell University, and the Agency for International Development, without which the study could not have been completed.

Part of a thesis submitted to Cornell University by the first author in partial fulfillment of requirements for the Ph.D. degree.

Accepted for publication 15 July 1982.

ABSTRACT

Zeigler, R. S., and Lozano, J. C. 1983. The relationship of some *Elsinoë* and *Sphaceloma* species pathogenic on cassava and other Euphorbiaceae in Central and South America. Phytopathology 73:293-300.

Isolates of *Sphaceloma* and *Elsinoë* spp. were collected from *Euphorbia brasiliensis, Eu. heterophylla, Eu. pulcherrima, Jatropha aconitifolia* var. *papaya, Manihot carthaginensis*, and *M. esculenta* in Mexico, Costa Rica, the Dominican Republic, and Colombia. *M. carthaginensis* and *J. aconitifolia* var. *papaya* had not been reported previously as *Sphaceloma* hosts, and cassava had not been previously reported as a host of *Elsinoë* spp. A connection between the *Elsinoë* from cassava with *Sphaceloma manihoticola* is established. Cross inoculations demonstrated that some isolates were pathogenic on several euphorbiaceous species. Pathogenicity on cassava of an isolate of *Elsinoë brasiliensis* from *Eu. brasiliensis* was enhanced by reisolation from cassava. Cultural characteristics on potato-dextrose agar were not sufficiently different to aid in separating the species. Conidial dimensions on the same medium were not significantly different among isolates from *Eu. brasiliensis, M. esculenta, M. carthaginensis,* and *J. aconitifolia* var. *papaya*. No significant differences were found between isolates from *Eu. pulcherrima* and *Eu. heterophylla*, but each was different from the other four. *Sphaceloma krugii* and *S. poinsettiae* both produced large, pigmented, spindle-shaped spores in addition to the more typical small, hyaline *Sphaceloma* conidia. In light of these studies, a combination of several species is proposed. *S. poinsettiae* and *S. krugii* are combined under *S. poinsettiae*. *E. jatrophae, E. brasiliensis* and the *Elsinoë* found on cassava are combined under the name *Elsinoë brasiliensis*.

The genus *Sphaceloma* de Bary is composed of more than 50 species, with the majority found in tropical and subtropical regions. The pathogen attacks flowers, fruits, leaves, and stems, causing characteristic scab lesions on these organs as well as necrotic spots on leaves. Conidia are small, unicellular, and hyaline, formed in more or less acervuluslike structures or, more commonly, on continuous, fertile layers of densely packed phialidic conidiophores. Under certain conditions, some species may form a larger, 0–2-septate, pigmented, thick-walled, spindle-shaped spore. This form, originally described from *Sphaceloma fawcetti* Jenkins (10), has been referred to as the "fawcetti" conidium (3) and is implicated in long-distance wind dissemination of the pathogen (21).

The genus *Elsinoë* Racib. contains over 40 species and has been shown, with one exception (*Bitancourtia* Thiram, and Jenkins), to be the sexual stage of *Sphaceloma*. Bitunicate asci, solitary in locules, usually contain eight hyaline or slightly pigmented ascospores that are commonly three-septate, often having a longitudinal septum in one or more cells (9,12,13).

In 1950, Bitancourt and Jenkins (5) described *Sphaceloma manihoticola* on cassava (*Manihot esculenta* Crantz). Their description and decision to consider it a new species were based entirely on symptomatology and on the host attacked, because no spores or other reproductive structures were visible in their specimens. They also observed symptoms that they attributed to the same pathogen on *M. glaziovii*, Muell. Arg. Bitancourt and Jenkins (5) stated clearly that they considered the new species designation provisional, pending later opportunity to examine fresh specimens containing reproductive structures.

Superelongation disease of cassava was first reported in the Tolima Valley of Colombia in 1972 (7). We have since observed it throughout Central America, the Caribbean, and northern South America. Symptoms include necrotic leaf spots, hypertrophic leaf veins, and cankers on petioles and stems, all characteristic of diseases caused by *Sphaceloma*. Severely affected plants showed marked elongation of the internodes, from which the disease named is derived. Krausz (15) identified the causal agent as a species of *Sphaceloma* and decided that it should be considered *S. manihoticola*, in spite of the impossibility of determining whether it

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was the same species described by Bitancourt and Jenkins, who made no mention of internode elongation in their description of symptoms.

Since 1942, several species of *Sphaceloma* and *Elsinoë* have been described as pathogens on weedy and ornamental cassava-related plants in Central and South America (Table 1). *Sphaceloma* and *Elsinoë* spp. occur on the common weeds *Euphorbia brasiliensis* L., *Eu. heterophylla* L., *Eu. hypericifolia* L., and *Eu. prunifolia* L.; on the common ornamental shrub *Eu. pulcherrima* Willd. (poinsettia); and on *Jatropha curcas* L. and *J. aconitifolia* Mill. var. *papaya* Arbelaez, which are trees often found in proximity to cassava plantings.

Because of the paucity of morphological characteristics suitable for distinguishing members of the *Sphaceloma-Elsinoë* complex, previous workers have relied on a number of other characteristics to justify taxonomic distinctions. These include colony characteristics on agar media, symptomatology, phylogenetic affinity of reported hosts and, to a limited extent, host range. Usually, information from cross-inoculation studies is based on tests made on a few host genotypes, making the general significance of nonpathogenicity on the plant species or genera as a whole difficult to evaluate. Symptomatology and pathogenicity are reflections of host-pathogen interaction and are, therefore, inappropriate characters for distinguishing pathogens taxonomically. We present data showing that host and symptomatology are not suitable bases for pathogen taxonomy in this group.

To date, five *Elsinoë* species and three *Sphaceloma* species have been described on euphorbiaceous hosts (Table 1). This study was undertaken to determine the possible relationships between *Elsinoë* and *Sphaceloma* on euphorbiaceous hosts and to determine which species are distinct.

MATERIALS AND METHODS

Isolates. During 1980 and 1981, samples of cassava plants affected with superelongation disease were obtained from sites in Colombia, Mexico, Costa Rica, and the Dominican Republic. Colombian sites included the Centro Internacional de Agricultura Tropical (CIAT) stations in Palmira and Popayan, CIAT-ICA (Instituto Colombiano Agropecuario) stations in Santander de Quilichao (Cauca), Caribia (Magdalena), and Carimagua (Meta). Additional samples were collected from farmers' fields in the Departments of Vichada and Casanare, Colombia. *Eu. pulcherrima, Eu. brasiliensis*, and *Eu. heterophylla* infected with *S. poinsettiae* and *E. brasiliensis* and *S. krugii*, respectively, and *J. aconitifolia* var. *papaya* Arbelaez infected by a *Sphaceloma* sp. were collected in the Cauca Valley of Colombia. *Manihot carthaginensis* Muell. infected by a *Sphaceloma* sp. was collected near Santa Marta (Magdalena), Colombia.

Isolates from young lesions on the various hosts were obtained in a manner similar to that described by Whiteside (22), with streptomycin (100 ppm) added to the agar. On very old material, where high populations of saprophytes prevented direct isolation of the slow-growing pathogen and when the host species could be propagated vegetatively, diseased stem pieces were planted in sterile soil and incubated at 25 C and 100% RH until the axillary buds sprouted and became diseased. The pathogen was then isolated from the newly infected young tissue.

Stock colonies were stored and maintained at 24 C in the dark under sterile mineral oil on Difco potato-dextrose agar (PDA) acidified with lactic acid. For studies on morphology and host range, the isolates were grown on acidified PDA in petri dishes.

Ascospore isolation. Single ascospore colonies were obtained by removing ascoma from surface-disinfested lesions and placing them in a sterile drop of 0.2% agar solution on a sterile glass microscope slide coated with Tween-60®. A sterile glass coverslip was then placed over the drop and pressure applied until the asci ruptured. The ascospores were transferred from the slide and coverslip to a 5% water agar surface with a strong jet of sterile distilled water. After permitting the spores to settle, the water was gently drawn off the agar surface. After 10–12 hr, germinating spores were located under magnification of 140, removed with a microspatula, and placed on acidified PDA + 100 ppm streptomycin.

Attempts were also made to isolate ascospores by placing lesions with ascoma on moist filter paper attached to the lid of sterile petri dishes to allow any mature ascospores to be forcibly ejected onto the agar, but these attempts failed.

Inoculation. Young cassava, poinsettia, *J. aconitifolia* var. *papaya, J. curcas*, and *J. nudans* were grown from stem cuttings rooted in sterile potting soil and grown under greenhouse conditions until they had approximately 20 cm of new stem tissue. *M. carthaginensis, Hevea brasiliensis, Eu. prunifolia, Eu. tovariensis*, and *Eu. heterophylla* were grown from true seed collected from plants in the Cauca Valley, Colombia. *Eu. hirta* and *Eu. brasiliensis* were grown from healthy young plants transplanted from weedy areas.

Inoculum was prepared by macerating colonies (21–28 days old) in a solution of 0.5% water agar and adjusting the concentration to 3×10^6 conidia per milliliter after removing mycelium by filtration. A few drops of Tween-20® were added to the inoculum. Plants were inoculated by spraying them at 3×10^4 Pa until they were completely covered with inoculum. They were then placed for 48 hr in a growth room with a 12-hr photoperiod (1.1×10^4 lux from General Electric 400-W multivapor lamps), 100% RH, and a temperature of 24–28 C. Thereafter, the plants were held in the same growth room under the same light-temperature regime but at

TABLE 1. Summary of *Sphaceloma* and *Elsinoë* species described on euphorbiaceous hosts

Species	Host	Dimensions[a] Ascospore (μm)	Dimensions[a] Conidium (μm)	Type specimen[b]	Reference
Elsionë antidesmae	*Antidesma heterophylla* Blume	14 × 2–3	...	...[c]	Raciborski, 1900
E. brasiliensis	*Euphorbia hypossifolia* L. (Sic) (= *Eu. brasiliensis* L.)	12–14 × 5–7	...	MSE 367	Bitancourt and Jenkins, 1942
E. hevae	*Hevea brasiliensis* Muell. Arq.	14–19 × 5–8	...	BPI 91270	Bitancourt and Jenkins, 1956
E. jatrophae	*Jatropha curcas* L.	12–15 × 4–6	...	MSE 473	Bitancourt and Jenkins, 1950
E. venezuelensis	*Croton glandulosus* L.	12–18 × 6–8	...	...[c]	Bitancourt, 1945
Elsinoë sp.	*Manihot esculenta* Crantz	(9.5–14 × 4–7)	...	...	...
Sphaceloma krugii	*Euphorbia prunifolia* Jacq. *E. heterophylla* L.	...	4–6 × 2–4	MSE 420	Bitancourt and Jenkins, 1949
S. manihoticola	*Manihot glaziovii* Mull. *M. esculenta* Crantz	...	Not seen (3–6 × 1.5–4)	MSE 477	Bitancourt and Jenkins, 1950
S. poinsettiae	*Euphorbia pulcherrima* Willd.	...	7–20 × 2.5–5.3	...[d]	Jenkins and Ruehle, 1942

[a] Dimensions in parentheses refer to specimens collected in Colombia by the authors.
[b] MSE = Myriangiales selecti exsiccati, Bitancourt and Jenkins. BPI = U.S. Mycological Herbarium, U.S. Department of Agriculture, Washington, DC.
[c] No type designated in publication with diagnosis.
[d] Type location not given.

only 50–80% RH, or they were transferred to a greenhouse. Disease evaluations were made 10–14 days after inoculation.

Fungal morphology. Measurements of mature ascospores and asci were made on water mounts of crushed or freeze-microtomed ascomata. Conidiophore dimensions were taken from water mounts of freeze-microtomed sections of stem lesions. Conidia were obtained from infected plants 10–14 days after inoculation and after holding the plants at 100% RH for 24 hr and collecting water drops from the lesions. "Fawcetti" conidia were produced from excised dry lesions with an olive or gray velvety surface by incubating them in a near-saturated moist chamber for 24 hr or by placing infected plants with well-developed lesions in a high-humidity environment and then scraping the lesion surface into a drop of distilled water. Conidia from colonies on PDA were obtained by crushing bits of mycelium in water between a cover glass and slide.

Studies on the induction of the sexual stage. Two susceptible cassava cultivars were inoculated with eight single-ascospore isolates obtained from one ascoma both singly and in all possible combinations of isolate pairs. Infected plants were grown for several months in the greenhouse.

The eight single-ascospore colonies were also grown on four different culture media singly and in all possible isolate pair combinations. The four media were acidified PDA, Czapek's agar (17), cassava leaf agar (CLA), and CLA + glucose. The CLA was prepared by grinding 300 g of cassava leaves from susceptible cultivars MCOL 113 and MCOL 22 (CIAT Cassava accession numbers), diluting to 1,000 ml with sterile distilled water, passing the mixture through several layers of cheesecloth, and adding 20 g of agar and water to make 1 L. The mixture was autoclaved at 10.3×10^4 Pa for 15 min. CLA + glucose was prepared by adding 15 g of glucose to the CLA mixture before autoclaving.

RESULTS

Symptomatology. *Sphaceloma* spp. were successfully isolated from the following euphorbiaceous species: *Eu. brasiliensis, Eu. heterophylla, Eu. pulcherrima, J. aconitifolia* var. *papaya, M. carthaginensis*, and *M. esculenta*. Symptoms did not differ appreciably from those published in the original pathogen species descriptions (Table 1). On the previously unreported hosts, *M. carthaginensis* and *J. aconitifolia* var. *papaya*, symptoms appeared as pale-buff, corky, raised, scab lesions on leaf veins and petioles. Lesions were circular to elongate, from 2 mm in diameter, coalescing to indeterminant length. Lesion centers were commonly deep red to black. Lesions on leaf lamina were typically necrotic, with the center often absent, forming a "shot-hole" effect, and bordered with red to black margins 1–2 mm wide. Leaf lesions on *J. aconitifolia* var. *papaya* were often markedly hypertrophic, as were those on the veins and petioles. They were indistinguishable from symptoms on the type specimens of *E. jatrophae*. No stem lesions were ever observed on *J. aconitifolia*. Stem lesions on *M. carthaginensis* were tan, frequently with dark red to brown or black raised centers, circular to elongate, from 2 mm in diameter, often coalescing to form lesions several centimeters long. They were very similar to those found on cassava.

Cultural characteristics. Isolates from all host plants typically formed slow-growing, pulvinate, or raised and deeply fissured, gummy to occasionally mucoid colonies on agar media. Tomentose colonies were found in all species but were more common in isolates of *S. poinsettiae* and the *Sphaceloma* state of *E. brasiliensis*. Ropey or hairlike aggregations of hyphae and white or pinkish aerial mycelial were commonly formed on the colonies for several transfers after the original isolation from the host. After four to five transfers, however, aerial mycelium production was limited to a few small tufts.

Colony color on PDA was found to be extremely variable even within the same isolates. All isolates, regardless of original host, ranged from orange to yellow or orange to bright red, rust, and brown. Yellow or orange colonies (from single conidia) frequently formed small red sectors. Reproducing selectively from these pigmented sectors for several transfers yielded red colonies. However, within these, small areas with yellow or orange pigmentations were produced occasionally. Isolates from *Manihot* or *Jatropha* frequently formed small black pigmented areas that, upon selective transfers, yielded pure black colonies. These proved to be very stable in culture.

Growth medium had a substantial influence on colony morphology. Single-ascospore colonies growing on CLA + glucose varied substantially and often contained a mixture of bright red, orange, and black sectors. They were pulvinate and produced relatively abundant whitish or pinkish aerial hyphae. Colonies of the same isolates on Czapek's agar were uniformly orange in color and produced no aerial mycelium (23).

The different *Sphaceloma* species proved impossible to distinguish using colony morphology and color. Colony morphology and color of isolates from non-*Manihot* hosts were all observed to fall within the range of morphological variants observed among 170 collections of *S. manihoticola* (23).

Pathogenicity and host range. The inoculation technique was satisfactory in that plants of known susceptibility to various isolates could be infected consistently. Nevertheless, disease levels (as estimated by the number or area of lesions) varied considerably among individual plants, making quantitative interexperimental comparisons difficult. Furthermore, a considerable range of susceptibility was observed within each host species. Individuals within the species *Eu. pulcherrima, Eu. brasiliensis*, and *M. esculenta* ranged from very susceptible to very resistant to the same isolate. The results of the cross inoculations with different isolates to test host specificity are summarized in Table 2. Some observations and variations in the results are not shown in the table. For example, a few individuals of *Eu. brasiliensis* were highly susceptible to a single ascospore isolate of the *Elsinoë* sp. from cassava, whereas others were only moderately susceptible. *J. curcas* showed no visible susceptibility to any isolates, but at a magnification of 20, minute lesions were observed on leaves, petioles, and stems of plants inoculated with the four isolates tested. *S. krugii* produced barely visible stem lesions with bright red margins on *Eu. brasiliensis*. Leaf symptoms on *J. aconitifolia* var. *papaya* inoculated with *S. manihoticola* were markedly hypertrophic, forming raised scabs around the margins of the necrotic areas similar to those formed when the species was inoculated with a *Sphaceloma* isolate from *J. aconitifolia*. Symptoms on cassava inoculated with *Sphaceloma* sp. from *J. aconitifolia* were indistinguishable from those caused by *S. manihoticola*.

Results of cross inoculations with pathogens reisolated from

TABLE 2. Susceptibility of various euphorbiaceous hosts to isolates of *Sphaceloma* spp.

Host	Pathogen[a]					
	Sm	Smc	Sj	Sb	Sp	Sk
Manihot esculenta	+++[b]	+++	+++	+	+	+
M. carthaginensis	+++	++	+++	+	+	++
Jatropha aconitifolia var. *papaya*	++	++	+++	+	−	−
J. curcas	+	+	+	±	−	−
J. nudans	−	−	−	−	−	···
Euphorbia brasiliensis	+	±	±	+++	−	+
Eu. hirta	−	−	−	+	−	···
Eu. heterophylla	+	+	±	−	+++	+++
Eu. prunifolia	+	+	±	−	+++	+++
Eu. pulcherrima	−	−	−	−	+++	+
Eu. tovariensis	−	−	−	−	−	−
Croton sp.	−	−	−	−	−	−
Hevea brasiliensis	−	−	−	−	−	−

[a] Sm = *Sphaceloma manihoticola* (single ascospore isolates from cassava), Smc = *S. manihoticola* from *Manihot carthaginensis*, Sj = *Sphaceloma* sp. from *Jatropha aconitifolia*, Sb = *Sphaceloma* state of *Elsinoë brasiliensis* from *Euphorbia hypericifolia*, Sp = *S. poinsettiae* from *Eu. pulcherrima*, Sk = *S. krugii* from *Eu. heterophylla*.

[b] − = no symptoms; ± = leaf symptoms only; +, ++, +++ = increasing degrees of leaf petiole and stem symptoms; ··· = not tested.

TABLE 3. Virulence of isolates of *Elsinoë brasiliensis* and *Sphaceloma poinsettiae* after passage through cassava compared with that of isolates of *Sphaceloma manihoticola*, as shown by disease levels on inoculated plants[a]

Inoculated plants	*Elsinoë brasiliensis*			*Sphaceloma poinsettiae*		*Sphaceloma manihoticola*	
	Original isolate	First reisolation from cassava	Second reisolation from cassava	Original	First reisolation from cassava	Least virulent isolate	Least virulent isolate
Manihot esculenta							
MCOL 113[b]	2[c]	162	357	0	0	136	362
MCOL 96[b]	13	172	···	0	0	295	472
Eu. brasiliensis	+++	+	+	−	−	±	±
Eu. pulcherrima	−	−	−	+++	+++	±	±

[a] Numerical values for cassava cultivars were computed by taking the product of the number of internodes infected and the proportion of the area of the internodes involved in disease. (Numerical system used for cassava not suitable for the other host species. Therefore, +++ = severe stem symptoms, + = few stem lesions, ± = leaf lesions only, − no symptoms observed, ··· = not tested.

[b] CIAT designation of cassava germplasm accessions: M = *Manihot esculenta*, COL = collected in Colombia; 113 = numerical designation of accessions.

[c] Values represent means of 6–8 plants, LSD = 102 ($P = 0.05$).

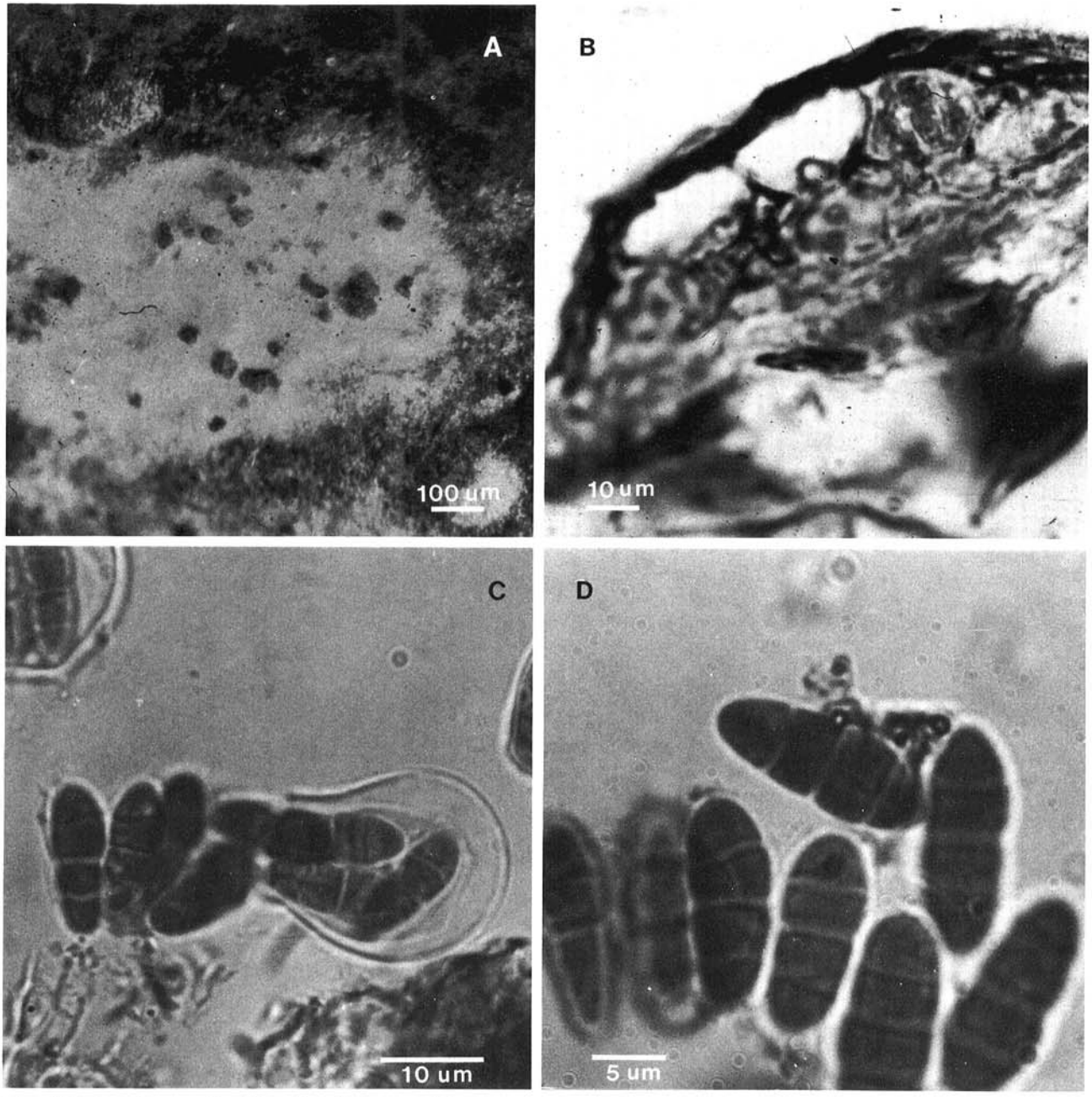

Fig. 1. A and **B,** Ascostromata; **C,** globose bitunicate ascus with ascospores; **D,** muriform ascospores of the sexual stage of *Sphaceloma manihoticola*. Ascospores were stained with cotton blue.

hosts other than the original host are presented in Table 3. Virulence of the *Sphaceloma* state of *E. brasiliensis* on cassava increased markedly after only one reisolation from cassava and decreased on *Eu. brasiliensis*, although not to the level of *S. manihoticola* on *Eu. brasiliensis*. Symptoms caused by reisolated *E. brasiliensis* on cassava were indistinguishable from those caused by *S. manihoticola*. No change in the virulence of *S. poinsettiae* was observed after one passage through cassava, and attempts at a second reisolation failed. Virulence of *E. brasiliensis* on *Eu. pulcherrima* and *S. poinsettiae* on *Eu. brasiliensis* were unaffected by these reisolations.

Field observations supported the data from the cross inoculation and reisolation studies (Tables 2 and 3). *Eu. brasiliensis* growing beneath cassava heavily infected with *S. manihoticola* showed moderate to heavy scab symptoms. No superelongation disease was observed on cassava where *Eu. heterophylla* was heavily infected with *S. krugii*. *Eu. pulcherrima* was scab-free in an area (CIAT-ICA Station, Carimagua) with extremely high levels of superelongation disease.

Morphology. Ascoma were observed on stromatic tissues of leaves, petioles, and stems of cassava plants collected during the early part of the rainy season, if the rains were frequent enough. These structures were present on material from Mexico (Tabasco), Costa Rica, the Dominican Republic, and Colombia (Departments of Casanare, Cauca, Magdelena, Meta, and Vichada). No sexual structures were seen on scab lesions on the other hosts examined. Attempts to induce the sexual stage in culture and on host plants failed.

Ascoma on cassava were pulvinate (occasionally applanate), convoluted to smooth, solitary, or coalescing, and 20–130 μm in diameter. They originated subepidermally and were composed of a hyaline pseudoparenchyma with a distinctly pigmented epithelium, giving the structure a dark appearance when viewed from above (Fig. 1). Asci (usually with eight ascospores) were bitunicate and globose (13–22 μm in diameter) and occurred singly in locules with well-developed walls. Mature ascospores (11–14 × 3–7 μm) were hyaline, had three transverse septa at which they showed slight constrictions, and commonly had a longitudinal septum in one or more internal cells. One end of the spore was usually somewhat broader than the other (Fig. 1). Germination was by production of conidia or was direct, with one or more germ tubes produced from each cell, near the septa. Fragmentation of ascospores at the septa was occasionally observed, particularly with dried specimens.

Conidiophores were occasionally found in a tightly packed layer in true acervuli, but more commonly they were present as a continuous or discontinuous layer on the lesion surface. Fascicles of conidiophores were fairly common. Conidiophores of isolates from cassava, *Eu. brasiliensis, J. aconitifolia* var. *papaya*, and *M. carthaginensis* were phialides, usually coming to a point, but occasionally showing a pronounced collaret. They were hyaline to slightly pigmented, 0–1 septate, isodiametric to elongated, and 5–24 × 2–5 μm. Conidiophores of *S. poinsettiae* and *S. krugii* were similar to one another. They were phialides (occasionally with a pronounced collaret), hyaline to brown, 0–2 septate, isodiametric to elongated, and 4–20 × 2–8 μm on lesions that produced hyaline conidia only and 4–28 × 2–8 μm on lesions that produced both hyaline and fawcetti conidia.

All isolates produced abundant hyaline conidia in culture and on their original hosts. On host lesions they commonly formed creamy to pinkish masses when dry. These conidia were small, thin-walled, elipsoid to (rarely) globose, and commonly had one or two polar gutullae and a thin gelatinous sheath. Fawcetti spores, when observed, were much longer, tapering at both ends, thick-walled with brown pigmentation, and slightly ornamented.

Hyaline conidia germinated directly by swelling and then forming hyphae that, after laying down several septa, frequently began to produce other hyaline conidia. The hyaline conidia also germinated by budding secondary conidia subapically or by forming them at the end of a sterigmalike structure. Fawcetti conidia were never observed to germinate directly. They always produced hyaline conidia either apically, subapically, or laterally.

Dimensions of conidia from the various isolates in culture and from their respective hosts are shown in Table 4. Considering only conidia taken from leaf lesions, populations of largest dimension for a given isolate are almost always from plants of the species from which the isolate was originally obtained. Table 5 presents conidial dimensions of 10 isolates of *S. manihoticola* and an isolate of the *Sphaceloma* state of *E. brasiliensis* from agar colonies and from

TABLE 4. Mean dimensions of hyaline and fawcetti conidia of isolates of *Sphaceloma* species on various substrates

Pathogen[a]	On substrates[b]							
	PDA	Me	Mc	Ja	Ebr	Epr	Ehe	Epu
	Length of conidia (μm)[c]							
Elsinoë brasiliensis (EB)	4.3 a[d]	4.2 a	4.0 a	4.4 a	4.6	...	...	...
S. manihoticola (as)	4.0 a	4.0 a	4.0 a	4.3 a	–	–	...	...
Sphaceloma sp. (J)	4.0 a	4.3 a	4.2 a	4.4 a	–	–	–	...
Sphaceloma sp. (MC)	4.4 a	4.8 b	4.6 b	4.4 a	–	–	–	...
S. krugii (EH)	6.1 b	4.0 a	4.2 a	...	–	5.3 a	5.7 a (13.6 b)	5.5 a
S. poinsettiae (EP)	6.2 b	5.2 c	4.9 c	...	–	6.2 b	5.6 a	6.8 b (11.7 c)
	Width of conidia (μm)[c]							
S. brasiliensis (EB)	2.5 c	1.7 b	1.4 a	1.8 b	1.8 a	–	–	–
S. manihoticola (as)	2.2 b	1.5 a	1.5 a	1.6 a	–	–	–	–
Sphaceloma sp. (J)	2.0 a	2.0 c	1.8 b	2.0 c	–	–	–	–
Sphaceloma sp. (MC)	2.0 a	2.0 c	2.0 b	1.9 b	–	–	–	–
S. krugii (EH)	2.5 c	1.6 ab	1.6 a	...	...	1.8 a	1.9 a (3.9)	1.9 a
S. poinsettiae (EP)	2.6 c	2.4 c	2.3 c	...	...	2.4 b	2.3 b	2.5 b (3.7)

[a] Letters in parentheses indicate origin of isolate: EB = *Euphorbia brasiliensis*, as = single ascospore isolate from cassava; J = *Jatropha aconitifolia* var. *papaya*; MC = *Manihot carthaginensis;* EH = *Eu. heterophylla;* EP = *Eu. pulcherrima.*

[b] Potato-dextrose agar colonies 21 days old; host lesions 14 days after inoculation. Me = *Manihot esculenta,* Mc = *M. carthaginensis*, Ja = *Jatropha aconitifolia* var. *papaya*, Ebr = *Euphoriba brasiliensis,* Epr = *Eu. prunifolia,* Ehe = *Eu. heterophylla,* Epu = *Eu. pulcherrima.*

[c] Dimensions given are means of 100 conidia; figures in parentheses are for fawcetti spore type. Absence of data indicates insufficient conidia produced to obtain comparable mean.

[d] Dimensions in a given column followed by the same letter are not significantly different at the 1% level.

lesions on plants inoculated with these same isolates. On PDA (Table 5) no significant differences were found among the 10 isolates from cassava and *J. aconitifolia* var. *papaya*, which were all smaller than conidia from the isolate from *Eu. brasiliensis*. Conidia of the same isolates taken from lesions that developed on a susceptible cassava cultivar (MCOL 113) showed no significant differences.

The fawcetti-conidium type (Fig. 2) was found for *S. poinsettiae* on *Eu. pulcherrima* and for *S. krugii* on *Eu. heterophylla* (Table 4). These were not always present, and specimens from these hosts not containing this spore type were quite common. These conidia were produced from pigmented conidiophores on lesions with an olivaceous and more or less velvety layer, and their formation could be induced on such lesions by treatment with high relative humidity. Free water on the lesion surface induced hyaline conidial formation only.

S. krugii on *Eu. prunifolia* formed fawcetti spores only sparsely. An exhaustive search yielded no evidence for the production of fawcetti conidia on cassava, *Jatropha, Eu. brasiliensis*, or *M. carthaginensis*.

DISCUSSION

Symptomatology, host relationships, and cultural characteristics have been previously used to consider taxonomic relationships within the *Elsinoë-Sphaceloma* complex (2,11). Jenkins considered conidia and ascospore morphology to be potentially important but pointed out problems in obtaining spores of equal maturity for comparison.

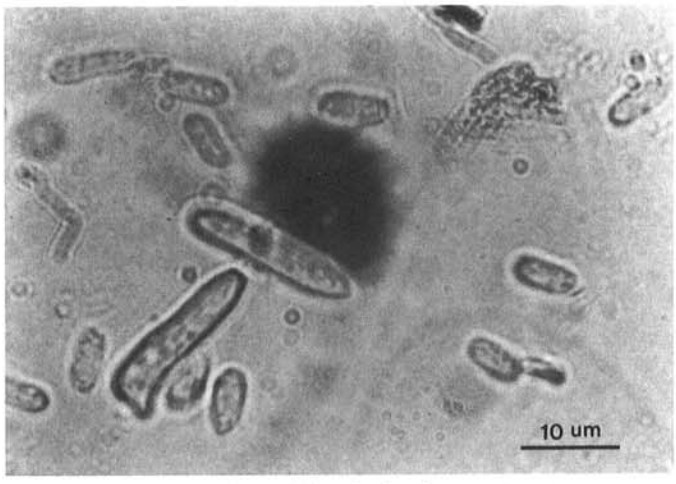

Fig. 2. Fawcetti and hyaline conidia of *Sphaceloma poinsettiae*.

Bitancourt and Jenkins (2) reported variability in colony morphology in *E. australis* Bitancourt and Jenkins but maintained that they could still distinguish this species from *E. fawcetti* Bitancourt and Jenkins by using other criteria. Our interpretation of their discussion (2) is that they could distinguish different isolates morphologically but could not assign them to a particular species without knowing their hosts of origin.

After examining large numbers of isolates from euphorbiacious hosts, we have found that within-species variability in cultural characteristics may exceed between-species differences (23). Furthermore, we have found cultural characteristics to be rather unstable. Placing heavy emphasis on cultural characteristics carries the risk of considering normal variants of one species to be different species.

In addition to the difficulties regarding host specificity, the problem of ambiguous host identifications also arises. *Eu. brasiliensis* L. (the legitimate name for *Eu. hypossifolia* L.) is very similar to several other species, eg, *Eu. hirta* L. and *Eu. hypericifolia* L. These species are physiologically similar (19,20) and, based on our results and on lesions found on some specimens in the Bailey Hortorium, Cornell University, *Eu. hypericifolia* is probably a host of *E. brasiliensis*.

Although Jenkins (11) cites several reports of host specificity, at the level of genus and even species, previous workers apparently never tested the stability of this specificity by passing the pathogens through related hosts. Similarly, they rarely, if ever, inoculated large numbers of individuals to confirm that an isolate was nonpathogenic to the species as a whole. Our results showed that the "specificity" shown by some pathogens may be quite plastic. Jenkins (11) also mentions that pathogens on genera placed in separate tribes within a family can be considered distinct species. We found that some pathogens are capable of infecting members of different tribes of euphorbiaceous plants (8), as with *Jatropha* and *Manihot* spp. According to some classifications of the Euphorbiaceae (18), *E. brasiliensis* crosses subfamilies from *Eu. brasiliensis* to *Manihot* spp., but not crossing subgenera (19) to *Eu. pulcherrima*.

Symptoms on different hosts tend to differ, restricting the usefulness of this character. This is particularly relevant when considering symptoms on *Eu. brasiliensis, J. curcas*, and *J. aconitifolia* var. *papaya*. Symptoms on *Eu. brasiliensis* are strikingly different from those on the *Jatropha* spp. and on cassava. Symptoms on the two *Jatropha* spp. are indistinguishable and very different from those found on cassava. However, symptoms on cassava caused by isolates taken from *J. aconitifolia* var. *papaya* and *Eu. brasiliensis* are identical to one another and to those caused by isolates of the *Elsinoë* sp. from cassava. Likewise, symptoms on *J. aconitifolia* var. *papaya* inoculated with an isolate from *Eu. brasiliensis* and from cassava were indistinguishable from those developing after inoculation with isolates from *J. aconitifolia* var. *papaya*. Such host influences on symptoms were also reported by

TABLE 5. Dimensions[a] of conidia from eleven monoconidial isolates of *Sphaceloma* growing on potato-dextrose agar (PDA) and cassava (MCOL 113) stem lesions

Parameter and substrate[b]	Isolate[c]										
	MS-069	MS-079	MS0075	MS0-56	MS-050	MS-051	MS-073	MS-070	MS-046	MS-038	MS-076
Length											
PDA	3.9 a	3.7 a	3.8 a	3.7 a	3.8 a	3.8 a	3.8 a	4.2 a	3.9 a	4.2 a	4.6 b
MCOL 113	4.9 d	4.8 d	4.0 a	4.4 bc	4.3 b	3.9 a	4.2 b	3.7 a	4.2 b	4.6 c	4.2 b
Width											
PDA	1.6 a	1.6 a	1.6 a	1.6 a	1.6 a	1.6 a	1.7 a	1.8 ab	1.7 a	1.9 b	2.2 c
MCOL 113	1.8 bc	1.9 c	1.7 ab	1.6 a	1.7 ab	1.6 a	1.7 ab	1.6 a	1.6 a	1.8 bc	1.7 ab

[a] Dimensions given are means of 100 conidia in microns. Numbers in the same row followed by the same letter do not differ significantly according to a Duncan's multiple range test ($P = 0.01$).

[b] PDA colonies 24 days old; conidia were removed from stem lesions 14 days after inoculation.

[c] Isolate MS-076 originally from *Euphorbia brasiliensis*; isolate MS-073 from *Jatropha aconitifolia* var. *papaya*; all others from cassava. Numbering system is that of CIAT cassava pathology single-spore fungus collection.

Bitancourt and Jenkins (2).

Our results on the variability of conidial dimension within and among our isolates (Tables 4 and 5) illustrate the problem of using this character for distinguishing species. We feel that it is best to consider only those dimensions obtained from colonies grown on an unbiased substrate, such as PDA. However, ability of a species to produce the fawcetti spore type may provide the strongest basis for clear-cut divisions.

Symptomatology and dimensions of hyaline conidia of the *Sphaceloma* pathogen on *Eu. heterophylla* were entirely consistent with published descriptions, photographs, and the type specimens of *S. krugii*. *S. krugii* had previously been considered a separate species from *S. poinsettiae* because of the larger conidial dimensions of the latter species (4,14). We believe the original description of conidia of *S. poinsettiae* (14) was based on the dimensions of fawcetti as well as of hyaline spores. Although the original description of *S. krugii* included no mention or implication of fawcetti spores, which were not found in the type specimens, we have found such spores on several field-infected plants and have demonstrated that they can be produced on plants inoculated with *S. krugii*. In view of the demonstrated ability of *S. krugii* and *S. poinsettiae* to produce fawcetti spore types on *Eu. heterophylla* and *Eu. prunifolia*, and the lack of other distinguishing morphological or pathogenic characters between them, retaining them as distinct species seems to have little justification.

Similar logic was used to consider the taxonomic status of other *Elsinoë* species studied. From the ascospore dimensions presented in Table 1, examination of herbarium species and results of pathogenicity studies (Table 4), there is no reason at this time to question the integrity of *E. antidesmae, E. heveae*, or *E. brasiliensis*. However, the ascospore, ascus, and ascoma dimensions of *E. brasiliensis* were similar to those of *E. jatrophae* and the *Elsinoë* state of *S. manihoticola*, based on published descriptions, and examinations of living, herbarium, and type specimens. Pathogenicity studies, conidial morphology, and the absence of the fawcetti conidium type for the conidial states of these organisms also strongly support arguments for their synonomy.

The results of these taxonomic studies are relevant to the epidemiology and control of superelongation disease of cassava. Alternative hosts of *E. brasiliensis* are cosmopolitan weeds and widely grown ornamentals. If the pathogen were introduced to cassava-producing areas of Africa or Asia, it probably would be impossible to eradicate if alternative euphorbiaceous hosts exist there. Many regions of Africa and Asia where cassava is the staple crop are climatologically very similar to the Llanos Orientales of Colombia, where the pathogen causes extreme losses in local plantings. The danger exists of introducing this pathogen to those areas on ornamental *Jatropha*, which may not be subject to the same stringent quarantine regulations placed on cassava. Because of the wide host range, inoculum will probably be present all year. Furthermore, highly genetically variable hosts (ie, several genera) may well maintain a very genetically variable pathogen population.

PROPOSED CHANGES AND SYNONOMY

Elsinoë brasiliensis Bitanc. and Jenkins, Proc. 8th Am. Sci. Conf., Washington, DC 1940 (Publ. 1942):160. *descr. emend.* Isotype: On *Euphorbia* ? *hyssopifolia* L. [*sic*] leaves and stems. Brazil, state of Paraiba, Alagoinha, Experiment Station. Types (examined): J. Deslandes 513, 1940. CUP Myriangiales Selecti Exs. 367, BPI 3581.

Elsinoë isotype *jatrophae* Bitanc. and Jenkins, Arq. Inst. Biol., São Paulo 20:13 (1950). Barcenz, Guatemala, on *Jatropha curcas* L. leaves, A. S. Muller, 1943. Types (examined): CUP Myriangiales Selecti Exs. 473, BPI 90158.

Sphaceloma manihoticola Bitanc. and Jenkins, Arq. Inst. Biol., São Paulo 20:15 (1950). Isotype: Brazil, state of Paraiba, Carcara, on *Manihot glaziovii* Muell. Arg. leaves, J. Deslandes, 1939. Type (examined): CUP Myriangiales Selecti Exs. 477; *stat. conid.*

Other specimens examined: BPI 90945, CUP 58983, 58985, 58986, 58987, 58990, 58991, 58993.

Hosts: *Euphorbia brasiliensis* L., *E. hypericifolia* L., *Jatropha aconitifolia* Muell. var. *papaya* Arbelaez, *J. curcas* L., *Manihot carthaginensis* Muell., *M. esculenta* Crantz, *M. glaziovii* Muell. Arg.

Leaf spots 0.5–5 mm, coalescing and much larger, amphigenous, circular to irregular, deforming leaf, light colored, necrotic, often with center gone, red or dark border and yellow halo, frequently on veins forming raised corky cankers; petiole and stem cankers usually hypertrophic, often with dark reddish borders or reddish to black centers when young, coalescing to produce large eliptical to fusiform lesions to 10 cm long, flat, depressed or slightly raised and somewhat fissured, becoming large and tumorlike on *Eu. brasiliensis*; pronounced internode elongation on severely infected members of some species (eg, *M. esculenta*), ascomata erumpant, pulvinate, convoluted, rarely coalescing, on surface of stem, petiole and leaf-vein lesions, 20–130 μm in diameter, composed of hyaline pseudoparenchyma and covered with a dark epithecium; locules with poorly developed walls; asci solitary in locules dispersed more or less regularly in one or, rarely, two rows in the pseudoparenchyma, globose, thick-walled, 13–20 μm in diameter, usually containing eight ascospores; ascospores hyaline, 3-septate, longitudinal septum in one or more of the internal cells when mature, constricted mostly at medium septum and to a lesser degree at others, often clavate, straight to slightly curved, 9.5–14 × 3–7 μm.

Status Conidialis, Sphaceloma manihoticola Bitancourt and Jenkins, Arq. Inst. Biol. São Paulo 20:13 (1950). Leaf spots light colored, small (0.5–3 μm), necrotic, pale buff, often with center gone and dark border, deforming leaf; on leaf veins corky, elongated; on stems and petioles, forming corky cankers often with dark borders or reddish internal areas when young, coalescing to produce elliptical to large fusiform lesions up to 10 cm long, flat, depressed to somewhat raised and somewhat fissured, usually with slightly raised margin, becoming large and tumorlike near nodes of *Eu. brasiliensis*, internodes elongated on heavily infected individuals of some species (eg, *M. esculenta*); conidiogenous surface continuous on young lesions, tending to the outer edge of progressing older lesions, frequently reddish below surface; conidiophores phialidic, often with pointed ends or collarettes, isodiametric to 3-septate and filamentous, hyaline to dark, 5–24 × 1–5 μm, producing conidia laterally and apically grouped into fasicles or forming a continuous layer; conidia hyaline, 0-septate, refringent, 2.5–6.5 × 1–4.5 μm, often with one or two refringent polar gutules, frequently producing secondary conidia laterally or subapically; germ tubes produced at one or both apices.

Sphaceloma poinsettiae Jenkins and Ruehle, Proc. Biol. Soc. Wash. 35:83 (1942). *descr. emend.* Type: Dade Co., FL, December 9, 1941 (location unspecified).

Sphaceloma krugii Bitanc. and Jenkins, Arq. Inst. Biol. São Paulo 19:03 (1949). Isotype (examined): On *Euphorbia prunifolia* Jacq. var. *repanda* Muell. Arg. stems, Brazil, State of São Paulo, Campinas, Institute Agronomico, H. P. Krug, April 15, 1936. CUP Myriangiales Selecti Exs. 420, BPI 72791.

Other specimens examined: CUP 419, 421, 422, 423, 424, 425, 426, 532, 533 1056, 1331, 58984, 58988, 58989, 58994.

Hosts: *Euphorbia heterophylla* L., *E. prunifolia* L., *E. pulcherrima.*

Leaf spots 1–5 mm usually confined to veins and margins; on veins forming pronounced raised cankers 3–10 × 2–6 mm with red to nearly black margins, on lamina usually raised below, occasionally coalescing, light to dark brown, causing leaf-curl when at margin; cankers abundant on stem, raised, circular to elongate, often with red to black margin, length and width exceeding 1 cm and coalescing, occasionally girdling stem; severely infected plants may show exaggerated internode elongation, fertile layers with pinkish hue or olivaceous and more or less velvety; conidiophores arise from more or less hyaline hyphae mingled with host tissue forming densely packed layer or groups; conidiophores pointed at apex or with collarette, 0–1 (occasionally 2) septate, pale to brown, up to 15–30 × 3–5 μm, commonly isodiametric; conidia eliptical, hyaline, often with polar gutules, 3–7.5 × 15.4 μm, 0-

septate and/or eliptical to spindle-shaped, pale brown, sparsely ornamented, 7–25 × 2.5–7 μm, 0–1 (occasionally 2) septate, with slight constriction at septa.

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