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Author(s): S. H. Sohmer

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A revision of *Chamissoa* (Amaranthaceae)<sup>1</sup>

S. H. Sohmer

Department of Biology, University of Wisconsin, La Crosse, Wisconsin 54601

SOHMER, S. H. (Dept. Biol., Univ. Wisconsin, La Crosse, Wisconsin 54601). A revision of *Chamissoa* (Amaranthaceae). Bull. Torrey Bot. Club 104: 111-126. 1977.— This revision, based on the study of approximately 1500 herbarium specimens and field work, recognizes two subgenera, including *Chamissoa* subgenus *Achlamys* (Moquin) comb. nov., and two species with five varieties, including *C. acuminata* var. *maximiliani* (Moquin) comb. nov., and *C. acuminata* var. *swansonii* var. nov. Illustrations and distribution maps are provided.

William Hillebrand commented in his classic Flora of the Hawaiian Islands (1888) on the resemblance between the Hawaiian genus *Charpentiera*, now also known from the Austral Islands, and the West Indian, Mexican, South and Central American genus *Chamissoa*. Sherwin Carlquist also implied a possible close relationship between the genera (1970, and pers. com.). These implied or suggested relationships stimulated my interest in undertaking a revision of *Chamissoa* shortly after concluding work with *Charpentiera* (Sohmer 1972), and in comparing these genera (Sohmer, 1976a).

**Important taxonomic features.** Taxonomically significant features of *Chamissoa* include: habit (clambering vines vs. suffrutescent herbs), leaf size and shape (ovate vs. lanceolate), and inflorescence type (paniculate vs. spicate). Characteristics of the gynoeceium and seed are also highly significant taxonomically. *Chamissoa* subg. *Chamissoa* is characterized by barrel-shaped ovaries which possess an emarginate, terminal wing (Figs. 1, 3, 9, and 10), although there is a tendency to suppress the wing in *C. altissima* var. *rubella* (Fig. 11), and these features are associated with a style that is shorter than the stigmas (in pistillate individuals). Correlated with these features is a large bi-valved aril that completely encloses the seed (Figs. 9 and 11). In *Chamissoa* subg. *Achlamys*, the mature ovary is smaller, the

walls are thinner, and the apex is either round with the base of the style broad (Figs. 2, 4, 6, 12, 14, and 15), or has a collar with the style base narrow and originating from within this collar (Figs. 8 and 13). The style in this subgenus is frequently as long as the ovary or longer, and the stigmas are shorter than the style. Members of this subgenus produce very small arils which are easily overlooked. *Chamissoa* subg. *Chamissoa* is gynodioecious (Figs. 5 and 7), whereas individuals of *Chamissoa* subg. *Achlamys* have perfect flowers (Fig. 4).

**Taxonomic treatment.** All measurements utilized in descriptions and keys were taken from herbarium material. Herbaria from which loans of *Chamissoa* were obtained are cited in accordance with the *Index Herbariorum* (Holmgren and Keuken, 1974). Observations and collections made during field trips to the Dominican Republic, Trinidad, and Mexico supplemented the study of herbarium material. Growth patterns of several individuals from Mexico and the Dominican Republic were observed in the greenhouse.

*Chamissoa* Humboldt, Bonpland, and Kunth (nom. cons.)

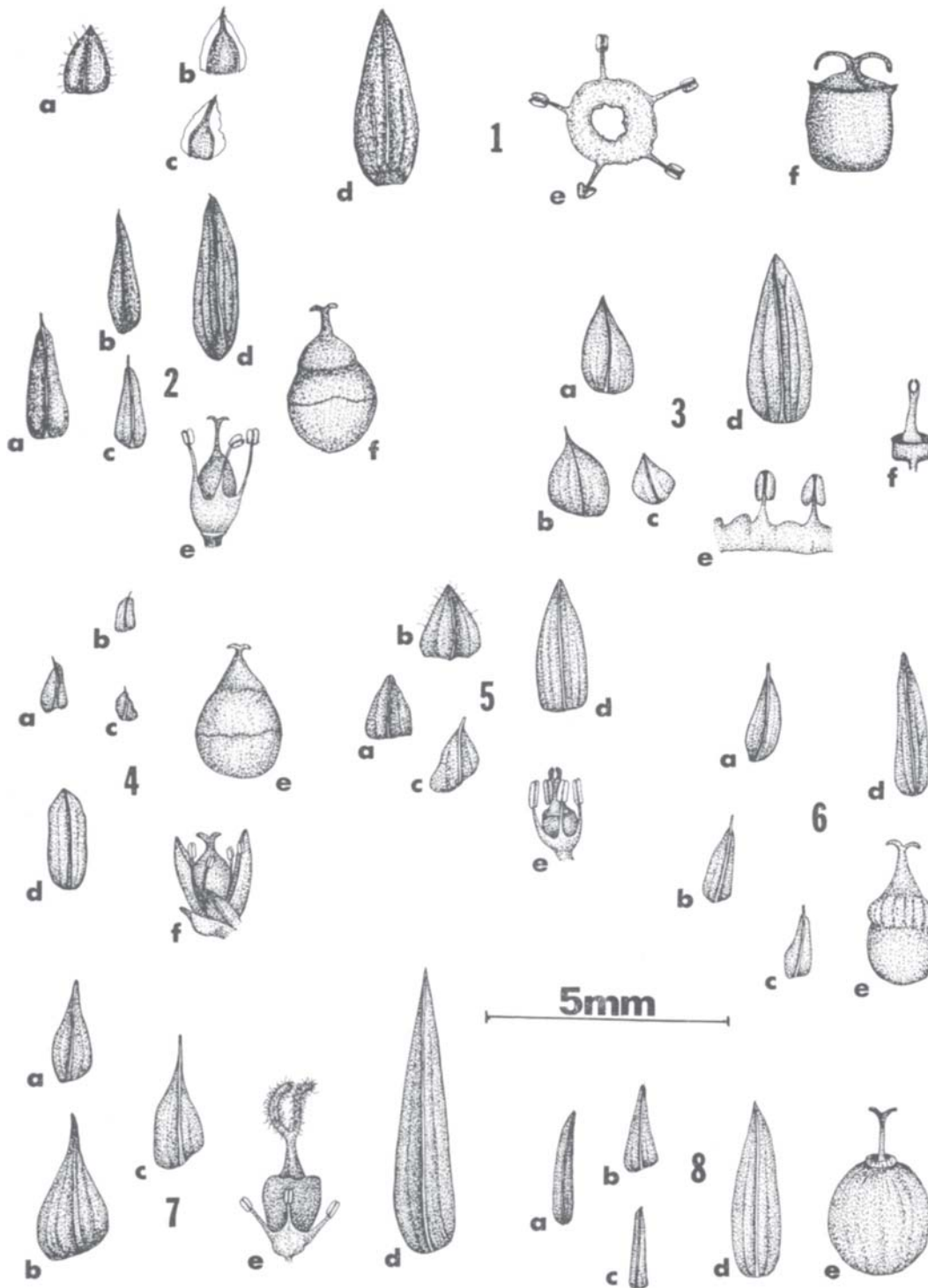
*Chamissoa* Humboldt, Bonpland, and Kunth, Nov. Gen. et Sp. Pl. 2(7): 196. 1818. Type species: *Chamissoa altissima* (Jacquin) Humboldt, Bonpland, and Kunth.

*Kokera* Adanson, Fam. Pl. 1: 269. 1763 (nom. rej.).

Plants either herbs becoming suffrutescent or shrubby to about 2 m in height, with arching branches, or woody vines climbing upon neighboring vegetation and then often densely covering small trees or

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Figs. 1-8. Floral parts in *Chamissoa*. The letters a, b, c, and d, refer respectively to the floral bract, first floral bracteole, second floral bracteole, and outermost sepal. Other structures are explained



the lower branches of tall trees; branches green, becoming brown with age, glabrous or pubescent (at least when young); leaves alternate, exstipulate, usually with well defined petioles, with blades 1.3–19.5 cm long, broadly ovate to narrowly lanceolate with rounded, truncate or acute bases and round to acute or long-acuminate apices, glabrous or pubescent, sometimes densely so when young, membranaceous to semi-coriaceous; inflorescences terminal and/or axillary, often with the leaves on the uppermost flowering nodes suppressed so that the inflorescence appears terminal, composed of cymose clusters of flowers densely or loosely arranged on the axes, each cymule with several to as many as 20 flowers, with the younger flowers appearing in the axils of the floral bracts or bracteoles of the older ones; flowers cream, yellow-green, whitish-green, white, pink, or magenta-purple, with short pedicels with 2 deltoid-ovate to lanceolate and acuminate bracteoles 0.6–2.6 mm long, the whole subtended by a deltoid-ovate to lanceolate floral bract 1.0–2.9 mm long, (if the oldest flower of a cymule), otherwise one of the bracteoles of an older flower acts as the floral bract), with five ovate to lanceolate, obtuse, acute, or acuminate sepals 2.0–5.5 mm long; stamens 5, with filaments fused at base into a short, membranous tube, the free parts of the filaments about 1–1.5 mm long at anthesis in the perfect-flowered species with the anthers 0.1–0.7 mm long, and with the free parts of filaments usually 2–3 mm long at anthesis with anthers 0.2–1 mm long in the perfect-flowered individuals of the gynodioecious species (*C. altissima*), the pistillate individuals of the gynodioecious species with staminodes only; pistils with unilocular, uniovulate, globose, or barrel-shaped ovaries 1.5–4.2 mm long at anthesis with basal placenta-

tion, with a round or acuminate apex, or truncate at apex with a narrow emarginate wing, or with a narrow collar at the top, with styles 0.4–1.5 mm long, slender or dilated at base and, if dilated, sometimes with a conspicuous spongy tissue developed at base, with stigmas 0.2–1.3 mm long; seeds black or mottled, smooth or foveolate, 1.0–2.7 mm long, with a large bivalved aril enclosing the seed or a very small aril. Fruit a circumscissile dehiscent capsule.

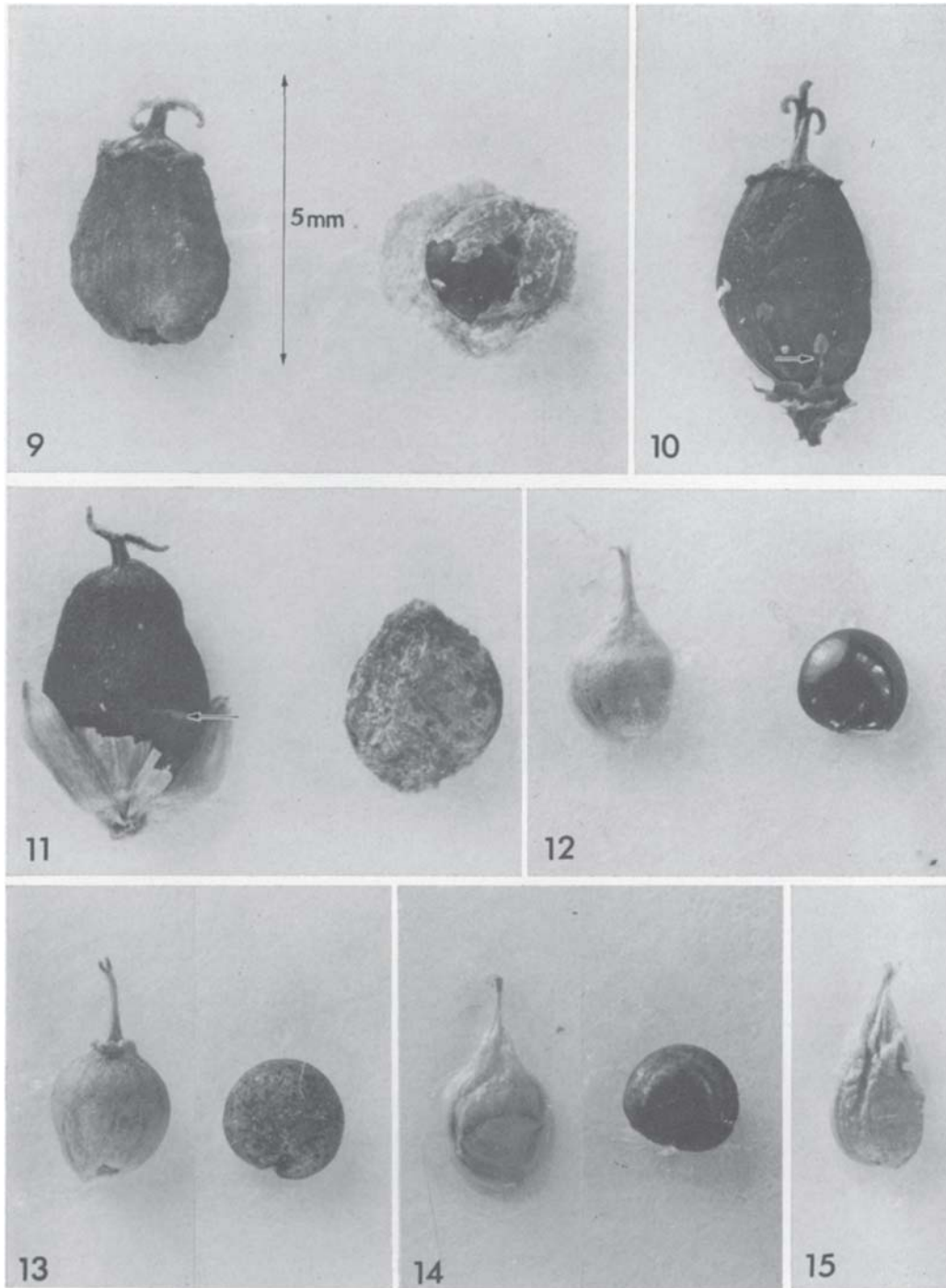
**DISTRIBUTION.** *Chamissoa* ranges through tropical and subtropical America from Mexico to northern Argentina and the West Indian Islands, usually below 2,000 m. It is very common in all parts of its range and appears to favor disturbed areas near clearings, roads, and banks of rivers and streams.

**INFRA-GENERIC DESIGNATIONS.** Moquin (1849) treated *Chamissoa* as consisting of three infrageneric sections: *Allmania*, *Euchamissoa*, and *Achlamys*. *Allmania* R. Brown ex Wight (1834) is excluded from *Chamissoa*, as has been commonly done since Moquin's day, primarily because of the absence of an aril. Moquin distinguished between his *Chamissoa* sections *Euchamissoa* and *Achlamys* on the basis of characteristics already discussed above: the presence or absence of a discernable aril, and the relative length of the style and stigmas.

#### Key to the taxa of *Chamissoa*

1. Plants usually with conspicuous, bivalved arils completely enclosing the mature seed; gynodioecious; pistillate individuals at anthesis with ovaries over 2 mm long and styles 0.4–1 mm long, usually shorter than the stigmas; usually becoming vines up to 20 m and tending to clamber onto and drape over surrounding vegetation (*Chamissoa* subg. *Chamissoa*) . . . . . 2
2. Flowers yellow-green, whitish-green, or cream colored, rarely, if ever pink or pinkish, usu-

in each figure where necessary. Since the drawings were made the same relative size they may all be compared to the scale shown. 1. *C. altissima* var. *rubella*, from Reitz and Klein 3501 (US); e, androecial tube with staminodes; f, pistil at anthesis with emarginate wing at top of ovary. 2. *C. acuminata* var. *swansonii*, from Matuda 16219 (US); e, pistil and androecial tube with 3 of the 5 stamens at anthesis; f, mature pistil showing a line of dehiscence on ovary wall. 3. *C. altissima* var. *altissima* from Abbott 1920 (GH); e, portion of androecial tube with 2 of the 5 stamens and the frequently encountered round lobes (= pseudostaminodia) that alternate with them; f, functionless pistil at anthesis—note the closed, unexpanded stigmas. This is a frequent occurrence in the structurally "perfect" flowers of this species. 4. *C. acuminata* var. *acuminata*, from Smith and Reitz 9200 (US); e, pistil; f, flower at anthesis with the two floral bracteoles. 5. *C. altissima* var. *rubella*, from Meyer 86058 (A); e, pistil and stamens of a "perfect" (functionally staminate) flower at anthesis. 6. *C. acuminata* var. *swansonii*, from Schunke 2950 (F); e, pistil with maturing ovary, note the conspicuous thickening at the base of the style. 7. *C. altissima* var. *altissima*, from Mexia 1284 (GH); e, pistil and staminodes of pistillate flower (this is a representative of populations with some of the largest flowers in the genus). 8. *C. acuminata* var. *maximilianii*, from Hassler 12174 (US); e, mature pistil showing the narrow style base characteristic of this variety.



Figs. 9-15. Pistils and seeds in *Chamissoa*. Sizes relative to the scale shown in Fig. 9. 9. *C. altissima* var. *altissima*, from *Rovirosa s.n.* (US): maturing capsule and mature seed (from another capsule not shown); part of the aril has been scraped away to expose the testa. 10 and 11. *C. altissima* var. *rubella*. 10. From *Hatschbach 14311* (US); note 3 stigmas and a staminode (arrow). 11. From *Ferreyra 7741* (US); mature pistil and a seed with the aril intact. Note the line of dehiscence



- ally drying brown or tan, including pistil, stigmas 2 and the top of the ovary usually truncate with a narrow emarginate wing . . .  
 . . . . . la. *C. altissima* var. *altissima*
2. Flowers often pinkish, red, or dark purple, or, if sepals yellow-green, whitish-green, or white, with the ovary of both the pistillate (male-sterile) and perfect-flowered individuals red, dark purplish, or pink, usually drying black or purple, and with a tendency to 3 stigmas and the elimination of the apical, emarginate wing . . . . .  
 . . . . . lb. *C. altissima* var. *rubella*
1. Plants with minute, inconspicuous arils; flowers perfect with ovaries at anthesis less than 2 mm long and styles 0.5–1.5 mm long, usually longer than the stigmas; plants usually less than 2 m tall (*Chamissoa* subg. *Achlamys*) . . . 3
3. Styles usually narrow to the base, originating within a collar-like structure at the apex of the ovary; seeds foveolate, black or mottled . . . 2b. *C. acuminata* var. *maximiliani*
3. Styles dilated toward the base; seeds smooth and black, or reticulate or minutely foveolate and black or mottled grayish-black . . . 4
4. Styles without a conspicuous dilation at the junction with the ovary; seeds smooth and black . . . . .  
 . . . . . 2a. *C. acuminata* var. *acuminata*
4. Styles usually with a conspicuous dilation at the junction with the ovary; seeds reticulate or minutely foveolate and black, or mottled grayish-black . . . . .  
 . . . . . 2c. *C. acuminata* var. *swansonii*

*Chamissoa* subgenus *Chamissoa*

1. *Chamissoa altissima* (Jacquin) Humboldt, Bonpland and Kunth, Nov. Gen. et Sp. Pl. 2 (7): 197, t. 125. 1818.

*Achyranthes altissima* Jacquin, Enumer. Syst. Pl. 17. 1760.

Type here designated: Sloane, Jamaica, Nat. Hist. Vol. I, Fig. 2, Plate 91. 1707. Lectotype.

*Celosia paniculata* L. Sp. Pl. Ed. 2. I:298. 1762.

*Kokera paniculata* (L.) Kuntze, Rev. Gen. Pl. 2:542. 1891.

Suffrutescent to woody shrubs to 2 m tall or, usually, woody vines to 20 m, fre-

quently with one or several main branches to 5 or 6 cm in diameter much branched at the upper nodes, clambering upon and draping over surrounding vegetation, with branches glabrous or more frequently pubescent, particularly on the younger parts; gynodioecious; leaves alternate, exstipulate, with petioles 0.5–7 cm long and ovate to narrowly lanceolate blades 1.3–19.5 cm long with round, acute, or infrequently, truncate bases and obtuse, acute or acuminate apices, somewhat membranous to semi-coriaceous, glabrous or pubescent, leaves associated with the flowers tending to be reduced, frequently extremely so; inflorescence 1–15 cm long, rarely longer, axillary, terminal or apparently terminal due to the repression of the upper nodal leaves, composed of cymules with up to 20 flowers, the cymules of the pistillate individuals usually more densely arranged on the axes than those of the structurally perfect-flowered individuals; flowers cream, yellow-green, whitish-green, white, pink, red or purple, each on a short pedicel in the axil of a deltoid-ovate to ovate floral bract and with 2 usually smaller ovate to lanceolate acute to acuminate bracteoles 2–4 mm long, with 5 ovate to lanceolate, acute to acuminate sepals 2–5.5 mm long; stamens 5, filaments fused at base into a short, membranous tube 2–3 mm long at anthesis with anthers 0.2–1 (averaging 0.7) mm long, pistillate individuals with staminodes only; pistils usually with barrel-shaped ovaries 2–3 mm long at anthesis (in the functionally pistillate flowers), usually with a short emarginate wing that completely encircles the truncate apex, although this is suppressed in some individuals that have a rounded apex, with a style 0.4–1 mm long, and 2 minutely papillose stigmas, sometimes with 3 stigmas, which are frequently longer than the style; fruit a circumscissile dehiscent capsule 3–4 mm long with a black, shining seed 1.5–2.7 mm long and usually completely

(arrow) and the nearly complete elimination of the emarginate wing at the top of the ovary that is so apparent on the ovaries in 9 and 10. 12. *C. acuminata* var. *acuminata*, from Reitz and Klein 14512 (US); in this variety the seed coat is without pitting or mottling of any kind. Note the smooth transition of the style base into the ovary. 13. *C. acuminata* var. *maximiliani*, from Morong 746 (US). In this variety the style is narrow at the base and surrounded by a collar-like outgrowth at the top of the ovary. The seed coat is relatively heavily pitted and is also mottled in appearance. 14 and 15. *C. altissima* var. *swansonii*. 14. From Garnier 273 (US); note the abrupt dilation of the style towards the base and the seed coat which is moderately pitted and mottled. 15. Schunke 1476 (US); immature pistil, note the amplification of the dilation of the style base shown in the previous figure; the wrinkling is due to the drying of the tissue.



enclosed within a white, or whitish, spongy, bivalved aril.

None of the material that Jacquin may have collected of this taxon has been located. Howard (1973) lists the taxa described by Jacquin in his *Enumeratio* (1760) and provides information as to whether these taxa are illustrated in Jacquin's later work, the *Selectarum* (1763). Jacquin did not illustrate the taxon but cited Fig. 2 of Plate 91 of Sloane (1707). Thanks to the kindness of Dr. William T. Stearn of BM, the existence of the Sloane specimen which was used as the model for the Sloane figure (Stearn, pers. com.) was confirmed. As pointed out to me by Dr. James Mears (pers. com.), the figure would best serve as lectotype, as Jacquin probably never saw the original specimen.

*Chamissoa altissima* ranges from the states of Sinaloa and Tamaulipas in Mexico, through Central America, into every country of South America, (save Chile), to northern Argentina. The species is also well-represented on nearly every island of the Greater and Lesser Antilles. It is common along clearings, road cuts, and the banks of rivers and streams usually to 1,000 m, infrequently up to 2,000 m. There are two varieties in the species. The varieties are distinguishable primarily on the basis of the color of the flowers, already indicated by the key above.

1a. *Chamissoa altissima* var. *altissima*

*Chamissoa macrocarpa* Humboldt, Bonpland, and Kunth, Nov. Gen. et Sp. Pl. 2: 197. 1818. Type: original material not located (See discussion below).

*Celosia tomentosa* Willd. ex Roemer and Schultes, Syst. 15: 531. 1819. Type here designated: Herbarium Willdenow, Cat. #05033 (B, holotype). Seen as microfiche reproduction.

*Chamissoa altissima* var. *laxiflora* Moquin in A. P. de Candolle, Prodr. 13: 251. 1849. Type here designated: Brazil: near Rio de Janeiro, *Gaudichaud* 396 (P!, lectotype).

*Chamissoa altissima* var. *densiflora* Moquin, l.c. Type here designated: Cuba: no further data, *Sagra* s.n. (P!, lectotype).

*Chamissoa altissima* forma *brevistyla* Seubert in Martius, Fl. Bra-

siliensis 5: 242. 1875. Type: same as for *C. altissima* var. *laxiflora* Moquin.

*Chamissoa altissima* forma *longistyla* Seubert in Martius, l.c. Type: same as for *C. altissima* var. *densiflora* Moquin.

*Chamissoa altissima* var. *glabrata* Seubert l.c. Type here designated: Brazil: no further data, *Seubert* s.n. 1874 (M!, lectotype).

*Chamissoa altissima* var. *grandispicata* Suessenguth, Repert. Spec. Nov. Regni Veg. 39: 6. 1935, excl. forma. Type here designated: Venezuela: Maracay, *Vogl* 70 (M!, lectotype).

Flowers usually greenish-white or greenish-yellow, ranging to white, ovaries never red, pink or purple, at least when mature; ovaries usually with truncate apex with a pronounced emarginate wing circling the top, sometimes the top 1/3 of the ovary constricted so as to give a flask-shaped appearance to the ovary; stigmas usually 2.

DISTRIBUTION. This variety is found in Mexico, Central America and the Antilles, and in South America in northern and western Colombia, Ecuador west of the Andes, Venezuela, the Guyanas, and the coastal areas of northern and eastern Brazil. It is particularly common on the larger islands of the Antilles (Figs. 16 and 17).

REPRESENTATIVE SPECIMENS EXAMINED: MEXICO: Sinaloa: Santa Maria, Culiacán, *Ortega* 6609 (M); Jalisco: Santa Cruz de Vallarta, *Mexia* 1284 (GH, MO, NY); Michoacán: Coalcoman: Aquilla, *Hinton* 12602 (F, GH, NY, US); Tamaulipas: near Tampico, *Palmer* 513 (BM, GH, MO, NY, US); Vera Cruz: Río Jalapilla near Orizaba, *Rosas* 152 (A), near Misantla, *Ventura* 3081 (F, NY); Oaxaca: Tuxtepec: near Chiltepec, *Martinez-Calderón* 451 (GH, US), near Concordia, *Makrinius* 582 (US), near Mogoña, *Alexander* 121 (F, NY); Chiapas: Triunfo, *Matuda* 390 (MO, US); Yucatán: Izamal, *Gaumer* 1011 (BM, GH, M, US). GUATEMALA: Escuintla: near San José, *Standley* 64030 (F, NY). BELISE: Corozal: without further data, *Gentle* 364 (F, MO, US); Stann Creek: S. of Lynam Agric. College, *Dwyer, Elias, & Maxwell* 578 (MO). EL SALVADOR: near San Salvador, *Benson* 83 (NY, US); San Miguel: S. of Lake Olomega,

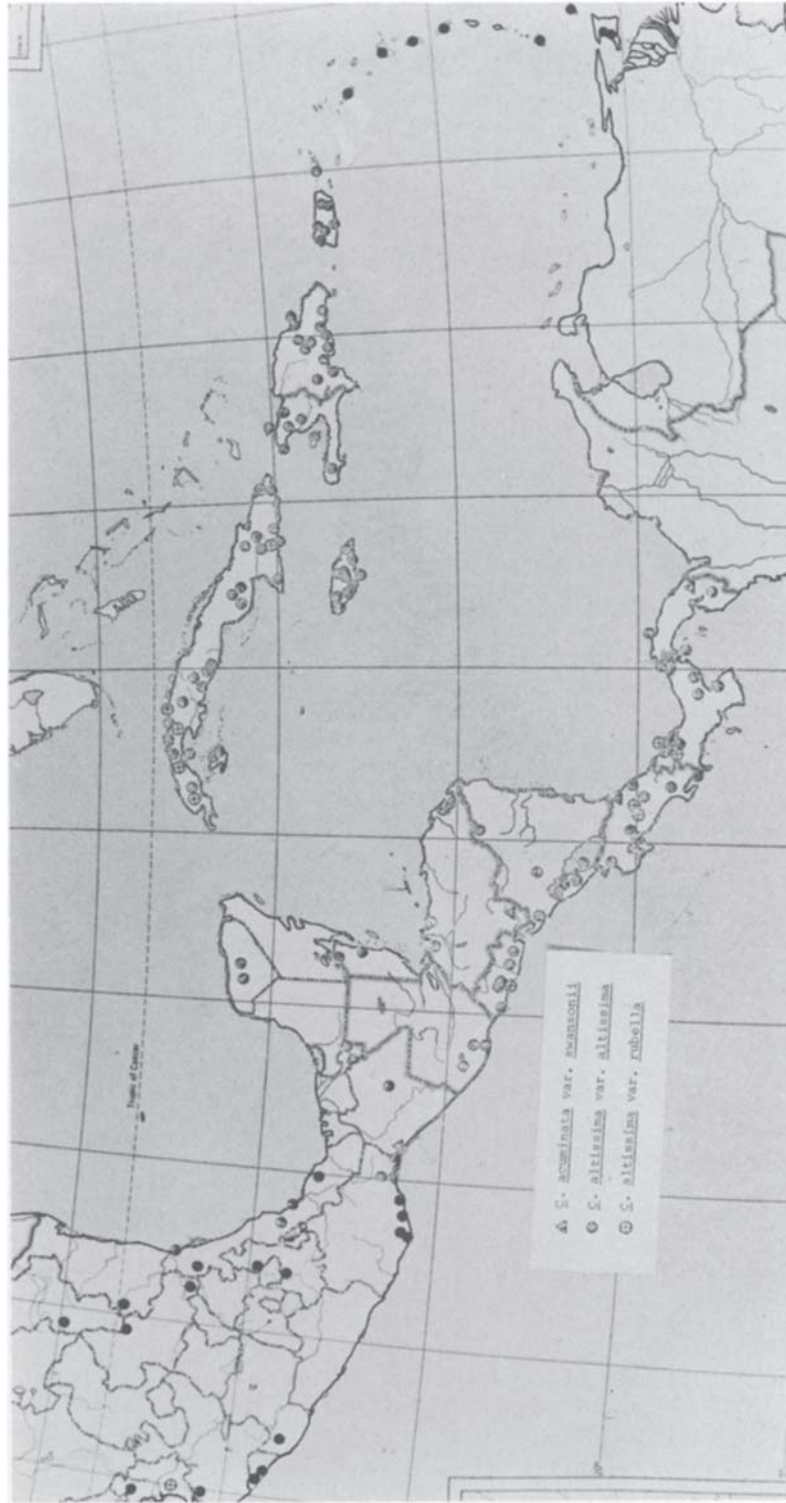


Fig. 16. Map illustrating general distribution of the *Chamissoa* taxa given in the figure in Central America and the Caribbean. Only those specimens with specific localities were mapped.





Fig. 17. Map illustrating general distribution of *Chamissoa altissima* in South America. Exact localities for two specimens of var. *rubella* for Venezuela not known and therefore not mapped.

*Tucker 950* (F, US). HONDURAS: Cortés: San Pedro Sula, *Thieme 5445B* (US). NICARAGUA: Segovia: Sangsansta, *Schramm 23* (US); Lake Nicaragua: Ometepe Island, *Shimek & Smith 122* (F, US). COSTA RICA: Limon: between Siguerres & Río Pacuare, *Burger & Liesner 6914* (F, MO, NY); Puntarenas: between Golfo Dulce & Río Terraba, *Skutch 5402* (US); Guanacaste: Liberia, Bahía de Santa Elena, *Jimenez 1548* (F, NY). PANAMA: Bocas del Toro: nr. Chiriquí

Lagoon, *Wedel 1896* (GH, MO, US); Los Santos: near Poeri, *Croat & D'Arcy 4207* (MO, NY). COLOMBIA: Atlantico: between Laña & Candelaria, *Dugand & Jaramillo 2776* (NY, US); Bolivar: Boca verde on Río Sinu, *Pennell 4230* (NY, US); Cundinamarca: near San Barnardo, *Cuatrecasas 9584* (US); Santander: near Puerto Wilches, *Killip & Smith 14818* (NY, US); Boyacá: Mt. Chapon, NW of Bogotá, *Lawrence 9* (F, GH, M, MO, NY, US); Meta: Villavicencio, *Cuatrecasas*

4511 (F, US). VENEZUELA: Mérida: Cano Zanuedo-Capazón, *Bernard 1033* (NY); Barinas: Rio Caparo, *Steyermark & Bunting 102,232* (NY), Ticoporo Forest reserve, *Breteler 3651* (NY); Apure: between Rio Orinoco & Piedra La Villa, *Wurdack & Monachino 41397* (F, NY); GUYANA: East Demerara: Mahaica, on coast, *Hitchcock 16772* (US). SURINAM: Nickerie: near Nieuw Nickerie, *Hekking 1139* (A). ECUADOR: Los Ríos; near Montalvo, *Jativa & Epling 239* (MO); Guayas: Milagro, *Hitchcock 20293* (GH, US). BRAZIL: Acre: Estrada Rio Branco-Xapuri, *Pires & Martin 10024* (NY); Pará: Rio Solimés, *Ducke 6744* (BM); Minas Gerais: Ponte Nova, *Macedo 1898* (NY, US). CUBA: Pinar del Rio: Sierra de Anate, *Wilson 11320* (NY, US) headwaters of Río Taco Taco, *Alain 736* (GH, US); La Habana: near Santiago de las Vegas, *Nicolas 2660* (F, NY); Camagüey: Sierra Cubitas *Shafer 477* (F); Isle of Pines: near Nueva Gerona, *Curtiss 269* (GH, M, NY, US); Las Villas: Soledad, Cienfuegos, *Jack 5597* (A, F), near Sancti Spíritus, *Shafer 12151* (F, MO, NY); Oriente: Puntón de Cuero N. of Imiás, *Morton & Bro. Alain 8854* (US). JAMAICA: Westmoreland: between Haddo & Mackfield, *Procter & Mullings 22029* (GH); St. Ann: Union Hill near Moneague, *Britton & Hollick 2730* (NY); Portland: near Port Antonio, *Wight 102* (F, NY). HAITI: near Mon Repos, *Miller 220* (US); near Carenage, *Ekman 7277* (US). DOMINICAN REPUBLIC: Barahona: near Barahona, *Abbott 1539* (GH); Azua: Azua-Peralta Road, *Sohmer & Swanson 9617*, (GH, MO, NY, US, UWL); Peravia: Baní River, *Liogier 17820* (NY); El Seibo: Hato Mayor-El Seibo Road, *Sohmer & Swanson 9615* (GH, MO, NY, US, UWL). PUERTO RICO: Adjuntas Road 8 miles from Ponce, *Heller 6197* (A, GH, MO, NY, US); Río Piedras, *Johnston & Stevenson 1130* (US): rocky seashore at Aguadilla, *Heller 4521* (NY, US). ST. THOMAS: Liliendal, *Eggers 214* (NY). GRENADA: St. John Parish: Belvidere, *Hunnewell 19473* (GH). MARTINIQUE: Parnasse, *Duss 91* (NY). TOBAGO: Mason Hall, *Broadway 4791* (BM, GH, MO, NY, US); Easterfield, *Broadway 4054* (F, NY). TRINIDAD: St. George: Tacarigua: St. Joseph, *Broadway 5609* (A, BM, F. MO); Caroni:

Chaguanas: Todd's Road to Talparo, *Sohmer & Swanson 9669*, (MO, US, UWL).

This variety of *Chamissoa altissima* appears to have its present center of diversity and abundance in the Caribbean where, if one is not misled by judging from herbarium specimens, it is extremely common. I can personally vouch for its abundance in the Dominican Republic. The capsule varies considerably in size: from the same length as the sepals to nearly twice as long. There is also a tendency in various localities for the top of the capsule to become constricted so that the overall appearance of the capsule is somewhat flask-shaped. Judging from the original description and locality ("*ripa obumbrata fluvii Magdalenae prope Mompox*") cited for *Chamissoa macrocarpa* (Humboldt, Bonpland, and Kunth, 1818). I believe that the authors had in hand a specimen of this variety with this kind of variation. As other authors have noted since, Suesenguth (1934), for example, it is impossible to maintain a taxon based on this feature (capsules lageniform, twice as long as sepals) when viewing the overall distribution and variation in *Chamissoa altissima* var. *altissima*. The attempt to segregate individuals with this kind of variation has frequently obscured the actual relationships that appear to prevail.

In the same manner, it becomes inappropriate to formally recognize variations based on inflorescence size and shape and the pubescence and the size of leaves. Attempts to do so become untenable when viewing the total variation and distribution. Giving formal nomenclatural status to such differences as forms also is unwise, in my opinion, as the genetic plasticity of these plants is considerable. Some of the differences in inflorescence morphology, in the nominate variety and the one following, is due to the sexual differentiation that occurs in the species. Perfect-flowered plants, i.e., the pollen-producing individuals, tend to have lax inflorescences on the axes of which the cymules are separated by a relatively greater distance than on pistillate individuals.

1b. *Chamissoa altissima* var. *rubella* Suesenguth, *Repert. Spec. Nov. Regni Veg.* 35: 306. 1934. Type here designated: Bolivia: Cochabamba: Chapare: Locotal-Jacinto, *Steinbach 9047* (GH!, lectotype; F!, NY! islectotypes)



*Chamissoa altissima* subsp. *albo-grisea* Suessenguth, Repert. Spec. Nov. Regni Veg. 39: 6. 1935. Type here designated: Bolivia: Guanaitipuaní, *Bang 1415* (M!, lectotype; BM!, F!, GH!, MO!, NY!, P! islectotypes).

*Chamissoa altissima* var. *densipaniculata* Suessenguth, Lilloa 4: 129. 1939. Type here designated: Argentina: Misiones: Santa Ana, *Rodríguez 287* (M!, lectotype; GH!, NY!, US!, islectotypes).

*Chamissoa frondosa* Hasimoto, Rodriguésia 13: 263. 1950. Type: Brazil: São Paulo: Lagoa Grande: "Margem do Rio Ribeira de Iguape", *Hashimoto 661* (SP!, holotype, seen as photograph).

Flowers often red, purple or pink, or at least with the mature ovary red, purple, or pink, drying dark, and the sepals, if not the same color, cream, yellow-green, or white; ovaries with a tendency to eliminate the emarginate wing at the flattened apex and sometimes with a round apex; stigmas usually 2 but with a pronounced tendency to 3.

**DISTRIBUTION.** This variety is centered in southern Brazil, northern Argentina, and Paraguay (Fig. 17). Amazon Basin members are probably very under-represented in herbaria. There are apparently representatives in Central America and Mexico and in Cuba and possibly Puerto Rico (Fig. 16). The questionable Puerto Rican collections are not mapped. In habitat and habit this variety closely resembles the nominate variety and it would be difficult, if not impossible, to separate individuals of this variety from the individuals of the nominate variety solely on vegetative characteristics.

**REPRESENTATIVE SPECIMENS EXAMINED:** MEXICO: Nayarit: near Tepic, *Lamb 613* (GH, MO, US). HONDURAS: El Paraíso: montaña Cifuentes between El Urraco & Cifuentes, *Molina 11425* (F). EL SALVADOR: La Libertad: Fuica Paraíso  $\frac{1}{4}$  mi. S. of Santa Tecla, *Carlson 88* (MO). NICARAGUA: Chontales: without further data, *Tate 337* (BM). COSTA RICA: Cartago: slope of Alto Patillos 4 km from Taparii, *Lent 1243* (MO), Instituto Interamericano in Turrialba, *Leon 2658* (M). PANAMA: Bocas del Toro: Water Valley, *Wedel 840* (MO). CUBA: La Habana: near

Vande, *Herman 417* (BM, F, MO, NY); Oriente: near Baracoa, *Pollard, Palmer & Palmer 33* (A, F, GH, MO, NY, US). COLOMBIA: Caldas: Río Quindío above Armenia, *Pennell, Killip & Hazen 8721* (GH, NY, US); del Valle: Cordillera Occidental between Brisas & La Carbonera, *Cuatrecasas 22706* (F); Nariño: Río Puelmambi, *Ewan 16041* (NY); Putumayo: Umbria, *Klug 1657* (BM, GH, MO, NY, US). ECUADOR: Pichincha: Salova W of the Cordillera Occidental. *Solis 5715* (F); Guayas: near village of Bucay, *Camp 3776* (NY); Tungurahua: Pastaza: Río Mapoto near confluence with the Pastaza, *Penland & Summers 194* (F, GH); Napo-Pastaza: Lena, Río Masaqualli, *Mexia 7226* (F, M, US). PERU: Loreto: Gamitanachocha: Río Mazan, *Schunke 263* (A, F, US); San Martín: Pucayacu 11 km S of Tarapoto, *Ferreyra 7741* (US), San Martín: 2.8 km S of Shapaya on trail to Tarapoto, *Belshaw 3214* (GH, NY, US) Mariscal Cáceres: Saule Grands, *Schunke 4388* (F); Huanuco: Tingo Maria: Cueva de los Huacharos, *Aldare & Fernandez 5605* (US); Junin: Tarma: 16 km S. of San Ramon, *Iltis, Iltis, & Ugent 246* (GH, US); Cuzco: Paucartambo: Cosnipata, *Weberbauer 6964* (F, GH). BRAZIL: São Paulo: Campinas: Abuna to Rio Branco road, *Forero, Coelho, & Farias 6418* (F, NY); Amazonas: Rio Purus between Campina and Tambaqui, *Prance et al. 13377* (F, NY); Pará: Santarem, *Spruce 635* (M); Paraíba: Alagoa Grande, *de Moraes 896* (NY, P); Pernambuco: Border of Tapacura River, *Pickel 555* (F, GH, P); Minas Gerais: Cidade de Caldas, *Henscheu 588* (US); Santa Catarina: Linha Coqueiro near Peperiquaea River, *Smith, Klein & Schnorrenberger 11786* (NY, US). BOLIVIA: El Beni: near Rurrenabaque, *Rusby 815* (NY); La Paz: S. Yugas: San Bartolome near Calisaya; *Krukoff 10398* (A, F, US); Cochabamba: Chapare: Todos Santos, *Steinbach 409* (F, MO, NY); Santa Cruz: San Javier, *Ocampo 5244* (US). PARAGUAY: San Pedro: Colonia Primavera, *Woolston 503* (GH, NY). ARGENTINA: Jujuy: Ledesma: Arroyo La Cantara 17 km N of Calilegua, *Everdam & Beetle 22666* (GH); Salta: Oran: Río Pescado, *Borsini 583* (F); Formosa: Pilcomayo: Rt. 86, 2 km N of km 45, *Morel 5842* (M, US); Tucumán: Paroquie Aconquija, *Meyer 4317* (A, F, NY); Misiones:



San Pedro: Río Alegria, *Bertoni 1036* (A),  
San Juan: Candelaria, *Schwindt 332* (M).

Suessenguth (1934) recognized the distinctiveness of this taxon when he first realized that there were individuals that differed from the typical in having red or purple flowers. His concept of this variety was limited to individuals whose flowers were these colors. I believe, however, that the taxon to which belong the paratypes he selected should be more broadly conceived, since one has to recognize that the flower color, particularly the sepal color, can vary considerably. Judging from information available on some specimen labels, the sepal color varies from red to whitish-red even on the same plant. It, therefore, becomes impossible to recognize, as Suessenguth did (1935), a subspecies based on individuals with white or whitish-gray flowers. Indeed, one of the paratypes he cites in his treatment of his subspecies *albo-grisea*, *Jorgensen 3335*, has a handwritten notation on the label stating that the color of the flowers was: "blanco a colorado." Suessenguth named another variety (1939), *C. altissima* var. *densipaniculata*, which was based on the nature of the inflorescence. This taxon also cannot be maintained due to reasons already discussed for the nominate variety . . . recognizing subspecific taxa based on these characters is untenable because of the continuous variation one finds in inflorescence morphology. The specimens Suessenguth cites for this variety are members of the taxon *C. altissima* var. *rubella*.

This taxon also includes those individuals that would be included in Hashimoto's concept of *C. frondosa* (1950), judging from the description and the photograph of the specimen cited as the holotype by Hashimoto, which was sent me by Dr. M. Cordeiro Marino, Instituto de Botânica, São Paulo.

*Chamissoa* subgenus *Achlamys* (Moquin)

Sohmer comb. nov.

*Chamissoa* section *Achlamys* Moquin in A.P. de Candolle, Prodr. 13 (2): 251. 1849. Type: *Chamissoa acuminata* Martius.

2. *Chamissoa acuminata* Martius, Nov. Actorum Acad. Caes. Leop.—Carol. Nat. Cur. 13: 286. 1826. Type here designated: Brazil: Minas Gerais: near "Sebastianopolis" (= Rio de Janeiro), *Martius s.n.* (M!, lectotype).

*Kokera acuminata* (Martius) Kuntze, Rev. Gen. Pl. 2: 543. 1891.

Herbaceous to suffrutescent, perfect-flowered plants to 2 m tall, but usually less than 1 m, erect to scandent, occasionally procumbent, rarely becoming a climbing vine, glabrous, pilose, or pubescent, particularly on the young parts; leaves alternate, exstipulate, with petioles to 7 cm long, with narrowly ovate to lanceolate, membranaceous or semicoriaceous blades 3.3–14.5 cm long with acute, round or truncate bases, often unequal, and obtuse, acute or acuminate apices, glabrous, puberulent or pubescent; inflorescences terminal or axillary, compound spikes to 30 cm long, or paniculate, with cymules of from 1–10, usually 3–7, flowers, the younger flowers appearing in the axils of the floral bract or bracteoles of the older flowers; flowers usually greenish-white or greenish-yellow, each on a short pedicel with 2 alternate, ovate to narrowly lanceolate, glabrous to puberulent bracteoles 1.2–2.6 mm long with round or truncate bases and with acute to long acuminate apices, in the axil of an ovate to lanceolate floral bract, (bracteoles of the older flowers in a cymule act as floral bracts for the younger flowers), 1.5–2.8 mm long; sepals 5, 1.8–4 mm long, lanceolate or narrowly ovate, with round to truncate bases and acute to acuminate apices; stamens 5, with the free portions of the filaments 1–2 mm long and anthers 0.1–0.7 (averaging 0.4) mm long at anthesis; pistil with a globose or somewhat ovate unilocular, uniovulate, basally placentated ovary, 1–2.5 mm long at anthesis with 1 narrow or basally dilated style 0.5–1.5 mm long, if narrow, usually surrounded at base by a narrow collar at the apex of the ovary, and if dilated at the base usually, in one variety, filled with a conspicuous spongy tissue, with stigmas usually shorter than the style; capsule usually, but not always, circumscissilely dehiscent, with a black seed 1–2.5 mm long with a smooth or foveolate, shining seed coat, sometimes with a mottled grayish overtone, and a small aril.

Martius (1826) cited 2 specimens from the state of Minas Gerais in his treatment of his new species. Both of these specimens are still preserved in M. The one selected as the lectotype has smooth seeds, whereas the other has foveolate seeds. It is apparent from Martius' treatment of his new



species, *C. acuminata*, as well as his subsequent action of recognizing another species, *C. maximilianii*, one of whose characteristics that distinguish it from var. *acuminata* is the possession of pitted seeds, that he considered the specimen with the smooth seeds to be representative of *C. acuminata* and it is here designated as the lectotype.

The present revision recognizes 3 varieties. The varieties are distinguished one from the other on the basis of the seed coat and the morphology of the style.

2a. *Chamissoa acuminata* var. *acuminata*.  
? *Chamissoa blanchetti* Moquin l.c. 251. Type here designated:

Brazil, *Blanchet 3576* (BM! lectotype; G, isolectotype (seen as photograph)). (This taxon is known only from this specimen).

*Kokera blanchetii* (Moquin) Kuntze, Rev. Gen. Pl. 2: 543. 1891.

Plants to 2 m tall, often less than 1 m; leaves with blades 3.3–14.1 cm long; inflorescences spicate or paniculate with main axes 3–15 cm long; flowers with ovate-deltoid bracts about 1 mm long and ovate bracteoles 0.5–1.0 mm long, with ovate-oblong sepals 2–3.2 mm long; pistil with a globose ovary 1.5–2.2 mm long at anthesis with a style 0.4–1.3 mm long dilated at base and with a black, smooth and shining seed 1–2 mm at maturity.

DISTRIBUTION. This variety is found in Brazil. The collections examined have been almost entirely from the eastern and southeastern parts of that country (Fig. 18).

REPRESENTATIVE SPECIMENS EXAMINED: BRAZIL: Bahia: without further data, *Blanchet 768* (NY). Minas Gerais: Caldas, *Regnell 229* (US). Rio de Janeiro: near Lidice, *Smith & McWilliams 15352* (US). São Paulo: Aguas de Prata, *Viegas & Zagatto 6189* (US); Aurora, *Loefgren 3945* (F). Paraná: Lapa: Rio Passa Dois, *Hatschbach 15993* (NY, P, US), Laranjeiras do Sul: Serra da União, *Hatschbach 3803* (US). Santa Catarina: Lajes: Passo do Socorro, *Reitz 6554* (US); Itapiranga do Oeste Forest Reserve W of Popi, *Smith, Klein & Schnorrenberger 11770* (US); São Miguel do Oeste: Forest above Rio Reperiguaguá, *Smith & Reitz 12793* (US); Riachuelo: Rio do Sul, *Reitz & Klein 8652* (US). Rio Grande do Sul: Pôrto Alegre: Colégio Anchieta, *Henz 35649* (MO, NY).

This variety is smaller than the other

varieties and more frequently has spicate inflorescences rather than paniculate ones. The sepals, bracts, and bracteoles tend to be ovate with acute to obtuse apices as compared to the other varieties. It is found near natural or artificial clearings in its range, tending, due to its smaller habit, to occur in more open situations than the individuals of the previous species.

2b. *Chamissoa acuminata* Martius var. *maximilianii* (Martius ex Moquin) Sohmer comb. nov.

*Chamissoa maximilianii* Martius ex Moquin in A. P. de Candolle, Prod. 13(2): 251. 1849 (“*Maximilianii*”). Type: BRAZIL: without exact locality, *Martius 180* (G, lectotype; F!, M!, MO!, NY!, isolectotypes). The lectotype was seen as a photograph.

*Chamissoa celosoides* Grisebach, Abh. Königl. Ges. Wiss. Göttingen 19:31. 1874. Type not located.

*Chamissoa maximilianii* forma *celosoides* (Grisebach) Suessenguth, Repert. Spec. Nov. Regni Veg. 35: 306. 1934.

*Chamissoa maximilianii* var. *procumbens* Seubert in Martius, Fl. Brasiliensis 5: 243. 1875. Type here designated: Brazil: without exact locality, *Reidel 702* (P! lectotype, GOET.!, MO! isolectotypes).

*Kokera celosoides* (Grisebach) Kuntze, Rev. Gen. Pl. 2: 543. 1891.

*Chamissoa maximilianii* var. *pubescens* Chodat, Bull. Herb. Boissier 7, Append. 1: 63. 1899. Type: *Chodat 467*. Specimen not located.

Plants usually 1–2 m tall; leaves with blades 2.9–14.5 cm long; inflorescence spicate or paniculate with main axes 5–30 cm long; flowers with narrowly ovate or deltoid to narrowly lanceolate floral bracts 1.5–2.5 mm long and narrowly deltoid to lanceolate bracteoles 1.0–2.5 mm long truncate or round at base, long acuminate at apex, with narrowly ovate, lanceolate to subulate sepals 1.8–3.8 mm long with truncate or round bases and acute to acuminate apices; pistil with a globose-lenticular ovary 1.5–2.5 mm long at anthesis with a style 0.5–1.5 mm long narrowed to base and usually surrounded at base by an emarginate collar at the apex of the ovary; seed 1.3–2.1 mm long, black, shining and foveolate at maturity.



Fig. 18. Map illustrating general distribution of varieties of *Chamissoa acuminata* in South America. Only specimens for which exact localities were available were mapped.

**DISTRIBUTION.** The specimens are those collected by Martius and represent one individual. The variety is found in Brazil, Paraguay, Bolivia, northern Argentina, and Peru (fig. 18). It is found in much the same kind of habitats as the nominate variety.

**REPRESENTATIVE SPECIMENS EXAMINED:**  
**BRAZIL:** Bahia: without further data, *Blanchet 2364* (P); Rio de Janeiro: without further data, *Gaudichaud 397* (P); Paraná: Jussara: Orto Florestal, *Hatschbach 21577* (MO, NY); Brazil without

further data, *Allemao 1290* (P). **PARAGUAY:** San Pedro: Alto Paraguay: Primavera, *Woolston 941* (NY); Central: Villa Elisa: bank of the Río Paraguay, *Pederson 3147* (US); Central: Yaguaron, *Balansa 3199* (P). **BOLIVIA:** Cochabamba: Chimoc: km 180, *Cardenas 2159* (GH); Santa Cruz: del Sara: Buenavista, *Steinbach 6318* (A); Tarija Villamontes, *Pflanz 2040* (US). **ARGENTINA:** Jujuy: Quinta Saguna de la Brea, *Fries 157* (US); Salta: Rosario, *Venturi 8215* (BM, GH, MO, US); Oran: Urondel, Arroyo



Nipan, *Hunziker 2015* (GH); Tucumán: Taci, *Venturi 151* (F, GH, M, US). PERU: San Martín: Juan Jui: Alto Río Huallaga, *Klug 4222* (A, BM, F, MO, NY, US); Junín: along Río Perene, *Killip & Smith 25163* (F, NY, US); CUZCO: Convencion: Echarate, *Stork, Horton & Vargas 10477* (F).

Martius recognized this taxon in his Herbarium Flora of Brazil, but it was not validly published until Moquin's treatment of the Amaranthaceae in the Prodrum in 1849. *Chamissoa acuminata* var. *maximiliani* is larger and somewhat coarser in habit than the nominate variety. The larger members of this taxon were segregated by Grisebach (1874) as *C. celosoides*. Suesenguth (1935), however, recognized that there was continuous variation in the size of individuals and reduced Grisebach's taxon to that of a form. I do not even see the value of maintaining the identity of this taxon as a form.

2c. *Chamissoa acuminata* var. *swansonii* var. nov.

Plantae 1–2 m altae inflorescentiis 3–30 cm longis; flores hermaphroditi bracteis et bracteolis 1.5–2.5 mm longis saepe acuminatis, sepalis anguste ovatis, lanceolatis vel oblongis 2.4–4 mm longis basibus truncatis vel acutis apicibus acutis vel obtusis, stylis basin versus conspicue dilatatis; semina nigra vel grisea-nigra et maculata saepe foveolata.

Plants usually 1–2 m tall; leaves with blades 4.9–14.8 cm long; inflorescence spicate or paniculate with main axes 3–30 cm long; flowers with ovate to lanceolate floral bracts and bracteoles 1.5–2.5 mm long often long-acuminate via prolongation of the mid-vein into a bristle and with narrowly ovate, lanceolate to oblong sepals 2.4–4 mm long with truncate to acute bases and acute to obtuse apices; stamens with anthers 0.1–0.8 mm long at anthesis, pistil with a globose ovary 1.5–2.3 mm long at anthesis with a style 0.5–1.4 mm long dilated at base with a conspicuous development of an areolate tissue at the base of the style; seed 1.3–2.5 mm long at maturity, black or grayish-black and mottled, shining and foveolate.

Type: PANAMA: Bocas del Toro: Water Valley near Chiriqui Lagoon, *Wedel 1695* (GH!), holotype: MO!, US!, isotypes). The type collection was selected as it was taken from an individual that well demonstrates

the features of this variety. It is illustrated in Fig. 19.

DISTRIBUTION. This variety ranges principally from Mexico through Central America, and is also found in Colombia, Peru, Paraguay, and Surinam (fig. 18). The taxon in the latter two countries is represented by only one collection each, neither with exact locality, and therefore not mapped.

SPECIMENS EXAMINED: MEXICO: México: Temascaltepec: Palmar, *Hinton 5178* (F, GH, NY, US); Chiapas: Arriaga, *Mell 2191* (NY, US), HONDURAS: Choluteca: near Choluteca, *Standley 24324* (F, US). NICARAGUA: Managua: Shore of Lake Managua, *Greenman & Greenman 5652* (MO). PANAMA: Bocas del Toro: Changuinola Valley, *Dunlap 354* (F, US); Darien: near Cana, *Stern, Chambers, Dwyer, & Ebinger 677* (GH, MO). COLOMBIA: del Cauca: Río Micay, Guayabal, *Cuatrecasas 14112* (F). SURINAM: without further data, *Hostman 1109* (BM, P). PARAGUAY: without further data, *Jørgensen 3733* (MO). PERU: Loreto: Lower Río Nanay, *Williams 432* (F); San Martín: Lamas, *Williams 6486* (F); Huanuco: near Puerto Inca, *Schunke 2950* (F).

*Chamissoa acuminata* var. *swansonii* appears to combine two characteristics of the other two varieties: basally dilated styles and foveolate seeds. Frequently, in this variety, the base of the style is very conspicuously thickened (Figs. 6 and 15). There is great variation in size of the entire seed, and the pits on the seed coat are smaller than in var. *maximiliani*. The seed color is often more a mottled grayish-black than pure black as in the latter variety.

The name is given for Steven D. Swanson who aided me in the field work relative to this revision.

#### Excluded or Dubious Names

*Chamissoa altissima* sensu Nees & Martius, Nov. Actorum Caes. Leop.-Carol. Nat. Cur. 11: 32. 1823. = *C. altissima* (Jacquin) Humboldt, Bonpland and Kunth?

*Chamissoa brasiliensis* (Moquin) Fries, Ark. Bot. 16: 2. 1920. *Banalia brasiliensis* Moquin in A. P. de Candolle, Prodr. 13(2): 278. 1849. = *Herbstia brasiliensis* (Moquin) Sohmer, Brittonia 28: 448–452. 1976.

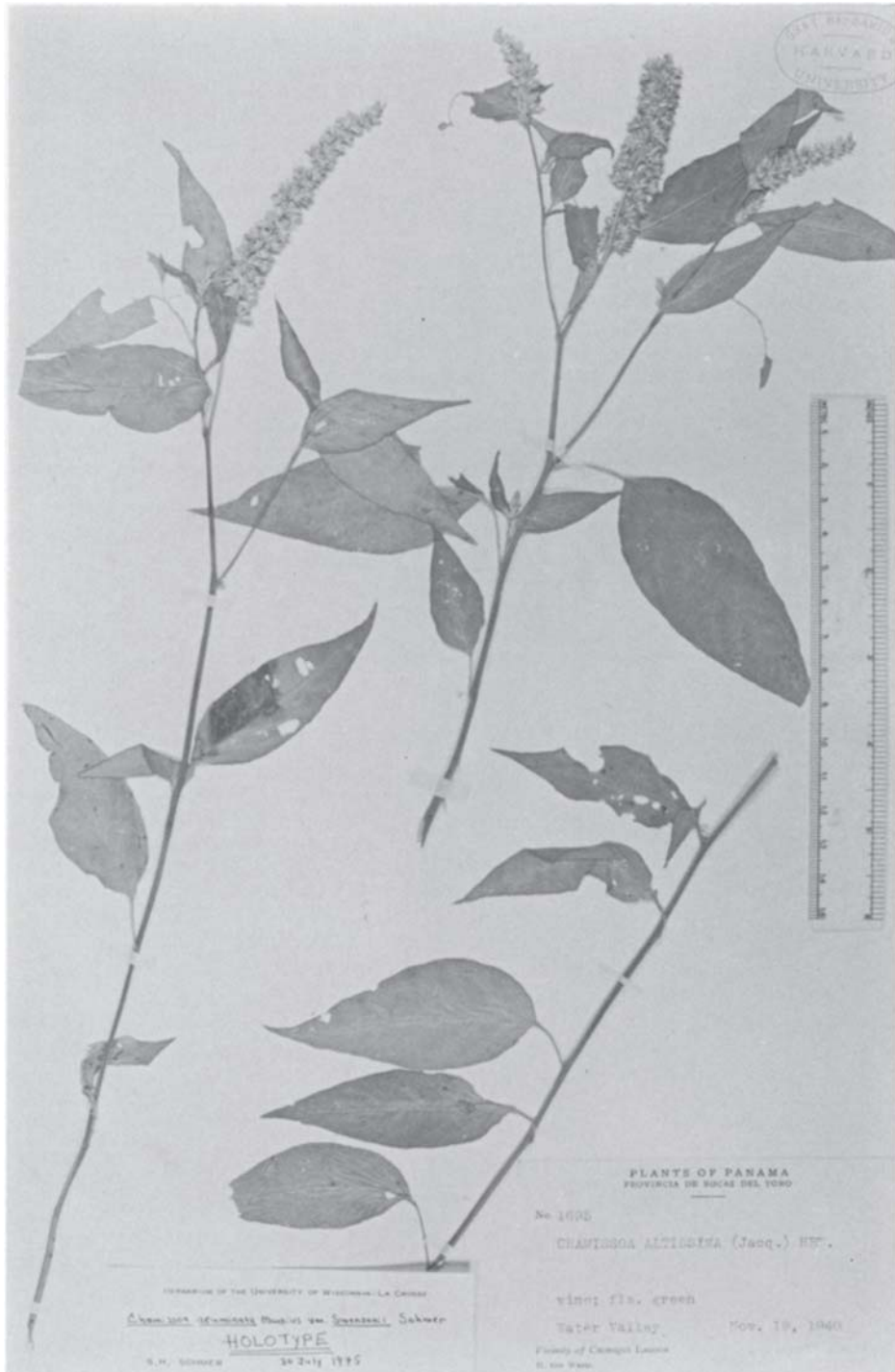


Fig. 19. *Chamissoa acuminata* var. *swansonii* Soehmer, *Wedel 1695* (GH, holotype).



*Chamissoa martii* Moquin in A. P. de Candolle, Prodr. 13(2): 252. 1849. = *Chamissoa altissima* sensu Nees & Martius.

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