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Recommended Citation

Simmons, Mark P., and W. John Hayden. "Revision of the Cerrado Hemicryptophytic Chamaesyce of Boissier's 'Pleiadeniae' (Euphorbiaceae)." *Brittonia* 49, no. 2 (April 1997): 155-80. doi: 10.2307/2807678.

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Revision of the cerrado hemicryptophytic *Chamaesyce* of Boissier's "Pleiadeniae" (Euphorbiaceae)

MARK P. SIMMONS¹ AND W. JOHN HAYDEN

Simmons, M. P. (Department of Biology, University of Richmond, Richmond, VA 23173, U.S.A.) and W. J. Hayden (Department of Biology, University of Richmond, Richmond, VA 23173, U.S.A.). Revision of the cerrado hemicryptophytic *Chamaesyce* of Boissier's "Pleiadeniae" (Euphorbiaceae). *Brittonia* 49: 155–180. 1997.—The species of *Chamaesyce* classified by Boissier as the "Pleiadeniae" are revised in light of presently available collections. Six species are accepted and new combinations are proposed for *C. nana*, *C. setosa*, *C. taman-duana*, and *C. viscoides*. Although these herbaceous perennials of cerrado vegetation of Brazil, northern Argentina, and adjacent countries are distinctive ecologically and geographically, cladistic analysis does not support their recognition as a monophyletic group.

Key words: *Chamaesyce*, *Euphorbia*, Euphorbiaceae, cerrado.

This systematic revision focuses on several *Chamaesyce* with hemicryptophyte growth habits that are endemic to the cerrado vegetation of southeastern Brazil and adjacent countries. These distinctive species of *Chamaesyce* are perennial plants that produce seasonal aerial stems from thickened rootstocks that extend deeply into the soil. Although uncommon in *Chamaesyce*, the hemicryptophyte habit is significant in several respects. Ecologically, it is clear that this habit is effective for survival of the seasonal droughts and periodic fires that characterize cerrado. Taxonomically, the co-occurrence of several hemicryptophyte species of *Chamaesyce* in a well-defined geographic and ecological setting led to their classification together in a group that Boissier (1862) termed the "Pleiadeniae." Phylogenetically, the hemicryptophyte growth habit is shared with certain *Euphorbia* species of subgen. *Agaloma* (Raf.) House and subgen. *Esula* Pers. and thus has been hypothesized to be the primitive con-

dition for *Chamaesyce* (Webster, 1967). Potentially, then, the species of Boissier's "Pleiadeniae" may prove pivotal in understanding the evolution of *Chamaesyce* within tribe Euphorbiae. This taxonomic revision presents a beginning step in exploring the phylogenetic position of these cerrado hemicryptophytes in the genus *Chamaesyce*.

A Note on Subgeneric Taxa in *Chamaesyce*

Among the plants presently known to constitute the genus *Chamaesyce*, Boissier defined eight taxa which he recognized as subsections of *Euphorbia* sect. *Anisophyllum*. Five of Boissier's subsections have been treated formally as subgeneric taxa of *Chamaesyce* (Hurusawa, 1954; Koutnik, 1987; Webster, 1967; Webster et al., 1982). As discussed below, there is doubt that the remaining groups, including "Pleiadeniae," constitute definable monophyletic groups. When referring to these dubious taxa, we therefore will employ the strictly informal device of placing the Boissierian names in quotation marks.

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Taxonomic History

The species that constitute Boissier's "*Pleiadeniae*" are based on early-19th-century collections of Blanchet, d'Orbigny, Lund, Pohl, Regnell, Riedel, Sellow, and Widgren. Prior to being grouped together in a formally defined taxon, the species treated herein were first named by Klotzsch and Garcke (in Klotzsch, 1859) as species of *Anisophyllum* Haw. or by Boissier (1860) as species of *Euphorbia* L. Subsequently, Boissier (1862) defined *Pleiadeniae* as a subsection of *Euphorbia* sect. *Anisophyllum* Roep. to include these hemicyptophyte species from Brazil, plus one other from Mexico. The Mexican species, *Euphorbia macropus* (Klotzsch & Garcke) Boiss., has since been recognized as extraneous and has been referred to *Euphorbia* subgen. *Agaloma* (Huft, 1979; Webster, 1967). It is significant to note that *E. macropus* possesses cyathia with five glands: as defined and described by Boissier, three of the Brazilian taxa also possess, at least sometimes, more than the usual four glands per cyathium found in other *Chamaesyce*—hence the name "*Pleiadeniae*" for the subsection (from the Greek *pleion* more, *adēn* gland). Other characters used in Boissier's loose definition of "*Pleiadeniae*" include the erect, often strigose stems, relatively large cyathia, and two leaf features unusual for *Chamaesyce*. Compared to other *Chamaesyce*, leaf bases in "*Pleiadeniae*" tend to be only weakly oblique. Further, instead of the usual strictly opposite condition, two of the species recognized by Boissier possess some leaves in verticils; we treat these two as a single species. In all, Boissier included seven Brazilian taxa in "*Pleiadeniae*" without further comment about their relationships *inter alia*: *E. caecorum* Mart. ex Boiss., *E. chamaerrhodos* Boiss., *E. potentilloides* Boiss., *E. selloi* Boiss., *E. selloi* var. *setosa* Boiss., *E. tamanduana* Boiss., and *E. viscoides* Boiss.

Although he did not use the subsectional designation, Mueller Argoviensis (1874) treated the species of "*Pleiadeniae*" much as had Boissier, the only important difference being the elevation of *E. selloi* var. *setosa* to specific status. Until the present

study, the publications of Boissier (1862) and Mueller Argoviensis (1874) were the most recent inclusive taxonomic syntheses of the group.

A number of piecemeal taxonomic adjustments pertinent to "*Pleiadeniae*" occurred sporadically in this century. Two new species were proposed, one by Chodat (1901) and the other by Pax and Hoffmann (in Emrich, 1937). Two new varieties were proposed, one each by Chodat and Hassler (1905) and Croizat (1943). We recognize none of these taxa. Croizat (1943) transferred four of the seven Brazilian taxa from *Euphorbia* to *Chamaesyce*, without comment about the other three. In terms of generic placement, we follow Croizat's (1943) lead and recognize all the cerrado hemicyptophytes of "*Pleiadeniae*" as elements of the genus *Chamaesyce*, an approach frequently adopted for these distinctive plants (see, e.g., Benedf & Orel, 1992; Koutnik, 1987; Lin et al., 1991; Webster, 1967, 1994).

Several members of Boissier's "*Pleiadeniae*" have been treated in regional floras (Allem, 1977; Allem & Irgang, 1975; Rambo, 1960; Subils, 1977), always as species of *Euphorbia* and often with circumscriptions somewhat at variance with earlier literature and/or our concepts. For example, Rambo (1960) and Allem and Irgang (1975) synonymized *E. chamaerrhodos* and *E. setosa* with *E. selloi*; however, Allem (1977) later recognized *E. chamaerrhodos* as distinct. It is noteworthy that, within the limits of their floristic studies, both Allem and Irgang (1975) and Subils (1977) referred *E. selloi* to subsect. *Hypericifoliae* and retained only *E. caecorum* within "*Pleiadeniae*."

Taxonomic Characters

The cerrado hemicyptophytes described herein possess irregularly thickened, somewhat twisted, more or less vertical rootstocks (Figs. 1A, 1F, 4, 5,) from which seasonal aerial stems diverge apically. Occasionally, bases of aerial stems persist through the winter/dry season. In most species, the annual stems first develop vegetatively for several nodes before producing

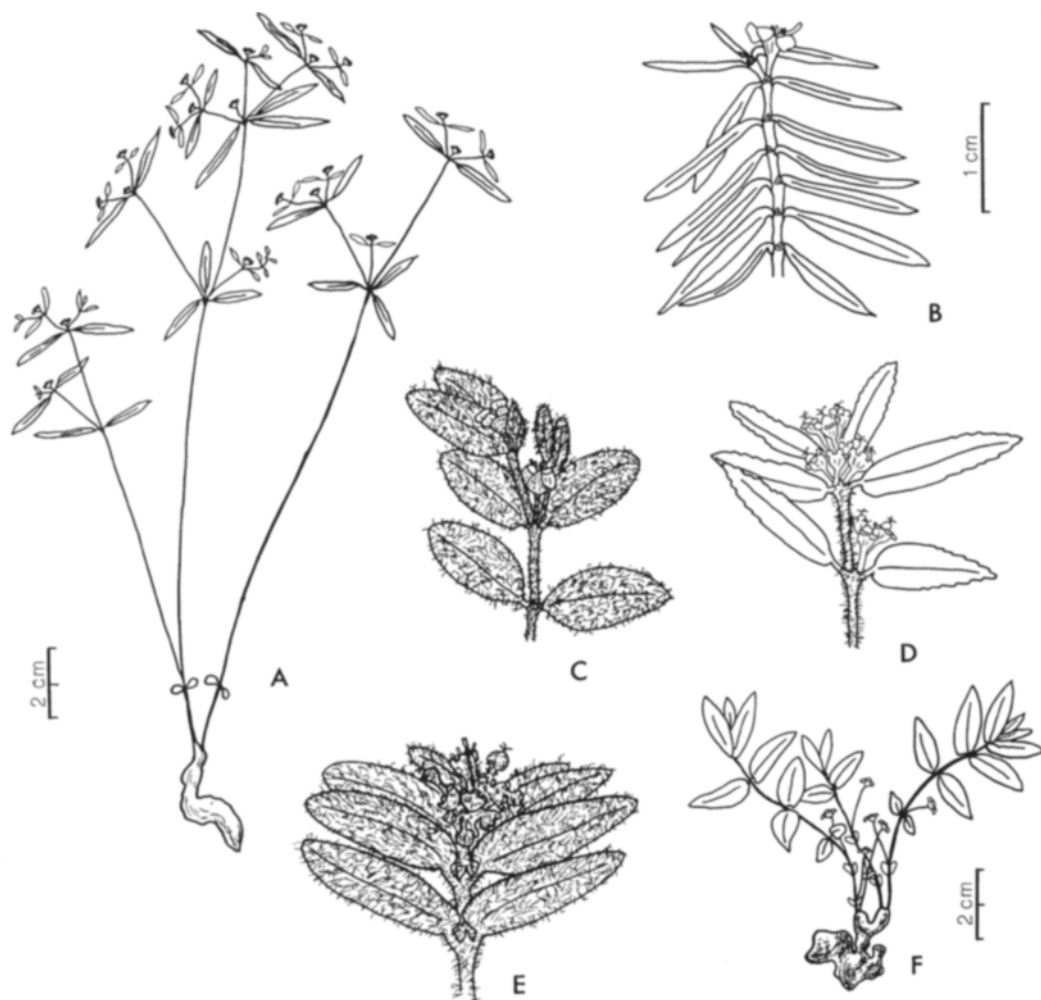
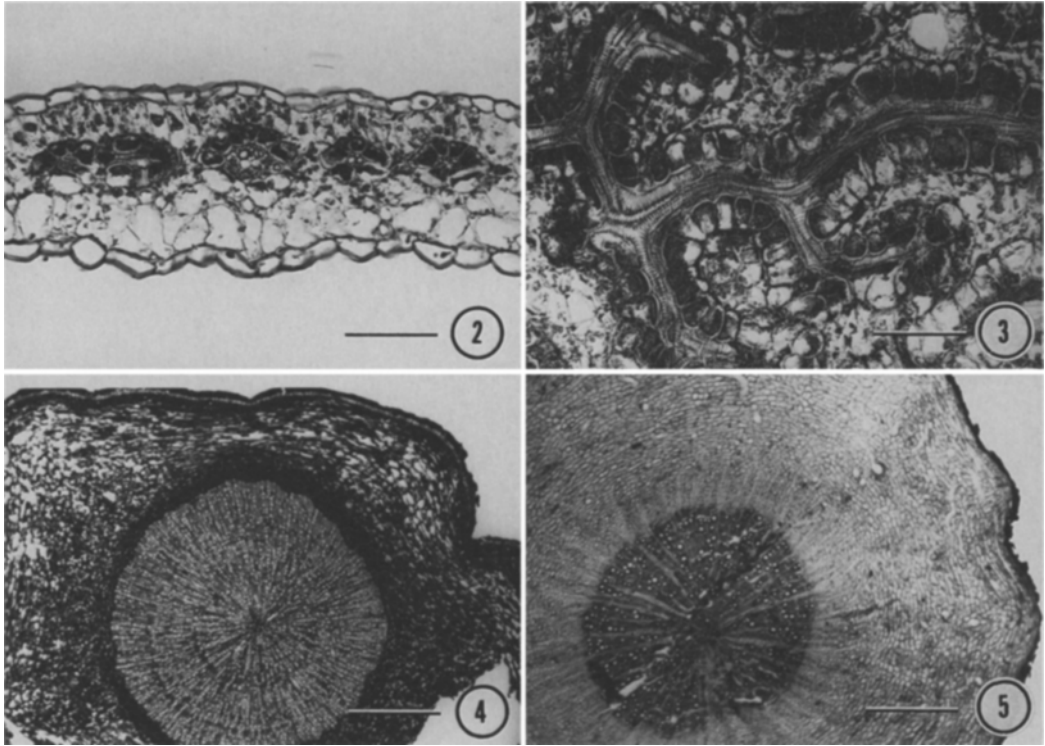


FIG. 1. Morphology of hemicyptophyte *Chamaesyce* species, from dried pressed material. **A.** Habit of common form of *C. potentilloides* (Mimura 131, NY). **B.** Distal nodes of *C. potentilloides* late-season form (Dawson 14584, RSA). **C.** Distal nodes of *C. tamanduana* (Blanchet 3841, G). **D.** Distal nodes of *C. setosa* (Schinini 12101, G). **E.** Distal nodes of *C. setosa* (Barreto 2600, F). **F.** Habit of *C. nana* (Hassler 8498, NY). (Scale bars: A, F, 2 cm bar; B–E, 1 cm bar.)

cyathia; however, this sequence is reversed in *C. nana* (Fig. 1F), in which vegetative shoots arise by apical proliferation of short, early-season-flowering stems. Unfortunately, seedling stages of cerrado hemicyptophyte species of *Chamaesyce* remain undescribed, so it is unknown whether epicotyls persist or exhibit the abbreviated (so-called abortive) ontogeny typical of *Chamaesyce* (Hayden, 1988; Koutnik, 1984, 1987; Lin et al., 1991).

Leaves grade continuously from basal cataphylls to foliage leaves and cyathophylls.

As is typical of *Chamaesyce*, leaves are strictly opposite and distichous, except for the characteristic production of at least a few verticils associated with early-season pleiochasial branching in *C. potentilloides* (Fig. 1A). A single anomalous ternate node was also observed in one specimen of *C. viscoides*. Foliage leaves and cyathophylls of all the species possess chlorenchymatous bundle sheaths characteristic of the C_4 photosynthetic pathway (Figs. 2, 3; see also Webster et al., 1975). Leaf bases are distinctly oblique except in *Chamaesyce po-*



FIGS. 2-5. Leaf and rootstock anatomy of hemicyptophyte *Chamaesyce*. 2. *C. potentilloides*, cross section of leaf (*Ezechias* 14134, US). 3. *C. potentilloides*, paradermal section of leaf (*Irwin* 18684). 4. *C. potentilloides*, cross section of root (*Eiten & Eiten* 8653, NY). 5. *C. nana*, cross section of root (*Pedersen* 6548, NY). (Scale bars: 2, 3 = 100 μ m; 4, 5 = 1 mm.)

tentilloides. Leaf margins are somewhat thickened, and apices are acute. Petiole bases are connected by persistent connate stipules that are generally triangular and acute but range from entire to deeply cleft.

The architecture of flowering stems of *C. potentilloides* (Fig. 1A) appears directly comparable to that of *Euphorbia* subgen. *Esula* and subgen. *Agaloma*, and is thus unique within *Chamaesyce*. In *C. potentilloides*, as in *Euphorbia* subgenera *Esula* and *Agaloma*, the transition from vegetative growth to flowering is marked by production of a terminal cyathium subtended by a whorl of leaves (cyathophylls); branches arise in the axils of each whorled leaf; these branches are leafless proximally, but terminate in another cyathium which is, in turn, subtended by either another whorl or pair of leaves; this pattern reiterates through several nodes. Verticils may occur for as many as three successive nodes formed ear-

ly in the flowering stage, but eventually this pleiochasial pattern becomes strictly dichasial, i.e., cyathia are subtended by paired cyathophylls and their axillary branches. A further simplification of this system occurs in stems of *C. potentilloides* that continue to grow and flower for an extended period of time (Fig. 1B); these late-season stems become pseudomonopodial by suppression of one branch at each node of the potential dichasium. The pleiochasial architecture of *C. potentilloides* differs from that of *Euphorbia* subgen. *Esula* and subgen. *Agaloma* in that the first cyathium-bearing verticil arises above cataphylls without intervening foliage leaves (Fig. 1A). Pleiochasial architecture would seem reasonably hypothesized as plesiomorphic for *Chamaesyce*; results of the phylogenetic analysis, however, suggest that this growth in habit in *C. potentilloides* may be an evolutionary reversal (see below). It is, perhaps, significant to

note that much of the range of phyllotaxy and branch architecture variation known in *Chamaesyce* can be found within *C. potentilloides*.

Cyathium production in other *Chamaesyce*, including the other hemicryptophyte species included in this study, does not routinely involve verticillate nodes or pleiochasial branching systems. In fact, aside from *C. potentilloides*, we have seen only one example of pleiochasial architecture in Boissier's "*Pleiadeniae*," a single stem of *C. viscoides*. Cyathium production is dichasial and/or pseudomonopodial in three of the hemicryptophyte species revised here, *C. nana* (Fig. 1F), *C. tamanduana* (Fig. 1C), and *C. viscoides*; their patterns of cyathium production are widespread in *Chamaesyce*. On the other hand, cyathia in *C. selloi* (Fig. 1D) and *C. setosa* (Fig. 1E) are solitary on main stems and clustered in groups of 2–12 in apparently lateral glomerules. Within these glomerules, peduncles are short and subtending cyathophylls are highly reduced to essentially obsolete; sometimes several cyathia may appear to arise from the same node or share a common short stipe. Glomerulate architecture of *C. selloi* and *C. setosa* appears directly comparable to that found in sect. *Hypericifoliae* and we agree with Lin et al. (1991) in hypothesizing that such glomerules are probably derived from equal dichasia by a process of overtopping.

As mentioned above, cyathia in *Chamaesyce* usually bear four appendaged glands, but additional glands and appendages occur in some "*Pleiadeniae*" (Fig. 6C). According to the taxonomy adopted herein, cyathia with more than four appendaged glands are routinely encountered only in *C. potentilloides*, for which glands may number up to seven. The "extra" glands are not merely unusual outgrowths at the rim of the involucre; they are an expression of the fundamental meristic organization of the cyathium itself.

The rim of the cyathial involucre in most *Chamaesyce* and, for that matter, a great many *Euphorbia* as well, reveals 10 more or less evenly spaced lobes that are interpreted to represent the tips of fused phyllomes and their stipules (Haber, 1925;

Schoute, 1937; Weberling, 1989). Five lobes end freely in acute apices and are referred to herein as primary lobes. Alternate with the primary lobes are five potentially glandular secondary lobes. In many species of *Euphorbia* subgen. *Esula* and subgen. *Agaloma*, each of the secondary lobes bears a terminal gland which in subgen. *Agaloma* also bears an appendage comparable to those found in *Chamaesyce*. In some species of subgenera *Esula* and *Agaloma* and in virtually all *Chamaesyce*, only four of the five secondary lobes are glandular. Thus, in *Chamaesyce* there is always one segment of the rim of the involucre that bears three adjacent acute lobes, the non-glandular secondary lobe flanked by two primary lobes. In the case of *C. potentilloides*, cyathia that bear more than four glands do so by the presence of additional pairs of primary and secondary lobes, but the number of glands is still, at most, one less than the number of secondary lobes. In other words, the overall meristic organization of the cyathium is greater than usual, with retention of at least one non-glandular secondary lobe.

The propensity for greater than 5-merous cyathia in *C. potentilloides* suggests the need for careful consideration of the apparently simple character of gland number. It appears that two factors may affect total gland number for any given cyathium: its overall meristic organization and the proportion of glandular secondary lobes, i.e., whether there are any non-glandular secondary lobes. Distinguishing these two factors may have phylogenetic implications. For example, it has been hypothesized that evolution from *Euphorbia* to *Chamaesyce* involved a decrease from five glands to four (e.g., Webster, 1967), but 4-glanded 5-merous cyathia are known in a significant fraction of the species of subgen. *Agaloma* (Huft, 1979); they may also be found in subgen. *Esula*, for example, in *E. lathyris* (Hayden, unpubl. obs.). Consequently, it appears that one often-cited distinguishing feature of *Chamaesyce*, gland absence or suppression on one secondary lobe, either pre-dates the origin of *Chamaesyce* or evolved more than once.

Variation in the meristic organization of

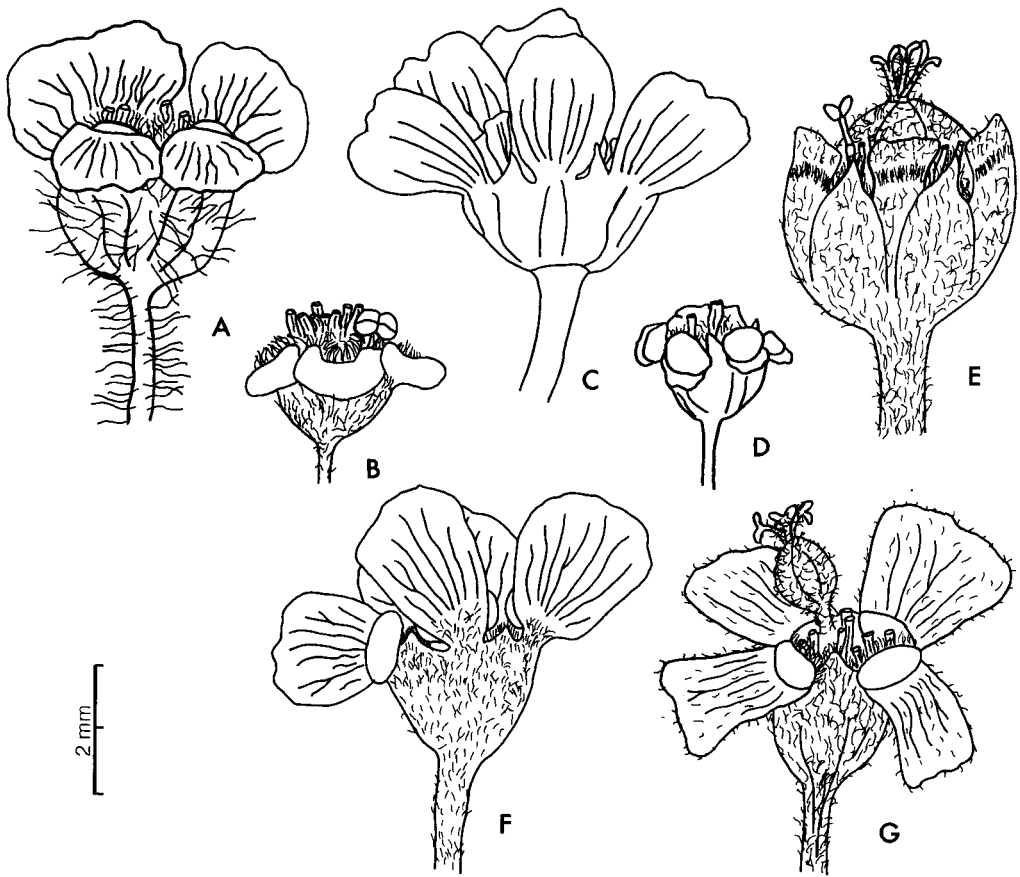


FIG. 6. Cyathia of hemicyptophyte *Chamaesyce* species, from dried pressed material. A. *C. viscoidea* (Fonsêca & Onishi 1042, UB). B. *C. selloi* (Cristobal et al. 2069, CTES). C. *C. potentilloides*, robust form (Irwin et al. 9924, UB). D. *C. potentilloides*, linear leaf form (Dusén 16450, NY). E. *C. setosa* (Irwin et al. 27209, NY). F. *C. nana* (Sellow 3131, MO). G. *C. tamanduana* (Blanchet 3841, G).

cyathia has not been well documented and is clearly in need of study across a wide range of species in tribe *Euphorbieae*. Huft (1979) noted that the first cyathium on flowering stems of *E. pubentissima* Michx. (sometimes included within *E. corollata* L.)—i.e., the cyathium subtended by the first order of pleiochasial branching—is often more than 5-merous and the same can be seen in *E. marginata* Pursh and *E. lathyryrus* L. (Hayden, unpubl. obs.); the phenomenon of pleiomerous early cyathia thus occurs in both subgenera *Agaloma* and *Esula*. It would seem reasonable to propose that such pleiomerism is plesiomorphic for *Chamaesyce potentilloides*; our phylogenetic analysis, however, suggests pleiomerous early cyathia may be a reversal for this spe-

cies. As far as is known, 5-merous cyathia seem fixed in all other species of *Chamaesyce*.

Glands of the six species treated herein are routinely very short stalked, concave above, minutely pitted, and appendaged. Cyathial appendages are more or less parallel veined and, in *C. nana*, *C. potentilloides*, and *C. setosa*, of equal size and shape. Cyathia of *C. selloi* rarely have two appendages slightly larger than the other two. *Chamaesyce tamanduana* has two wide and two narrow appendages of nearly equal length (Fig. 6G). In *C. viscoidea*, however, two appendages are distinctly smaller than the others (Fig. 6A). The appendages of *C. tamanduana* are distinctly papillate, whereas those of the other species are always smooth.

Another aspect of the meristic organization of cyathia involves the pattern of staminate flower production. Generally, staminate flowers of *Euphorbia* and *Chamaesyce* occur in five linear, radial, cincinnoid groups that are located opposite the primary lobes; the monandrous staminate flowers mature centrifugally. In *C. potentilloides*, the number of staminate cincinni corresponds to the number of primary lobes, i.e., up to eight. As is typical of most *Chamaesyce*, glands are four and staminate cincinni are five in the other hemicryptophyte species that constitute this revision.

Pollen grains of *C. nana*, *C. potentilloides*, *C. selloi*, and *C. setosa* were studied by SEM (Figs. 7–11). The grains of these species are similar to each other and consist of isopolar monads with elongate colpi. Shape is elliptical in equatorial view and deeply three-lobed in polar view. Polar dimensions range from 23 to 30 μm . The surface is minutely pitted. Similar grains are found throughout tribe Euphorbieae (Punt, 1962; Lopez & Diez, 1985).

As is routine in cyathia of *Chamaesyce* and *Euphorbia*, pistillate flowers are central, solitary, and exerted with age by means of an accrescent and reflexed gynophore. The 3-carpellate ovary bears a lobed hypogynous disk and three basally connate styles. Capsules are broadly ovoid, weakly keeled and ballistically dehiscent. The light brown to gray, ecarunculate seeds are sub-ovoid, narrowed apically, truncate and concave basally, and more or less tetragonal in cross section; the raphe is somewhat depressed (Fig. 12). Mature seeds of most species of *Chamaesyce* produce mucilaginous exudations upon exposure to moisture (Jordan & Hayden, 1992); except for *C. tamanduana*, which has not been tested because of lack of material, this phenomenon has been observed in the hemicryptophytic species of “*Pleiadeniae*.”

Phylogenetic Analysis

The purpose of this analysis was to ascertain whether the six species of *Chamaesyce* subsect. “*Pleiadeniae*” represent a monophyletic subsection and determine the

relationship of “*Pleiadeniae*” to other subsections in *Chamaesyce*.

TAXA INCLUDED IN THE ANALYSIS

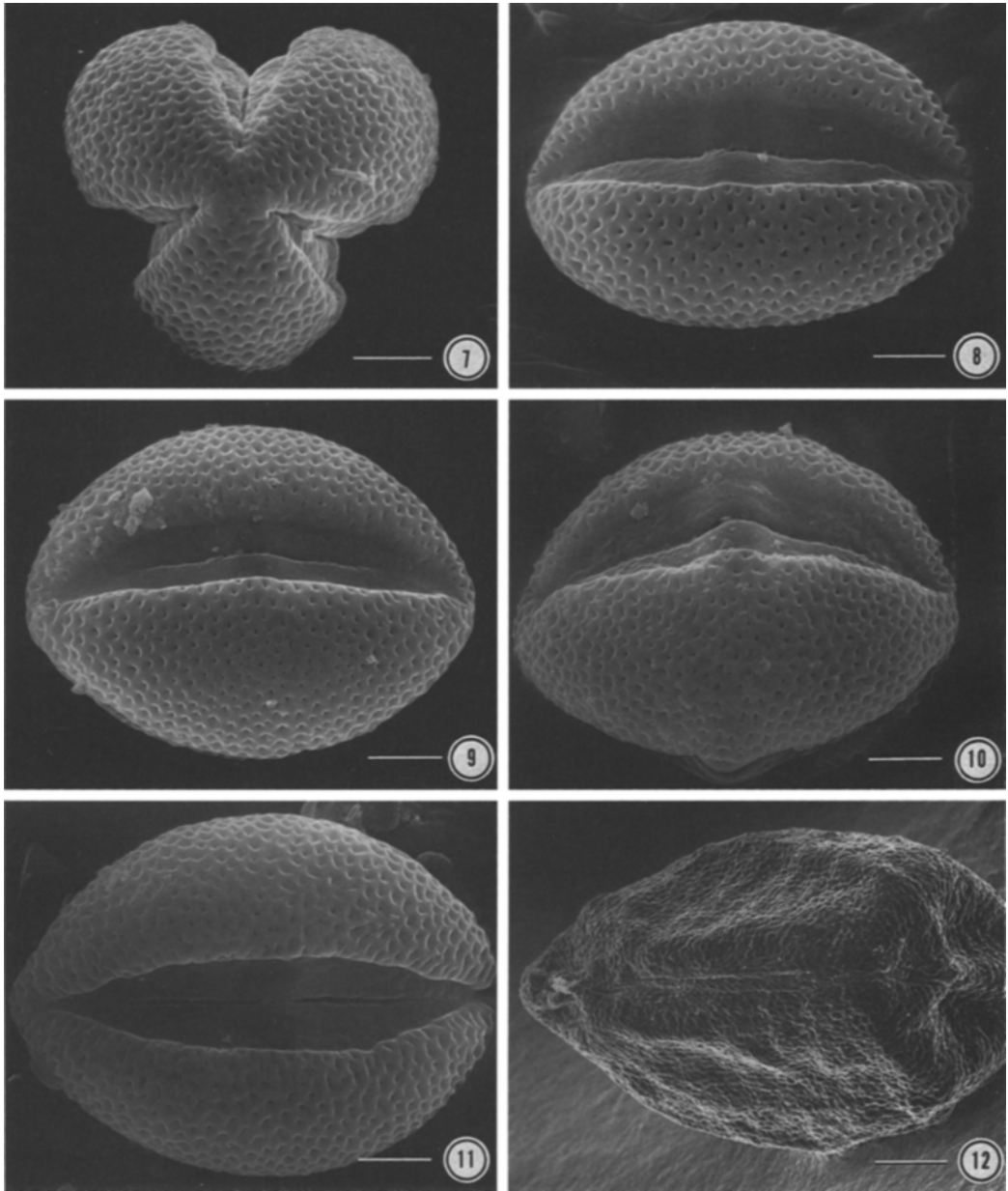
The taxa selected for inclusion in the analysis were a single outgroup, *Euphorbia corollata* L. from *Euphorbia* subgen. *Agaloma*, four species in “*Pleiadeniae*,” and representative species from the following subgeneric groups of *Chamaesyce*: *Acutae* (Boiss.) Webster, *Sclerophyllae* (Boiss.) Hurus., *Chamaesyce*, *Hypericifoliae* (Boiss.) Hurus., and *Gymnadeniae* (Boiss.) Koutnik. Subsections “*Cheloneae*” and “*Elegantes*” of Boissier (1862) were not included in this analysis due to lack of information and because they do not appear distinct from sect. *Hypericifoliae*, which was included in the analysis. Of the species revised here, *C. selloi* was not included in the analysis because it was coded identically to *C. setosa*. Further, *C. tamanduana* was not included because it would have coded identically to *C. viscoides* except that existence of seed mucilage in *C. tamanduana* is unknown. When *C. tamanduana* was included in the analysis, *C. tamanduana* formed a polytomy at the same node as *C. viscoides*.

CHARACTERS INCLUDED IN THE ANALYSIS

Thirteen morphological, developmental, and anatomical characters were included in the final data matrix (Tables I & II). Additional characters were considered, but problems of doubtful character independence, ambiguous character state coding, and/or the amount of missing data precluded their use. The two multistate characters, plant form and phyllotaxy, were coded as non-additive (unordered) because the relationships among the character states are unclear. Autapomorphic characters were not included. Seedling ontogeny is unknown for the four species in subsect. “*Pleiadeniae*” for which this character was coded as missing data.

ANALYSES PERFORMED

Hennig86 (Farris, 1988) was used with the ie* option to search for the most par-



FIGS. 7–12. Pollen and seed of hemicryptophyte *Chamaesyce* species. 7. *C. potentilloides*, pollen, polar view (Richards 6882, NY). 8. *C. potentilloides*, pollen (Macedo 3729, NY). 9. *C. selloi*, pollen (Schinini et al. 8313, G). 10. *C. setosa*, pollen (Irwin 25142, NY). 11. *C. nana*, pollen (Pedersen 6548, NY). 12. *C. potentilloides*, seed, ventral surface (Rosengurt 8898, MFVA). (Scale bars: 7–11 = 10 μm ; 12 = 500 μm .)

simonious unweighted trees by implicit enumeration. Implicit enumeration is certain to find all of the shortest trees (Farris, 1988). Pee-Wee (Goloboff, 1993b) was used for implied weighting with fifty replications and fifty trees held, and Hennig86

(Farris, 1988) was used for successive weighting. Pee-Wee searches by branch swapping for trees with maximum total fit. The fit of each character is based on a concave function of homoplasy. Characters with greater homoplasy are less fit and

TABLE I
CHARACTERS AND CHARACTER STATES USED IN THE
PHYLOGENETIC ANALYSIS

0. Plant form: hemicryptophyte (0); therophyte (1); phanerophyte (2) [nonadditive].
1. Plant habit: erect (0); procumbent (1).
2. Phyllotaxy: spiral (0); decussate (1); distichous (2) [nonadditive].
3. Leaf margin: strictly entire (0); entire to serrulate (1).
4. Kranz leaf anatomy: absent (0); present (1).
5. Pleiochasium presence: present (0); absent (1).
6. Cyathium arrangement: strictly solitary (0); solitary to glomerulate (1).
7. Cyathium meristic plan: some >5-merous (0); strictly 5-merous (1).
8. Appendage presence: present (0); absent (1).
9. Seed surface: smooth (0); rugose (1).
10. Seed mucilage: absent (0); present (1).
11. Mature seed size: reaching 1.5 mm or longer (0); strictly ≤ 1.1 mm (1).
12. Seedling ontogeny: continuous (0); aborted axis (1).

treated as less influential in comparing tree topologies. When there is conflict between two characters, the fittest trees have fewer steps for the character with the higher fit (Goloboff, 1993a). Implied weighting is similar to successive weighting (Farris, 1969) except for this difference: successive weighting does its first analysis using equal character weights, and it weights the characters by the rescaled consistency index (consistency index \times retention index) on the subsequent analyses, whereas implied weighting uses a modification of the consistency index (Goloboff, 1993a). The default concavity of 3 was used in implied weighting. Eve (Farris, 1991) was used to construct Adams consensus trees (Adams, 1972). Unlike a strict consensus tree (Sokal & Rohlf, 1981), in which only components identical in all trees are resolved (the unions), in an Adams consensus tree the intersections of components between trees are resolved. Adams consensus trees are particularly useful in discerning "wildcard" taxa (Nixon & Wheeler, 1990) which cause loss of resolution in the strict consensus tree. Bremer (1990) summarizes: "Adams (1972) consensus trees essentially work by pulling down unstable taxa and components with different positions in the cladograms to the first node summarizing the different positions." ClADOS version 1.4 (Nixon,

TABLE II
DATA MATRIX OF CHARACTERS USED IN THE
PHYLOGENETIC ANALYSIS

	0	5	10
<i>Euphorbia</i> subgen. <i>Agaloma</i>			
<i>E. corollata</i>	000000000000		
<i>Chamaesyce</i> sect. <i>Acutae</i>			
<i>C. acuta</i>	0010010100100		
<i>C. angusta</i>	0010010101001		
<i>Chamaesyce</i> sect. <i>Chamaesyce</i>			
<i>C. maculata</i>	1121110101111		
<i>C. serpens</i>	1120110100111		
<i>Chamaesyce</i> sect. <i>Hypericifoliae</i>			
<i>C. hirta</i>	1021111101111		
<i>Chamaesyce</i> "Pleadeniae"			
<i>C. nana</i>	002111010110?		
<i>C. potentilloides</i>	002010000010?		
<i>C. setosa</i>	002111110110?		
<i>C. viscoides</i>	00201?010110?		
<i>Chamaesyce</i> sect. <i>Sclerophyllae</i> subsect. <i>Gymnadeniae</i>			
<i>C. arnottiana</i>	2021111111001		
<i>C. atrococca</i>	2010111111001		
<i>C. celastroides</i>	202011111?101		
<i>C. multiformis</i>	2020111111001		
<i>Chamaesyce</i> sect. <i>Sclerophyllae</i> subsect. <i>Sclerophyllae</i>			
<i>C. chamissonis</i>	2020111100001		
<i>C. mesembryanthifolia</i>	2020110100001		

1993) was used to visualize character state changes and print cladograms.

RESULTS AND DISCUSSION OF THE ANALYSIS

Hennig86 produced four equally parsimonious unweighted trees with lengths of 27 steps, consistency index of 0.55, and retention index of 0.70. Successive weighting using Hennig86 resulted in the same four equally parsimonious trees with lengths of 27 steps when the characters are mapped as equal weights. Implied weighting using Pee-Wee resulted in ten trees of equal fit. When the characters are mapped as equal weights, one tree had a length of 27 and nine trees had a length of 28.

In the unweighted (and successively weighted) strict consensus tree (Fig. 13), which is also one of the four most parsimonious trees, *Acutae*, as previously defined, is paraphyletic and basal (a lineage that formed early in the evolution of a group) within *Chamaesyce*. *Sclerophyllae* is

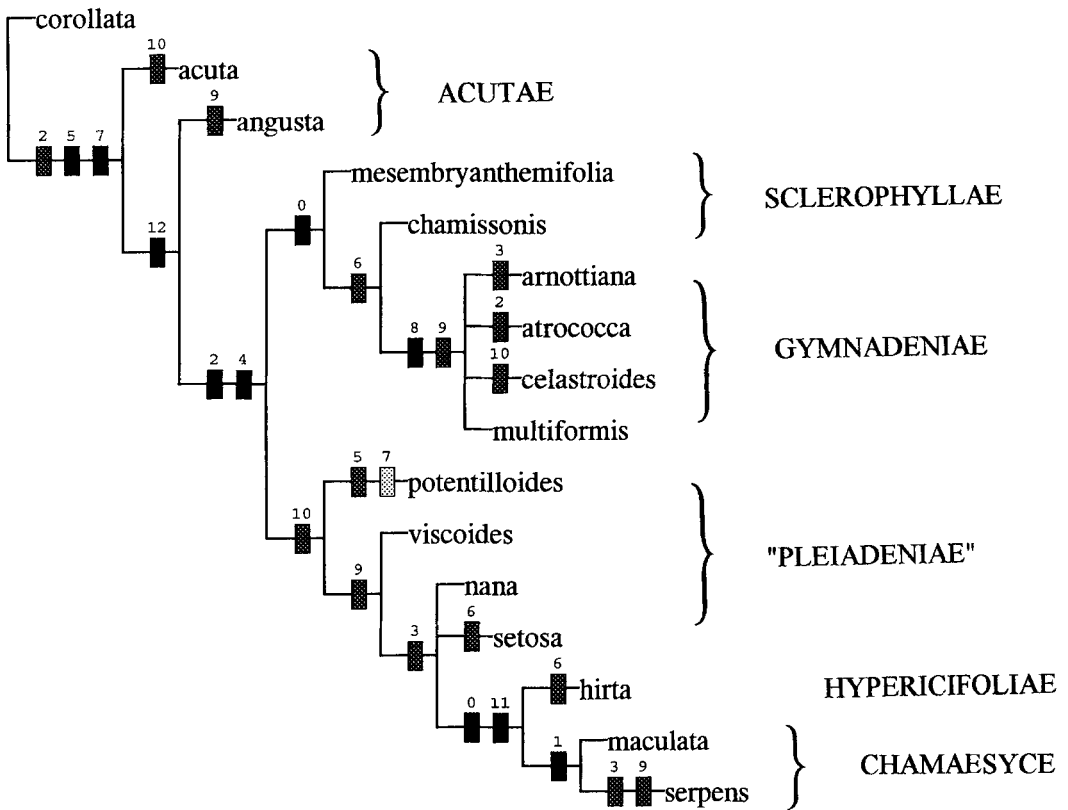


FIG. 13. Cladogram of *Chamaesyce*. Strict consensus of four most parsimonious unweighted trees; this is also one of the most parsimonious unweighted trees. Character numbers as in Table I. Solid box = synapomorphy; darkly shaded box = parallel change; lightly shaded box = reversal.

rendered paraphyletic if *Gymnadeniae* is separated from it at the same taxonomic level. “*Pleiadeniae*” is a pectinate paraphyletic group with *C. potentilloides* basal. *Chamaesyce viscoides* (and *C. tamandana*) is an ensuing lineage, and *C. nana* and *C. setosa* (and *C. selloi*) are derived (a lineage that formed later in the evolution of a group) within “*Pleiadeniae*.” Section *Hypericifoliae*, represented only by *C. hirta*, is the sister group to sect. *Chamaesyce*.

The unweighted strict consensus tree is more resolved than the implied weighted Adams consensus tree; there are four nodes in the unweighted strict consensus tree that are collapsed in the implied weighted Adams consensus tree (Fig. 14). However, both the *Hypericifoliae/Chamaesyce* and the *Sclerophyllae/Gymnadeniae* clades are still resolved in the implied weighted Adams consensus tree.

In the implied weighted Adams consensus tree, *C. potentilloides* is placed with *C. acuta* in a trichotomy, basal within *Chamaesyce*, in contrast to the unweighted strict consensus tree in which *C. potentilloides* is the first derived member of a paraphyletic “*Pleiadeniae*.” This placement of *C. potentilloides* represents the intersection of its positions in the 10 implied weighted trees of equal fit. One of the 10 trees has the same topology as the unweighted (and successively weighted) strict consensus tree (Fig. 13). In the other nine trees, *C. potentilloides* is represented as the sister group to the rest of *Chamaesyce* (i.e., it is the earliest derived member of *Chamaesyce*), which also results in a polyphyletic “*Pleiadeniae*,” with *C. acuta* and *C. angusta* derived after *C. potentilloides* but before the remaining members of “*Pleiadeniae*.” In none of the 10 equally fit implied weighted trees is “*Pleiadeniae*” a monophyletic group.

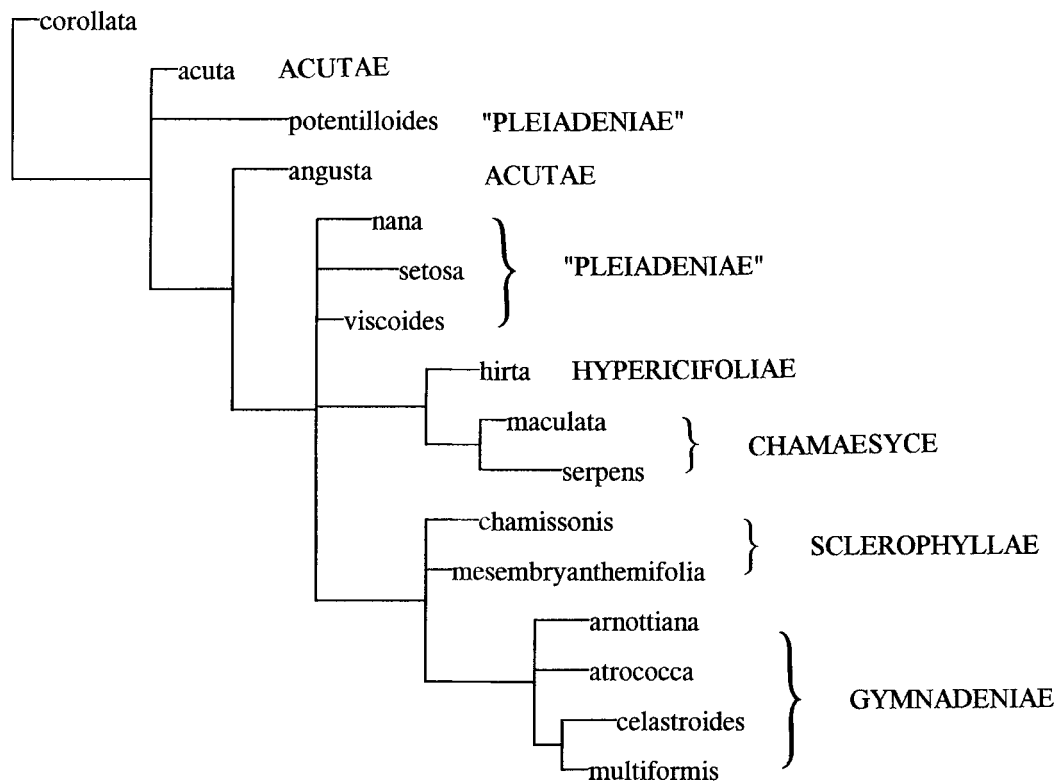


FIG. 14. Cladogram of *Chamaesyce*. Adams consensus of 10 equally fit implied weighted trees.

We prefer the use of implied weighting over equal character weighting because we believe that not all characters have equal explanatory value (and therefore equal weights) and consequently that character weighting based on their fit to tree topology is a logical extension of parsimony (Goloboff, 1993a). However, most of the conclusions we shall draw can be made with the unweighted strict consensus tree (Fig. 13) as well as the implied weighted Adams consensus tree (Fig. 14). Other than a few assertions as to relationships among one or more subsections expressed in the primary literature, there are no comprehensive previous studies on the phylogeny of *Chamaesyce*. Koutnik (1987) grouped *Gymnadeniae* within *Sclerophyllae*, an idea supported by our analysis. Webster (1967) suggested that *Acutae* is basal within the genus *Chamaesyce*, another idea supported by our analysis. Webster (1967) further suggested that "*Pleiadeniae*" is basal within the genus *Chamaesyce*, an idea partially sup-

ported by our analysis. Allem and Irgang (1975) and Subils (1977) opted not to maintain "*Pleiadeniae*" as constituted by Boissier (1862) and transferred some of its members (*C. selloi* and *C. setosa*) to *Hypericifoliae*. However, our analysis shows that inclusion of *C. selloi* and *C. setosa* would make *Hypericifoliae* paraphyletic (Figs. 13, 14).

Beyond supporting most of the earlier notions of phylogeny within *Chamaesyce*, there are two additional important points from the analysis. First, the *Sclerophyllae/Gymnadeniae* lineage is independent of the *Hypericifoliae/Chamaesyce* lineage (Figs. 13, 14). Second, "*Pleiadeniae*" is not a monophyletic group and should not be recognized in formal classifications. Furthermore, based on implied weighting, *C. potentilloides* may represent an independent lineage from the other members of "*Pleiadeniae*" (Fig. 14). This issue will need to be addressed with further studies using more characters.

Artificial key to the hemicryptophytic species of *Chamaesyce* from cerrado vegetation

1. Verticils present; cyathia in a pleiochasia or dichasia superinflorescence (pseudomonopodial in late season); seeds smooth; plant usually glabrous or sparsely pilose; leaves strictly entire. Central Brazil through northern Argentina, Uruguay, Paraguay, and Bolivia. *C. potentilloides*
1. Verticils absent, all leaves strictly opposite; cyathia in dichasia or pseudomonopodial positions; seeds rugose-punctate; plant usually pubescent; leaves entire to serrulate.
 2. Cyathia strictly solitary.
 3. Leaves serrulate to crenulate; cyathia strictly proximal, borne among scale-like cataphylls or the first few foliage leaves (distal regions of stems soon becoming strictly vegetative); peduncles usually 12–20 mm long. Goiás and Rio Grande do Sul, Brazil, and southeastern Paraguay. *C. nana*
 3. Leaves strictly entire; cyathia distal, borne among foliage leaves; peduncles usually <5 mm long.
 4. Stems usually 15–25 cm long, stems and cyathia long white hirsute-velutinous; appendages smooth. Goiás and Minas Gerais, Brazil. *C. viscoides*
 4. Stems usually <10 cm long, stems and cyathia short crispate-pubescent to short velutinous; appendages with papillate protuberances. Very rare, Bahia, Brazil. *C. tamanduana*
 2. Cyathia solitary and in glomerules of 2–12 per node (some late-season plants may exhibit only solitary cyathia).
 5. Cyathial appendages truncate, yellow, erect, crispate-pubescent; leaves often entire; stems sparsely branched, often woody at the base. Minas Gerais and Goiás, Brazil. *C. setosa*
 5. Cyathial appendages reniform, white to rarely pink or yellowish, perpendicular to rim of cyathium to erect, glabrous; leaves usually serrulate; stems often highly branched. Argentina, Paraguay, Uruguay, Rio Grande do Sul, Brazil. *C. selloi*

Chamaesyce nana (Klotzsch & Garcke) M. P. Simmons & W. J. Hayden, comb. nov. (Figs. 1F, 6F)

Anisophyllum nanum Klotzsch & Garcke in Abh. K. Akad. Wiss. Berlin 32. 1859. *Euphorbia chamaerrodos* Boiss. in Centuria Euphorbiarum 3. 1860. *Chamaesyce chamaerrodos* (Boiss.) Croizat, J. Arnold Arbor. 24: 184. 1943. TYPE: BRAZIL. *Sellow 3131*. (LECTOTYPE (designated here), MO; ISOLECTOTYPES, K, U, W–2 sheets).

Euphorbia Chamaerodos [sic] Boiss. var. *hirsuta* Chodat & Hassl., Bull. Herb. Boiss. (sér. 2) 5: 681 (616). 1905. TYPE: PARAGUAY: In campis combustis in regione cursus superioris fluminis Apa, *Hassler 8498* (BM, JEPS, NY).

Euphorbia macrorrhiza Glaziov non C. A. Mey. ex Ledeb., Mem. Soc. Bot. France 3: 637, nom. nud.

Aerial stems per rootstock varying seasonally, slender, ascending, degree of branching varying seasonally, up to 30 cm long (see below), short-crispate (sometimes hirsute-velutinous); stem trichomes uniseriate, multicellular, white (sometimes yellowish), 0.1–0.25 mm (to ca. 1 mm) long. Early season stems many from rootstock, floriferous, highly branched, 3–4(6) cm long; late-season vegetative stems arising by proliferation from some early-season-flowering stems, 1 to several per rootstock, sterile, sparsely branched, 4–10(30) cm long, to 1.8 mm diam. at base. Leaves either cataphylls or foliage leaves, strictly opposite; cataphylls scale-like, entire or ser-

ulate, persistent; foliage leaves largest at mid to upper stem; blades short ovate to ovate-elliptical to ovate-lanceolate, often weakly falcate, 9–27 × 6–9(13) mm, midrib and often blade short white crispate-pubescent (sometimes glabrous or hirsute-velutinous); adaxial surface drying pale to darker green; abaxial surface light brown or lighter green than adaxial surface; base oblique; margin serrulate; apex acute; petiole 1 mm long; stipules connate, rarely with distinct collar of tissue adnate with cataphylls, persistent, narrow to broadly triangular, 0.4–1.3 × 0.1–0.8 mm at base, glabrous to short crispate-pubescent (to few uniseriate multicellular hirsute-velutinous), not tufted hirsute-velutinous adaxially. Cyathia solitary, borne on early-season dichasia or pseudomonopodial stems, subtended by cataphylls or the most proximal 1–3 pairs of vegetative leaves; peduncles (3)12–20(25) mm long; involucre campanulate, externally yellowish (white-yellow) short crispate-pubescent (hirsute-velutinous), (1)1.2–1.6(2) × 1.3–2.3 mm at mouth; primary lobes 5, weakly keeled, entire, white- (sometimes yellowish-) ciliate; glands 4, transversely oblong, drying light to dark brown, not obviously pubescent on inner side, conspicuously stalked; gland bases narrow, crispate-pubescent; appendages ob-

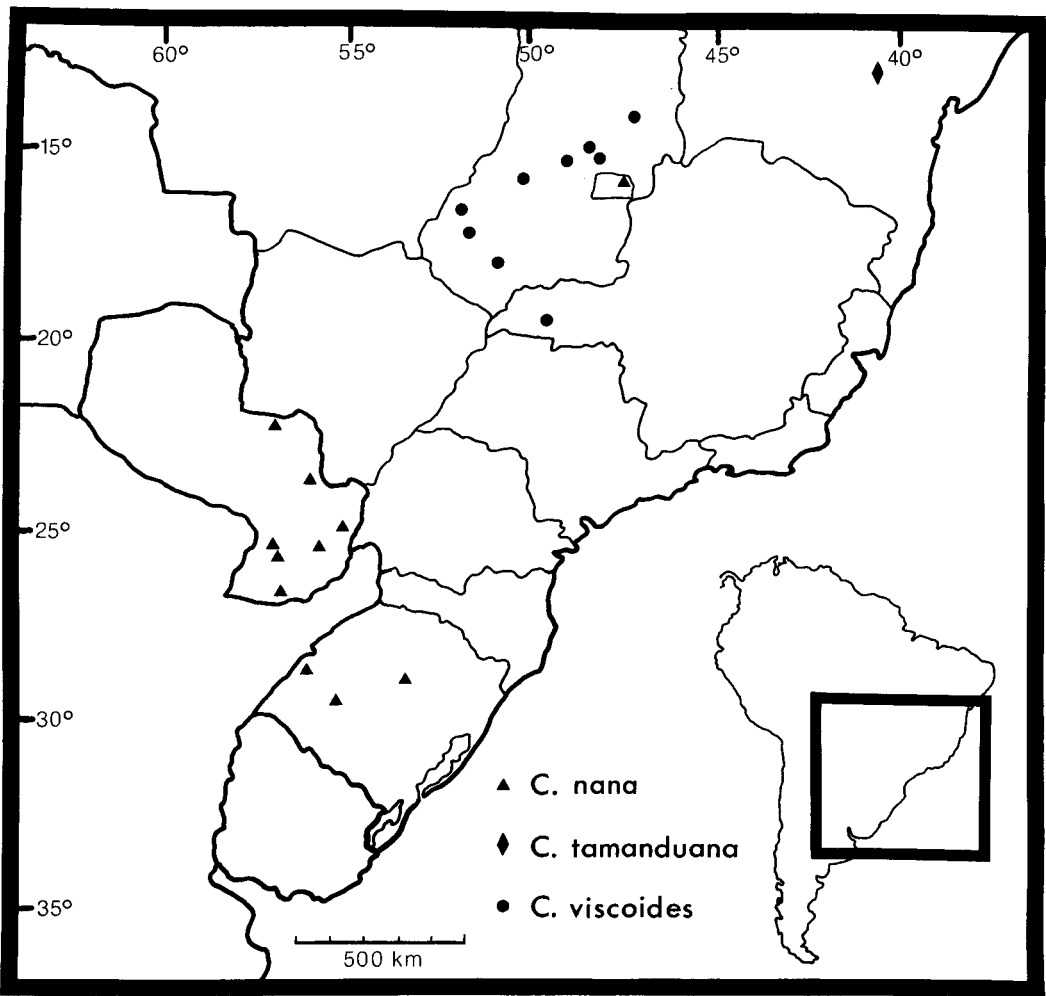


FIG. 15. Distribution of *Chamaesyce nana*, *C. tamanduana*, and *C. viscoides*.

ovate to rounded, 1–1.6(1.8) mm long, planar, perpendicular to rim of cyathium to erect, glabrous, weakly repand, white (sometimes pink). Staminate flowers ca. 25–30. Pistillate flower with gynophore to 2 mm long at maturity, densely crispate-pubescent (sometimes short uniseriate multicellular hirsute-velutinous); ovary yellow (sometimes white or yellowish) short (sometimes long) crispate-pubescent; styles (0.6)1(1.2) mm long, glabrous (sometimes crispate pubescent), connate basally, lower portion erect, bifid for $\frac{1}{3}$ – $\frac{2}{3}$ of length, tips recurved; stigmas thin or somewhat clavate. Capsule crispate-pubescent, (2.3)2.6–2.7 \times (2.5)3–3.3 mm; trichomes short (sometimes

long), uniseriate, multicellular, yellow (to white). Seed subovoid, \pm tetragonal, 1.5–1.7(2) \times 1.1–1.3 mm, rugose-punctate, brown, often with thin white surface at hilum; base truncate.

Habitat.—Cerrado and grasslands.

Distribution.—In Brazil in Goiás and central through western Rio Grande do Sul and southeastern Paraguay (Fig. 15).

Phenology.—Available evidence indicates cyathia present from early September through late February.

Specimens examined. BRAZIL. Without specific locality: *Sellow s. n.* (K, MO, U, W–2 sheets); *St. Hilaire 780* (A–fragment ex P, mixed collection with *C. viscoides*). Goiás: Between Planaltina and São Jose de Aliança

on the DF 17, *Ratter et al.* 4506 (UB); "le plateau central," *Glaziou* 22085 (G—mixed collection with *C. potentilloides*, MO). **Rio Grande do Sul:** *Gaudichaud* 1705 (F—fragment ex P); 1 km da Barragen do Itu-São Francisco de Assis, *Allem et al.* ICN 29885 (ICN); São Borja, *Allem et al.* ICN 29884 (ICN). **Soledade:** Rio Jacuhysinho, *Bornmüller* 639 (JE).

PARAGUAY. **Alto Paraná:** Reserva Biologica Tati Yupi, *Marmorì* 1274 (CTES). **Amambay:** Sierra de Amambay, Cabecera Río Aguidaban, *Rojas* 6354 (A). **Caaguazú:** Near Caaguazú, *Hassler* 9294 (BM, F, GH, MO, NY, S); near Igatimí, Yerbaliu de Maracayu, *Hassler* 4675 (BM, GH, JEPS, MO, NY, S). **Concepción:** Upper Río Apa, *Hassler* 8498 (BM, JEPS, NY). **Paraguari:** Carapegua, *Rojas* 3352 (A). **Misiones:** Santiago, Estancia "La Soledad," *Pedersen* 6548 (NY). **Without further locality data:** Est. Aomonia, *Regnell* 1970 (S); Lapyta, *Jorgensen* 4672 (C, F, MO—mixed collection with *C. Selloi*, NY—2 sheets, S, SI, US).

When *Chamaesyce nana* was first named as a species of *Anisophyllum* (Klotzsch, 1859), an unnumbered *Sellow* specimen was cited as its type. However, some *Sellow* collections of this plant bear the collection number 3131, notably, photographs of a type at B, now destroyed but most likely seen by Klotzsch, and also a specimen at MO. We have no reason to believe that the *Sellow* collections of this plant, whether numbered or not, constitute more than a single collection. At any rate, the sheet at MO, which consists of four separate plantlets and a packet bearing capsules and very immature seeds, serves well as a lectotype because of its comparatively abundant material and is numbered consistently with material most likely studied by Klotzsch. Upon transferring Klotzsch and Garcke's species of *Anisophyllum* to *Euphorbia*, Boissier (1860) coined the name *Euphorbia chamaerrhodos*, because of the existence of *E. nana* Royle, a different species.

Euphorbia Chamaerodos [*sic*] var. *hirsuta* is herein treated as a synonym of *Chamaesyce nana*. Besides the type specimen of this variety (*Hassler* 8498), *Rojas* 3352 is the only other specimen examined that has uniseriate multicellular hirsute-velutinous hairs on the stems, leaves, stipules, cyathial involucre, and pistillate gynophores. More-typical specimens have crispate hairs in the above-mentioned areas. However, an intermediate specimen, *Marmorì* 1274, has both crispate hairs and weakly velutinous uniseriate multicellular hairs. Besides the uniseriate multicellular hirsute-velutinous

hairs, no other features distinguish the variety. All three specimens were collected in southeastern Paraguay where more typical specimens were also collected. Because of the intermediate specimen, common geographical locations, and lack of further distinguishing characters, we do not believe that this variety should be recognized.

There are three details in which our morphological description for *C. nana* differs from that of Boissier (1860) and Mueller (1874). Boissier (1860) cited glands numbering four or five. Mueller Argoviensis (1874) concurred and further indicated two appendages to be distinctly larger. However, we saw only one cyathium on the several *Sellow* specimens examined that might have five glands, though we are not certain. On all other specimens we saw cyathia with only four glands. As for gland size asymmetry cited by Mueller Argoviensis, this pattern was not evident in any of the specimens examined. Glands on each cyathium appeared to be relatively equal in size, though occasionally there was some minor variation. Both Boissier and Mueller Argoviensis cited the capsule as flattened-keeled, and neither mentioned distal thickening of the stigmas. We interpret the "flattened" characterization of the capsules as an artifact of the very wide capsules being pressed somewhat flat during specimen drying. Though some stigmas are thin, many are thickened and somewhat clavate.

Geographically, *Chamaesyce nana* appears to consist of two disjunct populations, one in Goiás, Brazil, and one in southeastern Paraguay through Rio Grande do Sul, Brazil. We do not know of any reason for this peculiar distribution. In comparing the three specimens from Goiás with the other specimens from Paraguay and Rio Grande do Sul, there were no qualitative differences and only minor quantitative differences. We observed cyathia and appendages appreciably larger than average in *Glaziou* 22085 and *Ratter* 4506 from Goiás, but they are not separable in size from the full range evident in Paraguay and Rio Grande do Sul. *Ratter* 4506 is somewhat abnormal for the species because it has short hirsute hairs instead of crispate hairs and lacks crispate hairs on the short bases of the cyathial glands.

CHAMAESYCE POTENTILLOIDES (Boiss.) Croizat (Figs. 1A, B, 6C, D).

Chamaesyce potentilloides (Boiss.) Croizat, J. Arnold Arbor. 24: 184. 1943.—*Euphorbia potentilloides* Boiss. in Centuria Euphorbiarum 3. 1860. SYNTYPES (n.v.): BRAZIL, Goiás, Loco Chapadas de San-Marcos, *Riedel s.n.* (LE); *Lund s.n.* (G).

Anisophyllum caecorum Klotzsch & Garcke in Abh. K. Akad. Wiss. Berlin 38. 1859, nom. nud. *Euphorbia caecorum* Mart. ex Boiss. in DeCandolle, Prodrum 15(2): 51. 1862. SYNTYPES: BRAZIL, without specific locality, *Sellow s.n.* (BR, K, LD, W-2 sheets); Minas Gerais, *Widgren s.n.* (LD, S-sheet without additional collection, S-specimen at bottom of sheet shared with *Regnell s.n.*); BOLIVIA, Chiquitos, *d'Orbigny 944* (A, F, both are fragments ex P). *Chamaesyce caecorum* (Mart. ex Boiss.) Croizat, J. Arnold Arbor. 24: 187. 1943.

Euphorbia albiflora Taub., Bot. Jahrb. 21: 442. 1895. TYPE: BRAZIL, Goiás, Monte Morro do Salto, *Ule 3054* (n.v.).

Aerial stems one to many per rootstock, usually annual (some bases may winter over), slender, erect, unbranched below the inflorescence, (5)10–30(35) cm long, 0.4–1.6 mm diam. at base, glabrous to sparsely pilose or variously pubescent; stem trichomes uniseriate, multicellular, white (sometimes brown), highly variable in length. Leaves variable in size and shape depending on position, ranging continuously from persistent or deciduous cataphylls to foliage leaves and cyathophylls, largest at midstem or base of flowering region, in verticils of (2)3(5) below, strictly opposite and distichous above; blades ovate to oblong to lanceolate to linear, (3)10–30(45) × (1)1.5–6(10) mm, glabrous to sparsely pubescent; adaxial surface drying pale to dark green; abaxial surface somewhat lighter; base acute, obtuse, truncate, or weakly cordate, symmetrical to somewhat oblique; margin entire, somewhat thickened; apex acute, often cuspidate; petiole (0.3)0.6–1.3(2.3) mm long; midrib occasionally purple, depressed adaxially, protruding abaxially; stipules connate, persistent, narrowly to broadly triangular, acute, 0.3–0.5(1) mm long, entire or deeply cleft to base, serrulate, sparsely to densely hirsute adaxially. Cyathia borne continuously on aerial stems on pleiochasial (initially) or dichasial (later) or pseudomonopodial (late season) axes; internodes decreasing progressively from ca. 25 to 2.6 mm; peduncles 0.6–1.6(12) mm long; involucre campanulate (to hemispherical or urceolate), externally gla-

brous to short-pubescent, (0.5)0.6–1.3(2) × (0.6)1–2(2.6) mm at mouth; primary lobes 5 (to 8), keeled, entire, white ciliate; glands 4 (to 7), round to reniform or vestigial, concave, minutely pitted, drying yellow to tan (green), appendiculate, borne on a short base; gland bases pubescent; appendages reniform to oblong, 0.1–1(2.1) mm long, planar, perpendicular to rim of cyathium (or somewhat erect) glabrous, parallel veined, repand to erose, white to yellow (sometimes pink to maroon or green). Staminate flowers ca. 50. Pistillate flower with gynophore to 2.6 mm long at maturity, glabrous; ovary glabrous to puberulent; styles 0.4 mm long, glabrous to puberulent, connate basally, promptly spreading, bifid for 1/2 of length; stigmas clavate. Capsule essentially glabrous, broadly ovoid, 1.8–2.6 × 2–2.6(3.3) mm. Seed subovoid, ± tetragonal, 1.2–1.5(1.8) × 0.7–1.1 mm, smooth overall but minutely pitted, brown; base truncate, concave.

Habitat.—Primarily open cerrado, often in areas exposed by recent fires and with a stony, sandy, or clay substrate, also open grasslands, early successional woodlands, and disturbed areas. Altitude of 300–1350 m.

Distribution.—In Brazil from ca. 12°S in Mato Grosso, Goiás, and Bahia, through eastern Mato Grosso do Sul, Minas Gerais, São Paulo, Paraná, and Rio Grande do Sul; west to Santa Cruz, Bolivia, eastern Paraguay, and Misiones, Argentina; south to northern Corrientes, Argentina, and northern Uruguay (Fig. 16). No specimens seen from Santa Catarina, Brazil.

Phenology.—Flowers and fruits primarily August through December, often into April, occasionally throughout the year in the northern portion of the range.

Representative specimens examined. ARGENTINA. **Corrientes**: Estancia Garruchos, *Pedersen 2881* (C, US). **Misiones**: Apóstoles, *Ibarrola 1127* (A, NY); Lorteo, *Crovetto 9796* (CTES); Posadas, *Ekman 512* (G, LD, S, US).

BOLIVIA. **Santa Cruz**: Santiago de Chiquitos, *Cutler 7034* (A, US); Prov. Sara, Buena Vista, *Steinbach 5172* (F, GH, MO, NY), *Steinbach 6323* (A, G).

BRAZIL. **Without specific locality**: Megaponte, *Pohl 948* (W). **Bahia**: Aracatu, *Harley et al. 15025* (K, MO, NY, U, US); Espigão Mestre, *Anderson et al. 36575* (NY), *Anderson et al. 36896* (MO, NY, UB). **Distrito Federal**: *Aparecida da Silva & Azevedo 990* (DAV), *Cobra & Oliveira 215* (DAV), *Heringer s.n.* (UB 48613), *Irwin et al. 8077* (MO, NY), *Irwin et al.*

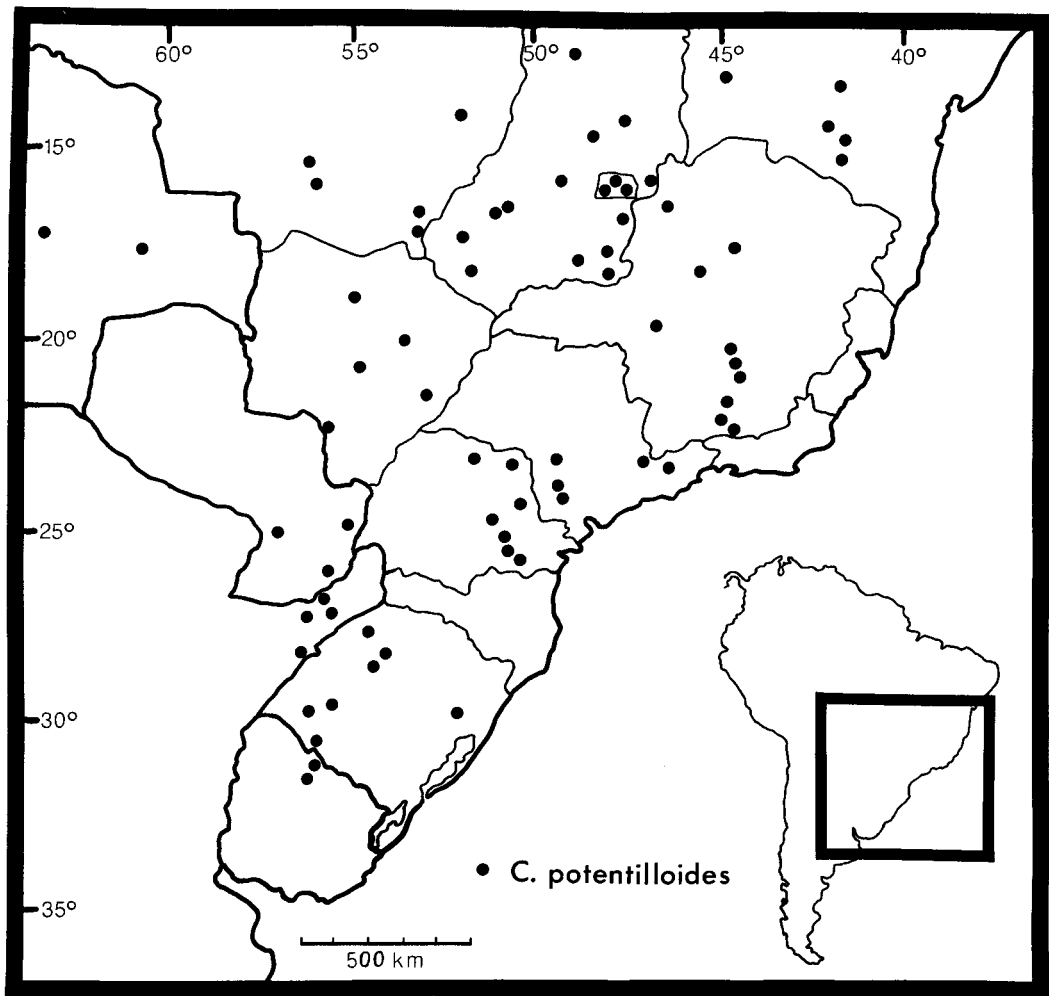


FIG. 16. Distribution of *Chamaesyce potentilloides*.

8380 (MO, NY), *Irwin et al.* 8655 (K), *Maguire et al.* 57076 (LD), *Philcox & Onishi* 4285 (K). **Goiás:** *Burchell* 7021 (B, K), *Glaziou* 22087 (A, B, BR, G, S, US); Chapada dos Veadeiros, *Dawson* 14584 (F, RSA); Niquelândia, *Irwin et al.* 35025 (MO, NY); Serra do Caiapó, *Irwin & Soderstrom* 6953 (F, NY); Serra dos Cristais, *Irwin et al.* 9921 (F-2 sheets, K, LD, UB), *Irwin et al.* 9924 (E, F, K, NY, UB); Serra dos Pirineus, *Irwin et al.* 18684 (F, MO, NY). **Mato Grosso:** Braço, *Baldwin* 3026 (US); Cachoeira Furada, *Prance et al.* 18850 (NY, U, US); Suia-Missu River, *Philcox et al.* 3262 (NY, UB). **Mato Grosso do Sul:** Barra do Garças, *Eiten & Eiten* 8484 (US); Campo Grande, *Archer & Gehrt* 148 (GH, NY, URV, US); Xavantina, *Irwin & Soderstrom* 6382 (NY); 75 km N of Xavantina, *Irwin & Soderstrom* 6704 (C, F, MO, NY, U, US); 250 km NNE of Xavantina, *Eiten & Eiten* 8533 (US). **Minas Gerais:** *Asemp* 25933, *Weddell* 1091 (A-fragment ex P); Caldas, *Lindberg* 429 (BR, S), *Lindberg* 649 (BR), *Regnell* 1407 (BR, S, US); Lagoa Santa, *Warm-*

ing s.n. (GH); São João d'el Rey, *Malme* 1243 (S). **Paraná:** Jaguaraiava, *Dusen* 10675 (AFS, F, GH, NY, S), *Dusen* 16450 (MO, NY, S); Município Lapa, *Hatschbach* 1002 (US); Palmeira, *Hatschbach* 20161 (JEPS, MO). **Rio Grande do Sul:** Cerro Armor-Livramento, *Porto et al.* 1834 (ICN); Pieda do Padre, *Adeliero* 280 (F); São Vicente do Sul, *Sorbal & Marchiori* 4549 (ICN); Tupancireta, *Normann & Gianluppi* 552 (ICN). **São Paulo:** Capão Bonito, *Dusen* 15027 (GH, S); Município de Moji-Guaçu, *Eiten & Eiten* 5078 (NY, US); Município de São José dos Campos, *Mimura* 131 (NY, URV).

PARAGUAY. Amambay: Sierra de Amambay, *Rojas* 6339 (A, BAF). **Caaguazú:** Yerbalium de Maracayu, *Hassler* 4181 (BM). **Without further locality data:** Cerros de Tobaty, *Hassler* 6110 (F, GH, JEPS, NY, S).

URUGUAY. Rivera: Rivera, *Berro* 1796 (MVFA), *Berro* 4814 (MVFA); near Galgo, *Herter* 271 (LD).

The epithet "*caecorum*" is the earlier and much more widely used of the names applied to this taxon in the past. Unfortunately, the publication of *Anisophyllum caecorum* by Klotzsch and Garcke was based on the transfer of an unpublished name that had been used by Martius. When Boissier published the name legitimately in the *Prodromus*, he had already named what we recognize as the same species, *Euphorbia potentilloides*, two years earlier.

Although we have seen neither of the two syntypes of *Chamaesyce potentilloides*, we are confident that *Chamaesyce caecorum* is the same entity. This judgment is based on analysis of the original descriptions of both taxa, Boissier's (1866) excellent lithograph of *C. potentilloides*, and an early comparison of the two taxa (Mueller Argoviensis, 1874). Mueller Argoviensis sought to distinguish the two by supposed differences in overall color and in structure of the involucre, styles, and fruit. Given the enormous and continuous range of variation evident in collections made since the last century, however, none of Mueller Argoviensis's distinctions can be upheld.

On the basis of the published description, we note that all but one of the features of *Euphorbia albiflora* fall easily within the range of morphological variation observed for *C. potentilloides*. Appendages of the type, *Ule 3054*, are described as 3.5 mm long, larger by one-third than any noted in *C. potentilloides*. We have not seen the type to verify the reported appendage dimensions but feel this minor discrepancy insufficient to prevent placement of *E. albiflora* in synonymy with the highly variable *C. potentilloides*.

Chamaesyce potentilloides is a remarkably variable species with extreme forms that intergrade. Variability is more pronounced in vegetative features than in reproductive characters. We have observed eight extreme forms, but none, in light of present knowledge, merits formal taxonomic status.

A robust form consists of plants with very large, wide, almost cordate leaves (Fig. 17H), often with cyathia and appendages larger (0.7–1.7 mm long) than usual. The most extreme specimen of this form is

Irwin et al. 9924, but intergradation from this form to more-typical forms (with leaves similar to Fig. 17E) is shown by *Irwin et al. 18684* and *Irwin et al. 8077*.

A dwarf form consists of plants with highly branched stems usually less than 8 cm in height bearing very narrow, linear leaves 12–18(27) mm long and only 1–1.5 mm wide (Fig. 17C), and cyathia with large oblong appendages 1.3–2.3 mm long. The most extreme specimen is *Irwin et al. 9921* in which the plants form dense mounds about 5 cm tall. The stems and internodes can become extremely elongated to 26 cm, as per *Macedo 3729* and *Maguire et al. 57076*. Intergradation with more-general forms is shown by *Irwin et al. 8655* and *8380*.

There are plants of normal height (greater than 10 cm) with very narrow, linear leaves which are similar to the dwarf form. However, the leaves are larger (14 × 1 mm to 35 × 2 mm) (Fig. 17D), and the plants have small cyathia with very small reniform appendages 0.1–0.3 mm long. The most extreme specimen of this linear leaf form is *Dusen 16450*. Intergradation with more-typical forms is shown by *Dusen 15027* and *Eiten & Eiten 5078*.

Plants with wide, oblong leaves (Fig. 17I) in apical clusters of closely spaced nodes on short stems are an uncommonly found form. An extreme specimen is *Heringer s.n.* Intergradation from this oblong leaf form with more typical forms is shown by *Archer & Gehrt 148* and *Philcox & Onishi 4285*.

Plants of another form have very long lanceolate leaves (Fig. 17A). The most extreme specimen is *Irwin & Soderstrom 6953*. *Irwin et al. 35025* and *Irwin & Soderstrom 6382* demonstrate intergradation from this lanceolate leaf form to more-general forms.

There are plants with thick leaves that often resemble cataphylls in size and shape, but are on widely spaced nodes (Fig. 17F). These plants also have cyathia with very small appendages, and the plants darken on drying. The most extreme specimen is *Philcox et al. 3262*. Specimens that intergrade with more typical forms have longer and/or wider leaves and/or shorter internodes, for

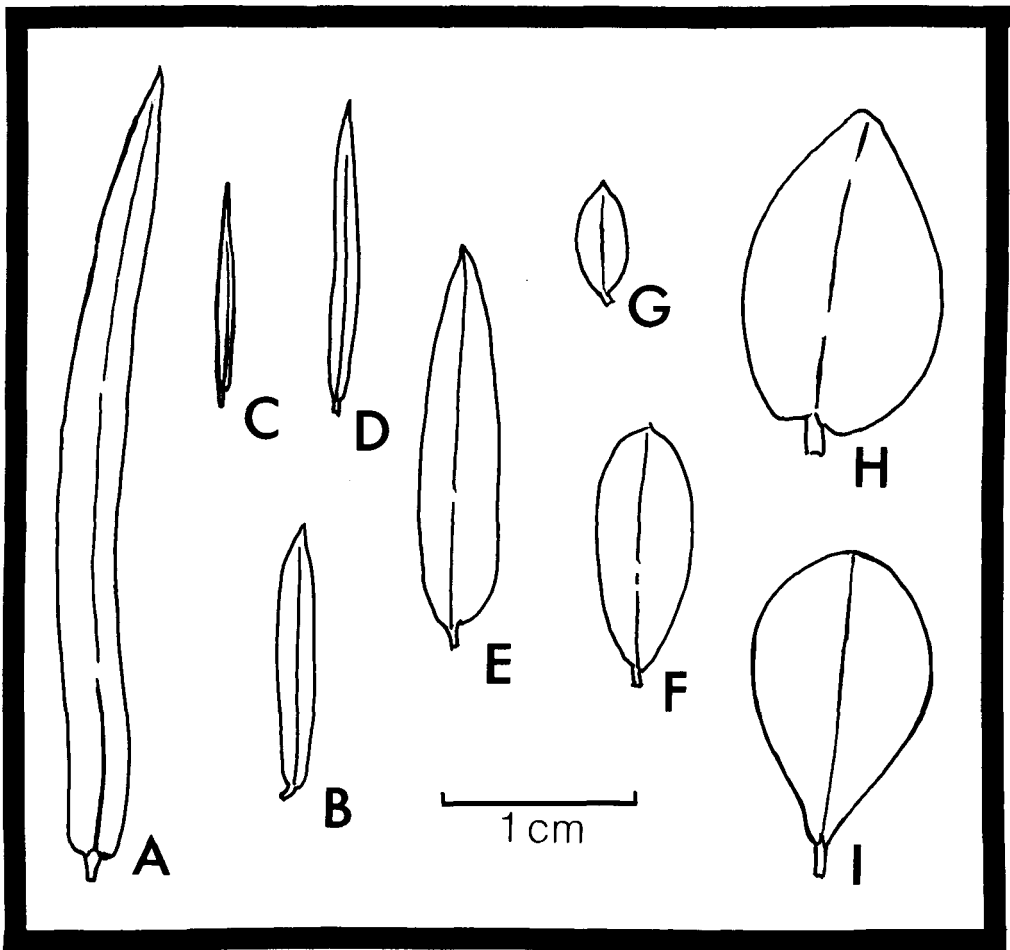


FIG. 17. Diversity of leaf shape in *Chamaesyce potentilloides*, from dried pressed material (see the discussion under *C. potentilloides* for vouchers). A. Lanceolate leaf form. B. Late-season form. C. Dwarf form. D. Linear leaf form. E. Common leaf of *C. potentilloides*. F. Cataphyll leaf form. G. Early season form. H. Robust form. I. Oblong leaf form.

example Eiten & Eiten 8484 and Irwin & Soderstrom 6704.

Another form consists of plants collected in early spring (August and September) with short stems and leaves similar in shape though slightly larger than cataphylls (Fig. 17G). Examples of this early-season form include Eiten & Eiten 8533, Asemp 25933, and Malme 1243.

A late-season form consists of plants collected in midsummer through fall (late December through April). These older stems have some secondary growth and bear opposite distichous cyathophylls (Fig. 17B). Stems are dichotomously branched below,

but pseudomonopodial above with seemingly axillary cyathia present toward the apex. The most extreme specimen is Dawson 14584 (RSA) with a distinctly woody, knotted perennial aerial stem. Other specimens include Anderson *et al.* 36575 and 36896.

None of these forms shows differentiation in seed, leaf anatomy, pollen, or cyathium structure characters. The variation is essentially restricted to characters of gross morphology such as overall plant size, leaf shapes and sizes, and shapes and sizes of various cyathium structures. Some forms show no geographical cohesion—e.g., the forms characterized by oblong leaves, lan-

ceolate leaves, and the early- and late-season forms. The robust and dwarf forms are geographically restricted to the region around Distrito Federal and adjacent Goiás (Brazil), but typical forms also occur in the same area. The long internode form occurs in Mato Grosso, Mato Grosso do Sul, and western Goiás of Brazil, also in the same general areas as more typical forms. The linear leaf form is found throughout the entire southern range including Argentina, Uruguay, Paraguay, and Rio Grande do Sul (Brazil), but occurs intermixed with more-typical forms in Bolivia and, in Brazil, Paraná and São Paulo. Population studies are necessary to address whether the linear leaf form should be treated as a distinct variety.

**CHAMAESYCE SELLOI (Klotzsch & Garcke)
Croizat (Figs. 1D, 6B).**

Chamaesyce selloi (Klotzsch & Garcke) Croizat, J. Arnold Arbor. 24: 184.—*Anisophyllum selloi* Klotzsch & Garcke in Abh. K. Akad. Wiss. Berlin 32. 1859. *Euphorbia selloi* (Klotzsch & Garcke) Boiss. in DeCandolle, Prodr. 15(2): 50. 1862. TYPE: BRAZIL. *Sellow s.n.* (LECTOTYPE (designated here), BR; ISOLECTOTYPES, BM—specimen on right, F, GH, S, U, US, W—2 sheets).

Euphorbia Hassleriana Chodat, Bull. Herb. Boiss. (Sér. 2) 1: 399 (93). 1902 ("1901"). TYPE: PARAGUAY: Without specific locality, *Hassler 1228* (G).

Euphorbia hebegyne Pax & K. Hoffm., in Emrich, Revista Sudamer. Bot. 4: 83. 1937. TYPE (n.v.): BRAZIL: Rio Grande do Sul: Porto Alegre, Caixa d'Água, *Emrich 11*.

Chamaesyce Selloi var. *brevisemina* Croizat, J. Arnold Arbor. 24: 184. 1943. TYPE: ARGENTINA: Entre Ríos: Concordia, *Burkart 822* (A).

Euphorbia selloi var. *setosa* sensu Subils (Kurtziana 10: 147. 1977), non Boissier.

Aerial stems 1 to many per rootstock, apparently annual, slender, erect to weakly ascending, sparsely to highly branched, (7)10–25(38) cm long, 0.8–1.5 mm diam. at base, sparsely to densely crispate and hirsute-velutinous or only crispate; stem trichomes uniseriate, multicellular, often with yellowish or reddish deposits at crosswalls, 1.3–4 mm long. Leaves either cataphylls or foliage leaves, strictly opposite; cataphylls smaller, ovate, serrulate, essentially persistent; foliage leaves largest at mid to upper stem; blades ovate to lanceolate, weakly falcate, (12)16–30(45) × 4–9 mm, sparsely to densely white crispate-pubescent and/or

velutinous; adaxial surface drying light to dark green, occasionally with a central reddish spot; abaxial surface lighter; base distinctly oblique; margin entire to serrulate; apex acute; petiole 1–2 mm long; stipules narrow triangular, 0.4–1.6 mm long, some strigose abaxially, not tufted hirsute adaxially. Cyathia on distal portions of stems, solitary or clustered in glomerules of 1–3(6), in pseudomonopodial (sometimes dichasial) positions, appearing terminal or axillary; peduncles 1.3–3.3 mm long; involucre campanulate or widely campanulate, green to red, externally densely white to yellow or pink crispate-pubescent, (1)1.2–1.6(2) × (1.1)1.3–1.6(2.2) mm at mouth; primary lobes 5, often distinctly keeled, entire or serrulate, whitish ciliate; glands 4, round to transversely oblong, drying dark green to brown, densely ciliate; gland bases densely white to pink crispate-pubescent; appendages reniform to reniform-auriculate, 0.4–0.6(1) mm long, planar or somewhat convolute, perpendicular to rim of cyathium to erect, glabrous, repand, white (sometimes yellowish or pink), rarely unequal (to somewhat larger). Staminate flowers ca. 25–35. Pistillate flower with gynophore to 1.7 mm long at maturity, long white to yellow or pink crispate pubescent; ovary long white to yellow or pink crispate pubescent; styles 0.6–1 mm long, glabrous or yellow crispate-pubescent at base, connate basally, lower portion erect, bifid for $\frac{1}{3}$ – $\frac{2}{3}$ of length, tips recurved; stigmas tapered or weakly thickened. Capsule crispate-pubescent, 2.2–2.5 × (2)2.2–2.5 mm; trichomes long, uniseriate, multicellular, yellow. Seed subovoid, ± tetragonal, 1.3–1.6 × 0.8–1 mm, rugose-punctate, brown, often with thin white surface at hilum.

Habitat.—Grasslands and dry, rocky countryside.

Distribution.—Southeastern Paraguay through Rio Grande do Sul of Brazil, northwestern Uruguay, and northern Entre Ríos, eastern Chaco, Corrientes, and southern Misiones of Argentina (Fig. 18).

Phenology.—Flowers and fruits present year-round.

Representative specimens examined. ARGENTINA. Chaco: Benitez, *Schulz 1531* (U); Río de Uro, *Nicken*

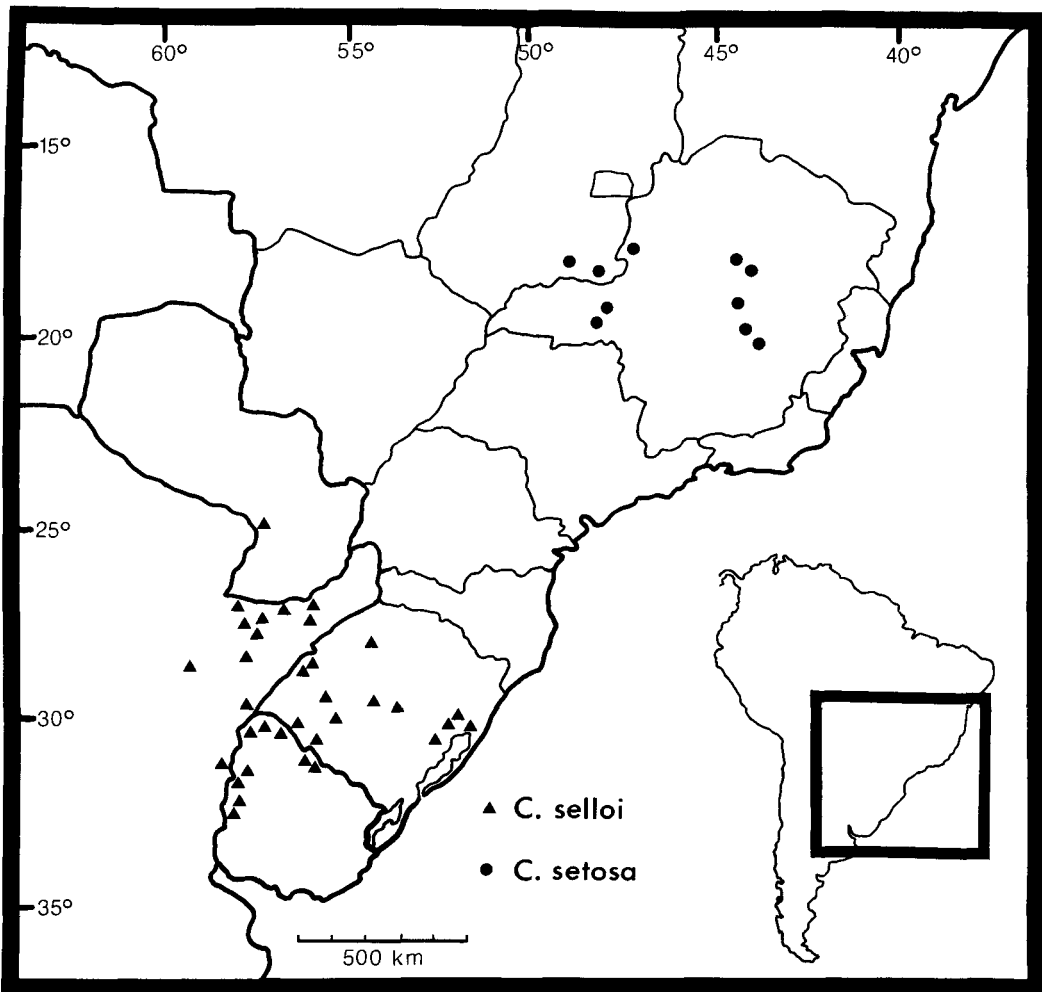


FIG. 18. Distribution of *Chamaesyce selloi* and *C. setosa*.

85 (A). **Corrientes:** Concepcion, *Arbo* 304 (CTES), *Krapovickas & Cristobal* 11642 (CTES, JEPS, US), *Pedersen* 8090 (C, L, NY, US); Ituzaingo, *Lourteig et al.* 2951 (JEPS, MO); Paso de los Libres, *Schinini* 7633 (CORD); Saladas, *Schwarz* 9550 (LIL); San Miguel, *Krapovickas et al.* 24777 (G, GB), *Schinini et al.* 8313 (CTES, G, JEPS); Santa Catalina, *Hunziker* 5779 (A). **Entre Ríos:** Concordia, *Burkart* 822 (A), *Castellanos* 271 (BA), *Gamerro* 1116 (LPS). **Misiones:** Apóstoles, *Renvoize* 3082 (NY, US); Candelaria, *Krapovickas et al.* 15444 (CTES); Posadas, *Ekman* 511 (G, LD, NY, S, US). **Santa Fe:** Reconquista, *Burkart* 5790 (A).

BRAZIL. Without specific locality: *Pohl s.n.* (K), *Sellow s.n.* (BM—specimen on right, BR, F, GH, S, U, US, W—2 sheets), *Sello* 170 (A—fragment ex G). **Río Grande do Sul:** L. Gomen, *Bornmüller* 252 (G, GH, JE, M, WU); Porto Alegre, *Emrich* 28 (U), *Malme* 487 (S), *Rambo* 37860 (B, S, W), *Schultz* 104 (ICN); S. Leopoldo, *Schmitt* 47474 (B).

PARAGUAY. Without specific locality: *Hassler* 1228 (G), *Jorgensen* 4336 (A, NY, S). **Without additional locality data:** Prairies de Dona-Juana, *Balansa* 1678 (G, S); Ybrimi, *Montes* 12935 (CTES, LPS).

URUGUAY. Without specific locality: Cerro de las Palmas, *Berro* 1448 (K, MVFA). **Paysandú:** Río Uruguay, Chapicuy, *Rosengurt* 3225 (A—2 sheets, HAS, MO, U, US); Río Uruguay, north of Río Quequay, *Rosengurt B-3303* (A). **Rivera:** *Flossdorf* 5209 (A).

Klotzsch and Garcke typified *Anisophyllum selloi* with two collections, those of Sellow and Pohl. The Pohl specimen is somewhat problematic. Our studies have uncovered only a single sheet (at K) bearing no collector's name that we nevertheless suspect was collected by Pohl. This judgment is based on comparison of the labels,

ink, and handwriting of the specimen at K with two Pohl collections of *C. viscoides*: Pohl & Burchell s.n. at G and Pohl 2179 at W. In contrast, the Sellow specimens cited by Klotzsch and Garcke are clearly labeled and widely distributed in herbaria; from these the sheet at BR has been chosen as lectotype because of its abundant material, including a rootstock and immature seed.

Chamaesyce selloi is a markedly variable species, a fact that has contributed to the proliferation of names that we have synonymized above. For the first of these, *Euphorbia Hassleriana*, Chodat (1901) thoroughly described vegetative structure but provided only a cursory and somewhat confusing comparison of its cyathia with those of *C. selloi* and *C. setosa*. Chodat focused on the number of cyathia per node and the angle of the "glands," which we interpret to mean the appendages of the glands. The type specimen, Hassler 1228, has one or two cyathia per node and appendages that are perpendicular to the rim of the cyathium, features that we find to be fully consistent with our concept of *C. selloi*, a concept that is probably somewhat broader than Chodat's. In comparison, *Chamaesyce setosa*, with most cyathia in glomerules and erect appendages, is clearly distinct. Subils (1977) accepted Chodat's species, but her treatment of this taxon reveals a number of inconsistencies. Specimens identified as *E. hassleriana* by Subils possess appendages that range from erect to perpendicular, often with both extremes on the same plant. Moreover, her illustration of this species has erect appendages whereas her key and description indicate appendages to be horizontal.

We follow Rambo (1960) and Allem and Irgang (1975) in treating *Euphorbia hebe-gyne* as a synonym of *Chamaesyce selloi*. Although we have not seen the type, the description and excellent illustration in Emrich (1937) purport this taxon to differ in its possession of subentire, linear leaves and non-capitate clusters of cyathia. However, we have found leaf width and cyathium number per node to vary considerably and independently in *C. selloi*, and consequent-

ly perceive no basis for distinguishing Pax and Hoffmann's taxon.

Chamaesyce selloi var. *brevisemina* Croizat is another problematic taxon. Croizat based this variety on seed morphology of three specimens—Burkhart 822 (the varietal holotype), Rosengurt B-3303, and Hunziker 5779—that he compared with Sellow 170, mistakenly believing the latter to be the holotype of the species. According to Croizat, var. *brevisemina* has ovoid seeds with a smooth raphe, in contrast to supposedly typical *selloi* with triangular-acuminate seeds and an impressed raphe. Reexamination of these specimens at A has failed to yield support for the proposed variant. No seeds could be found in the packets of Burkhart 822 nor Hunziker 5779. The specimen of Rosengurt B-3303 has mature seeds, but these seeds are identical to those found throughout *C. selloi*. Finally, the specimen of Sellow 170 bears only a single immature seed, suggesting that Croizat based var. *brevisemina* on an erroneous comparison of mature and immature seeds. *Chamaesyce selloi* var. *brevisemina* has been previously synonymized with *Euphorbia hassleriana* by Subils (1977).

We believe Subils (1977) misapplied Boissier's var. *setosa*. The specimens that she cited are discordant with our understanding of Boissier's variety and are better referred to typical *C. selloi*.

Variation within *Chamaesyce selloi* reveals considerable intergradation between weakly definable forms. One form may be characterized by a rather lax habit, short ovate-lanceolate leaves, and whitish pubescence including relatively few velutinous hairs on stems and leaves; this form is found throughout the range of the species but is rather infrequent in Misiones, Argentina, and Paraguay. Schinini 7783 is a good example of this lax form. Another form has an erect habit, long-lanceolate leaves, and yellowish pubescence including more densely velutinous hairs on stems and leaves; this form is frequent in Misiones, Argentina, and Paraguay. The erect form is illustrated by Ekman 511. Specimens transitional between these extremes are especially abundant in Rio Grande do Sul, Brazil.

Chamaesyce setosa (Boiss.) M. P. Simmons & W. J. Hayden comb. nov. (Figs. 1E, 6E)

Euphorbia Selloi var. *setosa* Boiss. in DeCandolle *Prodromus* 15(2): 50. 1862. *Euphorbia setosa* (Boiss.) Muell. Arg. in Martius *Flora Brasiliensis* 11(2): 672. 1874. SYNTYPES (n.v.): BRAZIL: near Tijuco, *Sellow s.n.*; Mount Urubu, *Pohl s.n.* (W). Goiás: *Riedel s.n.* (LD, LE).

Euphorbia villosissima Klotzsch pro syn. in Boissier (ibid).

Aerial stems 1–4 per rootstock, apparently annual, slender, erect (to ascending), sparsely branched, (7)20–30(55) cm long, 1.6–2 mm diam. at base, sparsely to densely short yellow crispate and hirsute-velutinous; stem trichomes uniseriate, multicellular, often with yellowish deposits at crosswalls, 0.6–2.8 mm long. Leaves either cataphylls or foliage leaves, strictly opposite; cataphylls smaller, ovate, entire to serrulate, somewhat fugaceous; foliage leaves large at mid- to upper stem; blades ovate-lanceolate to elliptic-lanceolate, (12)18–26(37) × 6–8(12) mm, sparsely to densely velutinous with white to light yellow trichomes; adaxial surface drying olive-green to brown; abaxial surface lighter; base distinctly oblique; margin entire to serrulate; apex acute; petiole 1–2 mm long; stipules connate, deciduous, narrow-triangular, (0.6)0.8–1.2(1.3) mm long, some strigose abaxially, not tufted hirsute adaxially. Cyathia on distal portions of stems, solitary or in glomerules of (1)2–12(20), in pseudomonopodial (sometimes dichasial) positions, appearing terminal; peduncles (1)1.5–2(3) mm long; involucre campanulate to widely campanulate, externally densely short yellow crispate-pubescent, (1)1.3–1.6 × (1.3)1.6–2.3(2.5) mm at mouth; primary lobes 5, obscurely keeled, entire or serrulate, yellowish ciliate; glands 4, transversely oblong, drying dark brown, ciliate; gland bases densely short yellow crispate pubescent; appendages short truncate, 0.3–0.5(0.6) mm long, planar to convolute, erect, densely short yellow crispate-pubescent, entire, drying light yellow. Staminate flowers about 30. Pistillate flower with gynophore to 2.6 mm long at maturity, long yellow crispate-pubescent; ovary long yellow crispate-pubescent; styles 0.6–1.1 mm long, short yellow crispate-pubescent throughout their length, connate basally, low-

er portion erect, bifid for $\frac{1}{3}$ – $\frac{2}{3}$ of length, tips recurved; stigmas either tapered or clavate. Capsule crispate pubescent, 2.2–2.6(3) × 2.5–2.8(3) mm; trichomes long, uniseriate, multicellular, yellow. Seed obovoid, ± tetragonal, 1.5(1.7) × (0.9)1.1 mm, rugose-punctate, brown, often with thin white surface above hilum.

Habitat.—Cerrado.

Distribution.—In Brazil in central to western Minas Gerais, into southeastern Goiás (Fig. 18).

Phenology.—Flowers and fruits present year-round.

Specimens examined. BRAZIL. **Without specific locality:** *Pohl 1674* (K). Goiás: *Glaziou 22079* (C, G-mixed collection with *C. viscooides*); unknown collector, possibly *Riedel s.n.* (C); 10 km S of Campo Alegre, *Hatschbach 42251* (MO); 22 km NE of Catalão, *Irwin et al. 25142* (DAV, MO, NY); Crominia-Mairipotaba, *Brooks et al. 80* (MO); Paracatu para Cristalina, *Duarte 9292A* (RB); Serra de Caldas, *Hatschbach 38746* (DAV). Minas Gerais: *Brade 13579* (RB), *Glaziou 19825* (C), *St. Hilaire 595* (F-fragment ex P), *St. Hilaire 597* (F-fragment ex P); 3 km W of Cantoni, *Irwin et al. 27209* (DAV, MO, NY); Ad Contendas, *Martius s.n.* (M); Estrada Curvelo-Corinto, km 40, *Ferreira & Marques 34* (SP); 17 km SW of Gouvêia, *Anderson et al. 35615* (UB); Joaquim Felício, *Silva et al. s.n.* (F); Lagoa Santa, *Barreto 2599, 2600* (F), *Warming 1662* (C-2 sheets), *Warming 1665* (C); Município de Jaboticatubas, *Joly et al. 4590* (SP), *Samir et al. 2847* (SP); Nova Ponte, *Stehmann & Teixeira 1063* (SP); Paracatu, *Glaziou s.n.* (F-fragment ex P), *Irwin et al. 25967* (DAV, MO, NY); Parãopeba, *Heringer 3874* (UB); Santa do Riacho, *Forero et al. 7994* (SP); Serra do Espinhaço, *Hatschbach 27795* (MO); 23 km N of Uberaba, *Goodland 3162* (UB); Cidade de Uberana, *Regnell III. 1049* (A, S-3 sheets, US-2 sheets); "Uniccate," *Irwin & Soderstrom 5480* (UB); Várzea de Palma, *Duarte 7456* (NY, RB).

Chamaesyce setosa has long been poorly understood. It was first proposed as a variety of *Euphorbia selloi* by Boissier (1862). Mueller Argoviensis (1874) elevated it to species status within *Euphorbia*, but subsequent authors have questioned this disposition or otherwise continued to confuse these two demonstrably distinct taxa. Herbarium specimens of these two taxa are frequently misidentified. The situation is exacerbated by the problematic nature of historically and nomenclaturally significant specimens.

Sellow specimens attributable to *C. setosa* have not been located in the course of this study, nor has the sheet of *Pohl s.n.* reported

TABLE III
COMPARISON OF *Chamaesyce setosa* AND *C. selloi*

Character	<i>C. setosa</i>	<i>C. selloi</i>
Leaves	Dry darker	Dry lighter
Stems	Often woody	Rarely woody
Stems	Sparsely branched	Highly branched
Leaves	Often entire	Usually serrate
Glomerules	Terminal position	Axillary and terminal positions
Appendages	Erect	Perpendicular to rim of cyathium to erect
Appendages	Truncate	Reniform
Distribution	Central Brazil	Southern Brazil to northern Argentina

to be at W. However, *Pohl 1674*, from K, matches descriptions of this taxon by Boissier (1862) and Mueller Argoviensis (1874), who also cites this specimen. We do not know if *Pohl 1674* is truly a duplicate of Boissier's syntype, but it is possible that Pohl's collection number was misplaced on the material studied by Boissier. Likewise, *Riedel s.n.* could not be located at LD nor at LE. A specimen at C, however, collected in Goiás but without documentation as to the collector, is perhaps a Riedel collection, judging by the handwriting; it is possible that the specimen is an isosyntype. We have also seen *Regnell III. 1049* from A, S, and US which is cited by Mueller Argoviensis (1874) as "*Regnell n. 1049*, Lund." Our concept of *C. setosa* is therefore based on the descriptions published by Boissier and Mueller Argoviensis in concert with *Pohl 1674*, the presumed *Riedel s.n.* collection at C, and *Regnell III. 1049*. Until unequivocal syntypes emerge from the fog of history, we feel unable to designate a lectotype with confidence.

Others have peered into the fog and reached conclusions at variance from ours. Rambo (1960), in a note on *E. selloi*, stated: "I do not know what is meant by *E. setosa* (Boiss.) M. Arg., l.c., and *E. chamaerhodos* Boiss.; but we suspect they are all the same as the present species," i.e., *E. selloi*. Rambo's study was based on specimens from Rio Grande do Sul and neighboring Santa Catarina, but *C. setosa* does not occur that far south. Following Rambo's lead, Allem and Irgang (1975) placed *E. setosa* in synonymy with *E. selloi*, citing as evidence a specimen annotated by Croizat; the specimen in question, however, proves to be *C. selloi* and not *C. setosa*. Again, since Allem

and Irgang's study was based on specimens from Rio Grande do Sul, none were of *C. setosa*.

On the other hand, Subils (1977) misapplied *C. setosa* as an element of the Argentine flora. She treated it as a variety of *E. selloi*, with a range extending northward to central Brazil. However, all Argentine specimens cited by Subils prove to be *C. selloi* rather than *C. setosa*.

The qualitative characters in Table III readily distinguish *Chamaesyce setosa* from *Chamaesyce selloi*.

***Chamaesyce tamanduana* (Boiss.) M. P. Simmons & W. J. Hayden comb. nov. (Figs. 1C, 6G)**

Euphorbia tamanduana Boiss. in Centuria Euphorbiarum 4. 1860. TYPE: BRAZIL. Bahia: Tamandua, Jacobina, and St. Thorne, *Blanchet 3841* (LECTOTYPE (designated here), G; ISOLECTOTYPES, BM, F—fragment ex P).

Aerial stems several per rootstock, usually annual (sometimes persisting longer), slender, erect or ascending, relatively sparsely branched, to 10 cm long, 0.8–1.2 mm diam. at base, densely short-crispate to short-velutinous; stem trichomes uniseriate, multicellular, white, 0.2–0.7 mm long. Leaves either cataphylls or foliage leaves, strictly opposite; cataphylls small, round-oblong, deciduous; foliage leaves largest at mid to upper stem; blades ovate-elliptical, 16 × 8 mm, pilose (densely so on abaxial surface, less so on adaxial surface); both surfaces dark green; base somewhat oblique; margin entire; apex acute to rounded; petiole 1 mm long; stipules connate, persistent, broadly triangular, ca. 0.3 mm long, strigose abaxially, tufted straight-hir-

TABLE IV
COMPARISON OF *Chamaesyce tamanduana* AND *C. viscoides*

Character	<i>C. tamanduana</i>	<i>C. viscoides</i>
Stem pubescence	Short crispate to short velutinous	Long hirsute-velutinous
Stem trichomes	0.2–0.7 mm long	1.3–2.3 mm long
Leaf base	Somewhat oblique	Distinctly oblique
Leaf color (dry)	Dark green	Light green to dark brown
Appendages	Papillate	Smooth
Appendages	Unequal size and shape	Unequal size, similar shape
Styles	0.7 mm long, short crispate	1 mm long, glabrous (sometimes short hirsute-velutinous)
Distribution	Central Bahia	Goiás to Minas Gerais

sute adaxially. Cyathia on distal portions of stems, solitary, in dichasial or pseudomonopodial positions; peduncles 1.8–2.6 mm long; involucre campanulate to somewhat hemispherical, externally short crispate-pubescent to short-velutinous, 1 × 1.2 mm at mouth; primary lobes 5, keeled, entire, white-ciliate; glands 4, transversely oblong, drying dark brown, white-ciliate on inner side; gland bases short crispate-pubescent; appendages 1.5 mm long, of unequal widths, planar, perpendicular to rim of cyathium, glabrous, repand, papillate, white; wider appendages 2, rounded, 1.6–2.6 mm wide at apex; narrower appendages 2, oblong to weakly obovate, 1–1.4 mm wide at apex. Staminate flowers about 30. Pistillate flower with gynophore crispate-pubescent; ovary somewhat crispate-velutinous; styles 0.7 mm long, somewhat crispate-pubescent, connate basally, lower portion erect, bifid for ½ of length, tips recurved; stigmas clavate. Capsule somewhat crispate-pubescent, 3 mm long, approximately 2.6 mm wide; trichomes short, uniseriate, multicellular, white. Immature seed subovoid, 1.8 × 1.1 mm, rugose, white.

Habitat.—Unknown, presumably cerrado.

Distribution.—Brazil, known only from Bahia near Jacobina (Fig 15).

Phenology.—Unknown.

Specimen examined. BRAZIL. Bahia: Tamandua, Jacobina, and St. Thome, *Blanchet 3841* (BM, F—fragment ex P, G).

Boissier (1860) cited the holotype, *Blanchet 3841*. The sheet from BM consists of but two stems, while that from G has numerous stems and cyathia including the only known capsule and an immature seed.

The sheet at G was therefore chosen as the lectotype because Boissier worked at G and undoubtedly saw this specimen with superior diagnostic material.

Chamaesyce tamanduana, known from but a single collection, is very similar to *Chamaesyce viscoides*; however, the two species are demonstrably distinct and their differences are contrasted in Table IV. These species occur in adjacent states of Brazil, but the nearest known specimens of *C. viscoides* were collected about 475 miles away from *C. tamanduana*. Though known from but a single collection in 1845, *Chamaesyce tamanduana* proves to be a distinct species. This species is very rare; the absence of collections for over 150 years suggests that it may indeed be extinct.

***Chamaesyce viscoides* (Boiss.) M. P. Simons & W. J. Hayden comb. nov. (Fig. 6A)**

Euphorbia viscoides Boiss. in *Centuria Euphorbium* 4. 1860. HOLOTYPE (n.v.): BRAZIL. Camapua, *Riedel s.n.* (LE).

Aerial stems 1–7 per rootstock, apparently annual, slender, erect, sparsely branched, (7)15–25(30) cm long, 0.7–2 mm diam. at base, sparsely to densely hirsute-velutinous; stem trichomes uniseriate, multicellular, white, occasionally with yellowish deposits at crosswalls, 1.3–2.3 mm long. Leaves either cataphylls or foliage leaves, strictly opposite; cataphylls smaller, round-oblong, deciduous; foliage leaves largest at mid to upper stem; blades ovate-elliptical, (15)20–26(33) × 8–12(15) mm, sparsely to densely pilose; adaxial surface drying pale green to brown or blackish; abaxial surface somewhat lighter;

base distinctly oblique; margin entire; apex acute; petiole 1–2 mm long; stipules connate, persistent, broadly (sometimes narrowly) triangular, 0.3–0.4 mm long, sparsely to densely hirsute abaxially, occasionally tufted-hirsute adaxially. Cyathia on distal and sometimes basal to middle portions of stems; solitary, in dichasial or pseudomonopodial positions; peduncles 2–5(13) mm long; involucre campanulate or sometimes hemispherical, externally short hirsute-velutinous, 1.3–1.6(2.1) × 1.6–2(2.6) mm at mouth; primary lobes 5, keeled, entire, white ciliate; glands 4, transversely oblong, drying light to dark brown to green, densely white ciliate on inner side; gland bases short hirsute-velutinous; appendages obovate-rounded, unequal (to somewhat larger), 1–2.5 mm long, planar, perpendicular to rim of cyathium, glabrous, repand to erose, white (sometimes pink). Staminate flowers ca. 30. Pistillate flower with gynophore 2.3 mm long at maturity, short hirsute-velutinous; ovary pubescence short, uniseriate, multicellular white hirsute-velutinous; styles 1 mm long, glabrous to sparsely short hirsute-velutinous, connate basally, lower portion erect, bifid for 1/3 of length, tips recurved; stigmas clavate. Capsule hirsute-velutinous, 2.7–3.3 mm × 3–3.3 mm wide; trichomes short, uniseriate, multicellular, white. Seed subovoid, ± tetragonal, 1.8 × 1.1 mm, rugose-punctate, brown; base truncate.

Habitat.—Cerrado, especially over serpentine and mafic substrates.

Distribution.—Brazil, from central and southern Goiás to western Minas Gerais (Fig. 15).

Phenology.—Flowering and fruiting year-round.

Specimens examined. BRAZIL. **Without specific locality:** *St.-Hilaire* 780 (A–fragment ex P, mixed collection with *C. nana*); Pouco do Ribeirão, *Glaziov* 22079 (A–fragment ex P, G–mixed collection). **Districto Federal:** Brasília e Niquelandia, *Pires et al.* 9670 (DAV). **Goiás:** *Burchell* 7205 (BR, K), *Weddell* 2623 (A–fragment ex P); Barro Alto, 11–12 km from town on rd. running SW through area of serpentinized peridotite, *Brooks & Reeves* 677 (K); Cana Brava, area between two chrysolite mines, *Brooks et al.* 445 (K); Cavalcante, *Burchell* 7660 (BR, K); Gammeleira, *Pohl* 2179 (W); Gaueuelevia, *Pohl & Burchell s.n.* (G); 35 km (by rd.) N of Goianesia, *Brooks et al.* 122 (MO); Macedo, ca. 15 km N of Niquelandia, *Brooks et al.* 193 (MO); Município Rio Verde, Cad. Alta, Faz. Eugauo, *Macedo* 2663 (MO, S, US); Niquelandia, south-

ernmost ultramafic hill of Tocantine complex, *Brooks et al.* 312 (MO); San Antonio de Laguna, *Brooks et al.* 115 (MO); Serra do Caiapó, roadside in cerrado ca. 20 km S. of Caiapônia on rd. to Jataí, *Irwin & Soderstrom* 7622 (UB); 9 km from estrada Caiapônia–Aragarças, *Fonseca & Onishi* 1042 (UB). **Minas Gerais:** Município Campina Verde, Botafogo, *Macedo* 626 (S).

Chamaesyce viscoidea is a poorly collected species known primarily from the province of Goiás, Brazil. The above description differs from that by Boissier and Mueller Argoviensis in which the cyathial involucre is described as campanulate; the available material shows they may also be distinctly hemispherical, e.g., *Macedo* 626. Also the leaves do not necessarily dry blackish but also pale green to gray or light to dark brown. An anomaly is evident in *Irwin & Soderstrom* 7622, in which a single stem bears a ternate node, reminiscent of *Chamaesyce potentilloides*.

Acknowledgments

We wish to thank the curators and staff of the following herbaria for providing loans or photographs of specimens: A, B, BA, BAF, BM, BR, C, CTES, DAV, E, F, FL, G, GB, GH, HAS, ICN, JE, JEPS, K, L, LD, LIL, LP, M, MICH, MO, MU, MVFA, NY, RB, RSA, S, SI, SP, U, UB, UC, US, W, WIS, WU. Grady L. Webster generously provided fluid-preserved specimens of *C. potentilloides*, and Antonio C. Allem and Michael J. Huft shared useful information in early stages of this work. We thank Kevin C. Nixon and Lawrence M. Kelley for providing constructive criticism of the phylogenetic section. Betty Tobias was indispensable in obtaining interlibrary loans for our use. Geoffrey Levin, Grady Webster, and an anonymous reviewer made a number of constructive suggestions for improvement of the text. Financial support was provided by the University of Richmond Undergraduate Research Committee and the D. A. Kuyk endowed chair research fund.

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