

THE NEW WORLD SPECIES OF CYNANCHUM L.  
SUBGENUS MELLICHAMPIA (A. GRAY EX S. WATS.)  
WOODS. (ASCLEPIADACEAE)

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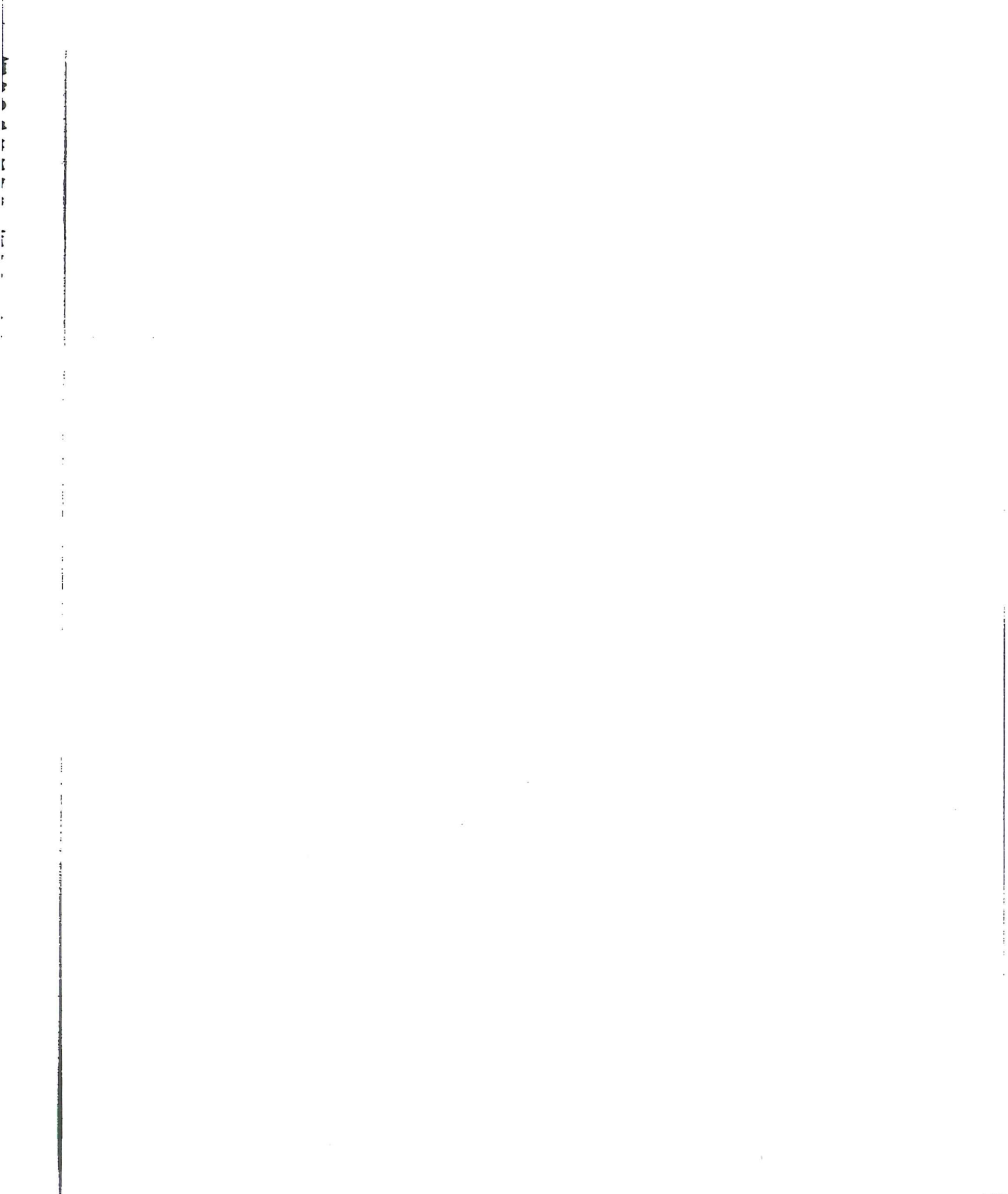
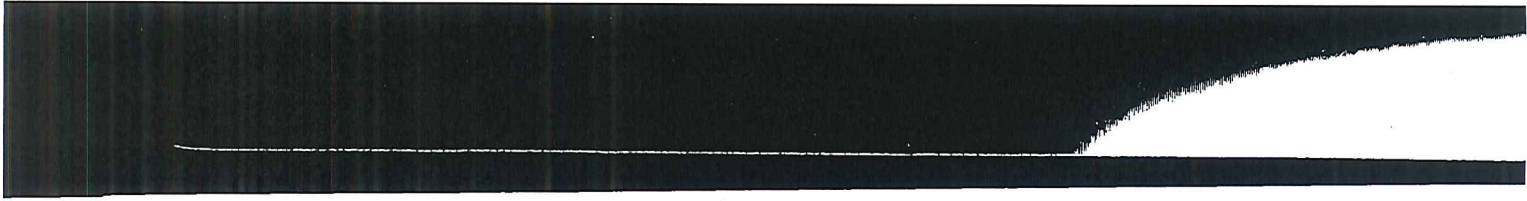


## ABSTRACT

This monograph comprises a taxonomic study of Cynanchum L. subgenus Mellichampia (A. Gray ex S. Wats.) Woods. (Asclepiadaceae), a group of tropical and subtropical, perennial, herbaceous, twining vines with milky sap. The study is based upon the examination of dried plant specimens from 32 European and American herbaria.

Subgenus Mellichampia is understood to include 11 species (including 2 species and 2 varieties described as new) in 4 sections, ranging from southern South America to the northcentral United States. The largely South American section Roulinia, closely related to paleotropical Cynancha of the Cynoctonum alliance and putatively the most primitive section of subgenus Mellichampia in the New World, consists of 3 more or less geographically restricted riparian species and a fourth species, Cynanchum montevidense Spreng., widely distributed from Jamaica and Panama south to the vicinity of Buenos Aires, Argentina. Section Metalepis, comprising 2 widely disjunct species of southern South America and Central America and the West Indies, is considered to be a relatively ancient group of uncertain affinities. Four species are recognized in the largely Mexican and Central American section Mellichampia: C. racemosum (Jacq.) Jacq. with 6 varieties is found from northern Colombia and Venezuela to southern Texas in the United States, while C. jaliscanum (Vail) Woods., C. foetidum (Cav.) H.B.K., and C. ligulatum (Benth.) Woods. are more narrowly distributed in the Mexican highlands, the last species extending into southern Arizona in the United States. Finally, C. laeve (Michx.) Pers., of the monotypic section Ampelamus, is a rather weedy species of temperate North America.

Nine species are treated in full. However, because the affinities with Mellichampia of the remaining two species, Cynanchum cubense (A. Rich.) Woods. and C. laeve, were not originally suspected, herbarium material sufficient for critical study was not obtained. In addition, Roulinia parviflora Decne. is excluded from subgenus Mellichampia, although its transfer to Cynanchum as well as a new name within that genus are proposed.



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## INTRODUCTION

Cynanchum subgenus Mellichampia is one of many infrageneric taxa created by Woodson (1942) in his controversial paper, "The North American Asclepiadaceae: Perspective of the Genera." Of some 85 segregate genera reviewed by Woodson, only nine were retained by him. But, whereas his consolidation of the genus Asclepias was based upon a critical investigation of the segregates in question, his solution to similar problems of generic inflation in the Cynanchum complex was, by his own admission, founded as much upon analogy with Asclepias as upon study of Cynanchum. A more detailed evaluation of Woodson's scheme, especially as it relates to subgenus Mellichampia, is given below.

As here understood, subgenus Mellichampia comprises 11 species (including 2 species and 2 varieties described as new) in 4 sections, ranging from southern South America (the vicinity of Buenos Aires, Argentina) to the north-central United States. Nine of those species are treated fully here. Because the affinities of the remaining two species (Cynanchum laeve (Michx.) Pers. and C. cubense (A. Rich.) Woods.) with Mellichampia were not originally suspected, herbarium material sufficient for critical study was not obtained. However, they are included in the key to the species, and their relationships to other members of Mellichampia are briefly discussed. Roulinia parviflora Decne. is excluded from subgenus Mellichampia.



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#### MORPHOLOGY

**Habit.** All species of Mellichampia are perennial, herbaceous to suffrutescent, twining vines with milky sap. No secondary growth is known to occur above ground, but the mature stems become more or less lignified before dying back at the end of the growing season. One herbarium specimen examined bears a cylindrical, woody rootstock. The stems possess a hollow pith (about  $\frac{1}{2}$  the diameter of the stem) and a ring of subepidermal bundles of bast fibers visible externally as numerous parallel ridges or striations. Bast fibers have been reported in the Asclepiadaceae by Metcalfe and Chalk (1950), Woodson (1954), and Stevens (1976).

**Indument.** Indument, when present on the vegetative parts, is of soft, uniseriate, multicellular hairs, which may be found on stems, petioles, leaf veins, and all parts of the inflorescences. The entire subgenus is remarkable for the conservative nature of the pubescence. All taxa, regardless of habitat, possess closely puberulent to tomentulose inflorescences and, to a lesser degree, petioles. Plants of Central and North America exhibit, in addition, a very delicate pubescence on stems and leaves. The stems are puberulent in decussate lines above the petioles and the leaves only sparingly so, with somewhat stiffer hairs, on the veins of either or both surfaces. Despite seasonal aridity of the habitat, such pubescence is not impressively functional, although perhaps it does provide some protection for delicate young stems and leaves. The pubescence of the inflorescence is one of the most stable characters



of the entire subgenus.

In addition to trichomes, all members of subgenus Mellichampia are consistently beset with glands in three places: on the nodal, inter-petiolar ridge, especially at the base of the petioles (2-6 per ridge), on the midvein of the upper leaf surface at its junction with the petiole (4-12 in a tight cluster), and in the throat of the calyx tube at and just below the sinuses (mostly 1-2 per sinus). In appearance, the glands are narrowly to broadly conic to digitate, dark and rubbery, and no more than 1 mm in length. They are especially prominent on new growth, tardily drying and deciduous. The number and distribution of glands within Mellichampia is mostly quite stable and of little taxonomic value within the subgenus.

Leaves. The leaves of all species of Mellichampia are opposite, chartaceous, ovate to ovate-lanceolate, with more or less cordate (to rounded) bases, entire margins, and adaxially canaliculate and at least distally puberulent petioles about half or more as long as the blades. In all species the leaf blades dry dark on the upper surface and remain paler beneath. Those of section Roulinia and section Metalepis are glossy and entirely glabrous, while those of section Mellichampia and section Ampelamus are dull and sparingly pubescent on the veins. The venation is plane above and raised beneath. The pattern of tertiary venation is reticulate varying to reticulate-scalariform (sensu Melville, 1976) in the Mexican and Central American species. Stipules are wanting but an inter-petiolar ridge is universally present, possibly representing ancestral stipular structures already lost at the evolutionary inception of the Asclepiadaceae.

Inflorescences. The inflorescences of many New World Asclepiadaceae are highly evolved and complicated structures derived directly or indirectly from a cymose type. Their point of attachment to the axis indicates further complexity, for the peduncles arise directly adjacent to one of each pair of opposite petioles, not from the leaf axils. Holm (1950) devoted much attention to this condition in the genus Sarcostemma, interpreting the main axis of the plant as sympodial and the inflorescences terminal. Woodson's (1954) interpretation of the inflorescences of Asclepias was fundamentally the same.

The nodal, interpetiolar inflorescences of Mellichampia are racemose, that is, scorpioid cymes or cincinni. With exceptions so few as to be called aberrancies, they are unbranched, bearing two pedicels at each node of the straight rachis and elongating regularly and rather indefinitely to as much as 15-20 cm. The small, more or less scarious bract at the base of each pedicel is often accompanied by one or two auxilliary bractlets which suggest a reduction and compaction of the asclepiad cyme resulting in these racemes. Peduncles are generally a little shorter than the petioles. Pedicels are evenly spaced along the rachis and are moderately stout, averaging 10 (5-20) mm in length. The numerous pedicel scars are circular, about 1 mm in diameter, with a single circular bundle scar. The even more highly specialized inflorescences of section Metalepis are discussed under Cynanchum ekmanii.

Perianth. The calyx is synsepalous in subgenus Mellichampia and rotate or campanulate in conformation to the shape of the corolla. (The calyx lobes remain rather stiffly erect in Cynanchum ekmanii.) The tube is indistinct, usually little more than 0.5 mm long, and generally bearing the same pubescence as the pedicels. The lobes are imbricate in bud, glabrous or glabrate, membranaceous to thin-chartaceous, more or less oblong to ovate with rounded apices and with the margins usually ciliate at least basally. In section Roulinia the calyx is about half or less as long as the corolla, but in section Mellichampia it tends to be somewhat greener and foliaceous and acquires a more prominent aspect due to the reduction of the corolla. Throughout the subgenus, corolla aestivation is contorted and the lobes overlap to the right in bud (externe visum). In addition, the corollas are always deeply cut, the five lobes always exceeding the tube, and rotate to campanulate in shape, glabrous to variously pubescent, and in color some shade of purple, green or white, often with white or yellow streaks on the lobes within.

Crown. The crown of subgenus Mellichampia is showy and petaloid, whitish in color, and invariably drying paler than the corolla, from which it is strongly exerted. It is inserted in the corolla throat at the junction between the corolla and the short



tube formed by the united staminal filaments. The crown is composed of 5 segments variously lobed at the summit and united at their bases into a short tube here designated the annulus. The primary form of the segments (and of the crown in general) is laminar, i.e., dorsiventrally flattened. A secondary, three-dimensional form is created by the segments becoming grooved within or the segment margins folded toward or away from the axis, or by the adaxial attachment of the annulus to the highly reduced staminal filaments.

One is accustomed to reading of a "staminal crown" in the Asclepiadaceae, and in the genus Asclepias, the association of the hoods with the staminal filaments or "column" is clear. The morphology of the Asclepias crown was elucidated developmentally at least as early as 1902 by Frye: "The filament pushes out on its dorsal side a crescentic protuberance...destined to become the hood." In Asclepias, the structures collectively referred to as the crown or corona comprise a double series, with the horn arising on the hood and not separately on the column. In other genera, such as Sarcostemma and Matelea, two and even three series of coronal structures are independently adnate to the corolla and androecium, and accurate developmental and histological characterization becomes more difficult. In an attempt to standardize coronal terminology, Woodson (1941) characterized the outer corona or "faucal annulus" as of corolline origin. Yet Holm (1950), in his developmental studies of Sarcostemma, was unable to confirm this. Early association of the annulus with both corolla and androecium makes it unclear to which floral series it pertains. Furthermore, although Woodson's restriction of the term "corona" to "various elaborations or enations of the staminal filaments only" clearly fits the hoods of Asclepias and the corona vesicles of Sarcostemma, its application to the crown of Mellichampia is problematical. Morphologically the Mellichampia crown may be construed as homologous to the Asclepias hood, however, like the faucal annulus of Sarcostemma, it is inserted at the junction of the corolla and androecium and cannot clearly be referred to either.

The Apocynaceae, the family ancestral to the Asclepiadaceae, are agreed to possess a corolline crown, and anatomical studies (Mulay et al, 1965) have shown the same for members of the Periplocoideae, a group transitional between the Apocynaceae and the true pollinium-bearing Asclepiadoideae. According to Sawfat (1962), both corolline and staminal crowns exist among the species of Secamone, also a transitional group, with four rather than two pollinia per anther, usually considered to be among the most primitive genera of Asclepiadoideae. Sawfat suggests that the evolution of the crown may have followed several different developmental lines to produce the most specialized forms in the Asclepiadaceae. Be that as it may, it is clear that Mellichampia and Asclepias, in regard to their crowns, are very similar. Although the Mellichampia crown is loosely termed "staminal" in this study (and in agreement with the related literature), it is emphasized that its point of origin between corolla and androecium remains to be critically examined.

Gynostegium. The term "gynostegium" refers to the structure in the center of the asclepiad flower formed by the fusion of the anthers to the more or less expanded stigma head. It is analogous to the column of the Orchidaceae and is a structural prerequisite to the formation of the translators (discussed below), in which an even more elegant fusion between parts of the androecium and gynoecium occurs. The sequential ontogeny of gynostegium and translators was first elucidated by R. Brown in 1810, and his description of those fascinating events is quoted in full by Woodson (1954).

In subgenus Mellichampia, the gynostegium is most often sessile, i.e., the staminal filaments are so highly reduced that the anthers themselves are attached more or less directly to the corolla tube. However, in three species (Cynanchum jaliscanum, C. ekmanii, and C. cubense), the anthers are elevated above the corolla on a short stipe. The functional and evolutionary significance of such "stipitate" anthers is discussed under the species in question.

Woodson (1954) divides the tube of staminal filaments in Asclepias into two distinct parts with regard to terminology: that between the corolla and the crown is called the "column," while that between the crown and the anthers is called the "stipe." The distinction is particularly useful in Cynanchum subgenus Mellichampia, in which the insertion of the crown directly to the corolla throat eliminates the column entirely.



As in all milkweeds, the five anthers of the Mellichampiae possess corneous lateral margins which are contiguous with one another, each pair of margins or "anther wings" framing a vertical groove termed the "stigmatic slit." The stigmatic surface in milkweed flowers is receptive only at the base of the five stigmatic slits, and it is into one or more of the slits that pollinating insects must inadvertently insert pollinia for successful pollination to be achieved. The length and orientation of the stigmatic slits constitute important taxonomic characters especially at the species level. A cylindrical gynostegium is one in which the stigmatic slits are entirely vertical and parallel to the axis of the flower. In a conic gynostegium the stigmatic slits lie at some acute angle to the axis and converge upward to their meeting with the stigma head.

Other unique features of the anthers in Asclepiadaceae are "anther appendages," hyaline, dorsiventrally flattened prolongations of the anther connectives. The outline of these appendages has proven to be of limited value in separating species of subgenus Mellichampia.

The gynoecium of the Asclepiadaceae is bicarpellate and secondarily apocarpous, the carpels entirely free from one another except at the expanded stigma head, where they are connate to one another and adnate to the anthers, forming the gynostegium. The ovaries themselves, as well as the free portion of their styles, are buried within and often beneath the tube of staminal filaments and rendered further inaccessible by elaborations of the crown.

Translators. The "translator" or "translator apparatus" as here defined comprises a "gland" and two "translator arms" (horny, non-cellular structures secreted by the stigmatic surface) which are joined while the flower is still in bud to two "pollinia" (waxy masses of pollen grains cemented together by a lipid secretion of the tapetum). In subfamily Asclepiadoideae (s.str., Secamonoideae excluded) five yoke-like translators encircle the stigma head of each flower. Taxonomically and functionally (that is, from the point of view of botanist and plant), the translator apparatus has proven to be a very significant structure.

At lower levels of classification, translator morphology has not been relied upon very heavily. For example, with few exceptions, the translators of Mellichampia are so uniform as to be nearly indistinguishable from species to species, sometimes differing in the dimensions, but usually not in the proportions of their parts. Glands are rhombic to cylindrical; translator arms are broad and tangentially flattened ("ribbon-like"), oriented laterally from gland to pollinia, and inserted sub-apically on the pollinia. The pollinia themselves are also somewhat tangentially flattened (although not nearly as two-dimensional as those of Asclepias) and are elliptic in outline with rounded ends.

A few abrupt discontinuities in translator morphology suggest significantly different pollination systems for certain species. Cynanchum jaliscanum and section Metalepis possess extremely long translator arms and correspondingly elevated gynostegia, while the pollinia of C. ligulatum are semi-orbicular, only slightly longer than broad. With regard to pollination, the implications of these structural innovations are discussed under the species in question.

Fruits and seeds. The characteristic fruit of subgenus Mellichampia is a narrowly ovoid, smooth to wrinkled-striate, glabrous follicle, mostly greater than 8 x 2 cm. With very few exceptions, only a single follicle matures from any one flower. In Asclepiadaceae the number of follicles developing from a single flower appears to correlate to some degree with fruit size. For instance, the commonly single follicles of Mellichampia and Asclepias are large, while, in contrast those of the Metastelma complex (such as Cynanchum angustifolium Pers.) are quite slender, less than 1 cm broad, and not infrequently mature in pairs from a single flower. The lack of sufficient fruiting material is a chronic problem in the study of the milkweed family, and available collections of the present subgenus are no exception.

The seeds are numerous in each follicle, closely overlapping one another upon the placenta. They are strongly flattened, smooth to somewhat wrinkled, broadly pyriform in outline with rounded, coarsely and irregularly toothed bases and truncate apices. All seeds bear at their apex a coma of white to pale brown silky hairs 2-4 cm in length.



## HISTORY AND GENERIC RELATIONSHIPS

Cynanchum and its segregates

Linnaeus (1753) included five species in his original treatment of Cynanchum. Of those original species, according to Stearn (1971), only two (C. acutum and the apparently conspecific C. monspeliacum) have been retained in Cynanchum by all subsequent authors. Robert Brown (1810) transferred the remaining three of Linnaeus' species to Gonolobus Michx. (C. suberosum and C. hirtum) and Marsdenia R. Br. (C. erectum), but added about a dozen new taxa. Apparently Brown felt uncomfortable with his circumscription of the newly defined genus: "...it appears still to contain the elements of several genera: I shall therefore add the characters of all the species I am acquainted with, divided into such sections as will probably hereafter be considered distinct genera." Brown's six sections are distinguished largely by coronal morphology and include species with crowns simple (uniseriate) and double, tubular and deeply divided, petaloid as well as fleshy. Had Brown been aware of the American species of subgenus Mellichampia, he would have had no difficulty accommodating them as yet another section.

For better or worse, future workers took Brown at his word and, on the basis of minor variations in coronal structure and the shape of the corolla, subdivided Cynanchum into numerous genera, of which the most important, outside the New World Mellichampiae, are Vincetoxicum Moench, with small flowers and reduced, fleshy crowns included in the corollas, and the larger-flowered Cynoactonum E. Mey., with exserted, showy, cup-shaped or tubular crowns. Schumann (1895) restored the genus to the limits originally set by Brown and divided it into two more or less natural groups, section Vincetoxicum (including Brown's sections V and VI) and section Cynoactonum (including Brown's sections I through IV). In 1941, in his revised circumscription of the genera of North American Asclepiadaceae, Woodson brought more than 20 additional generic allies into a much expanded Cynanchum, including such taxa as Ditassa R. Br. and Metastelma R. Br. which had never before been interpreted as congeneric with Cynanchum, even in Brown's rather broad concept of that genus. The current state of consensus in Cynanchum taxonomy worldwide is immediately apparent in Airy Shaw's (1973) most recent statement as to number of species in that genus: "S.str., 5 E. Eur., temp. As.; s.l., ?150 trop. & temp."

## The role of the crown in the taxonomy of Asclepiadaceae

Despite extensive morphological studies of the Asclepiadaceae in the 19th and early 20th centuries and an intense current interest in the pollination biology of this unique and highly specialized entomophilous family, the Asclepiadaceae are little studied and poorly known taxonomically. As might be inferred from the foregoing brief taxonomic history of Cynanchum, the criteria for generic delimitation are probably the most troublesome of many problems impeding a satisfactory system of infrafamilial classification. At the root of this disorder is the staminal crown, or corona, which has seduced taxonomists since R. Brown first removed the Asclepiadaceae from the Apocynaceae in 1810, and which has been invested with a taxonomic significance greatly out of proportion to its morphological stability.

Brown's (1810) initial key to the genera of his new family set a pattern for infrafamilial classification that nearly all subsequent research, at least until Woodson's (1941) revolutionary study, has sanctioned. Endlicher (1838) immediately comprehended the strengths and weaknesses of Brown's classification scheme. "Genera nimis fortassis nuper multiplicata, serie artificiali e corollae forma et coronae stamineae indole, per tribus ut videtur satis naturalis, disposita sunt." The consensus is still much the same. Infrafamilial, suprageneric taxa, based on characters of the androecium, seem to be natural and have undergone few taxonomic changes. On the other hand, the many genera, defined chiefly by the staminal crown which varies greatly from species to species, are probably artificial. Bentham's (1873) analysis of infrafamilial classification agrees with Endlicher's. "Tribus praesertim ad



modificationes androecii bene limitantur, genera perplurima praesertim ad coronam quae de specie in speciem magnopere variat definita, nimis artificialia sunt, characteres meliores tamen adhuc non occurrere."

Schumann (1895) placed such emphasis on coronal morphology in his subdivision of the Asclepiadeae into subtribes that he was able to refer the monotypic genus Mellichampia to the Cynanchinae and the genus Enslenia to the Asclepiadinae; the unfortunate result is that the same species, described as both Mellichampia rubescens Gray and Enslenia ligulata Benth., is classified in two subtribes.

Since the work of Woodson (1941), it is generally accepted by American students of the Asclepiadaceae that the staminal crown might be put to better taxonomic use at infrageneric levels. Holm (1950) observed perceptively that the milkweed crown exhibits an evolutionary plasticity normally associated with vegetative characters in most other groups. And Woodson (1954) described his newly circumscribed Asclepias as a large genus with species exhibiting differences (e.g., alternate vs. opposite leaves) of a magnitude often used to define genera in other families of flowering plants. Bullock (1952) was expressing the same thought (and echoing Bentham (1873) in particular) when he noted that not only have floral and especially coronal characters been taxonomically overstressed, but characters of habit, root, and fruit have been largely unavailable and hence neglected. Shinnars (1950) also repudiated the "...heavy reliance on technical minutiae of reproductive parts as generic criteria...", suggesting recourse instead to vegetative features and characters of the inflorescence for satisfactory generic definitions.

To my knowledge, wherever workers have examined a generic complex of Asclepiadaceae monographically, the concept of the genus has been broadened to embrace the satellite genera. Such a view is persuasively discussed by N. E. Brown (1890) when he argues against the dismemberment of the large genera Stapelia L. and Caralluma R. Br. In each of them, the crown is indefinitely variable: "...it cannot, when taken alone, be implicitly relied upon for generic distinction. If the various forms be not so grouped under these two genera, then a large number of small and often monotypic genera would have to be made, especially if the coronal structure is made the basis of classification as hitherto, and taking each variation as of equal generic value." Brown expressed the same view again, in 1933.

Recent work on the leafless asclepiads of Madagascar has yielded changes of circumscription paralleling those of Woodson (1941) for the family in North America. Also, with regard to African species of Cynanchum, Descoings (1961) casts the staminal crown into further disrepute as the prime morphological index of generic distinctions. As well as placing several small African genera into synonymy with Cynanchum, he goes further to say that the number and size of the lobes that ornament the summit of the coronal cup or the coronal segments must be used with great prudence even at the level of species. The infraspecific variation can be of such a magnitude that numerous artificial taxa are frequently described from a single biological species. This has proven to be the case in the present study with regard to the two most widely ranging species, C. montevidense and C. racemosum.

#### Woodson's concept of Cynanchum in North America

In the present study, Woodson's (1941) subgenus Mellichampia is maintained (and enlarged to include two other of his subgenera, Metalepis and Ampelamus). However, I hasten to add that the opinion expressed with regard to the rank of Mellichampia in no way extends to the numerous additional genera that were included by Woodson in his greatly expanded Cynanchum. A full discussion of that question must await a critical examination of some additional large and difficult taxa, such as Ditassa and Metastelma. But it may not be amiss to say a few words on the subject before proceeding to Mellichampia itself.

If one is to merge genera such as Metastelma and Ditassa with Cynanchum (largely on the basis of their similar coronal structures), upon what ground could the genus Asclepias remain distinct? Metastelma, Ditassa, and Asclepias agree (and differ from Cynanchum) in their possession of lanceolate to elliptic leaves with cuneate bases, umbelliform cymes, and, in the majority of species, free crown segments;



this is a strong correlation of conservative (in this family) vegetative and floral characters that are likely under the control of disparate parts of the genome, suggesting that the taxa sharing those characters might well form a group more natural than Woodson's enlarged Cynanchum. One could argue that Asclepias and Ditassa with their double crowns share an ancestor from which one or both have diverged but a short way, Asclepias radiating in temperate and subtropical North America, Ditassa in subtropical and tropical South and Central America. The only major evolutionary advances that may be credited to Asclepias are the herbaceous habit, valvate corolla lobes\*, and the substitution of hymenopteran for dipteran pollination, which has led to secondary morphological characters that have obscured the essential underlying similarities of their flowers and, in particular, their crowns. The correspondance of the ventral or inner crown segment in certain Cynancha to the horn of Asclepias was recognized by N. E. Brown (1902-03); and Ditassa oxypetala Decne. possesses a digitate inner crown lobe that is very like the horn of Asclepias.

Most American authors have adopted Woodson's (1941) treatment with regard to Metastelma and Ditassa, although their publications on Cynanchum largely have been limited to floristic works (e.g., Spellman, 1975) and a spate of new combinations (Spellman, 1973; Spellman & Morillo, 1976; Corell, 1977). It should be emphasized that many of the genera reduced to infrageneric rank by Woodson are centered in South America with only outlying species in Central and North America; with regard to those genera, Woodson's scheme has had mixed reception from workers in South America, where the biology of those groups is surely better known and understood. For instance, in a recent monograph of Tassadia Decne., Pereira (1977) countered Woodsonian doctrine to maintain that genus as distinct, principally on the basis of its axillary (rather than interpetiolar) inflorescence, an unusual and apparently highly modified and advanced condition. Other recent papers from South America (Alencastro et al, 1971; Pereira & Silva de Ferreira, 1975) indicate that many of Woodson's recommended consolidations have failed to gain acceptance there.

Although skepticism is apparent, my intent is neither to attack nor defend Woodson's (1941) treatment of the Cynanchum segregates outside subgenus Mellichampia, but only to make clear that the question is far from settled. In the paucity of hard evidence bearing on the status of segregates other than subgenus Mellichampia, it seems best, at least for the time being, to be not immoderate in any break with older tradition. Woodson's reevaluation of generic limits in North American Asclepiadaceae has stimulated new interest in the biology of milkweeds and has made the task of monographic work within the family more attractive by organizing many taxa into natural assemblages whatever their rank. Yet, his extravagant treatment also has stirred up new controversy, and if workers interested in the genus Cynanchum are to agree upon a stable precipitate, it will most likely be a generic concept very near that of Robert Brown, as it was limited and clarified from Linnaeus.

#### The subgenus Mellichampia

The species of subgenus Mellichampia constitute an easily recognized and defined, and apparently natural group which has escaped much of the taxonomic turmoil which marks the history of many Asclepiadaceae. Since the publication of the Prodromus (Decaisne, 1844), most species of the subgenus have been referred to the New World genus Roulinia. The name Roulinia Decne. is a later homonym of Roulinia Brogniart (1840) in the Liliaceae and was replaced by Rouliniella Vail in 1902. Decaisne distinguished Roulinia from Cynanchum on the basis of coronal insertion ("coron. foliolis fauci nec gynostegio insertis") and flattened stigma head ("stigmatate depresso...

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\*Corolla aestivation in Metastelma and Ditassa was considered by Schumann (1895) to be valvate. However, my own examination of representative flower buds of the former genus has determined the corolla lobes to be overlapping to the right at their extreme tips, a somewhat intermediate condition between contorted and valvate aestivation. The evolutionary distance between those two character states in this generic assemblage may not prove to be particularly significant.



nec apiculato"). As a generic distinction, the former character is baffling, for all species of Cynanchum with which I am acquainted, members of the Old World Vincetoxicum and Cynoctonum complexes especially, also have their crown joined to the corolla throat. In addition, the stigma heads of Central and North American Mellichampia (Roulinia) are no flatter than those of many Old World Cynancha. With the establishment of Roulinia, Decaisne had restricted Cynanchum to the Old World.

The genus Ensenlia Nuttall (a later homonym of a Rafinesque name) was established in 1818 with a single species (the North American Cynanchum laeve (Michx.) Pers.) distinguished from such closely related genera as Asclepias and Cynanchum by characters of habit, corolla shape, and, in particular, variations in crown morphology. Rafinesque provided the substitute name, Ampelamus, in 1819. Gray established the monotypic genus Mellichampia in 1887 for a Mexican species with large, maroon flowers and campanulate corollas, superficially quite remarkable, but in fact closely related to C. foetidum from Mexico. Several other members of subgenus Mellichampia had been variously referred to Cynanchum or Ensenlia before Decaisne's (1844) inauguration of Roulinia. Cynanchum ligulatum (Benth.) Woods., as will be discussed further, is based upon Ensenlia ligulata Benth., a taxonomic synonym of Mellichampia rubescens Gray.

As here defined, subgenus Mellichampia includes elements from three of Woodson's (1941) subgenera. Woodson included Rouliniella in his subgenus Mellichampia, but Cynanchum laeve was referred to the monotypic subgenus Ampelamus. The genus Metalepis, initiated by Grisebach (1866) for a single West Indian-Central American species (C. cubense), was also given independent subgeneric status.

#### The affinities of subgenus Mellichampia

There is no doubt in my mind that Rouliniella (Roulinia), Mellichampia, and Ampelamus (Ensenlia) are untenable entities at the rank of genus, and I fully agree with Woodson's decision to unite them with Cynanchum (but as comprising the single subgenus Mellichampia). Additionally, a cursory review of specimens of Cynanchum from the Old World tropics reveals many species that appear to possess all the morphological characteristics of tropical South American Rouliniella (i.e. section Roulinia of subgenus Mellichampia): stems glabrous; large, glossy, ovate-cordate leaves; racemose inflorescences; uniformly large and glabrous, often purplish, rotate corollas bearing erect, uniseriate, showy, petaloid, whitish crowns inserted in the throat. Closer investigation also discloses similarities with Rouliniella in the size, position, and form of the gynostegium, anther appendages, translators, and even stigma heads, all taxonomically significant characters, certainly at the generic level. Some Asiatic species, such as the Philippine endemic, C. suluense Schltr., are so close to section Roulinia in every significant morphological detail (except coronal incision) that the concept of Mellichampia may thus eventually have to be expanded to include some Old World taxa, in which case not only the circumscription but the correct name and rank of the group would require reexamination.

Such Old World species most closely allied to subgenus Mellichampia have often been segregated from Cynanchum as the genus Cynoctonum, mentioned above, which Meyer (1837) distinguished by their simple (i.e. uniseriate), as opposed to double, crowns; Endlicher (1838) and Decaisne (1844) also recognized Cynoctonum as distinct, but many subsequent authors were unable to find a sharp discontinuity from Cynanchum. Recent opinion has favored merger of those two genera (Schumann, 1895; N. E. Brown, 1902-03; Hutchinson & Dalziel, 1931).

Species of subgenus Mellichampia are like Cynoctonum in the possession of a simple, petaloid crown, but consistently differ in the depth to which the crown is cut. The Cynoctonum crown is generally cup-shaped or cylindrical (with or without internal ribs or wings on the tube) and divided at the summit into teeth or lobes; the crown of Mellichampia is more or less consistently deeply divided into five segments united only at the base, or the crown segments (Cynanchum laeve) are entirely free.

For convenience, I have described the Mellichampia crown as composed of five segments more or less united at their base and forming a short annulus. Such a crown may be derived from the tubular crowns so common in Cynoctonum. The direction of evolution is not entirely clear, but evidence based on morphological correlations and



geographic distribution suggests that the undivided or shallowly divided crown, relatively rare in New World Cynancha, represents the primitive condition. The Mellichampia annulus would be thus homologous to the Cynoctonum tube.

Comparing subgenus Mellichampia to other New World genera, it likewise becomes very tempting to speculate that the dominant trend in coronal evolution must indeed be toward the increased dissection of the crown into five free structures independently attached to the corolla or to the staminal filaments. In certain putatively advanced genera (e.g., Asclepias, Metastelma), free crown segments correlate strongly with umbelliform inflorescences and narrow leaves with cuneate bases, which are all probably derived conditions. Within subgenus Mellichampia itself, Cynanchum blandum and its allies, considered here to be the most primitive species assemblage, possess the least deeply divided crown, while the crown segments of the north temperate C. laeve are entirely free from one another.

The rank assigned to the Mellichampia complex ultimately depends upon its similarities to and differences from Cynanchum acutum L., the lectotype (Britton & Brown, 1913; Farr et al, 1979) of that Linnaean genus. Cynanchum acutum is a wide-ranging species of semi-arid regions of the Mediterranean and Near East. Its crown is deeply divided into five segments like that of Mellichampia. However, each coronal segment bears, attached to its adaxial wall, a second, inner segment; although such a double crown is not at all common in Mellichampia, it is exactly duplicated in one of its species, Cynanchum racemosum var. guatemalense (Dugand) E. Sundell, of Guatemala.

Cynanchum acutum may further be distinguished from both Mellichampia and Cynoctonum by its irregularly cymose inflorescences, which may be racemose, umbelliform, and paniculate on the same specimen, according to the number of flowers and the degree of meristematic activity at each node of the raceme. Numerous flowers at certain nodes create a raceme of umbels, and branching of the main axis of the raceme may elevate those umbels on rays (secondary peduncles), while additional rachis elongation within certain of the umbels further complicates the picture. Regardless of an appearance of irregularity verging on disorder, the inflorescence of C. acutum is probably not at any great evolutionary distance from that of subgenus Mellichampia, and its derivation from a more strictly racemose type (which may still be found in the Old World among the Cynoctonum alliance) is very likely.

Schumann (1895), in his rather broadly circumscribed genus Cynanchum, included C. acutum in section Cynoctonum. Indeed, Cynoctonum, in a stricter sense, with its more or less elongate racemes and cylindrical crown would appear to be very near the stem of both Old and New World Cynancha, the divergent groups differing principally in relatively minor features of crown and inflorescence.

Morphological evidence, geographical distribution, and pollination biology suggest that subgenus Mellichampia may occupy a rather primitive position in the phylogeny of New World Asclepiadeae. The pantropical Cynoctonum-Roulinia alliance has already been discussed, with particular reference to primitive and derived states of coronal morphology, and I would like here simply to summarize several other putatively primitive morphological character states common to most or all members of subgenus Mellichampia with contrasting character states to be found in other genera of New World Asclepiadeae. Interpretation of primitive states is based upon a cursory out-group comparison both to Old World Cynancha and to other genera of Asclepiadaceae, in-group correlation among primitive characters, and geographical distribution. The following character states of subgenus Mellichampia are suggested as primitive in New World Asclepiadeae:

- Twining habit (vs. herbaceous habit, Asclepias, Oxypetalum)
- Cordate leaf bases (vs. cuneate bases, Asclepias, Metastelma)
- Racemose inflorescences (vs. umbelliform, Asclepias, Sarcostemma)
- Crown insertion on the corolla (vs. on the column, Asclepias)
- Crown segments united at the base (vs. segments free, Asclepias, Metastelma)
- Crown serving role of both attraction (but without nectar) and manipulation of pollinators (vs. crown serving only to manipulate, Metastelma; or crown serving as nectar reservoir, Asclepias)
- Stigma heads flat to conic (vs. elongate, even exserted, and deeply bifid, (Araujia, Oxypetalum))



Translator arms simple (vs. ornamented, Oxypetalum)  
 Dipteran pollination (vs. hymenopteran or lepidopteran, Asclepias)

#### SECTIONAL RELATIONSHIPS AND DISTRIBUTION

Subgenus Mellichampia is here divided into four geographically and morphologically well defined sections, distinguished principally by the presence or absence of vegetative pubescence; the form, color, and size of the corolla; and the shape and especially the texture of the stigma head.

1. Sect. Roulinia (Decne.) E. Sundell, comb. & stat. nov.  
Roulinia Decne. in DC. Prodr. 8: 516. 1844.

Section Roulinia comprises four species almost entirely restricted to South America. The species are characterized by purplish (when mature), glabrous stems and leaves (although certain specimens of Cynanchum montevidense from the upper Amazon basin show a tendency toward puberulent stems) and by glossy to shiny leaf blades. Members of section Roulinia share comparatively large, purplish, rotate corollas, glabrous or (C. montevidense) pubescent in the throat below the crown with mixed unicellular and multicellular hairs. The corolla lobes are more or less lanceolate, 5-12 mm long. The relatively small, uniformly hispidulous corollas of the poorly known C. riometense suggest a possible link to section Metalepis. Exemplified by those of C. blandum, the corollas of section Roulinia, as already discussed, correspond closely to those of the Cynoctonum group of the Old World tropics and are here considered primitive within the subgenus in the New World. The stigma heads of section Roulinia are flat to depressed, pentagonal in outline with broadly rounded sinuses and a low, bifid umbo in the center. In texture they are considered smooth, although under high magnification minutely roughened in a somewhat areolate pattern.

Section Roulinia is largely restricted to low elevation, marsh and riverine habitats in South America east of the Andean cordillera. A single, wide-ranging species, Cynanchum montevidense, is found from Jamaica and Panama south to Buenos Aires. The remaining three species, C. blandum, C. rioparanense, and C. riometense, are more or less narrowly endemic to several widely scattered river basins in South America. Of the sections of subgenus Mellichampia in the New World, section Roulinia seems most closely related to the paleotropical Cynoctonum complex, and together they form a morphologically united, pantropical group of Cynancha which may well constitute one of the most primitive species assemblages, presumably originating in the Old World, in the subfamily Asclepiadoideae (Fig. 3).

2. Sect. Metalepis (Griseb.) E. Sundell, comb. & stat. nov.  
Metalepis Griseb., Cat. Pl. Cub. 179. 1866.

Section Metalepis comprises two widely disjunct and more or less narrowly endemic species (Cynanchum ekmanii & C. cubense) in the lowland tropics of South and Central America and the West Indies. Morphologically, its affinities lie with section Roulinia: the stems are glabrous and leaf blades both glabrous and glossy, and the stigma heads are flat and smooth. However, several unique morphological features, viewed in conjunction with geographic distribution, suggest that section Metalepis may be a very old group. The racemes are often organized into pseudo-panicles on an axillary branching system. The small, greenish to purplish corollas of both species are pubescent with appressed, unicellular hairs, and the anthers are elevated on a long stipe, while the translators exhibit a corresponding elongation of their arms. The morphology and taxonomy of section Metalepis are discussed in greater detail under C. ekmanii.

3. Sect. Mellichampia (A. Gray ex S. Wats.) E. Sundell, comb. & stat. nov.  
Mellichampia A. Gray ex S. Wats., Proc. Amer. Acad. 22: 437. 1887.

Section Mellichampia comprises four species of Central and North America characterized by soft stem and leaf pubescence, small greenish or whitish corollas



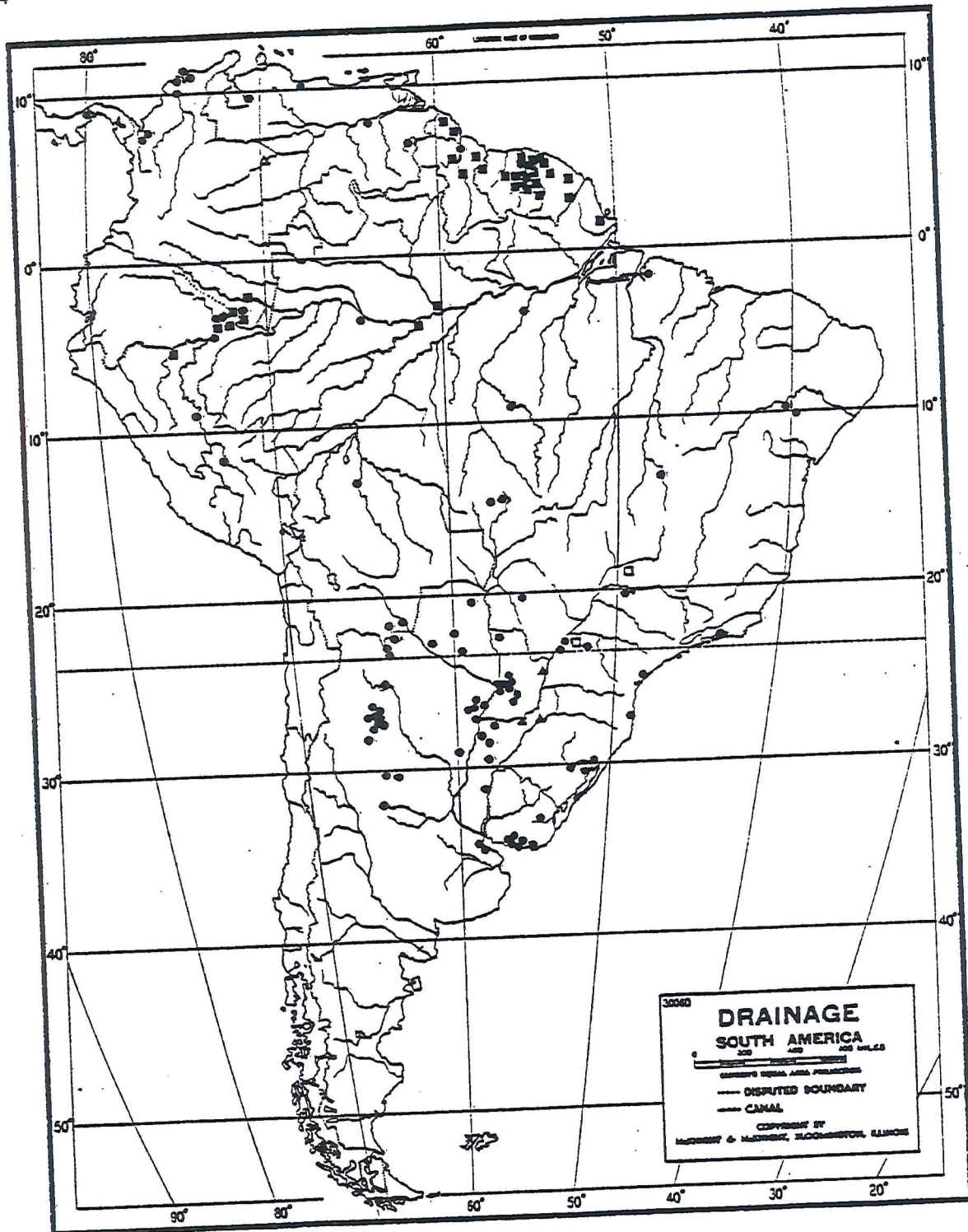


Figure 1. Collection localities for species of section *Roulinia* and for *Cynanchum ekmanii* of section *Metalepis*. Solid squares, *C. blandum*; open squares, *C. rioparanense*; open triangle, *C. riometense*; solid circles, *C. montevidense* (two stations in Jamaica are not indicated); solid triangles, *C. ekmanii*. (This material is reproduced through special permission from McKnight Publishing Company.)



(with the exception of Cynanchum ligulatum), and manifestly papillate stigma heads. The corollas of section Mellichampia are presumably derived from an ancestral type resembling those of section Roulinia. One transitional species seems to support such an assumption; Cynanchum racemosum is intermediate both geographically and with respect to corolla morphology, exhibiting the changes in color and size associated with section Mellichampia but retaining the rotate form and glabrous lobes of C. blandum of section Roulinia. Of the remaining three species, the corollas of C. jaliscanum are similar to those of C. racemosum, while C. foetidum is further modified by its campanulate corollas pilose with multicellular hairs on the lobes within. Secondary enlargement, in response to a change in pollinators, is the only plausible explanation for the showy corollas of C. ligulatum, the form and pubescence of which agree exactly with C. foetidum.

The stigma heads of section Mellichampia are invariably papillate. However, in shape (viewed laterally), they vary from broadly rounded in Cynanchum racemosum and C. jaliscanum to domed or conic in the other species. In outline (as viewed from above) the stigma heads give the appearance of a central dome with five radially oriented rays terminating at the glands. (The acute sinuses are indented halfway to the center of the stigma head). This contrasts sharply with the shallowly indented pentagonal disc of section Roulinia. Cynanchum racemosum, intermediate, as stated, between sections Roulinia and Mellichampia, appears to be transitional in stigma head morphology as well, retaining a scarcely elevated stigma head similar to the South American species but with the papillate texture of the Mexican group.

Section Mellichampia appears to have exploited coastal and upland habitats with ample summer rainfall and a more or less prolonged dry season. It has apparently undergone moderate radiation in the Mexican highlands, where three species are rather narrowly distributed in areas of higher elevation in southern and western Mexico, with a single species (Cynanchum ligulatum) reaching southwestern Arizona. One species, C. racemosum, occurs from the coastal slopes of Colombia and Venezuela through Central America and eastern Mexico into western and central Texas; a single specimen is also known from Cuba.

4. Sect. Ampelamus (Raf.) E. Sundell, comb. & stat. nov.

Ampelamus Raf., Amer. Monthly Mag. & Crit. Rev. 4: 192. 1819.

Section Ampelamus comprises a single species, Cynanchum laeve, a weed of disturbed areas, river banks and thickets from southcentral to northcentral United States west of the Appalachian Mountains. Both geographically and morphologically section Ampelamus is strongly tied to section Mellichampia. Vegetatively, members of the two sections are indistinguishable. However, with regard to inflorescence and especially to floral morphology, C. laeve exhibits several profound evolutionary changes. The racemose inflorescences elongate rather tardily, so that they appear umbellate in earliest stages of development. The corollas resemble those of C. foetidum in color, form and size, although they are glabrous within. The shape of the stigma head is strongly conic, but, in an apparent reversal of evolutionary direction, the texture is smooth. The most significant and informative discontinuity from section Mellichampia (and from all other members of the subgenus) is the division of the crown into five entirely free segments, each segment in turn deeply divided into a pair of ligulate lobes.

#### REPRODUCTIVE BIOLOGY

Numerous and sophisticated studies of life history and pollination relationships for various species of Asclepias have furnished valuable information about their reproductive biology. However, comparable studies of most other milkweed genera are lacking, and what little is known of the reproductive biology of Cynanchum subgenus Mellichampia is derived by inference alone.

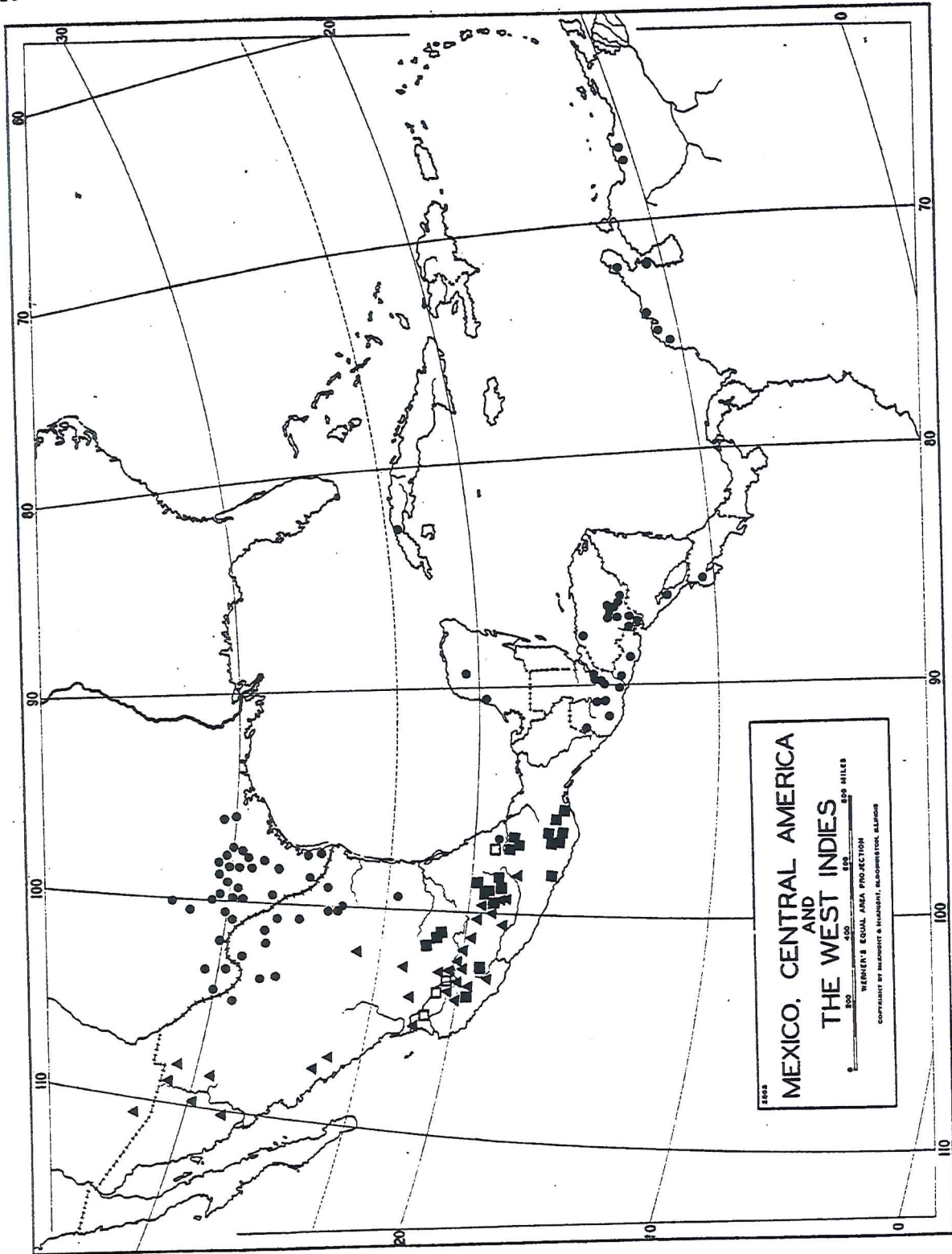


Figure 2. Collection localities for species of section Mellichampia. Solid circles, Cynanchum racemosum (only one locality per county is indicated in Texas, U.S.A.); open squares, C. jaliscanum; solid squares, C. foetidum; solid triangles, C. ligulatum. (This material is reproduced through special permission from McKnight Publishing Company.)



Delpino (1867) made the valuable observation that those asclepiads whose nectaries are opposite the stamens (and alternate with the glands), such as Asclepias and Hoya, are adapted to disperse their pollinia on the legs of insects, whereas those whose nectaries are alternate with the stamens (and opposite the glands), like Cynanchum, Matelea, and Stapelia, disperse their pollinia on insects' proboscides. Galil and Zeroni (1965) demonstrated the five stigmatic slits (i.e. the inner walls of the anther wings) of Asclepias curassavica to be lined with secretory tissue and to be the only nectaries of the flower. The same is very likely to be true of subgenus Mellichampia, which lacks the coronal hoods of Asclepias so often mistaken for the nectaries themselves but in which the nectar produced by the anther wings accumulates. In Mellichampia, nectar presumably produced in the stigmatic slits either remains within the slits or, in certain species, accumulates in a small, cup-shaped pocket-reservoir directly below each slit. An insect removing its proboscis from the stigmatic slit would find the path of least resistance to be upward; the proboscis would theoretically encounter and engage the gland and thus dislodge the entire translator.

With the possible exception of Cynanchum ligulatum, it is assumed that the purple flowers of section Roulinia and the white to greenish flowers of sections Mellichampia, Metalepis, and Ampelamus are attractive to flies whose rather short proboscides would be well suited to collect nectar made more or less readily available by the divergent corolla lobes and clefts in the crown often so deep as to fully expose the stigmatic slits. Drapalnik (1970) reports that the natural pollinators of species of Matelea in southeastern United States are small flies belonging to the families Chloropidae, Milichidae, Phoridae, and Anthomyiidae. Although Matelea (s.l., including Gonolobus) is in a different tribe from Mellichampia, the reader will recall that their flowers are superficially so close to the large, purple flowers of certain other members of Cynanchum, that Linnaeus (1753) was able to include species now referred to both genera under his original circumscription of Cynanchum. A possible change to lepidopteran pollination in C. ligulatum is discussed under that species.

During pollination, the Mellichampia crown likely performs two functions and, in this respect, is relatively unspecialized. Framed by the darker corolla, the erect, white, showy crown evidently plays an important role in the attraction of pollinators. This is especially true in section Roulinia, in which the corolla has undergone considerable reduction in size. A second and less obvious function of the crown may be to direct the proboscides of pollinating insects into the stigmatic slits. Structural modifications, artfully designed to this purpose in several species of section Mellichampia, include grooves and marginal folds of the segments, and differentially elevated attachment of the annulus below the anthers, which leaves pocket-reservoirs below the stigmatic slits.

The function of the translator is to bring about the insect-transfer of pollen grains en masse, no doubt in response to the selective pressure of a gynoeceum bearing numerous ovules in each of its separate carpels. The evolution of analogous structures in orchid flowers represents a response to similar pressures. It is generally believed that, with respect to the exploitation of insects in the service of pollination, the translator apparatus represents the most highly specialized structure developed by flowering plants.

In Asclepias, a well known and documented twisting of the translator arms brings about a 90° rotation of the pollinia upon their removal from the anther sacs. That phenomenon has never to my knowledge been reported for Cynanchum. Unlike the pendulous translator arms of Asclepias, those of Cynanchum are generally laterally oriented; although they probably do not twist, they likely bend towards each other, converging behind the adaxial face of the gland. In herbarium specimens, many Mellichampia translators immediately assumed this configuration upon removal from the flower. Such bending would produce the same results as twisting, i.e., to bring the pollinia into radial alignment with the stigmatic slits in order to both facilitate insertion, and to make the outer edge of each pollinium the leading edge, as the insect approaches the flower. It is from the outer edge of the pollinium that the pollen tubes emerge, a phenomenon generally described as asymmetrical germination.

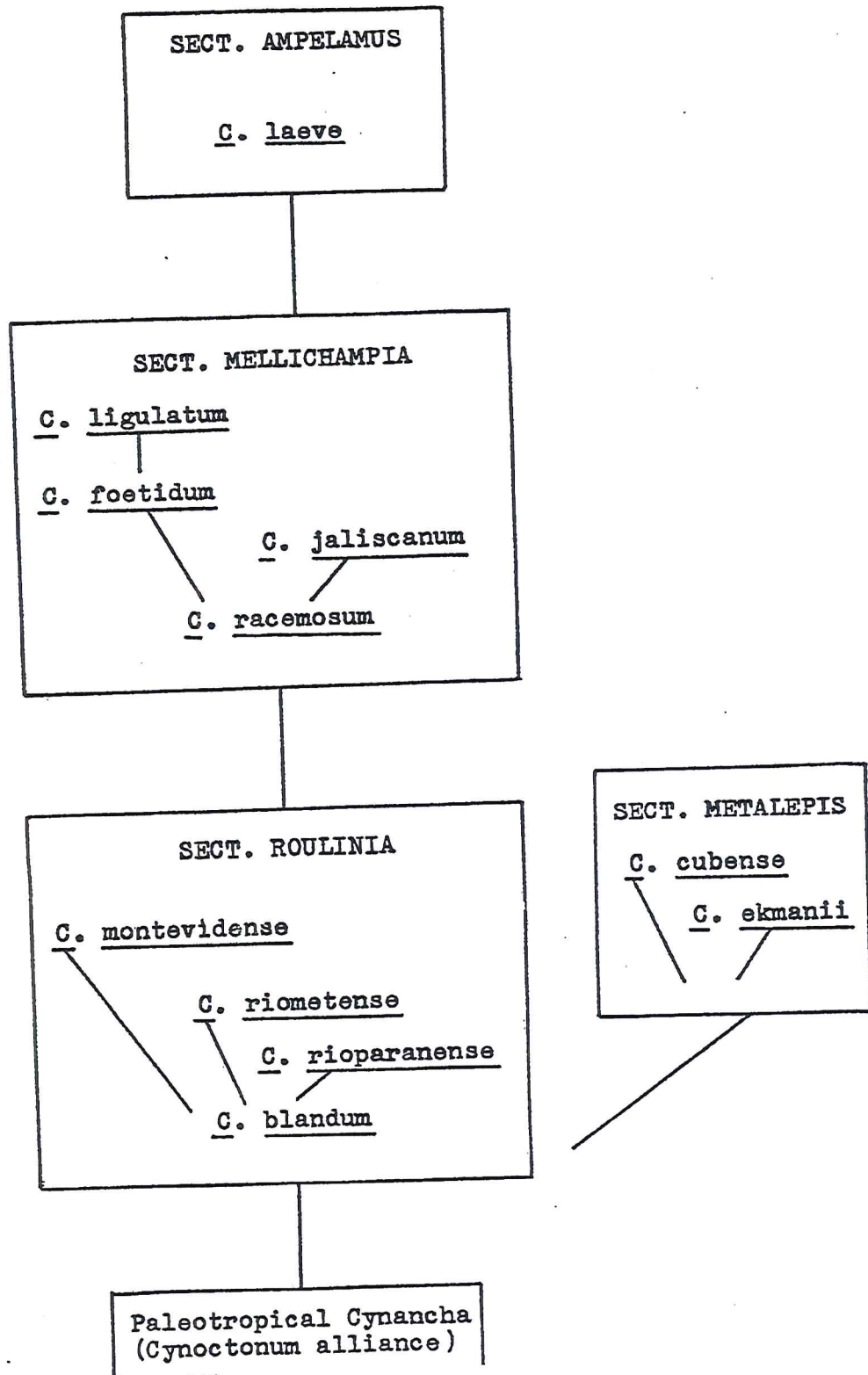


Figure 3. Schematic representation of probable phylogenetic relationships of Cynanchum subgenus Mellichampia in the New World.



Evidence is also accruing to suggest that the efficiency of this unique mechanism of pollen transfer may be quite high in the Asclepiadaceae (Wyatt, 1976; Stone, in ms.). According to Stone: "The pollination efficiency of Asclepias speciosa is the highest yet recorded for a xenogamous species; an average of 21.3% of all pollen (in pollinia) were successfully inserted compared to 1-9% for other xenogamous species." I should add, that successful pollinium insertion has proven to be a function of population size, among other factors, and, as far as I am aware, only temperate species of Asclepias have been studied at the populational level to any great extent. Tropical and subtropical vines such as the Mellichampiae may exhibit not only entirely different pollination systems but also entirely different population densities and distributions as well.

#### TAXONOMY

Cynanchum L. subgenus Mellichampia (A. Gray ex S. Wats.) Woods., Ann. Missouri Bot. Gard. 28: 209. 1941.

Enslenia Nutt., Gen. N. Am. Pl. 1: 16. 1818; Decne., in DC. Prodr. 8: 518. 1844; Benth., in Benth. & Hook. Gen. Pl. 2: 734. 1873; Schum., in Engl. & Prantl Nat. Pflanz. 4(2): 244. 1895; non Raf., 1817. Type species: E. albida Nutt.

Ampelamus Raf., Am. Monthly Mag. & Crit. Rev. 4: 192. 1819. ≡ Enslenia Nutt.

Roulinia Decne., in DC. Prodr. 8: 516. 1844; Benth., in Benth. & Hook. Gen. Pl. 2: 735. 1873; Fourn., in Mart. Fl. Bras. 6(4): 215. 1885; Schum., in Engl. & Prantl Nat. Pflanz. 4(2): 255. 1895; non Brogn., 1840. Lectotype species: R. corymbosa Decne., vide Rouliniella.

Metalepis Griseb., Cat. Pl. Cub. 179. 1866; Benth., in Benth. & Hook. Gen. Pl. 2: 736. 1873; Schum., in Engl. & Prantl Nat. Pflanz. 4(2): 298. 1895. Type species: M. cubensis (A. Rich.) Griseb.

Mellichampia A. Gray ex S. Wats., Proc. Am. Acad. 22: 437. 1887; Schum., in Engl. & Prantl Nat. Pflanz. 4(2): 255. 1895. Type species M. rubescens A. Gray ex S. Wats.

Rouliniella Vail, Bull. Torr. Bot. Club 29: 662. 1902. Lectotype species: R. corymbosa (Decne.) Bullock, vide Bullock, Kew Bull. 1958: 98. 1958.

Cynanchum subgenus Ampelamus (Raf.) Woods., Ann. Missouri Bot. Gard. 28: 211. 1941.

Cynanchum subgenus Metalepis (Griseb.) Woods., Ann. Missouri Bot. Gard. 28: 213. 1941.

#### Key to the species of Cynanchum subgenus Mellichampia

1. Racemes simple or aggregated into pseudo-panicles; flower buds obconic; corollas reflexed-campanulate, the lobes 2.5-5 mm long, minutely to rather long hispidulous within; crown cyathiform or the united segments deeply bifid with ligulate lobes: gynostegium manifestly stipitate, the stipe 1-2 mm; translator arms broadly filiform, 0.6-0.8 mm (section Metalepis).
2. Corolla lobes 5 mm long; crown 5 mm long, equaling the stigma head in height, deeply divided into 5 elliptic segments, the segments bifid nearly to the middle into ligulate lobes, 2-3 mm long. . . . .5. C. ekmanii.
2. Corolla lobes 2-3 mm long; crown about 1 mm long, shorter than the stigma head, cyathiform, shallowly divided into 5 orbicular to subquadrate lobes...6. C. cubense.



1. Racemes simple; flower buds ovoid-oblong to ovoid or orbicular; corollas reflexed to rotate or campanulate, the lobes 2.5-11 mm long, variably glabrous or pubescent but rarely (*C. riometense*) hispidulous; crown not as above, or if cyathiform, the annulus 1 mm high, and if the segments deeply bifid, these entirely free and the annulus wanting; gynostegium (except *C. jaliscanum*) sessile to subsessile, the stipe less than 1 mm high and the translator arms oblong-triangular and tangentially flattened, 0.1-0.3 mm long.
3. Mature stems purplish, the branchlets mostly glabrous; leaves glossy and glabrous, the tertiary nerves obscure; corollas rotate to reflexed, purplish, the lobes 4-11 mm long with plane tips; crown segment margins more or less revolute; stigmatic slits longer than the central, pollinium-bearing portion of the anthers; stigma heads smooth, flat to centrally depressed, in outline (viewed from above) nearly pentagonal with shallowly rounded sinuses (section *Roulinia*).
4. Corollas rotate, glabrous or rarely hispidulous on the lobes within or sparsely bearded in the sinuses; crown segments manifestly united, (the annulus 0.5-1.5 mm high), ovate in outline, three-dimensionally folded and narrowed to a short, oblong central lobe, 1-2 mm long, inflexed over the stigma head.
5. Flower buds 5-7 mm long; calyx lobes 2-5 mm long; corolla limb 15-25 mm across, glabrous or (rarely) sparingly bearded in the sinuses, the lobes 6-10 mm long; stigmatic slits 1.4-2.0 mm long.
6. Corolla limb 15-25 mm across, crown 4-6 mm long; stigmatic slits 1.6-2.0 mm long; pollinia 0.6-0.8 mm long . . . . . 1. *C. blandum*.
6. Corolla limb 15 mm across, crown 3.5-4 mm long; stigmatic slits 1.4-1.6 mm long; pollinia 0.55-0.6 mm long . . . . . 2. *C. rioparanense*.
5. Flower buds 3-4 mm long; calyx lobes 2-2.5 mm long; corolla limb 8-10 mm across, the lobes uniformly hispidulous within, 5 mm long; stigmatic slits 1.2-1.4 mm long . . . . . 3. *C. riometense*.
4. Corollas reflexed to rotate, pubescent in a ring at base of the crown and more or less bearded in the sinuses, rarely hispidulous on the lobes within; crown segments essentially free, (the annulus minute, mostly less than 0.2 mm high), rhombic to pyriform or broadly pyriform in outline with little three-dimensional folding, more or less abruptly narrowed to a broadly triangular to ligulate central lobe as much as 5 mm long, erect to inflexed over the stigma head . . . . . 4. *C. montevidense*.
3. Mature stems brownish, the branchlets puberulent in lines above the petioles; leaves dull, sparingly puberulent on the principal veins on either or both surfaces (rarely glabrate), the tertiary nerves prominent below; corollas rotate to rotate-campanulate or campanulate, white to pale green or yellowish, the lobes 2-5 mm long (8-10 mm and maroon in *C. ligulatum*) with recurved tips; crown segment margins plane to involute; stigmatic slits (except *C. laeve*) shorter than to equaling the central, pollinium-bearing portion of the anthers; stigma heads papillate, rounded to domed, or if smooth then strongly conic, in outline (viewed from above) mostly with acute sinuses cut halfway to the center.
7. Crown segments manifestly united (the annulus at least 0.2 mm high), the apices narrowed to a central, ligulate lobe to broadly rounded and emarginate, never deeply bifid; stigma heads papillate, rounded to domed, much less than 1 mm high, in outline (viewed from above) with acute sinuses cut halfway to the center (section *Mellichampia*).
8. Corollas rotate to rotate-campanulate, glabrous, pale green or yellowish; stigma heads rounded.
9. Gynostegium subsessile, the stipe no longer than 0.5 mm; translator arms oblong-triangular and tangentially flattened, 0.2-0.3 mm long...7. *C. racemosum*.
9. Gynostegium stipitate, the stipe 1.0 mm long; translator arms broadly filiform, 0.5-0.6 mm long . . . . . 8. *C. jaliscanum*.
8. Corollas campanulate, mostly pilose within (rarely glabrous), white or maroon; stigma heads rounded to domed-conic.
10. Corollas white, the lobes 2.5-5 mm long; crown inserted 0.3-0.6 mm below the corolla sinuses; pollinia elliptic to oblanceolate. . . . . 9. *C. foetidum*.
10. Corollas cream-white to maroon, the lobes 8-10 mm long; crown inserted near the base of the corolla tube, 1.5-2.5 mm below the sinuses; pollinia ovate



- to ovate-orbicular . . . . . 10. C. ligulatum.  
 7. Crown segments entirely free (the annulus wanting), deeply bifid into ligulate lobes; stigma heads smooth, strongly conic, more than 1 mm high, in outline (viewed from above) with shallow, rounded sinuses (section Ampelamus)  
 11. C. laeve.

1. Cynanchum blandum (Decne.) E. Sundell, comb. nov.

Figs. 1 &amp; 4 A-H, L-O.

- Roulinia blanda Decne., in DC. Prodr. 8: 517. 1844. Type: Surinam, without further locality, Hostmann 124 (holotype: P!; isotypes: G! K! W!).  
Roulinia corymbosa Decne., in DC. Prodr. 8: 517. 1844; Delessert, Ic. Select. Plant. 5: 27, pl. 62. 1846; Fourn., in Mart. Fl. Bras. 6(4): 216. 1885. Type: Brazil, without further locality and with no collector indicated (holotype: P!; photographs of holotype: F! GH!).  
Rouliniella corymbosa (Decne.) Bullock, Kew Bull. 1958: 98. 1958.  
Roulinia guianensis Decne., in DC. Prodr. 8: 517. 1844; Delessert, Ic. Select. Plant. 5: 27, pl. 62. 1846. Type: Guyana: East Berbice, Schomburgk 355 (holotype: P!; isotypes: BM! G! K! L! NY! OXF! W!; photographs of isotype at B (no longer extant): F! GH! NY!).  
Rouliniella guianensis (Decne.) Jonker, in A. Pulle, ed., Fl. Surin., Meded. K. Ver. Kol. Inst. Amst. 4: 348. 1940.  
Roulinia surinamensis Miq., Stirp. Sur. Sel. 169. 1851. Type: Surinam: interior region, Suriname River, Hostman & Kappler 1092 (holotype: U!; isotypes: C! F! G! K! LE! MO! NY! P! S! W! W! W!; photographs of isotype at C: F! GH! NY!).  
Roulinia Sprucei Fourn., in Mart. Fl. Bras. 6(4): 216. 1885. Type: Brazil: Amazonas. Amazon River, mouth of Rio Negro, Spruce 1490 (lectotype here designated: P!; isolectotypes: BM! BR! G! GH! K! LD! NY! NY! W!; photograph of isolectotype at G: F!).

Suffrutescent, twining vine; stems glabrous, terete, the older purplish, to 5 mm in diameter, the branchlets stramineous; petioles essentially glabrous or with a few adaxial hairs near the blade, 1.0-4.5 cm long, 1/4 to 1/2 the length of the blade; leaf blades chartaceous, glossy, drying dark green to brown or bluish black above, paler beneath or less commonly concolorous, ovate to lanceolate or lanceolate-oblong, 4.5-13.5 cm long, 2-8 cm broad, as much as twice as long as broad (Guianas), acute to acuminate at apex, shallowly cordate (Amazon) to rounded-truncate (Guianas) at base, indument entirely wanting or rarely with a few hairs near the petiole, the glands 3-10, the tertiary nerves obscure above; racemes bearing as many as 15 flowers when elongating (only 2-6 at once mature), 3-15 x 3-6 cm, the peduncle sparingly to densely adaxially tomentulose often with golden brown hairs, 1-6 cm long, equaling or longer than the petiole, the rachis and pedicels densely tomentulose, rarely glabrate (Guianas), the pedicels short and stout (Amazon) to filiform (Guyana), 5-25(-45) mm long; bracts ovate-triangular, 0.8-2.2 mm long, puberulent with ciliate margins; flower buds ovoid-oblong to rarely ovoid, 5-7 mm long, broadly rounded at apex; calyx rotate, mostly glabrous, the tube indistinct to 1 mm long, the lobes spreading, ovate to rarely ovate-lanceolate or broadly elliptic (Guianas), 2-4(-5) x 1.5-3.0 mm, at least the outer lobes ciliate at margin, the glands usually one per sinus; corolla rotate at anthesis, 15-20(-25) mm in diameter, white outside, purple to brownish-purple within with 3 yellow to white streaks on each lobe, glabrous, the tube 1.5-3.0 mm long, the lobes ovate to lanceolate, 6-9(-10) x 3-5 mm, acute to narrowly rounded at apex, mostly revolute at margin; crown inserted at the corolla throat, 0.6-1.5 mm below the sinuses, white, 4-6 mm long, the segments 5, manifestly united, (the annulus 0.5-1.5 mm high), erect to somewhat spreading and surpassing the gynostegium, ovate to obovate, 3-5 x 2.5-4 mm, more or less prominently and broadly channeled within, three-dimensionally folded and highly variable, often helmet-shaped, more or less abruptly narrowing to a short, broad 2- to 3-lobed or -toothed tip, 1-2 x 1 mm, inflexed-descending over the stigma head, the margins of the segments or their shoulders revolute; anthers sessile to rarely minutely substipitate, 1.2-1.7 mm broad below the glands, 1.6-2.0 mm long at the



stigmatic slits, the slits (anther wings) longer than the central, pollinium-bearing portion of the anthers, the appendages reniform, 0.5-0.8 x 0.8-1.6 mm, broadly rounded at apex; translators with pollinia elliptic-oblong to oval, 0.6-0.8 x 0.2-0.4 mm, the ends broadly rounded, the gland narrowly rhombic to rhombic-cylindrical, 0.3-0.5 x 0.2-0.4 mm, about half or more as long as the pollinia, the translator arms brown to yellow, tangentially flattened and more or less elongate-triangular (gradually to abruptly expanded at the pollinia or only slightly so), 0.15-0.30 mm long, sub-apically attached to the pollinia; gynostegium truncate-conic, about equal to the glands in height, the apex (stigma head) flat to centrally depressed, smooth, 1.8-3.0 mm in diameter, with a low, oval, bifid umbo; follicles (Lanjouw 533) narrowly ovoid, glabrous, finely wrinkled-striate, drying brownish, 8.5 x 3 cm; seeds ovate, minutely alveolate and sparingly wrinkle-ridged, brown, 7-8 x 5-6 mm, truncate at apex, coarsely and irregularly toothed at base and lower margins, the coma white, about 3 cm long.

Typification. The holotype of Roulinia blanda bears on the label both the collector's name and number, Hostmann 124, and the brief locality citation, "Surinam." In the Prodromus, Decaisne cites no collector and gives "Brasilia" as the type locality. Having worked at Paris, Fournier must have noted this discrepancy and dropped the species, unfortunately without explanation, from his treatment of Roulinia for Flora Brasiliensis. Decaisne's handwritten species name on the label of the holotype leaves no doubt as to its authenticity.

The holotype of Roulinia corymbosa provides no information about either collector or locality other than "Brésil." Decaisne examined the specimen at Paris, and the label bears in his handwriting the name of his new species. In the Prodromus, Decaisne suggests as type locality, "Para?", a Brazilian state in the eastern Amazon basin. Delessert's (1846, loc. cit.) illustration of Cynanchum corymbosum, cited by Decaisne with his original description, was no doubt drawn from the same specimen at P.

The type collection of Miquel's Roulinia surinamensis, Hostmann & Kappler 1092, is from the Suriname River in the interior of Surinam, a locality that must lie within the Administrative District of either Suriname or Brokopondo. Miquel's original herbarium and types are at Utrecht (Stafleu, 1967).

Fournier based his species Roulinia sprucei on Spruce 1490. Of the many duplicates distributed, the specimen at P was the most likely to have been seen by Fournier (Stafleu & Cowan, 1976) and is here designated lectotype.

Distribution. Cynanchum blandum is a riparian species of the Amazon River basin and the coastal rivers of the Guianas, ranging from the Orinoco to the Amazon River in the north, and thence westward along the Amazon and its tributaries to the states of Amazonas, Colombia, and Amazonas, Peru. Northern and southern populations have traditionally been treated as separate species, unquestionably on the basis of a geographical rather than morphological discontinuity. The two populations are isolated from one another by the Guiana Highlands, and collections from the eastern edge of the range, where northern and southern elements merge, are very rare. A mere 4 collections were seen from the Amazon basin of Brazil, 3 from French Guiana. Half of all Amazonian material was obtained in the state of Loreto, Peru, while Surinam accounts for two-thirds of all available collections of the species.

Altitudinal data are scanty (between 100 and 200 m for a few collections from Peru), but collection localities suggest that C. blandum is narrowly restricted to lower elevations both along the Amazon River and north of the Guiana Highlands. Flowering specimens have been collected throughout the year. A single collection with fruit is dated August 12.

Local names: Peru: "Bujcosacha," (Schunke 98, Loreto).

Guyana. North West: Sebai Creek, Kaituma River, Fanshawe 5159 (K, MO, NY). Essequibo: Soorooroo, upper Pomeroun River, Becket 8500 (NY); Mazaruni River, Jenman 773 (K); Rockstone, Essequibo River, Gleason 866 (NY).

Surinam. Nickerie: Kabalebo River, 30 km downstream of Kabalebo Airstrip, Florschütz & Maas 2585 (F, U), 2654 (A, LE, U). Saramacca: Tibiti River, Lanjouw & Lindeman 1872 (K, NY, U); Saramacca River, near plant, Catharina Sophia, Lanjouw 275 (U), vicinity of Brokolonka, Maguire 23789 (A, F, MO, NY, U), vicinity of Saron Creek,



Maguire 23772 (A, F, MO, NY, RB, U), Mama Dam, Florschütz 1152 (C, NY, U).  
 Brokopondo: Suriname River, vicinity of Brokopondo, Kramer & Hekking 2809 (U), south of Gansee on Kentoegoni Island, van Donselaar 1485 (U). Marowijne River, Lanjouw & Lindeman 2063 (K, NY, U), Hugh-Jones 43 (K, U), near Armina Falls, Lanjouw 533 (U), between Armina and Lakame Falls, Lanjouw & Lindeman 3474 (NY, U); Gran Rio, Lindkamp 228 (U); Tapanahoni River, Veersteeg 860 (U), below Kapoea Rapids, Rombouts 657 (K, MO, U); Gonini River, B. W. 1037 (U), Gonggryp 3666 (GH, U); Oelemari River, vicinity of airfield, Wessels-Boer 1003 (BR, F, U, UC). Uncertain locality: Saramacca River, Pulle 474 (U); upper Suriname River, Tresling 422 (U).

French Guiana. Inini: Mana River, Arouany Creek, Hallé 646 (P); Camopi River, Yanioyé Falls, Oldeman B-1410 (P, U); Haut Oyapock River at Trois Sauts, Sastre 4686 (U).

Peru. Amazonas: mouth of Pongo de Manseriche at Río Marañón, Tessman 5329 (G, NY). Loreto: Gamitanacocha, Río Mazan, Schunke 98 (F, MO, UC, US); Río Nanay, vicinity of Santa Maria de Nanay, Schunke 2514 (F, G, GH, NY); Río Marañón, vicinity of Iquitos, Mexia 6423a (F, MO, US), 6434 (F, MO, NO, U, US), Tessman 5038 (G, NY).

Colombia. Amazonas: Río Putumayo, near mouth of Igaraparaná, Schultes 3997 (MO).

Brazil. Amazonas: Amazon River, mouth of Río Purús, Silva 799 (NY). Amapa: Puchaca River, vicinity of Vila Nora, Emmerich 835 & Andrade 872 (R).

Specimens of Cynanchum blandum examined seem to fall into two groups on the basis of geographic distribution and leaf outline. The numerous collections from the Guianas possess broadly lanceolate leaves with rounded bases, scarcely if ever cordate, while the leaves of the comparatively few Amazonian collections are ovate (less commonly broadly lanceolate) with shallowly cordate to rounded bases. As already mentioned, those two populations have traditionally been recognized as the distinct and presumably allopatric species, Roulinia guianensis and R. corymbosa. However, the occurrence of intermediate forms with regard to leaf outline, and, most importantly, the essential similarity in floral morphology among the majority of specimens from both populations, provide ample justification for uniting them into a single species. At least a few collections are available from intermediate localities near the mouth of the Amazon River (Emmerich & Andrade 835/872 from the Brazilian state of Amapa is of particular interest).

With regard to leaf outline in the Amazonian material, careful examination shows that certain collections possess both broadly lanceolate and ovate leaves, with the ovate blades exhibiting both rounded and shallowly cordate bases (Schunke 98, Schunke 2514), while other collections have strictly narrowly ovate leaves with rounded bases (Tessman 5038, Tessman 5329, Mexia 6423a) characteristic of specimens from the Guianas. The strongest evidence for inclusion of the two populations under one species is obtained from floral morphology. The two type collections from Surinam of Roulinia blanda Decne. (Hostmann 124) and R. surinamensis Miq. (Hostmann & Kappler 1092), and the type collection of R. sprucei (Spruce 1490), from the confluence of the Rio Negro and the Amazon River, are morphologically indistinguishable in that respect, particularly in the details of the crown (Fig. 4 A-B, F-H). Decaisne's description of R. blanda in the Prodromus was, of course, available to Miquel, but the status of Hostmann 124, as the type of that name, was almost certainly not known to him (see discussion on typification). It is unlikely that Miquel ever saw the holotype at Paris which alone could shed essential light both on Decaisne's brief, original description and on his erroneous citation of Brazil instead of Surinam for the range of the species. Fournier's recognition of the Spruce material as a distinct species is not as easily explained, for, as mentioned, it is most likely that he did examine the R. blandum type at Paris.

Additionally, Fournier maintained Decaisne's Roulinia corymbosa, ostensibly from the Brazilian state of Para in the Amazon basin, but he did not offer any key characters by which to distinguish it from his own species, Roulinia sprucei. His description of R. sprucei diverges from his own and Decaisne's concept of R. corymbosa in three respects: the leaves are concolorous, not paler beneath; the petioles are equal to the peduncles, not longer; and the petals bear 5 streaks within rather than 3. My own examination of both types, and especially of additional material, suggests that these characters are highly variable and that the distinctions



are not significant. In fact, the label of the Kew specimen of Spruce 1490 bears these data: "Corolla...with three pallid streaks on each lobe." The holotype of R. corymbosa is indeed remarkable for the large size of its flowers but differs morphologically in no other way from the rest of the material examined. No other specimens are available from Para, Brazil, for comparison, nor do any of the other specimens of that species match the R. corymbosa holotype in floral dimensions. For the time being, this difference in flower size must remain unexplained.

Additional discontinuities in floral morphology are to be found in the type of Roulinia guianensis (Schomburgk 355) which was collected in Guyana toward the northwestern edge of the species' range and which exhibits several morphological extremes. The pedicels are entirely anomalous, almost twice the length of the longest pedicels found in any of the other material. The crown segments approach an orbicular outline rather than ovate-elliptic, a condition shared with Fanshawe 5159 (Fig. 4 C, D) from even farther to the west, and the annulus is higher than that generally found in specimens from Surinam and French Guiana. However, dimensions of the corolla, translator, and stigmatic slit, as well as the broadly lanceolate leaves with rounded bases mark the Schomburgk collection as unquestionably conspecific with the rest of the material from the Guianas and the Amazon Basin. With respect to inflorescence, the Amazon population also differs markedly from the Surinam norm in the possession of exceptionally stout peduncles, usually twice the breadth of the petiole, and relatively short, stout pedicels as well.

Cynanchum blandum is sympatric with the wide-ranging C. montevidense in the Amazon basin of Peru and Brazil. Although some hybridization is suspected (discussed under C. montevidense), the species remain remarkably distinct; with few exceptions specimens are easily referable to one or the other by the shape of their leaf bases (more deeply cordate in C. montevidense), presence or absence of corolla pubescence, height of the crown annulus, and the shape and outline of the crown segments.

2. Cynanchum rioparanense E. Sundell, sp. nov.

Figs. 1 & 4 I-J, P.

Type: Brazil: Minas Gerais. District of Ituiutaba, vicinity of Fundaõ, Macedo 1167 (holotype: MO!; isotypes: RB! S!).

Herba volubilis suffrutescens; caulibus glabris teretibus, demum purpurascens-  
fuscis, ad 4 mm diametro, ramulis stramineis; petioliis glabris, 2-3.5 cm longis;  
foliorum laminis nitidis, in sicco fuscis supra, subtus olivaceis, ovatis vel late  
ovatis, 5-13 cm longis, 3-9 cm latis, apice plus minusve abrupte acuminatis, basi  
subcordatis vel rotundatis, glabris, glandibus 2-6(?) aggregatis, nervis tertiariis  
utrinque obscuris; racemis in ramis lateralibus aggregatis, per nodum 1-2, tarde  
elongatis, cum 8-18 floribus (sed 1-4 simul maturis) et ad apicem inflorescentiae  
aggregatis, 3.5-5 x 2 cm, pedunculis adaxialibus puberulis, 1-2 cm longis et petiolum  
aequans vel brevioribus, rachidibus tomentosis, pedicellis adaxialibus tomentosis,  
sub anthesi 8-9 mm longis; bracteis inflorescentiae ovatis-triangularibus, circiter 1  
mm longis vel bracteis inferis longioribus, margine eciliatis; alabastris orbicularibus,  
6 mm longis; calyce rotato, basi puberulo, tubo indistincto, lobis late ovatis-ellipticis,  
4.5 x 2.5 mm, apice rotundatis, margine eciliatis; corolla rotata, limbo 15 mm diametro,  
extus alba, intus fusciori et per lobum cum 3-5 lineis violaceis, glabra vel in sinibus  
aliquantum barbata, tubo 1.5 mm longo, lobis effusis, lanceolatis, 7-7.5 x 3 mm, apice  
acutis, margine revolutis; corona fauci corollae inserta 0.5 mm infra sinus, 3.5-4 mm  
longa, in sicco fusca, corolla interius plus minusve concolora, segmentis coronae 5,  
manifeste connatis, (annulo 0.6 mm alto), convexis-erectis, in circumscriptione ovatis  
vel multum plicatis et tortuosis, intus late canaliculatis, quoque segmento ad humeros  
subito attenuato in brevem, triangularem vel oblongum lobum, 1-1.5 mm longum atque  
latum, lobi apice rotundato et integro vel obscure trifido, super stigmaticis capitulum  
inflexo, parte basale late oblonga, 2.5 mm longa (annulo excluso) et quam lobo longiore,  
2.3-2.6 mm lata, ad humeros rotundatos latissima, marginibus loborum, humerorum, et



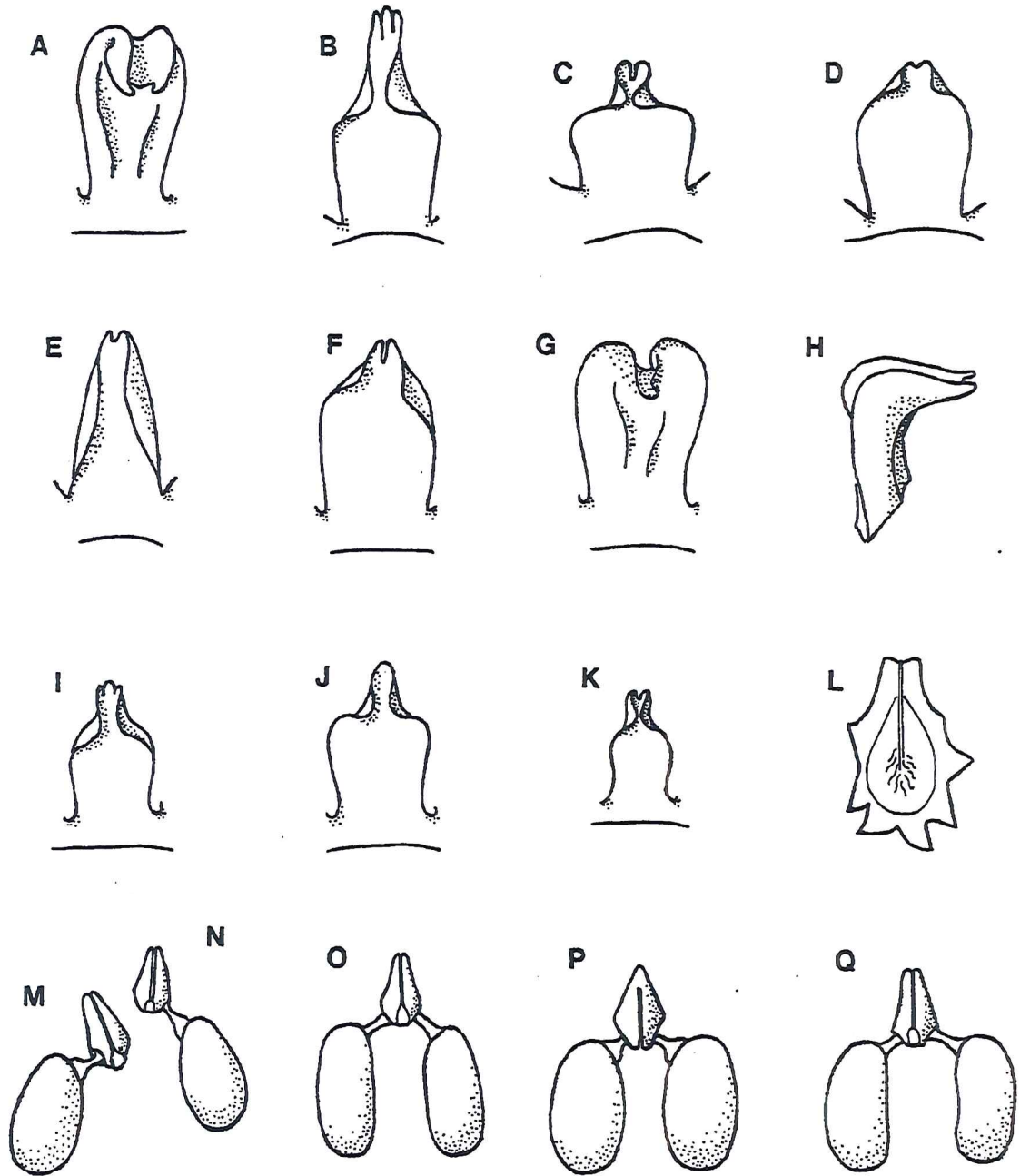


Figure 4. A-H, L-O, *Cynanchum blandum*; I-J, P, *C. rioparanense*; K, Q, *C. riometense*. A-K. Crown segments, abaxial surface (unless otherwise indicated), x 6.5 (A. Hostmann 124, adaxial surface; B. Hostmann & Kappler 1092, crown tip drawn erect; C. Schomburgk 355; D. Fanshawe 5159; E. Schunke 2514; F-H, Spruce 1490: G, adaxial surface; H, lateral view, gynostegium toward the right; I-J. Macedo 1167, from the same flower; K. Lehmann 8795. L. Seed, placental surface, coma detached, x 3.9 (Lanjouw 533). M-Q. Translators, abaxial surface (M. Tessman 5038, 1 pollinium and arm removed, x 32.5; N. Mexia 6423a, 1 pollinium and arm removed, x 32.5; O. Schomburgk 355, x 26; P. Macedo 1167, x 32.5; Q. Lehmann 8795, x 39).

partium basalium variabile revolutis; antheris sessilibus, infra corpuscula 1.3 mm latis, ad antherarum alas 1.4-1.6 mm longis, antherarum alis longioribus quam partibus centralibus polliniferis (ipsis 0.8 mm longis), appendicibus reniformibus, 0.8 x 1.3 mm, apice late rotundatis; polliniis late ellipticis, 0.55-0.6 x 0.3 mm, extremis late rotundatis, corpusculo rhombico, 0.4 mm longo, caudiculis 0.1 mm longis, complanatis et triangularibus, ad pollinia abrupte expansis et subapice affixis; gynostegio cylindricato vel subconico, 2 mm alto (ultra corpuscula aliquantum extenso), 2.5-3 mm lato, stigmati capitulo plano, laevi, umbonato vel parum tumido, plus minusve 2 mm diametro; folliculis ignotis.

Distribution (Fig. 1). Only two collections of Cynanchum rioparanense are known from sites approximately 200 miles apart in the states of Paraná and Minas Gerais, Brazil. The species is apparently endemic to the valley of the Rio Parana and its tributaries at low elevations. Flowering material has been collected in the months of January and August.

Brazil. Paraná: Rio Ivai, District of Terra Boa, Hatschbach 15734 (NO, US).

Cynanchum rioparanense grows sympatrically with C. montevidense in the basin of the Rio Paraná. Superficially, it is at once distinct from the latter in its leaves and inflorescences. The leaves are commonly quite large, longer than 10 cm, with bases shallowly cordate to subtruncate or rounded, and drying a characteristic glossy brown above and dull green beneath. At least in the two collections known, the racemes are relatively short and crowded on lateral branches, with 1 or 2 at every node along the flowering portions of the stems. With respect to floral structures, the pollinia and, especially, the stigmatic slits are longer in C. rioparanense than in C. montevidense, and crown morphology in the two species diverges significantly (Figs. 4 I, J & 5). Finally, the flowers of C. montevidense possess a ring of hairs at the base of the crown, lacking in C. rioparanense.

Cynanchum rioparanense is very closely related to C. blandum, although evidently disjunct by at least 1000 miles. Members of the C. blandum group (including as well C. riometense) share ovate, three-dimensionally folded, helmet-shaped crown segments that are united into an annulus at least 0.5 mm high. The species of this complex are so closely allied that they can be safely distinguished morphologically only by corolla pubescence and the relative dimensions of their floral structures, most usefully, corolla lobes, crown segments, stigmatic slits, and pollinia.

3. Cynanchum riometense E. Sundell, sp. nov.

Figs. 1 & 4 K, Q.

Type: Colombia: Rio Meta at the mouth of Rio Casanare, Lehmann 8795 (holotype: K!).

Herba volubilis, suffrutescens; caulibus glabratis, teretibus, demum atropurpureis, ad 3-4 mm diametro, ramulis stramineis, lineis supra petiolos parce puberulis; petiolis glabris, 1-3 cm longis, circiter 1/3 longis quam foliorum laminis; foliorum laminis nitidis, in sicco fuscis supra, subtus atro-olivaceis, anguste ovatis-oblongis, 3-9 x 2-5 cm, apice acutis, basi profunde cordatis, glabris, nervis tertiaribus utrinque obscuris; racemis confertim floriferis, cum 15-20 floribus (sed 4-8 simul maturis), demum magnopere elongatis, 6-12 x 2.5-3 cm, dense et subtiliter adaxialibus puberulis, pedunculis 2-4 cm longis, pedicellis gracilibus, 8-13 mm longis; bracteis inflorescentiae ovatis-triangularibus, circiter 1 mm longis; alabastris ovatis-orbicularibus, 3-4 mm longis, apice rotundatis; calyce rotata, basi minute puberulo, tubo 0.3 mm, lobis ovatis-ellipticis, 2-2.5 x 1.2 mm, apice rotundatis, margine eciliatis, glandibus 1 per sinus; corolla rotata vel reflexa, limbo 8-10 mm diametro, in sicco extus straminea, intus atrofusca et minute hispidula, tubo 1 mm longo, lobis effusis vel reflexis, ellipticis-oblongis vel lanceolatis-oblongis, 5 x 2.5 mm, apice acutis, margine revolutis; corona fauci corollae inserta 0.5 mm infra sinus, 3 mm longa, in sicco fusca, corolla interius



plus minusve concolora vel leviter pallidiora, segmentis coronae 5, manifeste connatis, (annulo 0.6 mm alto), erectis, gynostegium arcte cingentibus et parum superantibus, in circumscriptione ovatis-oblongis vel plicatis et complexis, intus distale late canaliculatis, quoque segmento ad humeros subito attenuato in lobum brevem oblongum, 1 mm longum atque latum, lobi apice bifido et super stigmatis capitulum abrupte inflexo, parte basale late oblonga, 2.5 mm longa (annulo excluso) et quam lobo longiore, 1.5 mm lata, marginibus loborum et partium basaliu[m] variabile revolutis; antheris sessilibus, infra corpuscula 1 mm latis, ad antherarum alas 1.2-1.4 mm longis, antherarum alis longioribus quam partibus centralibus polliniferis (ipsis 0.6-0.8 mm longis), appendicibus reniformibus-orbicularibus, 0.6 x 0.8-0.9 mm, apice late rotundatis; polliniis late ellipticis, 0.5 x 0.25 mm, extremis late rotundatis, corpusculo rhombico-cylindrico, 0.3 x 0.2 mm, caudiculis 0.1 mm longis, complanatis et oblongis-triangularibus, ad pollinia expansis et subapice affixis; gynostegio cylindricato, 2 mm lato, stigmatis capitulo plano, laevi, umbonato, 1.4 mm diametro; folliculis ignotis.

Distribution (Fig. 1). Cynanchum riometense is known only from the holotype, collected in eastern Colombia along the Rio Meta at the mouth of the Rio Casanare in July of 1897. Both paucity of collections and comparison to the low elevation, riparian habitat requirements of closely allied species of the C. blandum complex strongly suggest that C. riometense is restricted to the basin of the Rio Orinoco and its tributaries.

Future collections of Cynanchum riometense may demonstrate that it grows sympatrically with C. montevidense near the mouth of the Rio Orinoco. The two species are easily separable by their corolla pubescence, crown segment form and outline, presence or absence of an annulus, and by the longer stigmatic slits and shorter corolla lobes of C. riometense. In addition to floral characters, the racemes of C. riometense, crowded with small flowers, separate it not only from C. montevidense but from the much more closely related C. blandum and C. rioparanense, with racemes of fewer and less densely aggregated flowers.

4. Cynanchum montevidense Spreng., Syst. Veg. ed. 16. 1: 851. 1824. Figs. 1, 5, 6.

Type: Uruguay: Montevideo, Sello s.n. (lectotype here designated: photograph of holotype at B (no longer extant): GH!).

Vincetoxicum montevidense (Spreng.) O. Ktze., Rev. Gen. Pl. 424. 1891.

Roulinia montevidensis (Spreng.) Malme, Arkiv. Bot. Stockh. 16(15): 17. 1921.

Asclepias cordata Vell., Fl. Flum. 3:116, pl. 56. 1825. Lectotype here designated:

Brazil: (vicinity of Rio de Janeiro), Vellozo's description and illustration, 1825, loc. cit.

Roulinia cordata (Vell.) Macbride, Candollea 5: 401. 1934.

Roulinia fluminensis Decne., in DC. Prodr. 8: 517. 1844; Fourn., in Mart. Fl.

Bras. 6(4): 217. 1885; Malme, Kongl. Svensk. Vet. Akad. Handl. 34(7): 30,

pl. 5. 1900; Chodat & Hassler, Bull. Herb. Boiss. Ser. 2. 3: 65. 1903. Type:

Brazil: Rio Grande (do Sul), Gaudichaud 712 (holotype: P!; isotype (fragment): NY!).

Cynanchum tamifolium Hook. & Arn., J. Bot. (Hooker) 1: 294. 1834. Type: Brazil:

Rio Grande do Sul. Porto Alegre, ("Hedges of Portalegre." "In the woods of St.

Jorim" (São Joachim?)), Tweedie s.n. (lectotype here designated: K, photocopy seen).

Roulinia tamifolia (Hook. & Arn.) Decne., in DC. Prodr. 8: 517. 1844; Fourn., in Mart. Fl. Bras. 6(4):217. 1885.

Roulinia convolvulacea Decne., in DC. Prodr. 8: 517. 1844; Fourn., in Mart. Fl.

Bras. 6(4): 217. 1885. Type: Brazil: São Paulo, Gaudichaud 388 (holotype: P!; photographs of holotype: F! GH!; isotype: NY (fragment)!).

Roulinia modesta Decne., in DC. Prodr. 8: 517. 1844; Delessert, Ic. Select. Pl.



- 5: 27, pl. 62. 1846; Fourn., in Mart. Fl. Bras. 6(4): 216. 1885. Type: Brazil: Mato Grosso. Serra de Cujaba, Manso s.n. ("1832") (holotype: G (not seen); photographs of holotype: F! GH! NY!; isotype: P!).
- Roulinia acuta Decne., in DC. Prodr. 8: 517. 1844; Fourn., in Mart. Fl. Bras. 6(4): 215. 1885. Type: Brazil: São Paulo, Gaudichaud 378 (holotype: P!; photographs of holotype: F! GH!; isotype: NY (fragment)! ).
- Roulinia versicolor Lemaire, Herb. Gen. Amat. 4: 1. 1844. Lectotype here designated: Lemaire's description, 1844, loc. cit.
- Enslenia jamaicensis Griseb., Fl. Brit. W. Ind. 418. 1862. Type: Jamaica, Wilson s.n. (holotype: K!).
- Roulinia jamaicensis (Griseb.) Benth. ex Jackson, Ind. Kew. 2: 743. 1895.
- Rouliniella jamaicensis (Griseb.) Rendle, London J. Bot. 74: 340. 1936.
- Cynanchum jamaicense (Griseb.) Woods., Ann. Missouri Bot. Gard. 28: 210. 1941; Adams, Fl. Pl. Jamaica 599. 1972.
- Roulinia Selloana Fourn., in Mart. Fl. Bras. 6(4): 216. 1885. Type: Southeastern Brazil, without further locality. Sello 578 (lectotype here designated: GH!; isolectotypes: US (not seen), NY (fragment)!; photographs of isolectotype at US: F! NY!).
- Roulinia Riedelii Fourn., in Mart. Fl. Bras. 6(4): 217. 1885. Type: Brazil: Rio de Janeiro, Riedel 601 (lectotype here designated: P!; isolectotypes: GH! K! LE! M! S!; photographs of isolectotype at M: F! GH!).
- Roulinia Manii Rusby, Mem. N. Y. Bot. Gard. 7: 333. 1927. Type: Bolivia: Beni. Trinidad, Mamone River, Cardenas 9 Special (holotype: NY, 2 sheets!).
- Roulinia Voglii Suesseng., Mitt. Bot. Staatssamml. Munchen 1: 13. 1950. Type: Venezuela: Aragua, vicinity of Maracay, Vogl 1407 (holotype: M, 3 sheets!; isotype: BR, 2 sheets!).
- Cynanchum magdalenicum Dugand, Caldasia 9: 408. 1966; Spellman in Woodson, et al., Ann. Missouri Bot. Gard. 62: 122. 1975. Type: Colombia: Bolívar. Calamar, Killip & Smith 14715 (holotype: NY (not seen); isotypes: MO! US (not seen) ).

Suffrutescent, twining vine; rootstock elongate, cylindrical, slightly broader than the stems; stems glabrous, terete, the older purplish to pale brown, to 4 mm in diameter, the branchlets stramineous, rarely (Amazon basin) delicately pubescent in lines above the petioles; petioles glabrous or with adaxial hairs (especially distally), 1-9 cm long, 1/3-2/3 the length of the blade; leaf blades chartaceous, glossy to rather dull, drying brownish green, dark green, or blue-green above, paler beneath, olive- or blue-green, or nearly concolorous, ovate to ovate-triangular, 2.5-13 x 1.5-10 cm, acute to acuminate at tip, deeply or (upland Argentina) moderately cordate at base, indument entirely wanting or upper surface bearing a few hairs when young or these rarely persisting, glands 5-14, tertiary nerves obscure; racemes bearing at most 8-15 flowers (only 1-6 at once mature), greatly elongating in age, 2.5-13(-20) x 2.5-3.5(-5) cm, peduncle adaxially puberulent to tomentulose with white to golden brown hairs, occasionally glabrate, 1-7.5(-10) cm long, about equal to petiole in length, the rachis and pedicels puberulent to densely tomentulose (rarely short sericeous) with pedicel hairs mostly restricted to the adaxial surface, the pedicels slender, 4-25 mm long; bracts lanceolate-triangular to lanceolate-elliptic, 0.8-2.2 mm long, with ciliate margins; flower buds ovoid-oblong to ovoid-ellipsoid, uncommonly spherical, 4-7 mm long, broadly rounded at apex; calyx rotate, glabrous or with a few hairs below, the tube indistinct or to 0.5 mm long, rarely longer, the lobes broadly lanceolate to ovate-elliptic or ovate, 1.7-5 x 0.8-2 mm, rounded at apex, eciliate to ciliate at least below the middle at margin, glands 1-2(-3) per sinus; corolla rotate to reflexed, with the limb 10-17 mm in diameter, greenish white outside, purple to less commonly pinkish within with 3-5 white, yellow, or yellow-green streaks on each lobe, most often rather densely pubescent with a ring of hairs in throat at base of crown, usually bearded in the sinuses with hairs often extending to the proximal portion of lobes, rarely the entire inner surface of lobes hirtellous, the corolla tube 0.8-2.2 mm long, the lobes arcuate, reflexed to horizontally spreading, ovate to lanceolate to lanceolate-oblong, abruptly narrowing from the base and again near apex or tapering gradually throughout, 4-11 x 1.5-5 mm, 2-3 times longer than broad, acute at apex, mostly revolute at margins; crown inserted at corolla throat, 0.5-0.7(-1.2) mm below the sinuses, rarely inserted



on a minute to short column 0.1-1.0 mm long, drying pale brown to nearly white, always paler than interior of the corolla, the crown segments 5, essentially distinct (the annulus with few exceptions no more than 0.2 mm high), erect to spreading-erect, surpassing the gynostegium, with a central vertical groove within, but with little three-dimensional structure or folding, rhombic to broadly pyriform (abruptly narrowed more or less at the middle into a ligulate central lobe) in outline, the segment apices broadly triangular to ligulate, entire, bi- or trifid, the ligule when produced 2.5-6.5 x 2-3.5 mm, erect to more or less inflexed or descending over the stigma head, margins of segments plane or variously revolute, shoulders of segments rounded to prominently dentate-acute; anthers subsessile to indistinctly stipitate (the stipe to 0.5 mm high below the stigmatic slits, but usually about 0.2 mm when present), 0.8-1.4 mm broad below the glands, 0.5-1.5 mm long at stigmatic slits, the slits (anther wings) manifestly longer than the central, pollinium-bearing portion of the anthers to rarely (coastal Brazil) about as long, the appendages reniform to nearly orbicular, 0.4-1.0 x 0.6-1.4 mm, broadly rounded to truncate at apices; translators with pollinia broadly elliptic to elliptic-oblong or rarely obovate-elliptic, 0.4-0.7 x 0.2-0.4 mm, the ends broadly rounded, the gland rhombic-cylindrical, 0.2-0.4 x 0.15-0.3 mm, more than half as long as the pollinium, the translator arms yellow to brown, tangentially flattened and essentially triangular (gradually to abruptly expanded at the pollinia), 0.1-0.22 mm long, subapically attached to pollinia; gynostegium short-cylindrical, broader than high, equaling or slightly surpassing the glands in height, the apex (stigma head) flat, smooth, umbonate to somewhat tumid, 1.2-2.5 mm in diameter; follicles narrowly ovoid, glabrous, wrinkled to striate, drying pale brown to blackish gray, 6-16 x 2.5-3.5 cm; seeds ovate, smooth, brown 6.5-9 x 4.5-5 mm, truncate at apex, coarsely and irregularly dentate at base, the coma white to stramineous, 2.5-4 cm long.

Typification. The original Sello collection, designated by Sprengel as the type of Cynanchum montevidense, eventually found its way to Berlin as part of the Sprengel Herbarium and is, beyond any reasonable doubt, no longer extant. Dr. B. Leuenberger at Botanischer Garten and Botanisches Museum Berlin-Dahlem was kind enough to search both the general herbarium and the separate Willdenow Herbarium for surviving Sello type-collections but without success. A photograph of the original Berlin type exists at GH, with the acquisition of the specimen from the Sprengel Herbarium in 1890 clearly recorded on the label. This photograph is designated the lectotype.

It is disconcerting to read of glabrous umbels in Sprengel's original description of this species. However, inspection of the lectotype photograph reveals that the inflorescences are indeed racemose, although mostly in bud and with scarcely elongated internodes. In the southern part of its range, Cynanchum montevidense is characterized without exception by glabrous stems and closely puberulent inflorescences. Sprengel's description notwithstanding, there can be no doubt that the lectotype photograph represents a specimen conspecific with other of the material examined.

Neither collector nor type locality was cited in the original description of Asclepias cordata Vell. Types from Florae Fluminensis were deposited at the "Cabinet d'Histoire Naturelle de Rio de Janeiro" (Vellozo, 1825, loc. cit.; Stafleu, 1967). However, Vellozo's collections are not mentioned in Index Herbariorum (Holmgren & Keuken, 1974), nor were there any Vellozo specimens in material examined from the Museu Nacional (R) and the Jardim Botânico (RB) that might represent the original type collection. It is assumed that the collection did, indeed, come from the district of "Fluminensi," near Rio de Janeiro. In the absence of any surviving type material, the author's illustration and description (Vellozo, 1825, loc. cit., pl 56) are chosen as the lectotype of A. cordata.

Decaisne's Roulinia fluminensis, a superfluous name for Asclepias cordata Vell., is typified by Gaudichaud 712, the collection cited by Decaisne (1844, loc. cit.) (see Stafleu, 1978, art. 7.11). However, there is no possibility that the Vellozo species is based upon Gaudichaud's collection. Gaudichaud's second and third voyages (1831-33 & 1836-37), during which he visited the southern coast of Brazil, postdate the publication of Florae Fluminensis (Urban, 1906). In addition, the collection site of the Gaudichaud specimen, "Rio Grande" (do Sul), is significantly distant from the locus of Vellozo's Florae.

Two localities are cited with the original description of Cynanchum tamifolium



Hook. & Arn.: "woods about Rio Pardo, Rio Grande, and Maldonado in S. Brazil" Tweedie 267 and "hedges and woods at Port Alegre" Tweedie s.n. The former locality is, in fact, three localities, the first two in Rio Grande do Sul, Brazil, and the last in the state of Maldonado, Uruguay. Not surprisingly, there exist more than two specimens representing this type material: Tweedie s.n. (K), "Rio Pardo, S. Brazil"; Tweedie s.n. (K), "Maldonado"; and Tweedie s.n. (K), "Portalegre". An additional Tweedie specimen at OXF labeled "South Brazil" is yet another possible syntype, although many of the Tweedie specimens from that broad locality designation were collected after the 1834 publication of the Hooker and Arnott species. Of the Kew specimens, the authenticity of the Porto Alegre type seems most certain. The label data precisely match the original description in both collection number (there is none) and locality ("Hedges of Portalegre" and "In the woods of St. Jorim"). The Porto Alegre specimen is thus chosen as lectotype of C. tamifolium.

Lemaire's Roulinia versicolor was published with no specimen citation. The original description of plants under cultivation in Ghent and Paris, possibly originating in Buenos Aires, makes a suitable lectotype.

Two Sello collections (578 & 952) were cited as syntypes of Roulinia selloana Fourn., of which the former is designated lectotype for the following reasons. Only a single specimen of Sello 952 is known to exist (NY), and this is surrounded by some confusion, as Fournier erroneously cited the collection number as "592". On the other hand, Sello 578 is represented by material of equal quality but more ample quantity. At least 3 specimens are known to me: GH, US, and a fragment at NY. The specimen from GH is chosen as the lectotype.

Fournier cites Riedel 601 as the type of Roulinia riedelii. The specimen at P is the one most likely to have been seen by him (Stafleu & Cowan, 1976) and is designated the lectotype.

Distribution (Fig. 1). Cynanchum montevidense is a wide-ranging, somewhat weedy species, growing in periodically flooded habitats from Jamaica, Panama and the coastal slopes of Colombia and Venezuela south to Uruguay and Argentina. Generally, plants have not been collected at altitudes higher than 400 m. However, collections represent two populations in which plants are established in riparian habitats at higher elevations: one collection from the eastern slopes of the Peruvian Andes (Vargas 1697) records an elevation of 1200 m, and 7 collections from Argentina, from the northern states of Salta, Tucuman, and Catamarca, record elevations of 500-1100 m.

Habitat data available are mostly variations on a riparian theme. However, especially in Colombia, Paraguay, and Argentina, collections from marshes and swamps are quite common. Several specimens from thickets, railroad tracks, hedges, fences, and a cane field suggest that the species may also tolerate areas disturbed by man.

Cynanchum montevidense exhibits marked seasonality in growth and phenology, an adaptation which no doubt contributes to its breadth of geographic and ecological tolerance. It flowers (and shortly thereafter fruits) from July to January in Panama, Colombia, Venezuela, and Guiana, and from December to June in central and southern Brazil, Paraguay, Uruguay, and Argentina. Collections of flowering material from the Amazon basin of Peru and Brazil have been taken between the months of April and October.

Data on flower color is exceedingly variable and in some instances unreliable owing to the failure of the collector to distinguish between the petaloid crown and the corolla. The above species description provides details of floral coloration, and color variation at the population level is discussed below.

Jamaica. Purdie s.n. (P).

Panama. Panama: east of Bejuco, Duke 4551 (MO).

Colombia. Choco: Río Atrato near Río Sucio, Gentry 9292 (MO); Municipality of Río Sucio, Parque Natural Nat. Los Katyos, Río Cacarcas at Cristales, Léon 661 (MO). Atlantico: Vicinity of Barranquilla, mouth of Río Magdalena, Andre 179 (K). Magdalena: Salamanca Island, Romero & Nunez 11086 (MO); Cienega, H. H. Smith 1674 (BM, CM, G, NY).

Venezuela. Zulia: Vicinity of Méné Grande, Pittier 10607 (G). Bolivar: Ciudad Bolivar, mouth of Río Maruanta, Aristequieta 4860 (MO); Cuyuni River near Anacocco, Gentry et al. 10729 (MO).

Guiana. Essequibo: Essequibo River, Rockstone, Gleason 887 (NY).



Peru. Huanuco: Río Pachitea, 20 km upstream of confluence with Río Ucayali, Schunke 1851 (F, G, GH, MO, NY, U). Loreto: Río Marañón near mouth of Río Tigre, Killip & Smith 27512 (MO, US); Río Amazon, Nanay, Williams 512 (F); Río Amazon, Iquitos, Williams 8221 (F, MO); Iquitos, Williams 7900 (F); near mouth of Río Ucayali, Tessman 3288 (G). Cuzco: Convencion, Hda Portrero, Vargas 1697 (NY).

Brazil. Amazonas: Río Jurua, Paranagua, Tefé District, Krukoff 4536 (MO, U). Para: Río Tapajós, Boa Vista, Dahlgren & Sella 69 (MO); Tapaná, vicinity of Pará, Killip & Smith 30347 (MO, NY). Mato Grosso: Río Teles Pires ("Río São Manoel"), Pires 3744 (US); Barra do Bugre ("Santa Cruz do Barra"), Lindman 2833 (GH, LD, US); Salobra, without collector (R, Accession No. 94885). Goiás: Porto Real, Burchell 8478 (BR, K). Bahia: Juazeiro, Lehtner 781 (M); district of Coatinga, northeast Bahia, Luetzelburg 72390 (M). Minas Gerais: Manger, district of C. Verde, Macedo 200 (US). São Paulo: São Paulo railway near Río Grande, Wacket s.n. (W); Iguapé, "Morro das Pedras," Brade 9121 (R). Paraná: Río Paraná, district of Loanda, between Porto São Jose and Porto Camargo, Hatschbach 5605 (B, MO, US); Río Paraná, Cliffs of Araras, Hatschbach 15784 (NY, US); Río Ivahy, between Petropolis and Therezina, Dusen 11226 (BM, G, GH, MO, NY, S, US). Santa Catarina: Río Itajaí Açu ("Itahype"), Martius 2078 (M). Río Grande do Sul: Río Pardo, Tweedie s.n. (K); Porto Alegre, Malme 1358 (G, GH, LD, M, S, US); Porto Alegre, Río Guafba, Czermak & Reineck 188 (G), 323 (P); Río Grande, without further locality, Fox 22 (K), Tweedie s.n. "1837" (K). Brazil, locality uncertain: southeast Brazil, Sello 283 (K, NY, R), 952 (NY), 2553 (B, GH, NY), 3378 (US), s.n. "Roulinia Sellowiana" (F), s.n. "Roulinia fluminensis" (F), Tweedie s.n. (OXF); Río Branco, vicinity of San Marcos (Acre? Mato Grosso? Roraima?), Ule 7818 (B, G, K, L).

Bolivia. Tarija: Carapari, Fries 1345 (S); Río Pilcomayo, Fortin Crevane, Fries 1616 (S), 1627 (S). Locality uncertain: "im Palmar von Medanos (Alto Paraguay)" (Santa Cruz Department, south of Ravelo?), Herzog 160 (L).

Paraguay. Alto Paraguay: Chaco, 21° S., Fiebrig 1308 (G). Boqueron: Gran Chaco, Santa Elisa, 23° 10' S., Rojas 2729 (C, G, MO, NY, P, S, UC, W), 2729a (G, GH, NY, S, UC, W); Mennonite Colonies, Arenas 1462 (UC). Presidente Hayes: Camp Nanahua, 23° S., 59° W., Carter 75 (BM). Concepción: Villa Lana, between Río Apa and Río Aquidaban Fiebrig 4680 (BM, G, GH, K, L, M). San Pedro: Río Tapiracuay at San Estanislao, Krapovickas et al. 14301 (F, P, UC); without further locality, Woolston 343, (K, UC, US), 1160 (C, NY, S, UC). Central: Riacho Caracara, vicinity of Trinidad, Rojas 12562 (NY, UC); Asuncion, Balansa 1340 (P), Morong 183 (GH, MO, NY, US). La Cordillera: vicinity of Lake Ypacaraí, Rojas 14254 (P, W), Hassler 12601 (BAF, BM, C, G, GH, K, L, MO, NY, S, UC, US); San Bernadino, Hassler 3577 (G, GH, MO, NY, P, S, UC, W); Tobati, Fiebrig 802 (F, G); valley of Y-aca River, vicinity of Valenzuela, Hassler 6794 (BM, G, GH, K, MO, NY, P, S, UC, W). Guairá: Villarrica, Jorgensen 3835 (C, F, MO, NY, S, US). Locality uncertain: Río Pilcomayo, Morong 1037 (MO "1837", NY), Rojas 231 (G); Gran Chaco, Gilbert 6 (K); Santo Tomas (La Cordillera?), Hassler 1913 (G, NY).

Argentina. Salta: Dept. Oran, Tartagal, Schreiter 10853 (F, GH), Oran, Lillo 18093 (MO), El Tabacal, Meyer 4591 (F, UC), Río Capiasuti, Schreiter 3572 (MO); Pasaje o Río Juramento, Lorentz & Hieronymus 318 (F, NY, US); Dept. La Candelaria, vicinity of La Candelaria, Schreiter 5805 (F, GH, NY), 9370 (F, GH, NY). Catamarca: Río del Valle, Castillon 1075 (MO), Castillon s.n. (MO); without further locality, Spegazzini s.n. (S). Tucumán: Dept. Trancas, San Pedro de Colalao, Castillon s.n. (MO), Río de Cas Tipas, Castillon s.n. (MO); Dept. Burreyacu, Cerro del Campo, Venturi 8010 (MO, US); Dept. Tafi, Yerba Buena, Venturi 59 (MO, US); Dept. Capital, Parque de Julia, Schreiter 1412 (GH, MO); Dept. Leales, Leales, Venturi 730 (MO, US); Dept. Río Chico, los Sarmientos, Venturi 8474 (GH, US). San Luis: Sierra de San Luis, Bajo de Velis, Kurtz 8562 (NY, R, S). Córdoba: Serrezuela, Stuckert 17023 (G); between Soto and Cruz del Eje, Kurtz 6517 (S). Formosa: Pirané, Morel 255 (S, W); Formosa, Jorgensen 3188 (GH, MO, US), Jorgensen 3189 (MO), Kurtz 1673 (S); without further locality, Jorgensen 2602 (GH, MO, US). Chaco: Fontana, Meyer 593 (K), 757 (S); Colonia Benítez, Schulz 40 (S), 41 (S); Resistencia, Meyer 293 (A, S); locality uncertain, "Dept. San Fernando, Loc. Campo Kesqui," Schulz 15945 (G); "Dept. 1° de Mayo, Loc. Tres Horquetas," Schulz 109 (G). Santa Fe: Amores, Ragonese 3287 (MO). Corrientes: Dept. Empedrado, about 10 km north of Puente Descabezado, Pedersen 2632 (BR, C, MO, P, S, US); La Yela, Pedersen 3917 (BR, C, G, GH, NY); Dept. Mburucuyá,



Santa Teresa, Cañada Portillo, Pedersen 2616 (BR, C); Dept. Mercedes, Itá Caabó, Pedersen 5368 (C); Dept. Itatí, Ruta Nac. 12, 47 km east of Itatí, Ahumada et al. 712 (F, G). Entre Ríos: Dept. Uruguay, La Selmira, Isla Cupalen, Pedersen 8219 (C). Buenos Aires: Buenos Aires, Hanshel 651 (W); Ensenada, in Los Calas, Lefebvre s.n. (BR); locality uncertain, "Barracas al Sud: Estacion Grel Mitre," Aubray s.n. (BAF), "Barracas al Sud," Venturi 83 (BAF, S). Uruguay. San José: Río San José, Herter 1511 (MO, S, UC). Canelones: vicinity of Canelon Grande, Berro 1754 (G), 3376 (G); Carrasco, Gibert s.n. "1869" (S); Manga, Fruchard s.n. "1883" (P); Montevideo, Arechavaleta s.n. (W). Maldonado: Tweedie s.n. (K, photocopy seen). Treinta-y-Tres: Río Olimar, Berro 3024 (G). Locality uncertain: Río Santa Lucia, Fruchard s.n. "1875" (P), Gibert s.n. "1874" (W).

Despite the incorporation of a large number of taxonomic synonyms from localities as distant as Jamaica and Montevideo, Cynanchum montevidense is remarkable for its morphological uniformity. With few exceptions, the stems and deeply cordate leaf blades are devoid of pubescence, the rotate to reflexed corollas are bearded in the throat and sinuses, and the crown segments are essentially distinct or united by an annulus no more than 0.2 mm high. Only the outline of the crown segments and the overall dimensions of the flowers exhibit significant variability. Indeed, several local populations can be imprecisely defined accordingly. The validity of employing minor variations of the crown to distinguish species has been discussed previously. However, when all available material from South America is examined, such variability is seen to fit comfortably within the geographic patterns of a single morphological continuum; intermediates are many and significant discontinuities cannot be detected. Even the recognition of the most distinct of the local populations at the subspecific level is not considered warranted.

Five regions of South America, all generally east of the Andean cordillera, are represented by abundant collections of C. montevidense, an abundance which is interpreted to represent the emphasis of collectors rather than the distribution of the species. The five regions recognized (Fig. 1) are: the southeastern coast of Brazil and adjacent Uruguay and Argentina; the lowland marshes or Gran Chaco of Paraguay and adjacent Argentina, as well as the Rio Paraná and its tributaries (the eastern watershed of the Rio de la Plata); the upland areas of northern Argentina, particularly the states of Tucuman and Salta; the Amazon basin of Peru and Brazil; and the northern coastal slopes of Colombia and Venezuela. Populations of C. montevidense in each of these areas are more or less distinct from one another in certain combinations of morphological characters (see Table 1). However, specimens from intermediate localities, exhibiting every form of intermediate character, strongly suggest for all the South American populations the absence of insuperable geographic barriers to genetic exchange.

Three different designations of crown segment outline are taken to represent the full range of variability in C. montevidense: ligulate (Fig. 5 I, L, O, P, S, T, U, W), pyriform (Fig. 5 A, C, H), and rhombic (Fig. 5 B, D, F, J, K, M, Q). In general, these crown types, as well as floral dimensions and corolla lobe orientation, correlate well geographically (Table 1). Northern populations (Jamaica, Venezuela, Colombia, and Amazonian Peru) are characterized by rhombic crown segments, southern populations (Argentina, Paraguay, Uruguay, and Brazil) by ligulate segments; pyriform crown segments occur randomly in all populations except that of coastal Brazil, Uruguay, and Argentina. Segments of intermediate form are quite common (Fig. 5 E, G, N, R, V, X).

Specimens from the coastal population of southeastern South America are uniform in their possession of erect, ligulate crown segments. Proportion of ligule length to that of the broad, basal portion of the segment varies greatly, with ratios between 1:1 and 2:1 most frequent (Fig. 5 I, L, O, S, T, U, W). The holotype of Roulinia acuta (Fig. 5 P) from Sao Paulo, Brazil, represents the most extreme condition, with a ligule to base ratio of 3:1.

The coastal population attains its most distinctive overall morphology further to the southwest in the state of Rio Grande do Sul, Brazil, where are found plants with crowded racemes of rather small flowers and fully reflexed corolla lobes often unusually light in color, at least distally (Malme 1358 and Tweedie). Label data recording white flowers (entirely white?) are to be found for several collections from Uruguay and



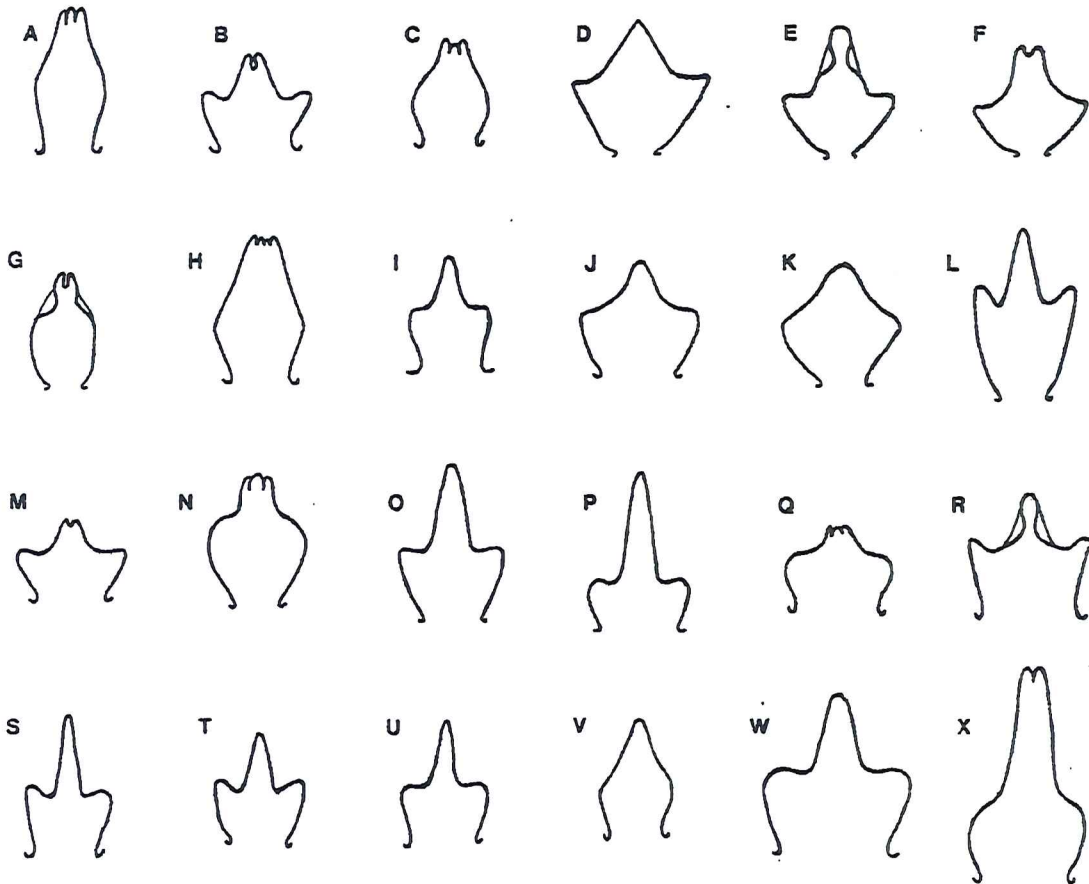


Figure 5. Crown segment outlines from selected specimens of *Cynanchum montevidense*, all  $\times 5.2$ . A. Duke 4551, Panama; B-C. Purdie s.n., Jamaica, different flowers; D. Vogl 1407, Aragua, Venezuela; E. H. H. Smith 1674, Magdalena, Colombia; F. Pittier 10607, Zulia, Venezuela; G. Krukoff 4536, Amazonas, Brazil; H. Killip & Smith 30347, Para, Brazil; I. Manso 1832, Mato Grosso, Brazil; J. Vargas 1697, Cuzco, Peru; K. Tessman 3288, Loreto, Peru; L. Riedel 601, Rio de Janeiro, Brazil; M. Cardenas 9 Special, Beni, Bolivia; N. Burchell 8478, Goias, Brazil; O. Gaudichaud 388, Sao Paulo, Brazil; P. Gaudichaud 378, Sao Paulo, Brazil; Q. Lorentz & Hieronymous 318, Salta, Argentina; R. Martius 2078, Santa Catarina, Brazil; S. Gaudichaud 712, Rio Grande do Sul, Brazil; T. Sello 578, South Brazil; U. Tweedie s.n., South Brazil; V. Spegazzini s.n., Catamarca, Argentina; W-X. Hassler 12601, La Cordillera, Paraguay, different flowers.

Argentina: Meyer 757, Ragonese 3287, Pedersen 5368 and 8219, Berro 1754, 3024, and 3376. Specimens to the northeast and southwest of Porto Alegre show a gradual increase in floral dimensions and a tendency for the corolla lobes to remain only partially reflexed and arcuate. Plants from the vicinity of Buenos Aires exhibit uniformly hirtelous corolla lobes (Venturi 83, Hanshel 651, Lefebvre s.n.), a condition duplicated in Malme 1358 from Porto Alegre but also in Cardenas 9 Special from Trinidad, Bolivia. A tendency toward union of the crown segments with a resulting annulus of as much as 0.5 mm high can also be seen in Buenos Aires collections: Hanshel 651 and Aubray s.n. However, the character occurs sporadically in other localities: Pedersen 5368 (Corrientes, Argentina), Hassler 12601 (La Cordillera, Paraguay), Venturi 8010 (Tucuman, Argentina), Killip & Smith 30347 (Para, Brazil).



Paraguayan collections from the vast marshlands of the central and northern states are strikingly robust. The corollas are large and dark with arcuate, horizontally spreading lobes, and the leaves often measure more than 10 cm in length and dry an extraordinary glossy blue-green color (Rojas 231, 2729, 2729a, 12562, 14254; Hassler 3577, 6794, 12601; Meyer 293, 593; Fiebrig 4680). That none of these collections was ever selected as type material for yet another new species of *Roulinia* is indeed remarkable. Judging from the diverse opinions represented on annotation labels, those specimens evidently have posed much difficulty of identification. Gustav Malme, for instance, an accomplished student of the Asclepiadaceae and monographer of the large South American genus *Oxypetalum*, had originally annotated the Stockholm specimens of Rojas 2729 and 2729a as *Roulinia fluminensis*. Some twenty years later, however, his 1933 reannotation labels read *R. convolvulacea*. A remarkably uniform gross morphology notwithstanding, crown segment outline within this population, and even within single collections (Hassler 12601, Fig. 5 W-X), is variable in the extreme.

Populations inhabiting the southeast coastal region between Buenos Aires and Rio de Janeiro, a region slightly more than a thousand miles long, have furnished a disproportionate number of type specimens for the genus *Roulinia*. Of the fourteen names that are here treated as synonyms, nine are typified by specimens from this geographically complex region. Unfortunately, not all material is still extant, but of that available for examination, collections from Rio Grande do Sul, e.g., original syntypes of *Cynanchum tamifolium* Hook. & Arn. and the holotype of *R. fluminensis* Decne., as well as the original syntypes of *R. selloana* Fourn., are all morphologically indistinguishable. Malme (*loc. cit.* 1921) considered the former two names synonymous with *C. montevidense*.

Decaisne established two additional species, *Roulinia acuta* and *R. convolvulacea*, based on two rather dissimilar collections from the state of Sao Paulo, Brazil (Gaudichaud 378 and 388, respectively). The former falls well within the range of character variability encountered in specimens to the southwest of Sao Paulo. On the other hand, the latter specimen possesses several characters that ally it to the populations of Argentina and Paraguay: darker, broader, more spreading corolla lobes, a longer stigmatic slit, and leaves scarcely longer than broad. Other specimens from the interior of the southeastern Brazilian coastal states are similarly robust and, at first glance, morphologically incongruous (Hatschbach 5605, 15785; Dusen 11226; Wacket s.n.). However, the complex morphological patterns encountered in these eastern Brazilian populations probably reflect the geographical complexity of the coastal highlands of the Sierra do Mar, whose major rivers flow westward toward the Rio de la Plata and not eastward directly into the Atlantic Ocean. It is not unreasonable to expect that plants of this lowland species collected along the Rio Paraná and the Rio Ivahy in the Brazilian coastal states of Sao Paulo and Paraná are elements of a population receiving more frequent genetic communication from the distant Paraguayan chaco than from the relatively nearby rivers on the opposite slopes of the coastal range.

That the western drainage system of these coastal highlands is to some degree geographically isolated is further emphasized by the occurrence of two narrowly endemic and rather closely related species in the basin of the Rio Paraná: *Cynanchum ekmanii* (discussed below) and *C. rioparanense*.

Riedel's collection (601) from the vicinity of Rio de Janeiro, the type of Fournier's *Roulinia riedelii*, exhibits characters of both the Paraguayan and coastal Brazilian populations. The pollinia are the shortest examined from among the coastal specimens (0.35 mm) while the length of the corolla lobes, crown segments, gland, and stigmatic slit is intermediate (Fig. 5 L & 6 B). The crown segments are ligulate with a relatively long basal portion. The corolla is entirely glabrous, a singular condition foreshadowed by the very sparsely pubescent corollas found in inland specimens farther to the west (Dusen 11226, Manso s.n., Martius 2078). It has already been mentioned that Vellozo's *Asclepias cordata* was more than likely based on a specimen collected in the vicinity of Rio de Janeiro. His illustration of the habit of that species, as well as details of crown segments and orientation of the corolla lobes, is certainly applicable to the Riedel specimens examined.

Collections from upland Argentina also share characters with lowland populations of both Paraguay and coastal Brazil. Orientation of the corolla lobes is intermediate--



reflexed to spreading. Leaves and flowers are generally small. Crown segment outline varies from pyriform (Fig. 5 V) to ligulate with frequent intermediates (Fig. 5 Q) that approach the deltoid outline characterizing more northern populations (Fig. 5 B, M). The Argentinean population is noteworthy for the small, ovate, and dull (rather than glossy) leaves, usually only slightly longer than broad, short racemes 3-7 cm in length, and the elevation of the gynostegium on a relatively long column (about 0.5 mm).

Collections from the Amazon basin of Peru superficially resemble those from the Gran Chaco of Paraguay; they are robust with large glossy leaves and equally large and showy flowers (Table 1), perhaps to some degree a response to abundant available moisture in both localities. By contrast, consistent differences in floral morphology between those populations are likely under rather tight genetic control. Dimensions of pollinia and stigmatic slits are considerably larger in the Amazonian material. Crown segments vary from rhombic to pyriform (Fig. 5 G-H, J-K) and suggest a close genetic affinity with Colombian and Venezuelan populations.

Several anomalous features mark certain of the collections from Amazonian localities. Peduncles may be exceptionally long (to as much as 10 cm in Tessman 3288 and Schunke 1851). Inflorescences may be tomentose (Pires 3744), especially when immature, or, in the single collection (Vargas 1697) from high elevation in Peru (1200 m), short sericeous. Occasional collections possess pubescent stems (Vargas 1697, Krukoff 4536). Finally, the crown may be inserted on the throat of the corolla or on a short column 0.1-1 mm high (Killip & Smith 27512, Dahlgren & Sella 69, Tessman 3288).

That those Amazonian specimens exhibit some unusual morphological features may perhaps be ascribed in part to low levels of hybridization with the sympatric Cynanchum blandum. A few specimens have characters that are intermediate, e.g., an unusually high crown annulus in Killip & Smith 30347 from Para, Brazil; rather intermediate crown segments in Krukoff 4536 (Fig. 5 G) from Amazonas, Brazil; and a ring of pubescence in the corolla throat in Schunke 98 from Loreto, Peru (a collection assigned to Cynanchum blandum). Cynanchum blandum is known to flower from January to August, Amazonian representatives of C. montevidense from April to October. In addition to crown morphology and corolla pubescence, those two species are separable by leaf shape, the leaves of C. montevidense being deeply cordate at the base while those of C. blandum are at most only shallowly so.

Collections of Cynanchum montevidense from upland areas of Brazil (Mato Grosso, Bahia) show affinities with populations farther north and south. Manso's collection (s.n., dated 1832) from Mato Grosso, designated by Decaisne as the type of Roulinia modesta, bears a rhombic-ligulate crown segment similar to those found in collections from as distant as Jamaica (Fig. 5 B, I). The type of R. manni (Cardenas 9 Special) from nearby Bolivia exhibits the same crown segment outline (Fig. 5 M) and compares well to the Manso type in floral dimensions. The Cardenas specimen is notable for its corolla lobes, which are short hirtellous throughout (rather than merely in the throat of the tube), a character already noted in some coastal Argentinean specimens.

A tendency toward the development of a short column below the crown (already noted in Amazonian plants) appears again in a few of those more upland collections (Burchell 8478, Goias, Brazil; Manso s.n., Mato Grosso, Brazil). However, this somewhat unusual character, like so many others of this variable species, is not geographically restricted but appears at intervals in several local populations, e.g., Brade 9121, Sao Paulo, Brazil; Schreiter 9370, Salta, Argentina; Venturi 730, Tucuman, Argentina; Fries 1345, Tarija, Bolivia; Meyer 293, Chaco, Paraguay; Carter 75, Presidente Hayes, Paraguay.

Likewise the pyriform crown segment continues to run through the upland Brazilian populations as a minor theme in counterpoint to the rhombic outline. The persistence of this alternate morphology from Amazon basin to Sao Paulo, Brazil, is remarkable. Pyriform segments from the following four Brazilian collections are practically indistinguishable: Killip & Smith 30347, Para; Lehntner 781, Bahia; Lindman 2833, Mato Grosso; Brade 9121, Sao Paulo.

Three species (Roulinia jamaicensis, R. voglii, and Cynanchum magdalenicum) are based upon collections from northern South America and Jamaica. Although the material from this part of the range of C. montevidense exhibits as much instability of crown morphology as other populations, the type specimens in question are quite similar.



Table 1

Selected floral character states in the five major regional populations of *Cynanchum montevidense*. A = corolla lobe orientation, B = corolla lobe length (mm), C = crown type, D = crown length (mm), E = pollinium length (mm), F = stigmatic slit length (mm). See text for explanation of population localities.

Population	A	B	C	D	E	F
Southeastern coast	fully reflexed	6-7.5	long ligulate	3-4	0.35-0.45	0.6
Gran Chaco	horizontally spreading	(6-)7-9(-10)	ligulate to pyriform	4-5	0.45-0.5	0.8
Upland Argentina	reflexed-spreading	5-7.5	short ligulate to pyriform	2.5-4	0.4-0.5	0.7-1.2
Amazon basin	reflexed-spreading	(6-)7-9(-10)	rhombic	3	0.5-0.7	0.9-1.4
Northern coast	fully reflexed	(5-)6-7	rhombic to pyriform	3-4	0.5-0.6	0.7-1.2



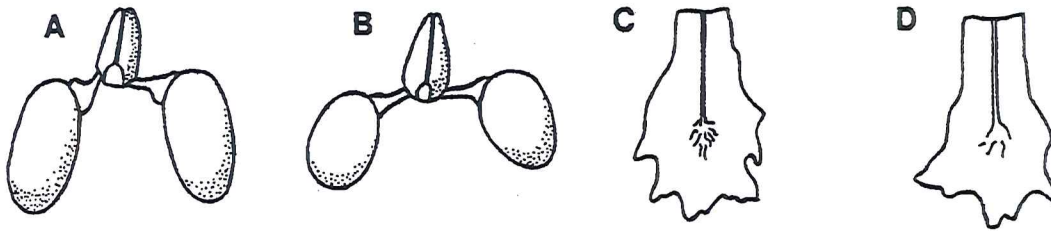


Figure 6. *Cynanchum montevidense*. A-B. Translators, abaxial surface, x 39 (A. Gaudichaud 388; B. Riedel 601); C-D. Seeds, placental surface, coma detached, x 3.9 (C. Killip & Smith 14715; D. Rojas 2729a).

The number of taxonomic synonyms, in this instance, can be attributed to factors other than the narrow species concept by which Decaisne and Fournier were able to generate such a large number of species out of collections from coastal Brazil.

*Roulinia jamaicensis* has, until the present, been known only from the holotype (Wilson s.n.) at Kew. However, a second Jamaican specimen, from Paris, has come to light during the course of the present study. Unlike the Wilson type, this specimen is in excellent condition, with ample flowering material permitting, perhaps for the first time, close comparison with collections from northern South America. No collector is recorded on the specimen, but the information, "donné par Sir W. Hooker," is strong evidence that the collection is one of many gathered by William Purdie and sent to Hooker at Kew (Ewan, 1948), and thence to Paris. Stearn (1965) notes (very conveniently) that some of the Purdie duplicates are indeed at Paris.

The presumed Purdie specimen without any doubt represents the same taxon as the Wilson type. Indeed, it also matches both the Venezuelan type (Vogl 1407) of *Roulinia voglii* and the Colombian type (Killip & Smith 14715) of *Cynanchum magdalenicum* in all details of floral morphology (Fig. 5 B-D). By its curious possession of pyriform and rhombic crown types (Fig. 5 B-C), Purdie's specimen allies the Jamaican population to the collection from Panama (Fig. 5 A) and to all southern populations with the exception of the southeastern coast of Brazil and adjacent Uruguay and Argentina.

5. *Cynanchum ekmanii* (Malme) E. Sundell, comb. nov.

Figs. 1 & 7 A-C.

*Roulinia Ekmanii* Malme, Arkiv. Bot. Stockh. 16(15): 18. 1921. Type: Argentina: Misiones. District of Posadas, vicinity of Bonpland, Ekman 406 (holotype: S!, 3 sheets).

Suffrutescent, twining vine; stems glabrous, terete, dull purplish brown to pale brown with age, to 7 mm in diameter, the branchlets stramineous; petioles glabrous, 4.5-7 cm long, to 2 mm broad, 1/3-1/2 as long as blade; leaf blades chartaceous, glossy, drying brownish green to blue-green above, paler beneath, the larger blades broadly ovate, the smaller ovate to broadly oblong-lanceolate, 6-16 x 2.5-13 cm, acuminate at apex, cordate to truncate at base, glabrous above and beneath, the glands 3-13, the venation of the lower surface prominulous, the tertiary nerves more or less obscure; racemes to 15-flowered (with 3-6 at once mature), congested distally, elongating in age, 6-11 x 2-4 cm, often pseudo-paniculate on axillary branch systems by reduction or loss of leaves, or less commonly the racemes producing short-stipitate umbels at the lower nodes, the peduncle sparingly to moderately puberulent, pedicels slender, 1 or 2 per node, densely adaxially puberulent, 12-18 mm long; bracts lanceolate, 2.5-4 mm long, ciliate at margins; flower buds oblong to obconic, 5-6 mm long, obtuse at base, broadly rounded-truncate at apex; calyx broadly campanulate, glabrate to densely puberulent at base, the tube indistinct to 1 mm long, the lobes chartaceous, erect, elliptic,



3-4.5 x 1-2 mm, broadest just below the middle, rounded at apex, ciliate especially distally at margin, the glands numerous, as many as 30 per flower, densely crowded in sinuses or spreading in a ring around calyx throat; corolla reflexed-campanulate, 8-10 mm in diameter, 5-6 mm long, drying dark brown to blackish brown outside, paler within, short-hispidulous with appressed unicellular hairs on lobes within, the corolla tube 1.6-2 mm long, 2 mm broad at the summit, the lobes spreading-erect but recurving below middle and distally reflexed, lanceolate, tapering abruptly near base or gradually throughout, 5 x 1.8-2 mm, acute at apex, revolute at margin; crown inserted at corolla throat, 0.4-0.8 mm below sinuses, 4.5-5 mm long, drying more or less dark brown, crown segments 5, manifestly united, (the annulus 0.2-0.4 mm high and minutely glandular in the sinuses), erect, about equaling stigma head in height, flat (with no three-dimensional structure), in outline elliptic, deeply bifid nearly to the middle, the twin lobes ligulate and converging at their tips, 2-3 x 0.4-0.5 mm, the sinus of each segment with or without a dentate lobe 0.5-1 mm long, the basal portion of the segments 2-2.5 x 2 mm, broadest at the summit; anthers stipitate (the stipe fully 2 mm high), 1.2-1.4 mm broad below glands, 0.6-0.8 mm long at stigmatic slits, the slits (anther wings) elevated above and manifestly shorter than the inflated-saccate, central, pollinium-bearing portion of anthers (0.8-1.2 mm), the appendages reniform-orbicular, 0.4 x 0.6 mm, broadly truncate-depressed at apex; translators with pollinia elliptic-fusiform, 0.6-0.75 x 0.2-0.25 mm, both ends acute or narrowly blunt, golden brown to yellow orange, the gland narrowly rhombic, 0.5-0.6 x 0.1-0.25 mm, broadest below middle, sharply acute and abruptly abaxially deflected at apex, about equaling the stigma head or slightly raised above, translator arms broadly filiform, 0.6 mm long, descending (after removal), apically attached to pollinia; gynostegium short-cylindric (stipe excluded), broader than long, 1.5 x 2.5 mm, the apex (stigma head) flat, smooth (more or less minutely rugose), umbonate to somewhat tumid, 1.5-2 mm in diameter; follicles unknown.

Typification. The citation of Stockholm as the institution at which Malme examined Ekman 406 appears on p. 11 (1921, loc. cit.), separate from the protologue.

Distribution. Three collections of Cynanchum ekmanii are known to me from the basins of the Río Paraná and the Río Uruguay in southeastern Paraguay and Misiones, the westernmost state of Argentina. Such a dearth of collections from a relatively populous area suggests that the known range may reflect the narrow endemism of this species with considerable accuracy.

Paraguay. Alto Paraná: Río Paraná, without further locality, Fiebrig 5868 (US).  
Argentina. Misiones: District of San Javier, vicinity of Acaragua, Bertoni 3288 (W).

Both Cynanchum ekmanii and C. rioparanense are endemic to the eastern drainage system of the Río de la Plata. The few collections presently available indicate that the species are allopatric, although some overlapping of their ranges in the basin of the Río Paraná would seem inevitable. Both species are restricted to low elevations where they are sympatric with the widespread C. montevidense. Collection data record that C. ekmanii flowers from December to March, suggesting a period of at least three months in which the three species are simultaneously in bloom.

Despite this geographical and phenological overlap, Cynanchum ekmanii is morphologically very distant from members of section Roulinia. Rather, it appears to be closely related to C. cubense (A. Rich.) Woods., a robust vine of low elevations in Cuba and from Colombia to southern Mexico. The two species share a number of interesting vegetative and reproductive features; both possess large, glabrous, glossy leaves with rounded to cordate bases as well as a tendency to develop pseudo-panicles by the aggregation of racemes on lateral (axillary) branching systems with reduced leaves, (a trend fully realized in the very different genera, Tassadia and Jobinia). In both species, the interior surface of the corolla lobes is rather uniformly pubescent with appressed, flattened, unicellular hairs. Lastly, the two species exhibit some extreme modifications of the gynostegium directly related to pollinium



transfer, in particular, the elevation of the anthers on a stipe at least 1 mm high and the closely correlated lengthening of the translator arms to at least 0.6 mm (Fig. 7 B, C).

The only significant differences between Cynanchum ekmanii and C. cubense lie in the form of the crown and the outline of its segments and in the number of their calyx glands. The crown of C. cubense is cyathiform, with segments reduced to more or less rounded lobes less than 1 mm long, scarcely longer than the annulus. The crown of C. ekmanii (Fig. 7 A) is more elaborate and showy, about 5 mm long, with the segments deeply bifid and the two ligulate lateral lobes 2-3 mm long. In addition, C. ekmanii has as many as 30 calyx glands per flower, densely crowded around the throat of the tube, while C. cubense (like C. blandum) has a single gland in each sinus. The follicles of C. ekmanii are unknown, but those of C. cubense are some of the largest in the Asclepiadaceae, specimens from Cuba (Wilson 11441, NY; Wilson & Leon 11623, NY) bearing fruits 16-17.5 cm long and 7 cm in diameter. Follicles of similar size in C. ekmanii would lend strong additional support to a claim of phyletic proximity between these two disjunct species.

6. Cynanchum cubense (A. Rich.) Woods., Ann. Missouri Bot. Gard. 28: 213. 1941.  
Fig. 7 D.

Spellman, in Woodson, et al. Ann. Missouri Bot. Gard. 62: 120. 1975.

Gonolobus cubensis A. Rich. Fl. Cub. Fanerog. 2: 98. 1845. Type: Cuba,  
Valenzuela (P).

Metalepis cubensis (A. Rich.) Griseb., Cat. Pl. Cub. 180. 1866.

For reasons already stated, Cynanchum cubense is not given detailed treatment in this study. The remaining taxa of the northern Metalepis complex (all closely related to C. cubense and some possibly conspecific) are listed below with information on place and date of publication and typification. I have not examined any of the types.

Cynanchum albiflorum (Urb.) Woods., Fl. Trin. Tobago 2: 168. 1947.

Metalepis albiflora Urb., in Fedde, Rep. Spec. Nov. 16: 37. 1919. Type: Tobago:  
near the district "The Widow," W. E. Broadway 4794.

Cynanchum (Metalepis) subpaniculatum Woods., Ann. Missouri Bot. Gard. 28: 275. 1941.

Type: Colombia: vicinity of Santa Marta, alt. 2000 ft., June 1898-1901,  
H. H. Smith 2410 (MO).

Cynanchum (Metalepis) Haughtii Woods., Ann. Missouri Bot. Gard. 28: 276. 1941.

Type: Ecuador: roadside near Paján, alt. ca. 200 m, Dec. 10, 1939, O. Haught 2985 (MO).

Cynanchum (Metalepis) Marsdenioides Woods., Ann. Missouri Bot. Gard. 31: 235. 1944.

Type: Ecuador: Los Rios, Oct. 1934, Mexia 6660, whence grown from seed at Puerto Rico Experiment Station, United States Department of Agriculture, Mayaguez, Puerto Rico, R. H. Moore 2163 (NA).

Cynanchum (Metalepis) peraffine Woods., Ann. Missouri Bot. Gard. 31: 236. 1944.

Type: Mexico: Oaxaca. in llanos, District Tuxtepec, Chiltepec and vicinity, alt. about 20 m, July 1940-Feb. 1941, G. Martinez-Calderon 258 (US, herb. no. 1,808,120). = C. cubense according to Spellman, 1975.

When Woodson (1941) merged Metalepis with Cynanchum, the distinctiveness of the former genus was emphasized by merely shifting the rank of the taxon to subgenus while maintaining the original monotypic circumscription. Woodson (1941 & 1944, loc. cit.) subsequently described four new species of subgenus Metalepis from Colombia, Ecuador, and southern Mexico (Oaxaca). Yet another species, from Tobago, came to his attention in 1947 (loc. cit.) In all, Woodson seems to have recognized six species



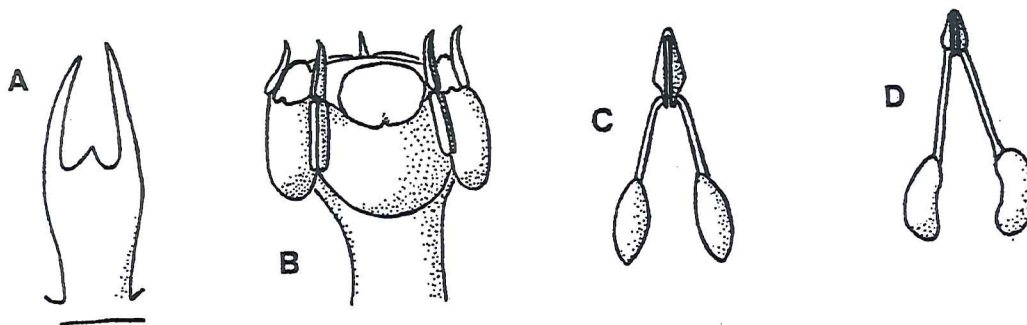


Figure 7. A-C. *Cynanchum ekmanii*. D. *C. cubense*. A. Crown segment, abaxial surface, x 7.8 (Ekman 406); B. Portion of anther stipe and gynostegium, x 13 (Ekman 406); C-D. Translators, x 19.5 (C. Fiebrig 5868; D. Croat 11175, MO).

in this complex occupying areas of low elevation from the West Indies and Central America (including southern Mexico) to northern South America.

Because the scope of the present revision did not originally include *Metalepis*, relevant herbarium material was not requested for study, and I cannot offer an opinion of Woodson's expanded *Metalepis* complex. The segregate species are based on minor variations of flower and leaf size, corolla shape and texture, and crown segment outline. My own experience with the numerous segregates of *Cynanchum montevidense* indicates that the significance of such characters dwindles as more abundant material, especially from intermediate localities, becomes available for examination. In addition, I have been able to examine two specimens, both probably referable to *C. cubense*, Croat 11175 (MO) from Panama and Howard 6238 (NY) from Cuba. Those specimens exhibit differences in corolla shape and pubescence, crown segment outline, and texture of crown and anther stipe of a magnitude which, by Woodson's standards, might perhaps merit specific recognition. Other differences may even be of greater importance: the Croat specimen has racemes aggregated into pseudo-panicles, calyx lobes only half the length of the corolla, and the principal crown segments opposite the anthers, while in the Howard specimen, the racemes are simple and interpetiolar (the usual condition in *Mellichampia*), the calyx lobes are equal in length to the petals, and the principal crown segments are alternate to the anthers. A third specimen from Ecuador (Dodson 5984, MO) further compounds the variability in *Metalepis* without shedding any additional light (at least that I am able to detect) on the status of the species recognized by Woodson. Whether there are one or as many as six species within this group remains to be determined.

Schumann (1895) has been criticized by Woodson (1941) for his incorporation of *Metalepis* into the tribe Gonolobeae, the only tribe of the subfamily Asclepiadoideae restricted to the New World, and distinguished principally by its horizontally oriented pollinia. (Schumann was in fact following Bentham's (1873) disposition of *Metalepis*). The pollinia of *C. cubense* are quite pendulous, and current opinion seems to be that that species is referable not only to the Asclepiadeae but to the genus *Cynanchum* as well. However, be that as it may, strong similarities do exist between *Metalepis* and the Gonolobeae, and if one were to search for a possible origin of the Gonolobeae among the more primitive New World Asclepiadeae, the comparatively ancient section *Metalepis* with its two greatly disjunct population centers would bear close investigation. Like Section *Metalepis*, many of the Gonolobeae possess an elevated but apically flat and radially expanded gynostegium with elongate translator arms oriented adaxially toward pollinia more or less concealed under the brow of the stigma head, interrelated structures that were no doubt the source of Bentham's and Schumann's error. Furthermore, certain of the subgenera of *Matelea*, as construed by Woodson (1941), bear their pollinia "more or less descending from the translator arms," in other words, in a somewhat intermediate position. Many other features common in the large and variable tribe Gonolobeae are available either in the same or in a theoretically ancestral condition in the tropical sections *Metalepis* and *Roulinia* of subgenus *Mellichampia*: large, ovate leaves with cordate bases (uncommon in other New World asclepiads); racemose cymes (certainly the



condition most closely ancestral to the umbelliform cyme, as exemplified by the transitional inflorescences of the Old World C. acutum discussed earlier); rather large flowers with rotate, purple (fly-pollinated?) corollas; large follicles (only one maturing per flower); seeds with irregularly and coarsely dentate bases.

It has already been observed that the tropical members of the New World Mellichampiae are a tightly circumscribed group, recognizable at a glance by their large cordate leaves, regularly racemose inflorescences, and purple, rotate corollas. They can be confused superficially not with any of the segregate genera of Cynanchum but only with members of the Gonolobeae. The reader will recall that of the five original species in the Linnaean genus Cynanchum, only two are now generally retained in that genus (and are in fact usually considered conspecific), while two others are referred to Gonolobus (Matelea s.l.). Whether the similarities are coincidental or reflect a profound phylogenetic relationship has never been investigated.

7. Cynanchum racemosum (Jacq.) Jacq., Select. Stirp. Am. Hist. 81, pl. 54. 1763. Figs. 2 & 8.

Suffrutescent, twining vine; rootstock (Stewart 1127) cylindrical, to 7 mm in diameter; stems terete, stramineous, to 3 mm in diameter, puberulent to less commonly tomentulose or short pilose in lines above the petioles, often more densely pubescent at and below interpetiolar ridges; petioles adaxially puberulent to tomentulose or uncommonly short pilose either distally or throughout, 1-6.5 cm long, about 1/2-2/3 as long as blade; leaf blades chartaceous, dull, drying dark green above, paler beneath, mostly ovate but occasionally narrowly so, ovate-triangular, or ovate-orbicular, 3-11 x 2-8 cm, acute to acuminate at apex, deeply cordate at base with broadly rounded or rarely shallow sinuses, sparingly to moderately pubescent with soft spreading, appressed, or lax hairs on the principal veins above, less so beneath, or either or (rarely) both surfaces glabrate, the margins glabrous to proximally ciliate, the glands 3-7(-13), the tertiary nerves prominent above and mostly scalariform; racemes unbranched or rarely (Texas) once-forked below the first flower, bearing 10-24 flowers (with 6-12 at once mature), at first congested, elongating in age, 2-10 x 1-2 cm, peduncle adaxially tomentulose to rarely short pilose distally, 0.5-3.5 cm long, somewhat shorter than to as long as the petiole, rachis and pedicels tomentulose, the pedicels adaxially and often more densely so, 4-12 mm long; bracts narrowly lanceolate, (1.0-) 1.8-2.3 mm long; flower buds spherical, 2-3 mm long, broadly rounded to (Central America) abruptly constricted at apex to a short-conic peak; calyx rotate, puberulent to short pilose below, the tube 0.2-0.6 mm long, the lobes lanceolate-oblong, 1.5-3.2 x 0.8-1.0 mm, nearly as long as corolla, rounded at apex, ciliate to long-ciliate at margin, the glands 1-2 per sinus; corolla rotate to broadly and shallowly rotate-campanulate, 5-7 mm in diameter, drying greenish brown to greenish white, mostly 3-5 striped within, the tube 0.8-1.5 mm long, the lobes spreading, distally pouched within and with two short ridges parallel to the margins between pouch and apex, entirely glabrous, narrowly to triangularly ovate, 2-3 x 1-1.5 mm, rounded at apex and plane to recurved, mostly plane at margin; crown abaxially inserted at corolla throat 0.2-0.6 mm below sinuses, adaxially joined to anther stipe and forming 5 rounded pocket-reservoirs between the segments and at the base of the stigmatic slits, the crown segments 5, manifestly united, (the annulus 0.2-0.6(-1.3) mm high), erect, 1-3 mm long, about equaling to surpassing the stigma head, variable in outline (see the key to varieties of C. racemosum), the margins variously involute and more or less attached below to the anther stipe to form 5 rudimentary hoods or pouches on the lower, inner segments opposite the anthers and precisely accommodating the anthers in bud; anthers substipitate, elevated at stigmatic slits by as much as 0.6 mm above floor of reservoirs, 0.8-1.2 mm broad below glands, (0.3-)0.4-0.6(-0.7) mm long at stigmatic slits, the slits (anther wings) slightly shorter than central, pollinium-bearing portion of anthers, the appendages drying white, orbicular to reniform-orbicular, broader than long, 0.6 x 0.7-1.0 mm, appressed to stigma head; translators with pollinia elliptic to moderately or broadly oblanceolate, 0.5-0.7 x 0.2-0.25 mm, equally rounded at each end or the top



more narrowly so, the gland rhombic to cylindrical, 0.2-0.3 x 0.15-0.2 mm, half or less as long as pollinia, the translator arms brownish above and usually paler and membranous below, tangentially flattened and triangular (expanding toward pollinia), 0.2-0.3 mm long, subapically attached to pollinia; gynostegium short-cylindrical, broader than high, the apex (stigma head) broadly rounded, 1.5-2 mm in diameter, densely and minutely papillate; follicles ovoid to narrowly so, drying pale to dark brown, glabrous, smooth to finely wrinkled-striate, 8-14 x 2.5-3 cm; seeds ovate, 7-9 x 4-6 mm, brownish to reddish, smooth, truncate at apex, irregularly erose-dentate with rather coarse, rounded teeth at base, the coma white to pale brown, at least 2-3 cm long.

Across a broad geographic range from northern South America to central Texas and embracing a variety of habitats, Cynanchum racemosum possesses a surprisingly uniform floral morphology. Dimensions vary little: the flowers are 5-7 mm in diameter, the corolla lobes 2-3 mm long, the pollinia 0.5-0.7 mm long. The most significant structural consistencies lie in the corolla, which is rotate to broadly rotate-campanulate, invariably glabrous, and distinctively marked (except var. guatemalense) by a distal pouch and two ridges on each lobe within. However, the extreme variability of the crown has led to the description of some half a dozen species. In contrast to C. montevidense of South America, much clearer geographic patterns in this coronal variability are detectable and intermediates uncommon; the recognition of segregate taxa at the varietal level is thus considered warranted.

The Cynanchum racemosum complex provides a good illustration of Charles Darwin's (1859) observation that, "wide-ranging, much diffused, and common species vary most." Several of the varieties here recognized, particularly those of the Guatemalan highlands, might indeed be considered "incipient species." On the taxonomic interpretation of such complex species, Darwin goes on to say: "We have seen that there is no infallible criterion by which to distinguish species and well-marked varieties; and when intermediate links have not been found between doubtful forms, naturalists are compelled to come to a determination by the amount of difference between them, judging by analogy whether or not the amount suffices to raise one or both to the rank of species."

Subgenus Mellichampia has not undergone prolific radiation in the New World. In comparison to such taxa as Matelea (s.l.) and Metastelma, its species are few and their differences rather well marked. Whether the broad species concept adopted in the present study would be equally suitable to those larger and more successful groups is open to question. However, in view of the more significant morphological changes that mark other species of subgenus Mellichampia, recognition at the specific level of the numerous, and in a few cases substantial, variations in coronal morphology exhibited by the C. racemosum complex, would seem to violate the idea of the species as it is conceived within this subgenus.

As discussed previously, section Mellichampia, largely a Mexican group, comprises four closely related species (Cynanchum racemosum, C. jaliscanum, C. foetidum, and C. ligulatum) distinguished from the more primitive section Roulinia by their stem and leaf pubescence and small whitish or greenish flowers with papillate stigma heads. The range of C. racemosum overlaps or is at least contiguous with that of section Roulinia in northern South America and in the West Indies. In addition, the corollas of C. racemosum, in being glabrous and more or less rotate, agree with those of the C. blandum complex of section Roulinia. Geographically and morphologically, then, C. racemosum seems closest to a hypothetical ancestor from which the other members of section Mellichampia may have been derived, the divergence of C. jaliscanum proceeding by gradual elevation of the gynostegium and corollary modifications of the translator, that of C. foetidum and C. ligulatum by the acquisition of campanulate, pubescent corollas (causing a change in the shape of the flower bud from spherical to ovoid-conic) and a general increase in flower size (Fig. 3).

#### Key to the varieties of Cynanchum racemosum

1. Crown 1.5-2 mm high, shallowly divided above the middle, the annulus 0.9-1.3 mm high, longer than the free portion of the segments (Guatemalan highlands)  
f. var. cyathiforme.



1. Crown 1-3 mm high, deeply divided below the middle, the annulus 0.1-0.6 mm high, shorter than the free portion of the segments.
2. Crown double, bearing 5 orbicular inner segments attached opposite to and at the base of the free portion of the outer segments, 1/3 to 1/2 as long as the outer segments or rarely reduced and represented by a fleshy pad (Guatemala)
  - e. var. guatemalense.
2. Crown single, inner segments wanting.
3. Central lobe of the crown segments narrowly elongate to ligulate, acute to uncommonly rounded or emarginate at the tip, 0.9-1.8 mm long, about equaling to longer than the basal portion of the segment; lateral lobes variable.
4. Crown segments apically 3-lobed, the central lobe 0.9-1.5 mm long, about equaling the basal portion of the segment and mostly about twice as long as the lateral lobes; the margins slightly if at all involute (Colombia and Venezuela)..... a. var. racemosum.
4. Crown segments with a single central lobe 1.0-1.8 mm long, equaling to longer than the basal portion of the segment, the lateral lobes reduced to rounded shoulders or rarely acute teeth; the margins involute (Yucatan to Costa Rica)..... b. var. rensonii.
3. Central lobe of the crown segments lanceolate-triangular to broadly reniform, rounded or emarginate to rarely acute at the tip, mostly less than 0.8 mm long (1.3 mm long in var. havanense), shorter than to rarely about equaling the basal portion of the segment; lateral lobes reduced to rounded shoulders.
5. Crown 2.9 mm high, the free portion of the segments ovate, 2.6 mm long, surpassing the stigma head, the central lobe lanceolate-triangular, rounded at the tip, 1.3 mm long, about as long as the basal portion of the segment (Cuba)..... c. var. havanense.
5. Crown 1-2 mm high, the free portion of the segments ovate-orbicular to reniform-rectangular, 0.8-1.8 mm long, about equaling the stigma head, the central lobe triangular to broadly reniform, emarginate or rounded to rarely acute at the tip, to 0.8 mm long, shorter than the basal portion of the segment (Texas to Vera Cruz)..... d. var. unifarium.

7a. *Cynanchum racemosum* var. *racemosum*.

Figs. 2 &amp; 8 A-B, K.

- Asclepias racemosa* Jacq., Enum. Syst. Pl. 17. 1760. Type: Colombia: Bolivar, vicinity of Cartagena (Lectotype here designated: Jacquin's description and illustration, Select. Stirp. Am. Hist. 81, pl. 54. 1763.).
- Cynanchum racemosum* (Jacq.) Jacq., Select. Stirp. Am. Hist. 81, pl. 54. 1763.
- Roulinia Jacquinii* Decne. in DC. Prodr. 8: 517, p.p. 1844, sensu typi; Hemsley, Biol. Centr. Am. 2: 329. 1882.
- Enslenia racemosa* (Jacq.) Griseb., Fl. Brit. W. Ind. 418, 735. 1864.
- Roulinia racemosa* (Jacq.) O. Ktze., Rev. Gen. Pl. 422. 1891.
- Rouliniella racemosa* (Jacq.) Vail, Bull. Torr. Bot. Club 29: 665, p.p. 1902.
- Rouliniella colombiana* Vail, Bull. Torr. Bot. Club 29: 663. 1902. Type: Colombia: Magdalena, vicinity of Santa Marta, near Bonda, thickets on low land near river, about 150 ft., H. H. Smith 1668 (holotype: NY!; isotypes: BM! CM! F! G! GH! L! LE! P! S! S! U! UC! UC! UC! VT! W!; photographs of US isotype: F! NY!).

Crown segments of the typical variety of *Cynanchum racemosum* are manifestly 3-lobed, the central lobe ligulate, acute, 0.9-1.5 mm long, about equal in length to the broadly oblong basal portion of the segment, the lateral lobes elongate-triangular, acute, mostly about half as long as the central lobe.

Typification. Stafleu (1967) states that the few and fragmentary Jacquin types from the West Indies (including coastal Colombia?) are to be found at the British Museum. However, a careful search of the collections at the British Museum, by J. F. M. Cannon, failed to locate a specimen which might be regarded as the type of *Cynanchum racemosum*. Jacquin's description of *C. racemosum* (1763, loc. cit.) is taken verbatim from the



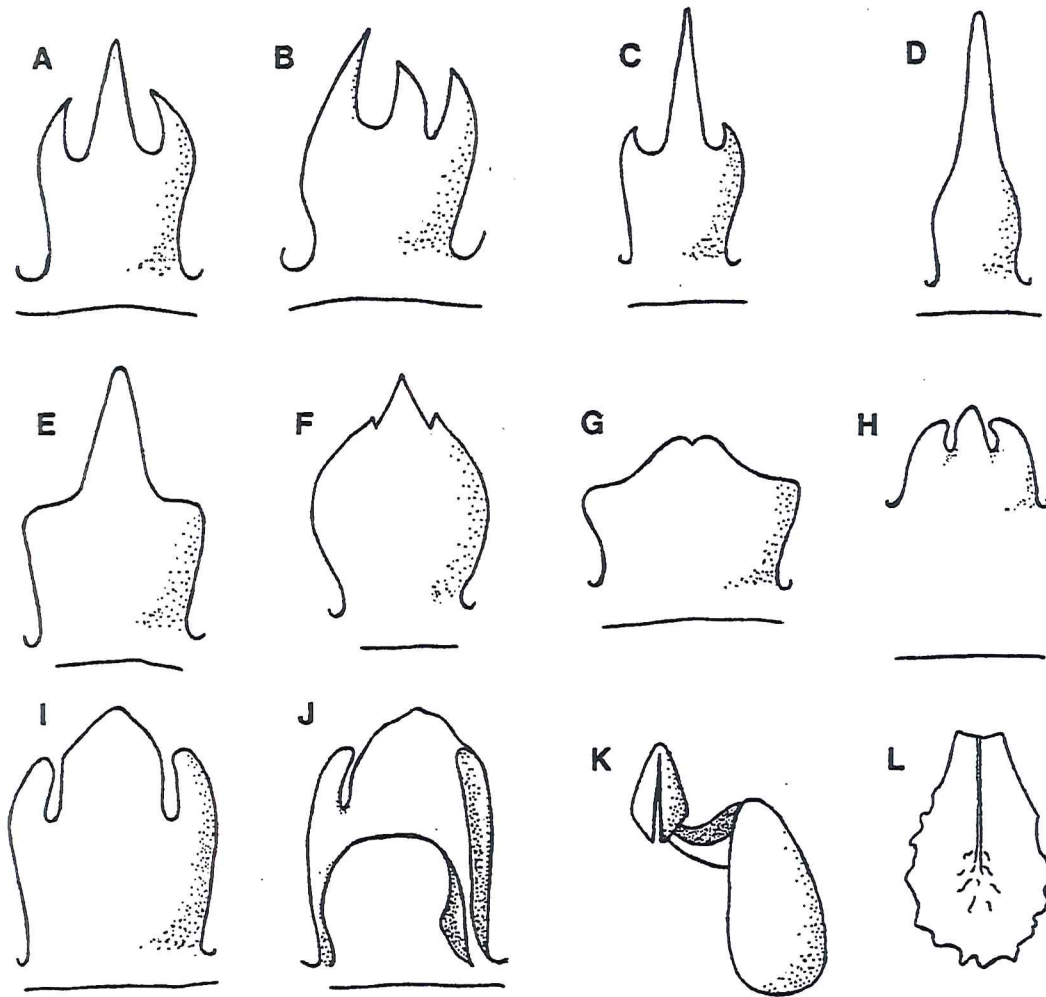


Figure 8. *Cynanchum racemosum*. A-J. Crown segments, abaxial surface (unless otherwise indicated): A-B. var. *racemosum*, x 15.6 (A. Killip & Smith 14033; B. H. H. Smith 1668); C-D. var. *rensoni*, x 15.6 (C. René 72; D. Gaumer s.n.); E. var. *havanense*, x 15.6 (Ruiz & Pavon s.n.); F-G. var. *unifarium*, x 32.5 (Bartlett 10150; G. Krukeberg 4872); H. var. *cyathiforme*, x 23.4 (Heyde & Lux 6187); I-J. var. *guatemalense*, x 32.5 (both Steyermark 29329; J, adaxial surface). K. Translator, abaxial surface, x 52 (H. H. Smith 1668). L. Seed, placental surface, coma detached, x 3.9 (Standley 75501).

earlier description of *Asclepias racemosa* (1760, *loc. cit.*); his later treatment, with its additional data on "habitat" as well as an informative illustration is chosen to lectotypify the typical variety of the species. A topotype collection (Killip & Smith 14033, "vicinity of Cartagena, near sea level") agrees quite well with this lectotype.

Decaisne considered his *Roulinia jacquinii* to be synonymous with two species, *Cynanchum racemosum* Jacq. and *Cynanchum foetidum* (Cav.) H.B.K. *R. jacquinii* is automatically typified by the type of *C. racemosum* var. *racemosum*, the older of those two names, despite Decaisne's citing of a Linden collection from Yucatan, here referred to *C. racemosum* var. *rensonii*, and of Galeotti 1538 from Oaxaca, here referred to *C. foetidum*. Decaisne did not indicate either of those cited collections as type (see art. 7.11, Stafleu, 1978). Hemsley's (1882, *loc. cit.*) concept of *R. jacquinii* followed that of Decaisne.

Distribution (Fig. 2). *Cynanchum racemosum* var. *racemosum* inhabits the coastal hills of eastern Colombia and western Venezuela. Recorded elevations vary from near sea



level to 1000 m. Detailed data from a Colombian collection (Dugand 5853) describe the habitat as deciduous thickets or subseric woodlands with sandy soil, suggesting arid (or at least seasonally arid) conditions ecologically approximating those that obtain along the water courses of the Chihuahuan desert of northern Mexico and southern Texas at the northern end of the species' range. Flowers described as having a white to greenish white corolla and white crown have been collected between the months of August and November.

Colombia. Bolívar: vicinity of Cartagena, Killip & Smith 14033 (GH, MO). Atlántico: between Baranoa and Galapa, Dugand 5794 (MO), 5853 (MO). Guajira: Cipanan, Finca de Nemesio Montiel, Castañeda 4449 (MO).

Venezuela. Zulia: Maracaibo, Moritz 1160 (BM, K). Aragua: hills above Guayas, Tuy Valley, Pittier 12200 (G). Distrito Federal: hills above Antimano, Pittier 12460 (G, MO, NY). Locality uncertain: Valley of Macarao (Miranda?), Fendler 1055 (GH, K, NY).

Vail's Rouliniella colombiana is based on a collection (Smith 1668) from the Department of Magdalena very close to the type locality of the original Jacquin species. It differs from the previously cited topotype (Killip & Smith 14033) and from other South American material examined only in that the 3 lobes of each crown segment are more or less equal in length (0.4-0.6 mm), i.e., the central lobe is unusually short (Fig. 8 A-B). Such a small distinction is, in my opinion, deserving of neither specific nor varietal recognition.

7b. Cynanchum racemosum var. rensonii (Pittier) E. Sundell, comb. nov. Figs. 2 & 8 C-D.

Roulinia rensonii Pittier, Contrib. U. S. Nat. Herb. 13: 101. 1910. Type: El Salvador: vicinity of San Salvador, Renson 313 (holotype: US!; isotype: NY!).  
Cynanchum rensonii (Pittier) Woods., Ann. Missouri Bot. Gard. 28: 210. 1941.  
Roulinia Jacquinii, sensu Decne. in DC. Prodr. 8: 517, p.p. 1844, non sensu typi.  
Roulinia foetida, sensu Standl. Fl. Yuc., Field Mus. Nat. Hist., Bot. Ser. 3: 389. 1930, non sensu typi.

Vine similar to the typical variety except the crown segments with a single ligulate central lobe, 1-2 mm long, about equaling or longer than the oblong basal portion, the lateral lobes reduced to rounded shoulders or rarely to acute teeth.

Distribution (Fig. 2). The wide geographic distribution and ecological amplitude of Cynanchum racemosum is reflected in several of its most widely ranging varieties. The present variety is found from Yucatan southward to Costa Rica, specimens having been collected at elevations between sea level and 1800 m, and in habitats as various as moist thickets, dry rocky hills, stone walls, athletic fields, and the walls of the Paul Standley Herbarium building in El Zamorano, Honduras. All but two of the collections examined were found in flower between September and November, with single collections taken in late August and January. Data on flower color vary from white or cream to greenish white, greenish yellow, and pale yellow. Since Cynanchum racemosum is not as yet known from Panama, varieties racemosum and rensonii are for the present considered allopatric. Collections from lowland eastern Guatemala may also bridge the disjunction between Yucatan and the Department of Cortes, Honduras.

Vernacular names. Honduras: "Chinchayote" (Standley 24290); "Cuchampera" (Standley 24368). El Salvador: "Cuchamper" (Padilla 149). Nicaragua: "Polla" (Chaves 248).

Mexico. Yucatan: Izamal, Gaumer 890 (BM, BR, C, F, LE, P, UC, W); without further locality, Gaumer 24223 (F, G, NY), Linden 351 (K), s.n. (P). Campeche: Campeche Linden 1119 (LE).

Honduras. Cortes: Río Arenales, 5 km from San Pedro Sula, Molina R. 3813 (F). Morazan: Río Guacerique, between Los Laureles and Las Tapias, northwest of Tegucigalpa, Molina R. 18620 (F, NY); Río Choluteca, Barrio Concordia, vicinity of Tegucigalpa,



Standley 24136 (F); Camino Viejo between Suyapa and Tegucigalpa, Standley 14171 (F); vicinity of Suyapa, region of La Travesia, Standley 12443 (F); La Travesia, Molina R. 1132 (F); between Santa Lucia and Valle de Angeles, Molina R. 3328 (F); between Toncontin and La Granja, Standley 28795 (F); vicinity of El Zamorano, Molina R. 13024 (BM, F, MO, NY, S), Rodriguez 3509 (F, MEXU), Standley 2196 (F), 12699 (F, MO), 13048 (F), 13241 (F), 14369 (F), 14442 (F, MO), 24652 (F); Río de la Orilla, southeast of El Zamorano, base of Cerro Majicarán, Standley 14025 (F), 24166 (F). Choluteca: vicinity of Choluteca, Standley 24290 (F), 24368 (F). Valle: Ampala, Rodriguez 3336 (F, MO); Salomar Beach, 2 mi. east of San Lorenzo Fonseca Gulf, Molina R. & Molina 22764 (F, G, MO, NY).

El Salvador. Ahuachapan: without further locality, Padilla 149 (MO, US). San Salvador: San Salvador, Calderón 1278 (F, MO, NY, US).

Nicaragua. Managua: Managua, Chaves 248 (US), René 72 (US).

Costa Rica. Guanacaste: La Pacifica, 4 km northwest of Canas, Opler 1977 (F, MO, UC).

7c. *Cynanchum racemosum* var. *havanense* E. Sundell, var. nov. Figs. 2 & 8 E.

Type: Cuba: Havana, Ruiz & Pavon s.n. (holotype: K!)

Herba volubilis eadem ac varietas typica sed coronae segmentis ovatis, 2.6 mm longis, 1.5 mm latis, stigmatibus capitulum excedentibus, lobo centrali lanceolato-triangulari, ad extremum rotundato, 1.3 mm longo, lobis lateralis redactis ad humeros rotundatos; et pollinibus brevissimis, 0.34 mm longis, 0.2 mm latis, et corpusculo pro ratione longo, 0.3 mm, differt.

*Cynanchum racemosum* var. *havanense* is known only from the holotype, a meager flowering specimen bearing only the above locality data. The chief distinction of variety *havanense* lies in the proportions of its translator apparatus; the elliptic-orbicular pollinia are relatively short and broad and the cylindrical gland relatively long, with the result that the pollinia are scarcely longer than the gland. On the other hand, the crown segments are not particularly distinct; they possess only the central lobe (like var. *rensonii*), the lateral lobes being suppressed to rounded shoulders, but; like var. *unifarium*, the central lobe is triangular-lanceolate and rounded at the apex, rather than ligulate and acute.

7d. *Cynanchum racemosum* var. *unifarium* (Scheele) E. Sundell, comb. nov.

Figs. 2 & 8 F-G.

*Gonolobus unifarius* Scheele, *Linnaea* 21: 760. 1848. Type: United States:

Texas: Comal County, Upper Guadalupe River, vicinity of New Braunfels, Lindheimer 460 (lectotype here designated: GH!; isolectotypes: BM! G! G! GH! K(not seen), NA! NY! P! P! UC! US! W! W!).

*Roulinia unifaria* (Scheele) Engelm. ex Torr., in Torr. *Bot. Mex. Bound.* 160. 1850; Hemsley, *Biol. Centr. Amer.* 2: 329. 1882.

*Rouliniella unifaria* (Scheele) Vail, *Bull. Torr. Bot. Club* 29: 663. 1902.

*Cynanchum unifarium* (Scheele) Woods., *Ann. Missouri Bot. Gard.* 28: 210. 1941.

*Ampelanus ligulatus*, sensu Heller, *Contr. Herb. Franklin & Marshall Coll.* 1: 79. 1895, non sensu typi.

*Roulinia Palmeri* S. Wats., *Proc. Amer. Acad.* 18: 115. 1883. Type: Mexico:

Coahuila: mountains 24 miles northeast by north from Monclova, Palmer 829 (holotype: K, not seen; isotypes: G! GH! NA! NY! NY! US! US! VT!).

*Rouliniella Palmeri* (S. Wats.) Vail, *Bull. Torr. Bot. Club* 29: 664. 1902.

*Cynanchum watsonianum* Woods., *Ann. Missouri Bot. Gard.* 28: 210. 1941.

= *Roulinia Palmeri* S. Wats.

*Vincetoxicum saepimentorum* Brandg., *Univ. Cal. Publ. Bot.* 4: 381. 1913. Type:

Mexico: Vera Cruz: Baños del Carrizal, Purpus 6019 (holotype: US!; isotypes: MO! UC!).



Cynanchum racemosum Brandg., Univ. Cal. Publ. Bot. 7: 331. 1920; non Jacq., 1763. Type: Mexico: Vera Cruz: vicinity of Acazonica, Purpus 8377 ("8378") (holotype: UC!; isotypes: MO! NY! US! US!).

Cynanchum veracruzianum Dugand, *Caldasia* 9: 413. 1966. = Cynanchum racemosum Brandg.

Vine similar to the typical variety, except the free portion of the crown segments ovate-orbicular to reniform or rectangular, 0.8-1.8 mm long, 1-1.5 mm broad, the margins sharply and vertically inrolled to produce a deep pocket reservoir below each stigmatic slit, the apex of the segments obscurely tri-lobed, the central lobe shorter than the basal portion of the segment but otherwise extremely variable, from triangular and acute or notched at the extreme tip to broadly rounded and emarginate, the lateral lobes more or less reduced to rounded shoulders.

Typification. Scheele cited a Lindheimer collection from New Braunfels, Texas, as the type of Gonolobus unifarius but supplied no collection number. Evidently, according to Blankinship (1907), certain of the Lindheimer sets, usually given exsiccatae numbers by Engelmann, were distributed without having been previously enumerated. Based on the Lindheimer specimens in the Engelmann Herbarium at the Missouri Botanical Garden, Blankinship is able to supply most of the missing numbers of those collections, many of which have served as types, particularly of Scheele. Blankinship confirms the type collection of Gonolobus unifarius to be Lindheimer 460.

Very little biographical information is presently available on Adolphe Scheele. He described numerous species of flowering plants in Linnaea between the years 1848 and 1852 based largely on Lindheimer's Texas collections from the vicinity of New Braunfels. However, I am unable to discover at which institution Scheele worked. Dr. R. S. Cowan (pers. comm.) informs me that he did not work at Berlin, a logical choice for a German speaking botanist publishing frequently in Linnaea. Therefore the choice of a lectotype specimen from among the many duplicates of Lindheimer 460 must be somewhat arbitrary. In the absence of compelling information, I have chosen as lectotype of Cynanchum racemosum var. unifarium the better of the two specimens at GH, where an important set of Lindheimer duplicates, that forming the basis for Engelmann and Gray's Plantae Lindheimerianae, is already located.

The description of a new taxon could scarcely be marked by more confusion and oversight than was that of Cynanchum racemosum Brandege. The name, with its separate type from Vera Cruz, is a later homonym of C. racemosum Jacquin (1763, loc. cit.) based on material from northern Colombia. Furthermore, Brandege's type is virtually indistinguishable from the type of Vincetoxicum saepimentorum, a species which Brandege himself described from the same state of Vera Cruz seven years earlier.

To make matters worse, the type collection, originally Purpus 8377 in the first two drafts of Brandege's description of "Philibertia racemosa" in his notebook of identifications of Purpus collections (unpublished, University of California, Berkeley), is mistranscribed as "8378" into the final draft under the name "Cynanchum racemosum." "No. 8378" along with "Herb. Univ. Calif. No. 200783" are then cited in the original publication. However, the same collection number and accession number appear earlier in the same work for another name in the Sterculiaceae, leaving little doubt that 8377, not 8378, is the type of C. racemosum Brandg. The error found its way onto several of the duplicate specimens distributed. Specimens at MO and US are incorrectly labeled "8378" while those at NY and UC bear the correct number, 8377.

Finally, Dugand (1966, loc. cit.) introduced a nomen novum for Brandege's later homonym, but evidently took his reference to "Purpus 8378 (Herb. Univ. Calif. No. 200783 Typus)" directly from the original publication. There is no record of such a specimen at Berkeley.

Distribution (Fig. 2). Cynanchum racemosum var. unifarium extends from Vera Cruz in southeastern Mexico northward into western and central Texas. Elevations as high as 900-1500 m are cited frequently for collections from the Chisos (Brewster Co.) and Davis (Jeff Davis Co.) Mountains in western Texas as well as for a few scattered localities in Chihuahua and Coahuila. Only four collections from Nuevo Leon and Tamaulipas bear elevational data, all indicating stations between 300-600 m. At least



one collection from southernmost Texas (Cameron Co.) was unquestionably made near sea level.

Abundant collections, especially from Texas, provide much habitat information. The plant is found in oak-juniper chaparral and desert scrub communities, growing in sandy creek bottoms, canyons, and arroyos, as well as on limestone, granite, and lava ledges, rocky slopes, talus slopes, and dry hillsides. A few fencerows, hedges, and overgrazed pastures are the weedy situations indicated.

Flowers described with about equal frequency as whitish, greenish-white, greenish, yellow-green, or yellowish, have been most commonly collected between the months of May and September. Fruiting specimens are dated June through November, with a single anomolous April collection from Uvalde Co., Texas.

United States. Texas: Taylor Co. Abilene State Park, Correll 31734 (GH, LL). Tom Green Co. Christoval, Cory 24344 (GH). Jeff Davis Co. Davis Mountains, Little Ajuga Canyon, Correll 33336 (LL), Palmer 34547 (NY), Warnock & Turner 8101 (LL); Fern Canyon, Cory 48419 (NA); Fort Davis, Ferris & Duncan 2713 (NY); 12 mi. N of Alpine, near Hwy. 18, Powell 2745 (LL); without further locality, Steiger 473 (NY). Presidio Co. 2H Canyon, Miller Ranch, ca. 11 mi. W of Valentine, York 48154 (TEX); Lower Musgrave Canyon, Tierra Vieja Mountains, Hinckley 1953 (NY, TEX); vicinity of Old Ross Mine, south side of Chinati Mountains, about 5 mi. W of Shafter, Hinckley 3228 (NY), 3416 (NY). Brewster Co. Kokernot Ranch, 6 mi. NW of Alpine, Warnock 5574 (TEX); Musquiz Canyon, N of Alpine, Steiger 1221 (NY); W of Alpine, Steiger 1679 (NY); Glass Mountains, Old Blue, Warnock 21089 (GH, TEX), Altuda Pass, Warnock 173 (GH, TEX, UC); S of Alpine, Steiger 605 (NY), 1285 (NY); summit and upper slopes of Nine Point Mesa, ca. 60 mi. S of Alpine, Correll 33800 sheet 1 (LL); Horse Canyon, 100 mi. S of Alpine, Warnock & Hinckley BG-125 (LL); Chisos Mountains, vicinity of Burro Mesa, Moore & Steyermark 3398 (GH, UC), Ward Spring, Warnock 12993 (LL), Panther Canyon, Sperry 241 (US), without further locality, Mueller 8124 (F, GH, NY, TEX, US), Young s.n. (TEX); locality uncertain, NW Brewster Co., Williams T554 (GH, UC, US), mouth of Heath Canyon, Correll 31563 (LL, NA). Terrell Co. Independence Creek, near Pecos River, Demaree 48407 (NO), 50912 (GH, NO), Blackstone Ranch, 18 mi. S of Sheffield, Webster 438 (TEX). Val Verde Co. 6 mi. N of Pandale, Correll 34149 (LL, NA, UC); Hwy. 30, S of Vinagarone, Cory 3318 (GH); 13 mi. S of Loma Alto, Cory 39472 (TEX), 39475 (GH); Devil's River, ca. 1 mi. NW of confluence with Dolan Creek, Smith & Butterwick 177 (LL), without further locality, Eggert s.n. (GH); near mouth of Devil's River, Correll & Wasshausen 27777 (GH, LL), Devil's Cave, Thompson 192 (TEX); San Felipe Creek, near Del Rio, Correll 14947 (LL). Edwards Co. Hwy. 30, 30 mi. S of Sonora, Cory 3320 (GH); 23 mi. NE of Rocksprings, Cory 23772 (GH); 15 mi. SE of Carta Valley, Correll 31545 (GH, LL, NA). Mavarrick Co. Eagle Pass, Havard s.n. (US). Kimble Co. Along South Llano River, ca. 3 mi. SW of Telegraph, Correll 31530 (LL, TEX). Real Co. 2-3 mi. NE of Camp Wood, Correll & Wasshausen 28007 (LL, NA, UC). Uvalde Co. Garner State Park, Cory 43318 (TEX), 43320 (GH); 1.5 mi. SE of Uvalde, Correll & Rollins 32530 (LL, NA). Kerr Co. Vicinity of Kerrville, Heller 1899 (G, GH, LE, NY, UC, US). Gillespie Co. Bear Mountain, N of Fredericksburg, Correll & Douglas 31185 (LL), Correll & Johnston 17249 (GH, LL, NA). Llano Co. Enchanted Rock, Tharp s.n. (TEX). Burnet Co. Below Inks Dam, Correll & Correll 36381 (LL); 4 mi. E of Longhorn Cavern State Park, Webster & Rogers 6487 (TEX, W); Fairland, Pennell 10480 (NY). Brazos Co. Texas Agriculture and Mining College campus, Reeves 489 (NA). Blanco Co. Rte. 165, ca. 7 mi. SW of Henly, Webster 13773 (TEX). Travis Co. Above Mt. Bonnel, N of Austin, Ferguson s.n. (TEX); West Lake Hills, W side of Austin, Nee & Whelan 11818 (LL); vicinity of Austin, Winnous s.n. (TEX); Austin, Schulz 722 (US), Tharp s.n. 19-VII-1940 (GH, TEX, UC), s.n. 18-VIII-1941 (GH), Whitehouse s.n. (TEX); locality uncertain, Daffan, Bodin 235 (US); without further locality, Strandtmann s.n. (TEX). Bastrop Co. Without further locality, Duval s.n. 15-V-1928 (TEX), s.n. 10-IX-1928 (TEX), Matthes 411 (G). Comal Co. New Braunfels, Lewton 926 (LL, NA); Comanche Spring, New Braunfels, Lindheimer 995 (BM, BR, C, F, G, GH, LE, M, NY, P, TEX, UC, US, W), 996 (BM, BR, C, F, G, GH, LE, M, NY, TEX, UC, US, W), 997 (BM, BR, C, F, G, GH, NY, TEX, UC, US, W). Bexar Co. Vicinity of Bracken, Groth 170 (F, NY, US); San Antonio, Jermy 104 (US), Palmer 827 (G, GH, NA, NY, US, VT); without further locality, Jermy



70 (NY), s.n. (NY). Gonzales Co. Without further locality, Bogusch 1510 (TEX). Wilson Co. Sutherland Springs, Cory 15108 (GH). Karnes Co. Railroad cut N of Union Leader School No. 2, between Kenedy and Runge, Johnson 1373 (TEX). Live Oak Co. Grant Ranch, Tharp s.n. (GH, TEX, UC). Starr Co. 15 mi. N of Rio Grande City, Johnston 2774 (TEX). Kenedy Co. A few mi. E of headquarters, Norias Division of King Ranch, Johnston s.n. (TEX). Cameron Co. Banks of Resaca, at Olmito, Runyon 3105 (NA, TEX). Uncertain locality. Chiefly Valley of the Rio Grande above Donana, Parry et al. (Mexican Boundary Survey) (LE, NY, US); Rio Grande, Wright s.n. (1848) (GH); Devil's River, Clark 4101 (G, M), Wright 1672 (GH, NY, US); Waller Creek hills (Waller Co.?), Ferguson 500 (TEX); Mountains of Muerte, Bigelow 1059 (NY); western Texas, Neally s.n. (F), Wright 546 (GH, K, NY, US); "Texas," Wright s.n. (NY, US), "Distributed by P. V. le Roy" (NY).

Mexico. Chihuahua: Sierra del Diablo, 3 km S of Rancho de la Gloria, Chiang et al. 8991 (LL). Coahuila: SW flank of Sierra del Carmen, Chiang et al. 9250a (LL); eastern foothills of Sierra de las Cruces, 7 mi. E of Santa Elena Mines, on road from Castillon to San José, Johnston & Muller 328 (LL); Puerto de San José, along road from Esmeralda N (100 km) to Santa Elena Mines, Stewart 1127 (BM, F, LL); Santa Anna Canyon, vicinity of Músquiz, Marsh 441 (F, TEX); Sabinas, Nelson 6215 (6815?) (US); Municipio de Castenos, Cañon Bocatoche, Muller 3114 (LL, NA, UC). Nuevo Leon: Municipality of Santiago, Horse Tail Falls, Chase 7799 (F); Monterrey, ½ mi. above gate to Chipinque, Smith M546 (TEX); floodplain above mouth of Cañon de Huestecas, ca. 10 mi. S of Monterrey, Kruckeberg 4872 (NY); El Carrizo (= Carrizal), Pringle 11840 (CM, F, G, K, L, M, MO, NY, P, UC, VT, W). Tamaulipas: Vicinity of Victoria, Palmer 243 (F, MO, NY); uncertain locality, vicinity of San José, Bartlett 10150 (LL, US).

Cultivated plants: at Brownsville, Texas, from seed taken at Olmito, Cameron Co., Texas, Runyon 4371 (M, TEX).

I can find no way of separating taxa based respectively on Lindheimer 460 (type of Gonolobus unifarius) and Palmer 829 (type of Roulinia palmeri). The collections correspond in all respects of floral morphology, including the size and shape of crown segments and pollinia, the characters by which variety unifarium, as here recognized, can be distinguished from its nearest relative, variety rensonii. Shinnars (1964) referred all Mexican material formerly treated as Roulinia palmeri (Cynanchum watsonianum) to C. unifarium.

Nor can I make a case for the recognition, even at the varietal level, of Brandege's Vera Cruz species. The two Purpus collections upon which are based Vincetoxicum saepimentorum and Cynanchum racemosum are indistinguishable, although they are more or less distant from the Palmer and Lindheimer types. Their crowns are cyathiform (but with a very short annulus which separates them from variety cyathiforme), about equal to the stigma head in height and to varying degree surpassed by the anther appendages. The segments are reniform or even rectangular, broader than long, with a broadly obtuse, emarginate central lobe and rounded shoulders. Such a crown differs significantly and abruptly from the ligulate form in variety rensonii from Yucatan.

To the north, however, no such convenient discontinuity of coronal morphology is to be found. Collections from the vicinity of Monterrey in Nuevo Leon are intermediate between Cynanchum unifarium (sensu typi) and Vincetoxicum saepimentorum. The segments of Kruckeberg 4872 (Fig. 8 G) and Chase 7799 are broader than long, those of Smith M546 longer than broad. From Chase to Kruckeberg to Smith the central lobe varies from broadly obtuse-emarginate to triangular-emarginate to triangular-rounded-acute. Furthermore, emarginate central lobes occur sporadically across the range of variety unifarium, for example, Lindheimer 460 (Comal Co., Texas, both acute and emarginate lobes in the same collection) and Johnston & Muller 328 (Coahuila, Mexico). Crown segments of plants from Tamaulipas, to the south of Nuevo Leon, are unequivocally C. unifarium-like, despite their intermediate geographic position.

Finally, it should be noted that crown segments representative of the extreme forms of Cynanchum unifarium and Vincetoxicum saepimentorum agree at least in their unusually small size, less than 2 mm high and scarcely if at all surpassing the stigma head. In contrast, the flowers of variety unifarium are generally the largest of the Cynanchum racemosum complex, and the dimensions of floral parts (corolla, pollinia, stigmatic slits) tend to fall at the upper end of the scale of variability.



Most of the data for follicles and seeds recorded for Cynanchum racemosum are taken from numerous fruiting specimens of variety unifarium collected in Texas. Very little Mexican and Central American material is available in fruit.

Two unusual morphological conditions occur with slight regularity and are worth mentioning. The maturation into follicles of both ovaries of a single flower (a common condition in slender-fruited taxa, such as Metastelma) occurs in two collections, Correll & Rollins 32530 and Webster 438. Also several collections (Runyon 4371, Palmer 827, Cory 38057 & 38058, Sperry 241) bear one or more inflorescences consisting of twin scorpioid cymes or cincinni, the two branches arising directly below a single terminal flower.

7e. Cynanchum racemosum var. guatemalense (Dugand) E. Sundell, comb. nov.

Figs. 2 & 8 I-J, L.

Cynanchum guatemalense Dugand, Caldasia 9: 412. 1966. Type: Guatemala: Sololá, vicinity of Patulúl, alt. 3000 ped., Heyde & Lux 6349 (holotype: NY!; isotypes: F! G! K(not seen), M! MO! NY!).

Rouliniella racemosa, sensu Vail, Bull. Torr. Bot. Club 29: 665. 1902, p.p.; non sensu typi.

Cynanchum Rensoni, sensu Standley & Williams, Fl. Guat., Fieldiana, Bot. 24: 421. 1969, non sensu typi.

Vine similar to the typical variety, except the crown segments double, the outer segments scarcely united (the annulus 0.1-0.2 mm high), ovate-oblong, 1-1.2 mm long, 0.9-1 mm broad, slightly longer than broad, slightly surpassing the stigma head, apically 3-lobed, the central lobe broadly ovate-triangular, 0.3-0.4 mm long and about as broad, shorter than the basal portion of the segment, at the extreme tip entire, emarginate, or 3-fid, the lateral lobes narrower and shorter than the central, inrolled at the margins, the 5 distinct (e.g. not connate) inner segments inserted basally upon (and opposite to) the outer segments at the level of the top of the annulus, more or less orbicular, 1/3-1/2 as long as the outer segments but nearly as broad, slightly shorter than the anthers and (from closely investing the anthers in bud) concave, or rarely the inner segments reduced and represented by scarcely elongated, fleshy pads.

Typification. Among the collections cited by Vail under Rouliniella racemosa, Heyde & Lux 6349 was considered representative of that species. Dugand recognized the distinctness of the Heyde & Lux collection, making it the type of still another segregate species, Cynanchum guatemalense. Actually, the inner crown segments of this type collection are rather poorly developed, reduced to fleshy pads, and not particularly representative of the remainder of the material here referred to variety guatemalense.

Distribution (Fig. 2). Cynanchum racemosum var. guatemalense is known from a few scattered localities in the Guatemalan highlands from 200-1000 m. Habitat data record thickets, rocky slopes, hedges, and railroads, the expected mix of undisturbed and weedy situations. Flowers described as yellowish white, yellowish, and greenish white have been collected between the months of September and January.

Vernacular names. Guatemala: "Cuchamper" (Standley 75349 & 75501, "young fruits eaten").

Guatemala. Baja Verapaz: slopes above Río Mantagua, 12 km southwest of Granados, Harmon & Dwyer 4200 (MO). Zacapa: between San Pablo and Pepezca, Steyermark 29329 (F, MO); vicinity of Zacapa, Standley 74636 (F, MO). Chiquimula: vicinity of Ipala, Steyermark 30348 (F). Jutiapa: vicinity of Jutiapa, Standley 75349 (F, MO), 75501 (F).

A more unusual coronal morphology does not exist among the New World Mellichampiae. However, such a double crown is quite common among Old World Cynancha, and the wide-ranging and extremely variable C. acutum (s.l.), like C. racemosum,



exhibits both single and double forms, although in the former species the double crown is much the more common condition. Variety guatemalense is distinct in several other respects: the calyx lobes are quite broadly ovate, about 2/3 as broad as long, and the corolla lobes are uniformly flat, with ridges and pouches obscure or wanting.

Among the various innovations of the crown that mark the Cynanchum racemosum complex are several conditions so close to what might well be considered ancestral to the hood and horn of the genus Asclepias that it is impossible not to speculate on homologies. Throughout the species, with the exception of variety guatemalense, the tendency is well developed for the segment margins to become involute and create a three-dimensional, rudimentary hood. In many specimens, the inrolled margins join at their base directly below the anthers which in bud are closely invested by the more or less convex crown segments. In other words, the rudimentary hood may essentially be a morphological by-product of floral aestivation. However, in Asclepias, the necessity is made a virtue, with the structurally refined and elegant hood assuming the function of nectar reservoir and thereby allowing insects' legs instead of proboscides access to the stigmatic slits. The pollination system of the ancestors of Asclepias could thus be utterly transformed to exploit as pollinators the large hymenopterans of North America.

Cynanchum racemosum variety guatemalense introduces a second structural novelty, the inner crown segment, inserted on the adaxial wall of the outer segment. However common such a condition may be in the Old World, the New-World double crown (at least in the Mellichampiae) must be interpreted as a parallel, not homologous, development. The inner crown segment of variety guatemalense fulfills all requirements of a structure ancestral to the horn of the Asclepias crown. The implications of such a homology are profound. Not only must the genus Asclepias itself originate at not too great a distance from the C. racemosum complex, but a different point of view would be brought to bear on the much-argued question of the relationship between Asclepias and its African segregate, Gomphocarpos, probably suggesting that these widely disjunct taxa represent separate phylogenetic lines.

I hasten to reiterate that such a descent is merely speculative and the available evidence circumstantial, however intriguing. A close relationship between Asclepias and Cynanchum has traditionally been granted on the basis of their similar and rather primitive translators and pollinia. In addition to the hood and horn, other specialized features of the Asclepias crown (its dissection into 5 free segments and its disassociation from the corolla) can be found in Cynanchum subgenus Mellichampia, although not commonly. It is also of interest that other New World taxa phylogenetically close to Cynanchum (e.g., Metastelma, Ditassa) possess cuneate leaf bases and umbelliform cymes, stable character states that also mark Asclepias. Finally, one of Woodson's (1954) six centers of Asclepias concentration falls in the Mexican highlands at no great distance from Guatemala.

7f. Cynanchum racemosum var. cyathiforme E. Sundell, var. nov. Figs. 2 & 8 H.

Type: Guatemala: Department of Santa Rosa: Cuajiniquilapa, alt. 900 m., Heyde & Lux 6187 (holotype: US!; isotypes: K(not seen), M! NY! US! VT!).

Herba volubilis eadem ac varietas typica sed coronae segmentis in cupulam connatis, (annulo 0.9-1.3 mm alto et quam segmentorum parte libera longiore), et segmentis reniformibus, 0.6-0.7 mm longis, 1 mm latis, stigmatibus capitulum excedentibus, ad apicem tri-lobis, lobo centrali ovato-triangulari, ad extremum rotundato, 0.4 mm longo, lobis lateralibus 1/2-2/3 longitudine lobi centralis et marginibus involutis et in pariete adaxiali supero cupulae 10 plicas verticales facientibus differt.

Distribution. Cynanchum racemosum variety cyathiforme is known only from three collections taken at elevations between 900 and 1600 m in western Guatemala. Molina R. and Molina (26512) provide the following data: "vine on moist thickets; flowers greenish-cream." Flowering material has been gathered in the months of September and October.



Vernacular names: Guatemala: "Cuchamper" (Molina R. & Molina 26512).

Guatemala. Huehuetenango: Vicinity of San Sebastian, Molina R. & Molina 26512 (F, U). Guatemala: Vicinity of Guatemala, Aguilar 230 (F).

It has been suggested previously that the cup-shaped or tubular crowns of paleotropical Cynancha represent the primitive coronal condition in this cosmopolitan genus. Thus the most notable morphological advancement of New World Mellichampiae, the tendency toward a deeply divided crown of 5 nearly free segments (the trend is fully realized in Cynanchum laeve and in more advanced taxa) is here reversed and a cyathiform crown is reinvented. The 10 vertical folds on the upper adaxial walls of the cup probably represent the inrolled margins of formerly nearly free segments that have become secondarily webbed. Other novelties further distinguish this narrowly endemic variety: the anther stipe is folded outward directly below the stigmatic slits (a similar condition is described by Holm (1950) for species of Sarcostemma) to form more or less parallel twin ridges, about equal to the slits in length, which no doubt serve to guide the pollinator's tongue upward into the slits. In the type collection, these ridges are bowed rather than parallel and form a pocket-reservoir below each slit; they appear to be folds of the very base of the coronal cup rather than of the anther stipe. Unusually short (about 0.4 mm) oblanceolate pollinia further separate variety cyathiforme from allied taxa.

Varieties guatemalense and cyathiforme are evidently sympatric in the Guatemalan highlands, although a few collections with pertinent data suggest that they may segregate by elevation at about 900-1000 m. Whether their respective coronal innovations are responses to the pressures of local pollinators or merely the result of random mutational drift is, in view of the number of available collections, impossible to answer at this time.

8. Cynanchum jaliscanum (Vail) Woods., Ann. Missouri Bot. Gard. 28: 209. 1941.  
Figs. 2 & 9 A, F-G.

Rouliniella jaliscana Vail, Bull. Torr. Bot. Club 29: 668. 1902. Lectotype here designated: Mexico: Jalisco, vicinity of Guadalajara, Pringle 4494 (NY! isolectotypes: BM! BR! F! G! K(not seen), L! LE! MO! P! UC! US! VT (fructu excluso)! W!).

Suffrutescent, twining vine; stems sparingly to moderately puberulent in lines above the petioles, densely so at nodes, the older stems glabrate, terete, pale brown, to 4 mm in diameter; petioles sparingly adaxially puberulent, 1-7 cm long, about 1/2 as long as blade; leaf blades chartaceous, dull, drying brownish green above, pale green beneath, ovate to broadly lanceolate, 4-16 x 1.5-9 cm, acuminate and abruptly narrowed at apex, truncate to deeply cordate at base, sparingly pubescent on veins of both surfaces (less so above) with rather straight, spreading or appressed hairs, or leaves glabrate, the glands about 6, the tertiary nerves prominent, scalariform; racemes crowded, bearing up to 20 flowers at maturity (mostly with 4-6 at once mature), 2-8 x 1.5-2 cm, the peduncle adaxially puberulent to sparingly tomentulose, 1-4 cm long, the rachis and pedicels matted tomentulose to puberulent, pedicels 4-11 mm long; bracts lanceolate-oblong, 2 mm long, margins ciliate; flower buds ovoid-pyriform, with a short, rounded beak, 3.5-4 mm long; calyx rotate to rotate-campanulate, the tube 0.3 mm long, the lobes more or less spreading, ovate-oblong, 2-2.5 x 0.8-1 mm, punctate within, margins ciliate to sparsely so, the glands 1-2 per sinus; corolla broadly rotate-campanulate, 8 mm in diameter, drying dull greenish outside, paler within, with streaked lobes, glabrous, the tube 1 mm long, the lobes narrowly ovate-triangular, 4 x 1.5-2 mm, broadest at base, gradually and evenly tapering to rounded apex, somewhat revolute at margin, recurved at the tip, bearing (within) two ridges of



elevated tissue parallel to the margins and extending between sinus and recurved tip, the area between the distal half of the ridges pouched; crown inserted in corolla throat 0.2-0.4 mm below sinuses, pale in color, 4-5 mm long, the crown segments 5, manifestly united (the annulus 0.4-0.6 mm high), erect, greatly surpassing the stigma head, abruptly narrowed from the broad, oblong basal portion (2 x 1.4-1.6 mm) to a ligulate central lobe 2-2.5 mm long, the shoulders acute, the margins plane to in-rolled; anthers manifestly stipitate, (the stipe 0.4-0.5 mm high below anthers, 1 mm high below stigmatic slits), 1.2-1.5 mm broad below the glands, the stigmatic slits (anther wings) tangentially 0.3-0.4 mm long but bending sharply inward and prolonged radially for about the same length, the tangential portion manifestly shorter than the central, pollinium-bearing portion of the anthers (1 mm), the appendages reniform, 0.6 x 1-1.1 mm, appressed to dome of stigma head; translators with pollinia oblong-ovate, acute at apex, at base rounded, 0.7-0.82 x 0.2 mm, the gland rhombic, brown, 0.2-0.25 x 0.15 mm, projected radially beyond the plane of the anthers by 0.5 mm, translator arms brown, broadly filiform, 0.5-0.6 mm long, oriented laterally from the gland, minutely expanded at the pollinia and attached apically; gynostegium short-cylindric, the apex (stigma head) broadly rounded, 2-2.5 mm in diameter, densely papillate; follicles unknown.

Typification. Vail cited three collections in her original description of Cynanchum jaliscanum: Palmer 384, Pringle 4494, and Botteri s.n. No holotype was designated, but the author did state that the "type" is at NY. Of the syntypes the Pringle collection is chosen as lectotype because the original drawings for the new species (mounted with the Botteri fragment at NY) are clearly taken from Pringle 4494. In addition, the Pringle specimen has more abundant flowering material and duplicate collections are more numerous.

The Pringle specimen at VT bearing flowers and fruit represents two collections and merits brief discussion. The flowering material undoubtedly corresponds to Pringle's printed label which bears the following data: "1893. State of Jalisco. In thickets on cool banks near Guadalajara. 19, August." Handwritten on the label is this information: "Fr. Valley of Oaxaca. 1894." Evidently the single mature follicle was collected the following year in a different and quite distant locality from that which furnished the abundant flowering material of Pringle 4494. The fruit must in no way be construed as belonging to the type collection (all other specimens of Pringle 4494 are without fruit). In fact, it is extremely doubtful that the follicle attached to the VT specimen is conspecific with material here taken as representative of Vail's species. The pubescence of rachis and pedicel attached to the follicle is extremely dense and that of the pedicel not restricted to the adaxial surface. The follicle itself is densely canescent, a condition which does not correspond satisfactorily to that of the ovaries at anthesis, which are sparsely and minutely papillate near the base. Neither the pubescence of the fruit nor the evenly rounded outline of the seed base finds a comparable character state in any other New World Mellichampia.

Distribution (Fig. 2). Only four collections are known to represent this unusual species, three of which were cited with the original description in 1904. Although poorly collected, Cynanchum jaliscanum appears to have a relatively large geographical range. The few available data record the species as somewhat weedy or successional in its habitat preferences, inhabiting riverbanks and hedgerows in upland areas of southern Mexico, from Vera Cruz westward to Nayarit and Jalisco. The only collection label with altitudinal data records an elevation of 1000 m. Flowers have been gathered in August and September.

Mexico. Nayarit: Rancho de las Delicias, Mexia 563 (BM, F, G, NY, UC). Jalisco: Tequila, Palmer 384 (BM, G, LE, MO, NY, P, US). Vera Cruz: Orizaba, Botteri s.n. (GH, NY).

Cynanchum jaliscanum is unique among Mexican species of section Mellichampia in the possession of an elevated gynostegium and correspondingly long translator arms (Fig. 9 F-C), conditions that seem to match those in Metalepis. The question must be



asked, whether such modifications, presumably directly related to pollinium transfer, might arise more than once or whether they are homologous and clearly delineate a natural, monophyletic group.

Evidence bearing on the question can be found in the tropical African segregate of Cynanchum, Schizostephanus Hochst., which possesses similar modifications of the gynostegium. N. E. Brown (1902-03) united Schizostephanus with Cynanchum, observing that the elevated gynostegium has appeared independently in Asclepias and thus should be considered of specific importance only. Certainly a disjunction between high elevations (1800 m) of East Africa and sea level Central and South America (section Metalepis) is not readily explicable. In addition, it should be noted that Woodson (1954) considered Asclepias subgenus Podostigma of the southeastern United States, with its Metalepis-like gynostegium, to represent one of the most highly modified and advanced of the erstwhile Asclepias segregates and to be connected to the most primitive members of that large genus "through innumerable intergrading mutations amongst the intervening scores of species." It may well have been Podostigma to which N. E. Brown was referring.

On the basis of what appear to be more conservative characters (delicate stem and leaf pubescence and the papillate surface of the stigma head) as well as its small greenish white flowers and the overall morphology of the crown, Cynanchum jaliscanum lies firmly within the section Mellichampia complex of Mexico and Central America. It seems best to treat the species as an extremely specialized member of that group, its resemblance to Metalepis the result of a convergent response to insect pollination, a convergence of a kind that has occurred in several other genera of Asclepiadaceae. Additionally, the dish-shaped (rotate-campanulate), glabrous corollas of C. jaliscanum suggest a rather direct relationship with the C. racemosum complex, the widely distributed and putatively ancestral group for all the Mexican Mellichampiae. An elevated gynostegium is foreshadowed in C. racemosum by the gynostegium substipitate above deep nectar reservoirs.

9. Cynanchum foetidum (Cav.) H.B.K., Nov. Gen. Sp. 3: 202. 1818. Figs. 2 & 9 B, H.

Asclepias foetida Cav., Icon. 2: 45, pl. 158. 1793. Lectotype here designated:

"Mexico imperio," Cavanilles' description and illustration, 1793, loc. cit.

Roulinia foetida (Cav.) Standl., Field Mus. Nat. Hist., Bot. Ser. 3: 389. 1930.

Rouliniella foetida (Cav.) Vail, Bull. Torr. Bot. Club 29: 667. 1902.

Roulinia Jacquini, sensu Decne. in DC. Prodr. 8: 517, p.p. 1844; Hemsley, Biol. Centr. Am. 2: 329, p.p. 1882; non sensu typi.

Rouliniella lignosa Vail, Bull. Torr. Bot. Club 29: 665. 1902. Lectotype here designated: Mexico: Jalisco, Rio Blanco, Palmer 314 (NY!; isolectotypes: BM! G! GH! K(not seen), LE! MO! NY! US! VT!).

Cynanchum lignosum (Vail) Woods., Ann. Missouri Bot. Gard. 28: 210. 1941.

Suffrutescent, twining vine; stems terete, reddish brown, to 3 mm in diameter, the branchlets stramineous, puberulent to less commonly short pilose or sericeous in lines above petioles, mostly more densely pubescent at nodes; petioles adaxially tomentulose, short pilose, or uncommonly glabrate, to tomentose near axils, 2.5-6.5 cm long, 1/3-2/3 as long as blade; leaf blades chartaceous, dull, drying brownish green to dark green above, paler beneath, ovate to narrowly so or ovate-triangular, 3-12 x 1.5-9 cm, acuminate at apex, deeply to shallowly cordate at base, indument of soft, spreading to lax hairs, the lower surface sparingly puberulent on principal veins, the upper surface somewhat less so, the glands 5-12, the tertiary nerves prominent, scari-form at least proximally and on young leaves; racemes bearing as many as 12-15 flowers (with 4-8 at once mature), elongating in age, 1-10 x 2-4 cm, the peduncle adaxially tomentulose, 1-4.5 cm long, about equaling to somewhat shorter than petiole, the rachis and pedicels sparsely to densely tomentulose, or the pedicels short pilose distally, 3-12 mm long; bracts narrowly lanceolate, about 2 mm long, caducous; flower buds



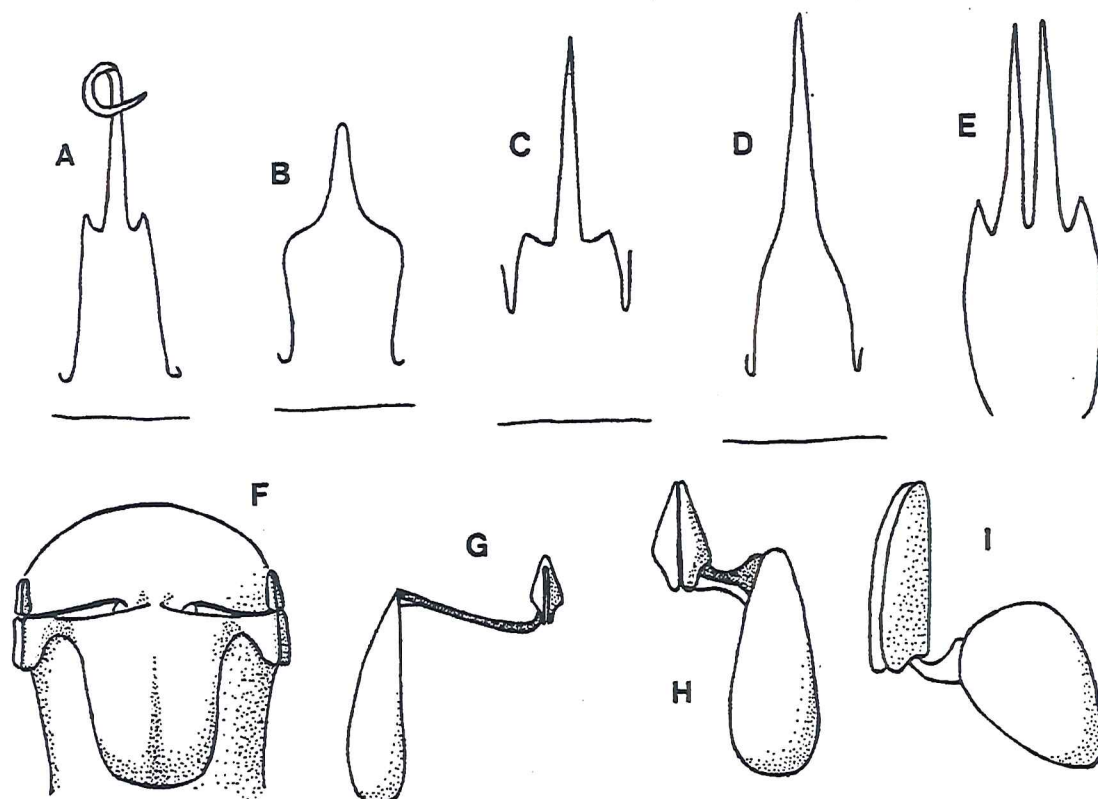


Figure 9. A, F-G. *Cynanchum jaliscanum*. B, H. *C. foetidum*. C-D, I. *C. ligulatum*. E. *C. laeve*. A-E. Crown segments, abaxial surface (A. Botteri s.n., x 13; B. Palmer 314, x 13; C. Walker 73H43, x 6.5; D. Palmer 280, x 6.5; E. McDaniel 2097, NO, x 13). F. Portion of anther stipe and gynostegium, x 26 (Botteri s.n.). G-I. Translators, 1 pollinium and arm removed from each (G. Palmer 384, x 39; H. Conzatti 4948, x 65; I. Palmer 280, x 52).

ovoid, 4-6 mm long, evenly tapering and bluntly rounded at tip; calyx campanulate, sparingly pubescent below, the tube 0.3-0.4 mm long, the lobes lanceolate to lanceolate-oblong (rarely ovate-lanceolate), 1.5-4 x 0.8-1.2 mm, acute at apex, sparingly ciliate to sub-fimbriate at margin, the glands 1-2 per sinus; corolla campanulate to reflexed-campanulate, 5-7 mm in diameter, drying whitish outside, somewhat darker within, the tube 1-1.6 mm long, the lobes abruptly spreading near middle and distally reflexed to recurved as much as 360°, lanceolate, 2.5-5 x 1.2-2 mm, gradually tapering to a bluntly rounded apex, the margins mostly plane, the lamina mostly with two ridges of more darkly pigmented tissue parallel to the margins within or ridges indistinct and represented by bands of either darker color or denser pubescence or both, moderately to densely short pilose (rarely glabrous) within with hairs more or less restricted to or rather abundant on ridges, absent on marginal strips; crown inserted at the corolla throat 0.3-0.6 mm below sinuses, drying whitish and paler than interior of corolla, 2-6 mm long, the crown segments 5, manifestly united, (the annulus 0.3-0.6 mm high), erect, surpassing the stigma head by as much as 2-3 mm, abruptly narrowed from the usually oblong basal portion (1.2-2 x 1.2-1.6 mm) to a ligulate (rarely lanceolate-triangular and very short) central lobe 1-4 mm long, the shoulders rounded to acute and about equal to the glands in height, the margins of basal portion variously inrolled and directed basally to a pocket below each stigmatic slit; anthers sessile, 0.8-1 mm broad below glands, 0.5-0.65 mm long at stigmatic slits, the slits (anther wings) about equal to and slightly lower than the central pollinium-bearing portion of anthers, the appendages ovate-triangular to reniform-triangular, 0.6 x 0.6-0.9 mm, rounded at apex; translators with pollinia



elliptic to oblanceolate, 0.38-0.5 x 0.2-0.22 mm, with rounded ends, the gland rhombic to nearly cylindrical, 0.25-0.3 x 0.12-0.2 mm, more than half as long as pollinia, translator arms brownish above and usually paler and membranous below, tangentially flattened and elongate-triangular (more or less abruptly expanded at pollinia), (0.1-)0.15-0.2 mm long, subapically to rather laterally attached to pollinia; gynostegium short-cylindric, broader than to nearly as broad as high, 1-1.5 mm high, the apex (stigma head) broadly rounded to domed, surpassing the glands and occasionally the anther appendages, 1.5-1.8 mm in diameter, densely papillate; follicles glabrous, finely striate, 9 cm long.

Typification. Cavanilles' types are located at the Instituto "Antonio José Cavanilles" in Madrid (Holmgren & Keuken, 1974), but inquiry there has failed to turn up any original material of Asclepias foetida (P. Blanco, pers. comm.). No specimen was originally cited. Cavanilles' illustration, with insets of crown segments, pendulous pollinia, and gynostegium, as well as his rather detailed description are quite helpful in fixing the identity of the species; illustration and description are chosen as the lectotype. The "type" photograph at F of a Humboldt and Bonpland specimen (postdating the protologue of A. foetida) at P, although conspecific with the Cavanilles' species, cannot represent original material of that species.

Rouliniella lignosa was originally based upon three collections from the Mexican states of Jalisco and Oaxaca: Palmer 314, Pavon s.n., and Ghiesbreght s.n. As might be expected, the Palmer collection surpasses the other syntypes in quality and quantity. Vail saw the NY specimen from "herb. Columbia University" which is chosen as the lectotype.

Distribution (Fig. 2). Cynanchum foetidum is restricted to the Sierra Madre Occidental and the Sierra Madre del Sur of southern Mexico. Elevations between 600 and 2100 m have been recorded for collections from Guanajuato and Queretaro south to Oaxaca. Habitat data give a picture of broad ecological tolerance within this upland range. The species seems to have made an easy transition from desert scrub and chaparral communities to the disturbed environments of stone walls, hedges, and roadsides. Flowers recorded as white to yellow-white and pale yellow have been collected from May through October, with the great majority between July and September. Two September collections, Nelson 1302 and Rose 10154, bear immature fruits.

Mexico. Guanajuato: San Felipe, Liebmann 12045 (C). Queretaro: Vicinity of Queretaro, Humboldt & Bonpland s.n. (F, photograph); vicinity of San Juan del Río, Rose 9618 (NY); without further locality, Kuntze 23447 (NY). Michoacan: Aquililla, District of Apatzingan, Hinton 15149 (F, MO, NY). Mexico: District of Temascaltepec, Carboneras, Hinton 1856 (BM, G, MO); vicinity of Luvianos, Roe et al. 1628 (NY); Tejupilco, Hinton 4688 (MO); "Tenayac," Hinton 4849 (MO, NY), 8372 (NY); "Volcan," Hinton 2226 (BM, F, G). Distrito Federale: "Huipulco," Smyth 115 (US); "lava beds near Enslava," Rusby 46 (NY). Morelos: Cuernavaca, Schmitz 730 (W), Smyth 129 (US); Yautepec, Pringle 11021 (CM, F, G, MO, US, VT). Puebla: Vicinity of Tehuacan, Rose & Painter 9911 (MO); vicinity of San Gabriel Chilac near San Juan Atzingo and San Andrés, Smyth et al. 4034 (NY); San Sebastian, Rose 10154 (MO, US); vicinity of San Luis Tultitlanapa, near Oaxaca, Purpus 2623 (BM, MO, UC, US), 3236 (F, MO, NY, UC); "El Riego," Purpus 1257 May (F, MO, UC); "Río de San Francisco," Purpus 3999 (G, UC). Guerrero: District of Mina, Campo Morado, vicinity of Otatlan, Hinton 14491 (F, MO, NY). Oaxaca: Huitzo, Conzatti & Gonzales 336 (NY); El Parian, vicinity of Nochixtlan, Conzatti 1943 (F); Valley of Etla, Alvarez 768 (NY); vicinity of Oaxaca, Conzatti 217 (NY); Valley of Oaxaca, Nelson 1302 (US); Plain of Oaxaca, Galeotti 1538 (BR, G, K, LE, NY, W); mountains west of Oaxaca, Galeotti s.n. (P); 23 miles northwest of Totolapan, Dwyer et al. 858 (MO); mountains in vicinity of Tehuantepec, Gonzalez s.n. (W); uncertain locality, "Ferrenos de Aguilar," Conzatti 4948 (F); without further locality, Ghiesbreght s.n. (F, LE). Uncertain locality: Ruiz & Pavon s.n. (K); "Tehuacan, Jalisco," Purpus 1257 July (F, MO, NY).

The flowers of Cynanchum foetidum are quite variable in size and proportion of their parts. Generally, the variation is marked by an increase in size from north to



south, most notably of the corolla lobes and crown ligules. Several Hinton collections (1856 & 4849) from the state of Mexico possess central crown lobes almost as broad as long (1 x 0.8 and 1.1 x 0.6 mm) and scarcely ligulate. On the other hand, the ligule of Roe et al. 1628 from the same area of Mexico measures 1.5 x 0.3 mm, like that of more northern collections.

It is not hard to understand how Vail, looking at no intermediate collections, was able to recognize the Palmer and Ghiesbreght specimens, from Jalisco and Oaxaca, as the distinct species, Rouliniella lignosa. Various Oaxaca collections, although no woodier than northern material, are certainly more robust. On the other hand, measurements of translators and stigmatic slits yield more uniform figures. Furthermore, the campanulate to campanulate-reflexed corollas, with longitudinal ridges parallel to the margins within, seem to be consistent throughout most of the geographic range of the species.

Cynanchum racemosum resembles C. foetidum in its small, whitish flowers, vegetative pubescence, and papillate stigma heads. The two species are nowhere sympatric, yet are superficially quite similar and can be separated by characteristics given in my key to species of subgenus Mellichampia. A glabrous form of C. foetidum from Queretaro is represented by several collections (Rose 9618, Kuntze 23447, as well as, according to the description, the Humboldt & Bonpland collection), but if not suggesting hybridization with C. racemosum, it culminates a reduction series in corolla pubescence from south to north.

10. Cynanchum ligulatum (Benth.) Woods., Ann. Missouri Bot. Gard. 28: 210. 1941.  
Figs. 2 & 9 C-D, I.

Enslenia ligulata Benth., Pl. Hart. 290. 1849; Hemsley, Biol. Centr. Am. 2: 328.

1882. Type: Mexico: Aguascalientes, Hartweg 1612 (holotype: K (Herbarium Benthamianum, photocopy seen); tracing of holotype: NY!; isotypes: K (Herbarium Hookerianum, photocopy seen), LD (very poor)!).

Ampelanus ligulatus (Benth.) Heller, Contr. Herb. Franklin & Marshall Coll. 1: 79. 1895.

Mellichampia ligulata (Benth.) Vail, Bull. Torr. Bot. Club 26: 425. 1899.

Roulinia ligulata (Benth.) Pittier, Contr. U. S. Nat. Herb. 13: 111. 1910.

Mellichampia rubescens A. Gray ex S. Wats., Proc. Amer. Acad. 22: 437. 1887.

Type: Mexico: Jalisco, Guadalajara, among underbrush in wet ground, Palmer 280 (holotype: GH!; isotypes: BM! G! LE! NY! NY! P! US!).

Roulinia sinaloensis Brandg., Zoe 5: 243. 1908. Lectotype here designated: Mexico: Sinaloa, vicinity of Culiacan, Brandegee s.n. (Sept. 19, 1904) (UC!; isolectotype: US!).

Mellichampia sinaloensis (Brandg.) Kearney & Peebles, J. Wash. Acad. Sci. 29: 488. 1939.

Cynanchum sinaloense (Brandg.) Woods., Ann. Missouri Bot. Gard. 28: 210. 1941.

Suffrutescent, twining vine; stems terete, pale brown (rarely purplish), to 3.5 mm in diameter, the branchlets stramineous, sparsely to densely puberulent to short pilose in lines above the petioles; petioles adaxially puberulent to (distally) tomentulose, 1-5.5(-7) cm long, mostly 1/4-1/2 as long as blade; leaf blades chartaceous, dull, drying brownish green above, pale green beneath, ovate to narrowly so, 3.5-12 x 1.5-7.5 cm, narrowly acute at apex, deeply to moderately cordate at base, the indument of soft, spreading to appressed hairs, the lower surface sparingly puberulent on veins, the upper surface glabrate, the glands 2-7, the tertiary nerves prominent, scalariform to irregularly reticulate-areolate; racemes bearing 1-10 flowers (with 1-7 at once mature), 3-12.5 x 2.5-4.5(-6) cm, the peduncle adaxially tomentulose, 1.5-9 cm long, slightly shorter to much longer than petiole, the rachis tomentulose, pedicels 1-2 per node, adaxially tomentulose, 5-18 mm long; bracts linear-lanceolate, 1.5-5 mm long, caducous, ciliate at margin; flower buds narrowly ovoid-conic, tapering their entire length, 9-17 mm long;



calyx funnelform to campanulate, sparingly puberulent in sinuses, the tube indistinct to 0.5 mm, the lobes erect to spreading-erect, narrowly to less commonly broadly lanceolate or lanceolate-oblong, 3-6 x 1-1.6 mm, acute at apex, ciliate to eciliate at margin, the glands mostly 1-2 per sinus; corolla campanulate, 15-30 mm in diameter, longer than to about as long as broad, drying maroon to cream white outside, usually paler and 3-5 streaked within, the tube 2-6 mm long, 5-7 mm broad at summit and somewhat pouched at base, the lobes spreading-erect with tips recurved 180-360°, lanceolate to broadly so, 8-10 x 2-3 mm, gradually tapering from base, blunt to sub-obtuse at apex, more or less plane at margin, the lamina mostly with two ridges of minutely pustular tissue parallel to margins within, moderately to densely pilose (rarely glabrous) within, the hairs mostly restricted to or more or less abundant on the ridges, with the unraised marginal and central strips sparingly pubescent to glabrous and often paler or darker than the ridges; crown inserted near base of corolla tube 1.5-2.5 mm below sinuses and but loosely adherent to corolla below point of insertion, drying whitish and always paler than exterior surface of corolla, 8-11.5 mm long, crown segments 5, manifestly united, (the annulus 1-2.5 mm long), erect and conspicuous, at least 4 mm longer than stigma head, each segment more or less abruptly narrowed from the usually oblong basal portion (2-5 x 2-3 mm) to a ligulate central lobe, 4-8 x 0.8-1.5 mm, the shoulders dentate-acute or obsolete and the segment tapered gradually from base to ligule, plane at margin; anthers sessile, 0.9-1.2 mm broad below glands, 1.2-1.8 mm broad at base, 1-1.2(-2) mm long at stigmatic slits, the slits (anther wings) straight to arcuate, only slightly longer than the central pollinium-bearing portion of anthers, the appendages ovate to ovate-orbicular, mostly longer than broad, 1-1.5 x 0.8-1.2 mm, equaling to exceeding the stigma head, rounded at apex; translators with pollinia ovate to ovate-orbicular, 0.42-0.5 x 0.25-0.3 mm, the ends broadly rounded or somewhat narrowed toward the base, the gland cylindrical to broadly so, (0.22-)0.3-0.5 x 0.2-0.24 mm, nearly as long as pollinia, the translator arms pale brown, tangentially flattened and triangular (abruptly expanded at pollinia), 0.15-0.2 mm long, subapically attached to pollinia; gynostegium short-conic, 2-3 mm high, 2-3 mm broad at glands, 2.5-4 mm broad at base, the apex (stigma head) broadly rounded to domed and surpassing the glands by as much as 0.8 mm, 1.2-2 mm in diameter, densely papillate; mature follicles unknown, but immature follicles (1.5-4 cm long) narrowly ovoid-fusiform, longitudinally wrinkled, glabrous, black to dull purple, broadly rounded at base, acute at apex; immature seeds coarsely and irregularly dentate at base.

Typification. According to McVaugh (1970), Bentham's own set of Hartweg duplicates, upon which are based the descriptions in Plantae Hartwegianae, is located at Kew. An additional set of duplicates came to Kew from the Hooker Herbarium. Only the holotype, stamped "Herbarium Benthamianum," bears the name of the new species and the number "290," the page number of the original description in Plantae Hartwegianae. A tracing of the holotype, sent to NY, enabled Vail (1899, loc. cit.) to recognize Ensenlia ligulata as conspecific with Mellichampia rubescens.

Brandegee cited no specimens with the original description of Roulinia sinaloensis but offered the following information: "Climbing over bushes in the vicinity of Culiacan and Yervacito, Sinaloa, Mexico." Apparently, the species is based on two of Brandegee's own unnumbered collections made Sept. 19, 1904 (vicinity of Culiacan: UC, US) and Sept. 26, 1904 (vicinity of Yervacito: UC, US). The former collection comprises the more abundant flowering material. The specimen at UC, repository of Brandegee's first set of duplicates and his manuscript notes, is designated the lectotype.

Distribution (Fig. 2). Cynanchum ligulatum is widely distributed in the Sierra Madre Occidental of Mexico, from the southern states of Michoacan and Morelos northward into the Baboquivari Mountains of southern Arizona in the United States. Label data record a gradual increase in elevation from 450 m in the north (Sinaloa) to 1350-1800 m in the south (Jalisco and Michoacan). A single, and perhaps disjunct, collection (Galeotti 1571) exists from Oaxaca, but no subsequent collections have reconfirmed the species' presence that far south.

Collection labels indicate a variety of habitats from oak and pine chaparral to desert scrub and grassland, fences, open fields, and meadows. Habitat designations from Sonora, Chihuahua, and Sinaloa ("valley forest," "canyon bottom," "lowland forest")



suggest that in the drier, northern portion of its range this species may be restricted to better-watered bottomlands. It seems to attain the status of a weed only at rather high elevations in Jalisco and Michoacan.

Throughout the range of Cynanchum ligulatum, flowering collections have been made almost exclusively in the month of August. Only four collections are dated July, September, or October, and a single specimen (Arsène s.n.) from Michoacan collected in February is quite anomalous. Ferris (5333, Nayarit) records the flowers as fragrant.

Vernacular names: Mexico, Sonora: "Paneywa" (H. S. Gentry 1619).

United States. Arizona: Pima Co. Baboquivari Mountains, Goodding s.n. (U), Proctor 2913-crp (NA, US).

Mexico. Sonora: 21 miles south of Moctezuma, road to Mina Zaragosa, Wiggins 7453 (US); 10 miles south of Mazatan toward Colorado, Wiggins & Rollins 371 (MO); Río Mayo at San Bernadino, H. S. Gentry 1619 (F, MO, UC, US). Chihuahua: Río Mayo at Wisiego, H. S. Gentry 2390 (F, MO, UC, US); Río Bonito, LeSueur 947 (F, TEX, UC). Sinaloa: Yervacito, vicinity of Culiacan, Brandege s.n., Sept. 26, 1904 (UC, US); Baromena, H. S. Gentry 6131 (MO). Zacatecas: Vicinity of Escobedo, Rose 2676 (MO, NY). Nayarit: Vicinity of San Blas, Ferris 5333 (F, NY, US). Jalisco: Road between Colotlan and Bolaños Rose 3658 (MO); vicinity of Guadalajara, Pringle 5432 (US, VT); road to Tapalpa, Walker 73 H 43 (NY); near Río Grande de Santiago, 17 km east of Guadalajara, W. & M. Leavenworth 1805 (F); 15 miles south of Guadalajara on Hwy. 54, Wallace et al. 260 (MO); 14.5 miles south of Guadalajara on road to Chapala, W. R. & C. Anderson 5161 (NY); 73 km south of Guadalajara on Hwy. 33, Barch 5168 (MO, NY); 15 miles southeast of Jocotepec, Barkley et al. 7582 (TEX). Guanajuato: Morolón ("State of Michoacan, Monte Leon"), Pringle 8653 (BM, C, CM, F, G, L, LE, MO, NY, P, UC, US, VT, W). Michoacan: 35 km east of Tizapan el Alto on Hwy. 15, Cruden 1151 (MEXU, TEX, UC); 10 km west of Sahuayo and east of Cojumatlan Iltis et al. 830 (MEXU, MO, UC); Morelia, Arsène s.n. (G, R); Tancitaro region, Municipality of Apatzingan, above Acahuato, Leavenworth & Hoogstraal 1693 (F, MO); District of Zitacuaro, Zitacuaro-Los Pinsanes, Hinton 13092 (G, LL, NY, P, UC, W); District of Huetamo, Santa Cruz, Hinton 6429 (MO, NY). Mexico: District of Temascaltepec, Limones, Hinton 4737 (F, NY, US). Morelos: Xochitepec, Lyonnet 1034 (US); vicinity of Yautepec, Rose & Painter 6585 (NY). Oaxaca: Chinantla, Galeotti 1571 (BR, G, P). Uncertain locality: Sessé et al. 831 (F), 1477 (F), 3585 (F).

Cynanchum ligulatum is the only showy member of the Mexican Mellichampia, but, so far as I am aware, its horticultural potential in arid areas has not been exploited, and only one collection records a vernacular name. The species is remarkable for its consistently large flowers, so large, in fact, that Pittier (1910, loc. cit.) could assume that the floral dimensions cited in Bentham's original description were in error and equated Ensenlia ligulata with a Pringle collection (11021) of C. foetidum. Heller (1895, loc. cit.) had earlier misinterpreted Bentham's species, forcing the original description to conform to Texas specimens of C. racemosum var. unifarium. As previously mentioned, the species appears twice, and in different subtribes of the Asclepiadeae, in Schumann's (1895) treatment of the Asclepiadaceae for Die Natürlichen Pflanzenfamilien, as E. ligulata Benth. (Asclepiadinae) and as Mellichampia rubescens A. Gray ex S. Wats. (Cynanchinae). These plausible errors serve to emphasize the need for very thorough descriptions of these complicated flowers.

Historical misinterpretations notwithstanding, a number of diagnostic features mark Cynanchum ligulatum as unique. Calyx lobes, corolla, crown, and crown annulus are all very long, while, in contrast, the pollinia are rather short (scarcely if at all longer than the gland) and in outline ovate to ovate-orbicular and not at all oblong. Corolla lobes uniformly bear two ridges of pustular tissue (or at least two bands distinguishable by color, pubescence, or both) parallel to the margins within. The crown is inserted near the base of the corolla tube rather than in the throat, a condition unique to C. ligulatum and uniform throughout the species.

Vail (1899, loc. cit.) was the first worker to realize that Gray's Mellichampia rubescens was identical to the troublesome Ensenlia ligulata. Indeed, the two species are based on types from neighboring states in the southern portion of the range, and



Bentham's description, excepting the outline of the crown segments, could as well describe Palmer 280 as Hartweg 1612.

On the other hand, Brandegee's syntypes from Sinaloa, in the northern portion of the range, diverge markedly from the Bentham and Gray types, and are well representative of the majority of specimens from Nayarit, Sinaloa, Chihuahua, and Sonora, and from Arizona in the United States. The corollas of northern specimens are creamy white, contrasting with the striking maroon color of the corolla exterior in specimens from Michoacan and Jalisco. Additionally, calyx, corolla, crown, and pollinia are smaller in northern specimens. Proctor's collection (2913-crp) from Arizona and Brandegee's (Sept. 26, 1904) from Yervacito, Sinaloa, are noteworthy in their possession of extremely short glands, 0.22 and 0.25 mm, scarcely half the length of their pollinia.

Despite salient morphological differences between northern and southern populations, the recognition of separate species or even infraspecific taxa does not appear justifiable. Similarities between the populations, such as the large size of the flowers generally, pollinium shape, and crown insertion, are here judged more important than the differences. And collections intermediate in flower color and size are not uncommon: Morelos, Rose & Painter 6585 (flowers small, but maroon) & Lyonnet 1034 (flowers small and creamy brown); Mexico, Hinton 4737 (flowers small and brownish maroon); Michoacan, Hinton 13092 (flowers small and brownish maroon); Zacatecas, Rose 2676 (flowers rather large and white). And finally, much of the variation displayed does not correlate geographically at all. Two collections from Jalisco (Palmer 280 and Walker 73H43, Fig. 9 C-D) exhibit the full range of crown segment outline and annulus height within the species, while the Brandegee paratype (Sept. 26, 1904) from Sinaloa is intermediate.

Phylogenetic proximity between Cynanchum ligulatum and C. foetidum is suggested by similarities of corolla form and pubescence. However, certain unique features of C. ligulatum may be interpreted to reflect a possible change from a dipteran to a lepidopteran pollination system. A longer-tongued insect would be required to reach the gynostegium of C. ligulatum hidden deep in the coronal tube and further secluded by the erect, campanulate corolla. And the change in pollinium size and shape, from elliptic-oblong (as in all other Mellichampiae) to nearly orbicular, no doubt allows for the easier removal of the translators (with less breakage of the arms) from their new and rather inaccessible position. Notes accompanying one collection (Iltis et al. 830) record visits of sphingid moths to the large purple flowers of a Michoacan population of C. ligulatum.

Brandegee's Sinaloa collection (Sept. 19, 1904) had inadvertently included a small, metallic green wasp in one of the comparatively small, white flowers. The wasp was apparently trapped by its proboscis in the stigmatic slit but bears a translator of the same species on the anterior tarsal claw of a hind leg. It is not known what role, if any, in the pollination of Cynanchum ligulatum, the wasp species in question might play, but it is probably worth noting that its broad mouth parts would appear unsuited for obtaining nectar directly from the stigmatic slits.

#### 11. Cynanchum laeve (Michx.) Pers., Syn. 1: 274. 1805.

As mentioned in the introduction, a full monographic treatment of Cynanchum laeve is deemed beyond the scope of the present study. The species is widely distributed from the southcentral to the northcentral United States, its range being contiguous with that of C. racemosum var. unifarium in central Texas. Species descriptions and illustrations are given in numerous floristic works, e.g., in Small, 1933 (Gonolobus laevis), and in Steyermark, 1963. The morphological characteristics of greatest interest and the phylogenetic relationships of C. laeve are briefly discussed in the introduction under section Ampelamus. An elucidation of the singularly confused typification and historical interpretation of this species is provided by Woodson (1941).



## EXCLUDED SPECIES

- Roulinia connivens (Hook. & Arn.) Decne. in DC. Prodr. 8: 518. 1844. (Cynanchum connivens Hook. & Arn., J. Bot. (Hooker) 1: 294-295. 1834.) = Jobinia sp.
- Roulinia barbata Turcz., Bull. Soc. Nat. Mosc. 21(1): 253-254. 1848. = Metastelma sp., vel aff.
- Ensenia volubilis (Turcz.) Karst., Fl. Colomb. 2: 117. pl. 162. 1866; Ampelanus volubilis (Turcz.) Dugand, Calsasia 9: 404. 1966. (Nematuris volubilis Turcz., Bull. Soc. Nat. Mosc. 21(1): 254. 1848.) = Ditassa sp.
- Roulinia chlorantha K. Schum., Bot. Jahrb. 25: 729. 1898. = Jobinia sp.

Cynanchum contrapetalum E. Sundell, nom. nov.

Roulinia parviflora Decne. in DC. Prodr. 5: 518. 1844; Fourn. in Mart. Fl. Bras. 6(4): 218. 1885; non Cynanchum parviflorum Sw., Prod. Veg. Ind. Occ. 53. 1788; Sieber ex Steud., Nom. ed. 2. 1: 462. 1841; Link ex Fourn. in Mart. Fl. Bras. 6(4): 210. 1885; Alain, Bull. Torr. Bot. Club 90: 191. 1963. Type: Brazil: Mato Grosso, Serra de Cujaba, da Silva Manso s.n. (holotype: G (not seen); photographs of holotype: F! NY!; isotype: P!).

Cynanchum contrapetalum is known from the states of Mato Grosso, Goias, Ceara, and Minas Gerais in central Brazil. Decaisne (1844, loc. cit.) cites a da Silva Manso specimen from Serra de Cujaba, Minas Gerais, as the type. The holotype specifies "Serra de Cujaba," but the state of Minas Gerais was apparently a guess on the part of Decaisne. Although a small village in Minas Gerais bears the name Serra de Cujaba, the more likely type locality is the extensive mountain range in Mato Grosso of the same name. The isotype from P that I examined has no data other than "Brasil (ex herb DC)." However, the handwritten species name matches an orthograph of Decaisne in the possession of Joseph Ewan (Tulane University), and the authenticity of the specimen is beyond any reasonable doubt.

Morphological similarities between Cynanchum contrapetalum and Cynanchum subgenus Mellichampia include vegetative pubescence, leaf outline, racemose inflorescences (tending to pseudopaniculate), shape and proportions of the stigma head and translators, and the coarsely dentate seeds. However, the species is unique among the Cynancha of the New World with which I am familiar in its coronal structure. The 5 segments of the deeply divided crown are opposite the petals, not opposite the anthers and sepals, and the central groove of each segment rather than its margins guides the pollinator's proboscis into the facing stigmatic slit.

Further study of Cynanchum contrapetalum will be necessary to determine the nature of its affinities to both Old and New World groups. It may well be that the species will merit recognition as a monotypic subgenus, but that remains to be seen.

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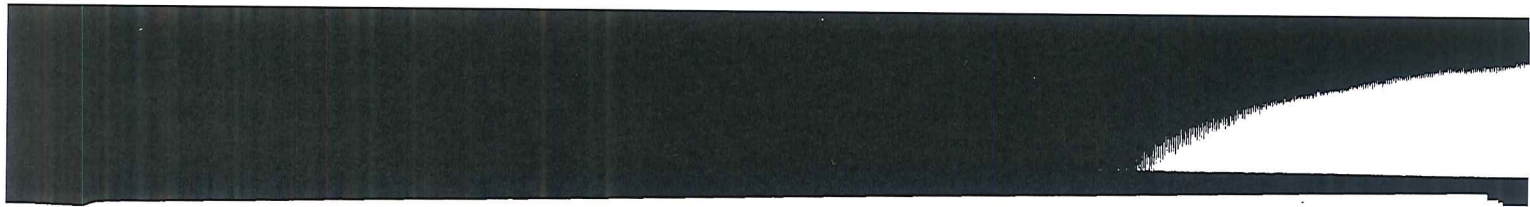


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