

## ABSTRACT

KRINGS, ALEXANDER. Systematics of *Gonolobus* and the Gonolobinae (Apocynaceae, Asclepiadoideae): Circumscription Based on Evidence from Molecules and Morphology; New Species and New Combinations; Typification, Revision, and Conservation in the West Indies. (Under the direction of Drs. Jon M. Stucky and Qiu-Yun (Jenny) Xiang.)

*Gonolobus* Michx. (Apocynaceae, Asclepiadoideae) is a New World genus comprising an estimated 100–150 species. The degree of variation in estimated species numbers is largely the result of still poorly known tropical taxa and differences regarding generic limits.

Characters historically used to delimit genera such as *Gonolobus* within Gonolobinae—such as laminar dorsal anther appendages and various follicle morphologies—have been controversial and their evolution remains unknown, not having been explored in a phylogenetic framework. The primary objectives of the current research were to (1) test the monophyly of *Gonolobus* in the context of a phylogeny of New World Asclepiadeae and (2) explore the evolution of laminar dorsal anther appendages and winged follicles with respect to their potential utility in generic circumscription. Secondary objectives were to revise a tractable monophyletic group as borne out by the phylogenetic analyses and to provide typifications and new combinations as appropriate for Gonolobinae in the West Indies (ca. 50 spp.). Evidence from the chloroplast (*trnL-F*, *rps16*) and nuclear genomes (*Leafy*) presented here supports the monophyly of both the subtribe and the genus *Gonolobus* in a narrow or broad sense. A transversion in the *trnL-F* spacer is shown synapomorphic for *Gonolobus* s.s. Two indels in *Leafy*, as well as winged follicles, are shown synapomorphic for *Gonolobus* s.l. Several earlier subgeneric circumscriptions in *Matelea*, including *Ibatia*, *Heliostemma*, *Pachystelma*, and *Ptycanthera*, are not monophyletic. Considering the support for a monophyletic *Gonolobus* s.s., recent

taxonomic changes in West Indian taxa, and that several species have been published from the area since the last comprehensive treatment over a hundred years ago, a revision of the genus in the West Indies seemed appropriate and is provided. An index of names and typifications for Gonolobinae in the West Indies is also provided, including numerous lecto- and neotypifications. Twelve new species are described for the West Indies (5 *Gonolobus* spp., 5 *Matelea* spp.) and South America (2 *Matelea* spp.).

**SYSTEMATICS OF *GONOLOBUS* AND THE GONOLOBINAE (APOCYNACEAE,  
ASCLEPIADOIDEAE): CIRCUMSCRIPTION BASED ON EVIDENCE FROM  
MOLECULES AND MORPHOLOGY; NEW SPECIES AND COMBINATIONS;  
TYPIIFICATION, REVISION, AND CONSERVATION IN THE WEST INDIES**

by

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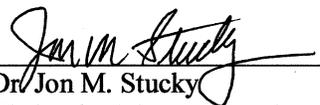
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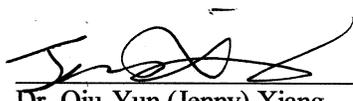
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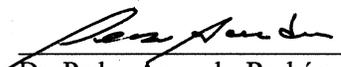
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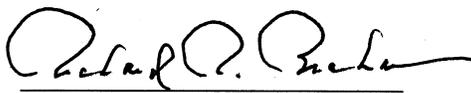
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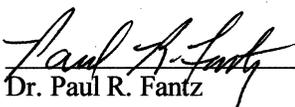
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## INTRODUCTION

*Gonolobus* Michx. (Apocynaceae: Asclepiadoideae) is a New World genus comprising an estimated 100–150 species (Rosatti 1989; Mabberley 1997; Stevens 2001). Over 300 names have been published in the genus, largely due to different, and sometimes confused, interpretations regarding morphology (see Woodson 1941). The genus was erected by Michaux in 1803, based on a taxon from the southeastern United States—*Gonolobus suberosus* (L.) R.Br. Reveal and Barrie (1992) reviewed the complicated nomenclatural history of the type species and Krings and Xiang (2004, 2005; Chapters 1 & 2) its taxonomy. The degree of variation in estimated species numbers in *Gonolobus* is largely the result of still poorly known tropical taxa and differences regarding generic limits. The genus has most recently been accepted as a member of subtribe Gonolobinae (Liede-Schumann et al. 2005). Evidence from the chloroplast genome supports the monophyly of the subtribe, although the sample size has not exceeded seven species (Rapini et al. 2003; Liede-Schumann et al. 2005; Rapini et al. 2006). Over thirty genera have been referred to the subtribe, but Woodson (1941) recognized only *Fischeria* DC., *Gonolobus*, and *Mateleia* Aubl., submerging twenty-nine genera, many monotypic, into a broadly circumscribed *Mateleia* that is in large part still followed today (Stevens 2001). A few genera, such as *Dictyanthus* Decne. (16 spp.), *Labidostelma* Schltr. (monotypic), *Polystemma* Decne. (2 spp.), and *Prosthecidiscus* Donn. Sm. (monotypic) have been resurrected in recent syntheses and floras (Vethacke 1994; Stevens 2001), but without accompanying phylogenetic analyses. Overall, generic circumscriptions in the subtribe remain poorly defined (Stevens 1988). One controversy has been the circumscriptions of *Gonolobus* and *Mateleia*. Woodson (1941) considered that the genus *Gonolobus* should contain plants

characterized by only long, eglandular trichomes, laminar dorsal anther appendages (Cd sensu Kunze 1995), and smooth, angled or winged follicles, whereas *Matelea* should contain plants characterized by glandular and eglandular trichomes, anthers lacking dorsal appendages, and muricate follicles. Unconvinced that laminar dorsal anther appendages should serve as a generic character and citing examples of smooth—but not angled or winged—fruits in *Matelea*, Shinnery (1950) argued against Woodson's generic concept and later included twelve of Woodson's (1941) *Gonolobus* combinations in *Matelea* (Shinnery 1950, 1964). Drapalik (1969) essentially followed Shinnery by maintaining the type of *Gonolobus* (i.e., *G. suberosus*, syn. *G. gonocarpos* (Walter) L.M. Perry) in *Matelea*, although noting its morphological distinctness vis-à-vis other subtribal members in the southeastern United States. Some more recent flora authors have also continued to recognize the type in *Matelea* (Wunderlin 1998). Taking a broader geographical perspective of generic morphology, Rosatti (1989) argued for renewed circumscription of *Gonolobus* based on the presence of laminar dorsal anther appendages. Most recently the concept of *Gonolobus* as characterized by short, capitate-glandular, short acicular, and long acicular trichomes, laminar dorsal anther appendages (typically), and smooth, winged follicles has been used by Stevens (2001, 2005). However, glandular hairs, although thought characteristic of *Matelea* by Woodson (1941), appear without circumscriptional value in the *Gonolobus-Matelea* question, being present in both the type of *Gonolobus* (i.e., *G. suberosus*) and numerous species lacking dorsal anther appendages (Rosatti 1989; Krings, pers. obs.). The utility of the follicle character (primarily winged in *Gonolobus* vs. primarily muricate in *Matelea*) is also problematic. With greater collections since Woodson (1941), it has become clear that several taxa apparently lacking dorsal anther

appendages bear winged instead of muricate follicles. The evolution of characters historically used to delimit genera in Gonolobinae, such as laminar dorsal anther appendages and various follicle morphologies, remains unknown and cannot be understood outside of a phylogenetic framework. Because taxonomic revisions will continue to prove ‘ephemeral’ unless improved resolution of relationships within New World Asclepiadeae can provide better generic assignments (Rapini et al. 2003), the primary objectives of the following studies were to (1) test the monophyly of *Gonolobus* in the context of a phylogeny of New World Asclepiadeae and (2) explore the evolution of laminar dorsal anther appendages and winged follicles with respect to their potential utility in generic circumscription. Secondary objectives were to revise a tractable natural group as borne out by the phylogenetic analysis above and provide typifications and new combinations as appropriate for Gonolobinae in the West Indies (ca. 50 spp.). Although not anticipated at the outset, the description of new taxa became necessary as a result of field and herbarium studies related to the primary and secondary objectives. Many of the following chapters were published at various times over the past few years and are arranged here in three sections, not chronologically, but by subject matter: (1) systematic studies in *Gonolobus* in the southeastern U.S. and the West Indies, (2) additional studies in West Indian Gonolobinae, and (3) additional studies in South American Gonolobinae.

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**Systematic studies in *Gonolobus***  
**in the southeastern United States and the West Indies**

# Chapter I

## **The *Gonolobus* complex (Apocynaceae: Asclepiadoideae) in the southeastern United States**

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## ABSTRACT

Taxonomic limits of *Gonolobus* (Apocynaceae – Asclepiadoideae) in the southeastern United States have been controversial, with some authors recognizing two species and others only one. Over the past thirty years, most authors have tended toward recognition of a single species. However, the morphological variation within the taxon appears complicated and has not been analyzed using a quantitative approach. We analyzed the morphological variation within southeastern *Gonolobus*, based on 143 herbarium specimens from thirteen southeastern states, using ANOVA, and mapped taxon distributions. Two distinct *Gonolobus* entities, based on differences in floral character states and geographic tendencies, appear to exist in the southeast, although questions regarding rank recognition remain.

Climbing milkweeds (Apocynaceae: Asclepiadoideae and Periplocoideae) encompass at least two taxonomically difficult genera in the southeastern United States – *Matelea* and *Gonolobus* (Drapalik 1969; Sundell 1981; Rosatti 1989; Liede 1997). Two closely-related species of *Gonolobus* Michx. have until recently been recognized from the southeastern United States, although opinions over generic placement have differed. Woodson (1941) considered that the genus *Gonolobus* should contain plants characterized by only long, eglandular trichomes, dorsal anther appendages, and smooth, angled or winged follicles, whereas *Matelea* Aubl. should contain plants characterized by glandular and eglandular trichomes, anthers lacking dorsal appendages, and muricate follicles. Unconvinced that dorsal anther appendages should serve as a generic character and citing examples of smooth [but not angled or winged] fruits in *Matelea*, Shinnors (1950) argued against Woodson's

generic concept and transferred the southeastern *Gonolobus* taxa to *Matelea*. Later, Shinnery (1964) also included twelve of Woodson's (1941) *Gonolobus* combinations in *Matelea*. Drapalik (1969) maintained Shinnery's generic view, although admitting to the characteristic differences of southeastern *Gonolobus* from southeastern *Matelea* species in bearing dorsal anther appendages and smooth, winged follicles. Taking a broader geographical perspective of generic morphology and citing the importance and development of anther appendages in the 150 some species of *Gonolobus* outside the southeastern United States, Rosatti (1989) argued for renewed placement of the southeastern taxon in *Gonolobus*. Most recently the concept of *Gonolobus* as characterized by short, capitate-glandular, short acicular, and long acicular trichomes, dorsal anther appendages (typically), and smooth, winged follicles has been used by Stevens (2001). The two *Gonolobus* species historically recognized from the southeastern United States -- *Gonolobus suberosus* (L.) R. Br. and *Gonolobus gonocarpos* -- have been distinguished primarily by the ratio of corolla lobe length to sepal lobe length and the presence or absence of pubescence on the adaxial corolla surface (Small 1933; Perry 1938; Fernald 1950; Gleason 1952; Radford et al. 1968). Most authors essentially followed Small (1933) in referring the taxon with glabrous corollas and lobes more than twice as long as the sepals to *G. gonocarpos* and the taxon with pubescent corollas and lobes twice as long or less than the sepals to *G. suberosus* (Perry 1938; Fernald 1950; Gleason 1952; Radford et al. 1968). In contrast, Drapalik (1969) considered the two taxa synonymous, having found "plants that would represent both [...] taxa and every conceivable intermediate." However, he stressed that in no manner should his decision be taken to acknowledge that the taxon was uniform throughout its range. Considering that *G. gonocarpos* is state listed as threatened in Florida

(Florida Administrative Code Ch. 5B- 40.0055), this study seeks to re-examine the taxonomy of the southeastern *Gonolobus* complex by critically analyzing patterns of morphological variation and their geographical relationships using a quantitative approach.

## METHODS

A total of 326 herbarium specimens (from nineteen herbaria) were examined from throughout the range of the southeastern *Gonolobus* complex (i.e., AL, AR, FL, GA, KY, LA, MS, NC, OK, SC, TN, TX, and VA). We selected 143 herbarium specimens (the OTUs in the analysis) for our analyses - the rest were either too poor in condition or lacked some or all organs. Six characters (Table 1), three quantitative and three qualitative, showed variation within the group and were thus chosen for the analysis. Only mature flowers were chosen for scoring of floral characters.

Leaf shape/size and vestiture characters were not chosen for inclusion in the analysis. These characters were not rejected due to high variability, but due to lack of basic understanding regarding intra-individual variation. Leaf size and shape may be influenced by position on the stem (e.g., sun vs. shade leaves) and habitat (e.g., edge vs. forest interior) (Krings, pers. obs.). As collectors rarely indicate the stem position from which samples were taken, parallel comparisons of herbarium specimen leaf material (i.e., comparing sun leaves to sun leaves) is essentially impossible. Leaf pubescence characteristics were also considered uninformative with regard to southeastern *Gonolobus*. Our chi-square tests suggested no correlation between leaf pubescence and either floral character states or the environment (i.e., habitat), as might be expected (unpubl.).

Although inflorescence characters (type and number of flowers borne) have been useful in higher level analyses in the Asclepiadoideae (e.g., Liede 1996, 1997), inflorescence characters were not included in our study based on results of a preliminary analysis of 48 *Gonolobus* specimens chosen primarily from the extremes of the range (i.e., Florida and Texas). ANOVA results showed no significant difference ( $F=0.865 < F_{\text{crit}}=4.05$ ) in the mean number of flowers per inflorescence between uniformly-colored and multi-colored specimens (Klings, unpubl.). In the preliminary analysis, flowers were counted for any inflorescence bearing at least one fully opened flower (i.e., corolla lobes completely extended). As flowers are produced sequentially over the life of the inflorescence, visible flower buds were included in the total count of flowers per inflorescence. Specimens chosen for inclusion were those most robust overall – a somewhat arbitrary judgment of the number of inflorescences available and their condition.

Due to the high similarity of fruits of *Gonolobus* in the southeast, collections of the same individuals in flower and fruit would be required to allow correlative evaluation of fruit character utility. Unfortunately, the extremely small number of such collections is inadequate for such an evaluation at this time.

A data matrix was produced by scoring the character states of five characters for all 143 OTUs (see below & Table 1). There were no gaps in the data matrix. A neighbor-joining tree was generated using PAUP 4.0 (Swofford 2002). Frequency distributions were also

determined for selected floral character states and tested for significant differences using ANOVA.

## CHARACTERS

1. FLORAL COLOR. Individuals of the southeastern *Gonolobus* complex exhibit flowers that are either uniformly green from corolla lobe base to apex or conspicuously dark at the base (variously described as maroon to brown) with lighter tips (typically green). Specimens bearing the former were scored as uniformly green (1) and specimens exhibiting the latter as multi-colored (0) for corolla lobe coloration. On senescing, greenish flowers tend to turn yellowish.

2. ADAXIAL COROLLA VESTITURE. Adaxial corolla vestiture is an important character that has been used to recognize species in the southeastern *Gonolobus* complex (see Small 1933; Gleason 1952; Radford et al. 1968). Adaxial corolla lobe pubescence tends to be laterally distributed. Pubescence is generally concentrated on the right side of corolla lobes (from apex to base) and may extend longitudinally to various degrees across the lobe center to the left. The far left margins (from apex to base) tend to be glabrous in otherwise pubescent flowers. The same asymmetry was also evident in Caribbean species available to us for inspection and may be the case for all pubescent *Gonolobus* species - although such analysis was presently beyond our scope. Specimens were scored as pubescent (0) if pubescence to any degree was observed on the adaxial corolla lobes and glabrous (1) if no pubescence was evident.

3. CORONA. Corona characters have in the past been used to distinguish asclepiad genera (see Liede 1996), although caution must be employed if the true homology is not known (see Liede 1996; Liede & Täuber 2002). In our study, we evaluated only the shape of the corona lobes among members of the southeastern *Gonolobus* complex. All coronas in the complex are lobed. However not all lobes are further lobed (i.e., emarginate at the apex). We scored corona lobes to be either lobed (i.e., emarginate at the apex)(0) or truncate (i.e., squared off at the apex) (1).

4-6. QUANTITATIVE FLORAL CHARACTERS. Measurements of sepal and petal length were taken from between 1 to 5 flowers per specimen, depending on availability and measurability. Flowers with excessive contortion and folding of petals and sepals were avoided. In general, measurements were taken from different flowers, although in a few cases, when availability was poor and lobe length varied infraflorally, multiple corolla lobes were measured from a single flower. For generation of a nearest-neighbor tree, continuous sepal and corolla lobe lengths were coded into one of five range classes and treated as unordered in the analysis (Table 1). The ratio of mean corolla lobe length to mean sepal length was not used in the generation of the nearest-neighbor tree.

## RESULTS

It appears that at least two distinct groupings of *Gonolobus* taxa exist in the southeastern United States. The clustering of taxa exhibits strong geographic tendencies (Fig. 1), although petal and sepal length intergrade among OTUs when graphed in a scatterplot (Fig. 2). Based on corolla coloration, taxa can be assigned to one of two groups: (1) a uniformly

colored corolla group (UCCG) and a multi-colored corolla group (MCCG). The UCCG is considerably more widespread and exhibits a more western center of gravity relative to the MCCG (Fig. 1). Adaxial corolla pubescence is nearly invariable in the UCCG. Only 3.7% (3 of 81) of the examined individuals exhibit pubescent adaxial corolla surfaces (Fig. 3). Although individuals with uniformly colored petals have been collected in the far eastern states of Georgia, North Carolina, and Virginia, these tend to be rare collections disjunct from the main range of occurrence (Fig. 1). Adaxial corolla pubescence is much more frequent among members of the MCCG (Fig. 3). In fact, two thirds of the examined individuals in this group were pubescent (41 of 62). The MCCG appears to be restricted to a more narrowly defined southeastern range east of the Mississippi (Fig. 1).

Except for a few outliers (e.g., GA2, NC20, VA1, VA23), the geographic clustering is supported by the midpoint-rooted neighbor-joining tree (Fig. 4). Although bootstrapping yielded little support for any one branch of the tree (due to the small number of characters employed), the tree remains informative. Members of the MCCG and UCCG are grouped together – indicating greater within-group similarity across the five morphological characters than between groups.

Individuals of the UCCG exhibit longer mean corolla lobes (mean=7.68) and higher mean corolla lobe length to mean sepal length ratios (mean=2.48) than individuals of the MCCG (Table 2). Results of analyses of variation (ANOVA) indicate the differences in both mean corolla lobe length and corolla:sepal length ratio to be highly statistically significant between the two groups (Table 3).

It is interesting to note that the rare pubescent individuals of the predominantly glabrous UCCG appear to exhibit a similar frequency distribution of corolla lobe lengths and corolla:sepal ratios as pubescent members of the MCCG. ANOVA tests show no significant difference between pubescent UCCG and pubescent MCCG in both mean corolla lobe lengths ( $F=0.042 < F_{\text{crit}}=3.99$ ) and the ratio ( $F=0.604 < F_{\text{crit}}=3.99$ ) - although this may be a factor of the small sampling size of pubescent UCCG members ( $n=3$ ). Glabrous members of the MCCG appear to exhibit corolla lobe lengths much larger than the more frequent (in terms of specimens examined) pubescent members of the MCCG (Fig. 5B). However, the difference in mean corolla lengths between glabrous and pubescent MCCG is not quite significant ( $F=3.559 < F_{\text{crit}}=3.96$ ). The difference in the corolla:sepal ratio between glabrous and pubescent MCCG members is also not quite significant ( $F=3.746 < F_{\text{crit}}=3.96$ ). Although the frequency peak for corolla:sepal ratios of glabrous MCCG members appears to graphically coincide with the peak of glabrous UCCG members (Fig. 5C & D), ANOVA results show a strong statistical difference between the two ( $F=9.467 > F_{\text{crit}}=3.93$ ).

## DISCUSSION

The issue of whether more than one *Gonolobus* species should be recognized for the southeastern United States has long confronted taxonomists and has been additionally complicated by the nomenclatural confusion surrounding *Gonolobus suberosus* (L.) R.Br. (see Drapalik 1969; Reveal & Barrie 1992). Small (1933), and later Perry (1938), recognized two species of *Gonolobus* in the Southeast based on corolla pubescence and the

ratio of corolla lobe length to sepal length. Small (1933) referred the taxon with glabrous corollas and lobes more than twice as long as the sepals to *G. gonocarpos* (*Vincetoxicum gonocarpos* sensu Small), whereas the taxon with pubescent corollas and lobes twice as long or less than the sepals was referred to *G. suberosus* (*V. suberosum* sensu Small). Fernald (1950) added some less than distinct characters to the mix, including flower bud (“abruptly acuminate” vs. “gradually acute or acuminate”), calyx pubescence (“practically glabrous” vs. “glabrous or ciliolate apically”), and corolla lobe shape (“broadly lanceolate” vs. “linear-lanceolate”), while basically maintaining Small’s (1933) pubescence and ratio characters. Gleason (1952) treated only *G. gonocarpos*, stating that *G. suberosus* was “erroneously” accredited to the range of Britton and Brown’s flora. However, in a footnote, Gleason (1952) maintained the distinction between the taxa based on adaxial corolla pubescence, forwarded by previous authors (Small 1933; Perry 1938; Fernald 1950). In light of the present analyses, these concepts of specific delimitation are untenable as stated.

Drapalik’s (1969) findings of overlapping combinations of character states among *Gonolobus* taxa in the southeast are upheld by our study. However, overlapping character presence/absence combinations are insufficient argument against recognition of multiple taxa. Especially at the infraspecific level and in hybrid zones, some level of character overlap can be expected between individuals sharing some range continuity. Our data support the notion of previous workers (e.g., Small 1933; Perry 1938; Fernald 1950; Gleason 1952), that at least two *Gonolobus* entities occur in the Southeast that could be accorded formal rank. However, contrary to previous workers, we propose that the two

groups respectively be defined by uniformly-green versus multi-colored corolla lobes, rather than by corolla/sepal length and adaxial corolla lobe pubescence. Although there are significant differences in mean corolla lobe lengths and the ratio of corolla lobe length to sepal length (Table 3), these character states can overlap at the individual level and cannot consistently separate the taxa. Similarly, adaxial corolla pubescence cannot consistently separate the taxa, being present in both members of the UCCG and the MCCG. However, distinct differences are apparent in the frequencies of the pubescence trait (Figs. 3 & 5). In addition, with respect to their geographic distribution, the frequency of glabrous, multi-colored flower collections increases conspicuously in the zones where the UCCG meets the MCCG (e.g., in Alabama). Similarly, the rare individuals bearing adaxially pubescent, uniformly green corollas occur well within the range of the MCCG. Thus, the respective changes in pubescence frequencies in the MCCG or occurrence of rare character states in the UCCG outside its primary range may be cautiously hypothesized to be an effect of genetic interchange between two taxa intergrading in distribution.

Unfortunately, frequency histograms of corolla lobe length and ratio of corolla lobe length:sepal length size classes within the UCCG and MCCG shed weak light on the matter of intergradation (Fig. 5). Although our analyses support the recognition of two *Gonolobus* entities in the Southeast, the question remains whether these should be recognized at the species level or below. Our data can be interpreted either way – two morphologically divergent species potentially hybridizing in overlapping zones, resulting in some morphological intergradation, or two diverging subspecies with morphological intergradation in zones of range overlap. The former interpretation could result from

application of a quantitative or phenetic species concept, in which species are distinguished based on differences in means of variables. Although commonly applied, the underlying theory of this concept remains unclear (see Luckow 1995). In contrast, application of a phylogenetic species concept suggests two infraspecific taxa – populations exhibiting high frequencies of unique traits that may become ‘fixed’ in the future (Nixon & Wheeler 1990). However, a cladistic analysis that includes other congenics is necessary to test this hypothesis (Nixon & Wheeler 1990). In the absence of additional data, we cautiously choose to follow (Drapalik 1969) in recognizing a single species until additional evidence is available. Interestingly, the overall biogeographic pattern exhibited by the two *Gonolobus* entities has been observed for other taxa (including fish!) in the Southeast (see Avise 1994) and may be the result of past environmental shifts such as the oceanic incursions and retreats that define today’s southeastern Coastal Plain (Sorrie & Weakley 2001). To further elucidate both the question of rank and evolutionary history of the complex, we are conducting genetic analyses of southeastern *Gonolobus* populations using molecular markers and integrating phylogenetic data from Caribbean *Gonolobus* species - some of which have been suggested to be nearest relatives of the southeastern taxa (Scheele 1848).

Should workers choose to formally recognize the two entities, we provide a brief discussion regarding available names. For more detail regarding the particularly complicated history and nomenclature involved, readers are urged to see Reveal & Barrie (1992) and Krings (2001). In choosing a name for the taxon with uniformly colored petals, past names published for southeastern *Gonolobus* taxa were examined. Walter’s type of *Gonolobus*

*gonocarpos* (Walter 687, BM!) contains only leaves and roots. In addition, no mention regarding the pubescence of the corolla is made in his protologue (Walter 1788). Thus we cannot be certain to which species the plants that Walter based his description on belong. However, due to the rare occurrence of uniformly colored species in the Carolinas, we propose that his type be considered to belong to the multi-color group. Types for *Gonolobus macrophyllus* Michx. and *Gonolobus laevis* A. Gray, non Michx. are relegated to the multi-color group for the same reason. The protologue of *Gonolobus granulatus* Scheele (1848) is based on the only eligible type specimen collected west of the Mississippi (*Lindheimer s.n.*) and notes glabrous adaxial corolla lobes. Thus, the correct name for the uniformly green-flowered taxon should be based on *Gonolobus granulatus* Scheele and the name for the multi-color flowered taxon should be *Gonolobus suberosus* (L.) R.Br. Alternatively, if the two entities are recognized at the infraspecific level, the correct species name is *Gonolobus suberosus* (L.) R.Br.

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TABLE 1. Floral characters and character states. Character 6 used in ANOVA only and not in generation of neighbor-joining tree due to lack of independence vis-á-vis characters 4 and 5.

<i>Character</i>	<i>Character State</i>	
1. Adaxial corolla coloration	Multi-colored (dark center, lighter tips) [0]	Uniformly green [1]
2. Adaxial corolla vestiture	Pubescent [0]	Glabrous [1]
3. Corona	Lobed [0]	Truncate [1]
4. Mean sepal length (mm)	1.5-2.5 [0], 2.51-3.5 [1], 3.51-4.5 [2], 4.51-5.5 [3]	
5. Mean corolla lobe length (mm)	2.01-4 [0], 4.01-6 [1], 6.01-8 [2], 8.01-10 [3], >10.01 [4]	
6. Ratio of Mean corolla lobe length: Mean sepal length	Continuous	

TABLE 2. Descriptive summary statistics for continuous floral characters of the uniformly colored corolla group (UCCG) and the multi-colored corolla group (MCCG).

	<i>Mean sepal length</i>	<i>Mean corolla lobe length</i>	<i>Mean ratio (corolla lobe length: sepal length)</i>
Uniformly colored	3.21 (SD=0.76)	7.68 (SD=1.47)	2.48 (SD=0.61)
Multi- colored	3.08 (SD=0.74)	5.59 (SD=1.73)	1.83 (SD=0.44)

TABLE 3. ANOVA results for floral character comparisons between the uniformly colored corolla group and the multi-colored corolla group. In both cases, the null hypothesis of no significant difference is rejected.

Mean corolla lobe length

<i>Source of Variation</i>	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P-value</i>	<i>F crit</i>
Between Groups	153.1516	1	153.1516	61.08722	1.15E-12	3.908255
Within Groups	353.5008	141	2.507098			
Total	506.6524	142				

Ratio of mean corolla lobe length: mean sepal length

<i>Source of Variation</i>	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P-value</i>	<i>F crit</i>
Between Groups	14.78613	1	14.78613	50.19068	6.1E-11	3.908255
Within Groups	41.53849	141	0.294599			
Total	56.32462	142				

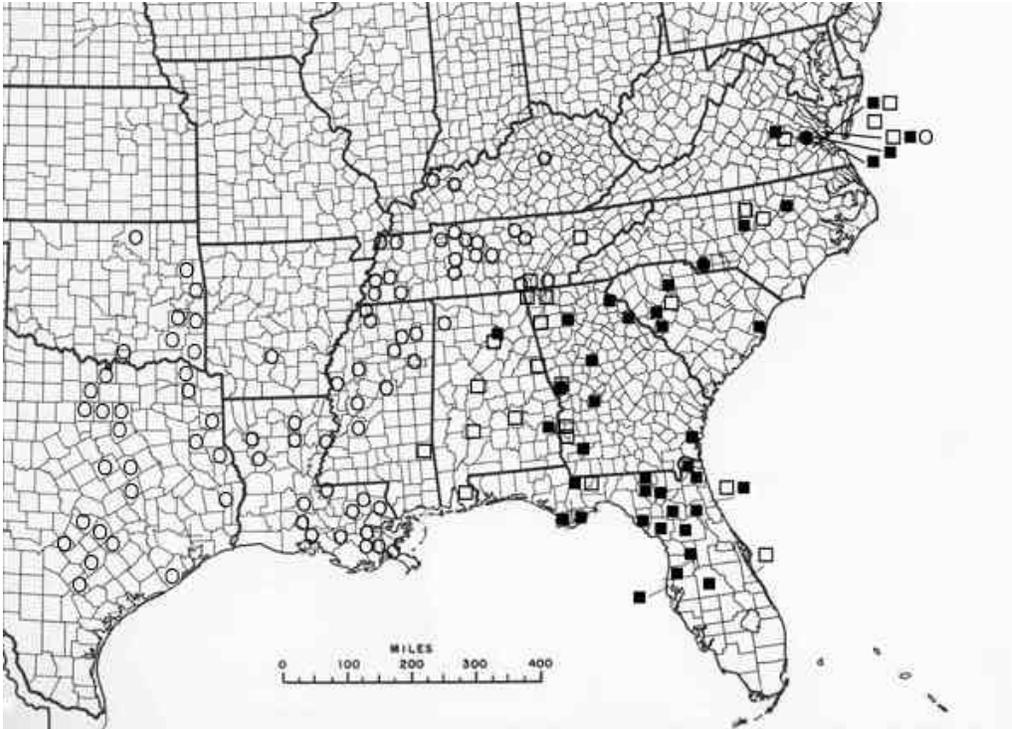


FIG. 1. Distribution map of southeastern United States *Gonolobus* entities. Circles represent individuals with uniformly green corollas - either glabrous adaxially (open circle) or pubescent (closed circle). Squares represent individuals with multi-colored corollas - either glabrous adaxially (open square) or pubescent (closed square).

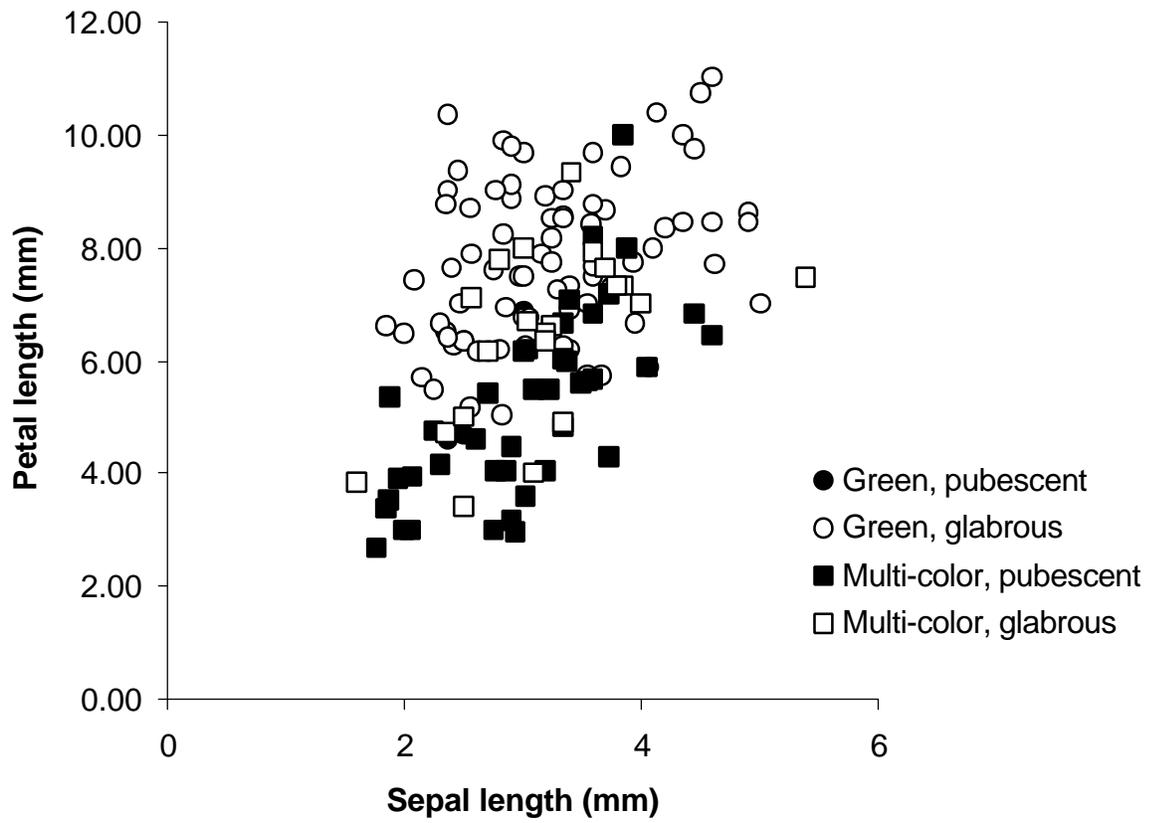


FIG. 2. Scatterplot of sepal vs. petal length by flower color and adaxial petal vestiture for *Gonolobus* entities in the southeastern United States.

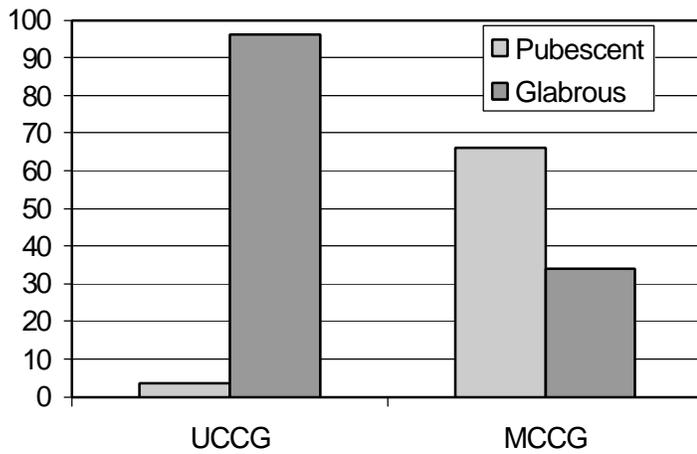


FIG. 3. Percentage of *Gonolobus* specimens exhibiting pubescent or glabrous adaxial corolla lobes in the respective uniformly colored corolla group (UCCG) and the multi-colored corolla group (MCCG).

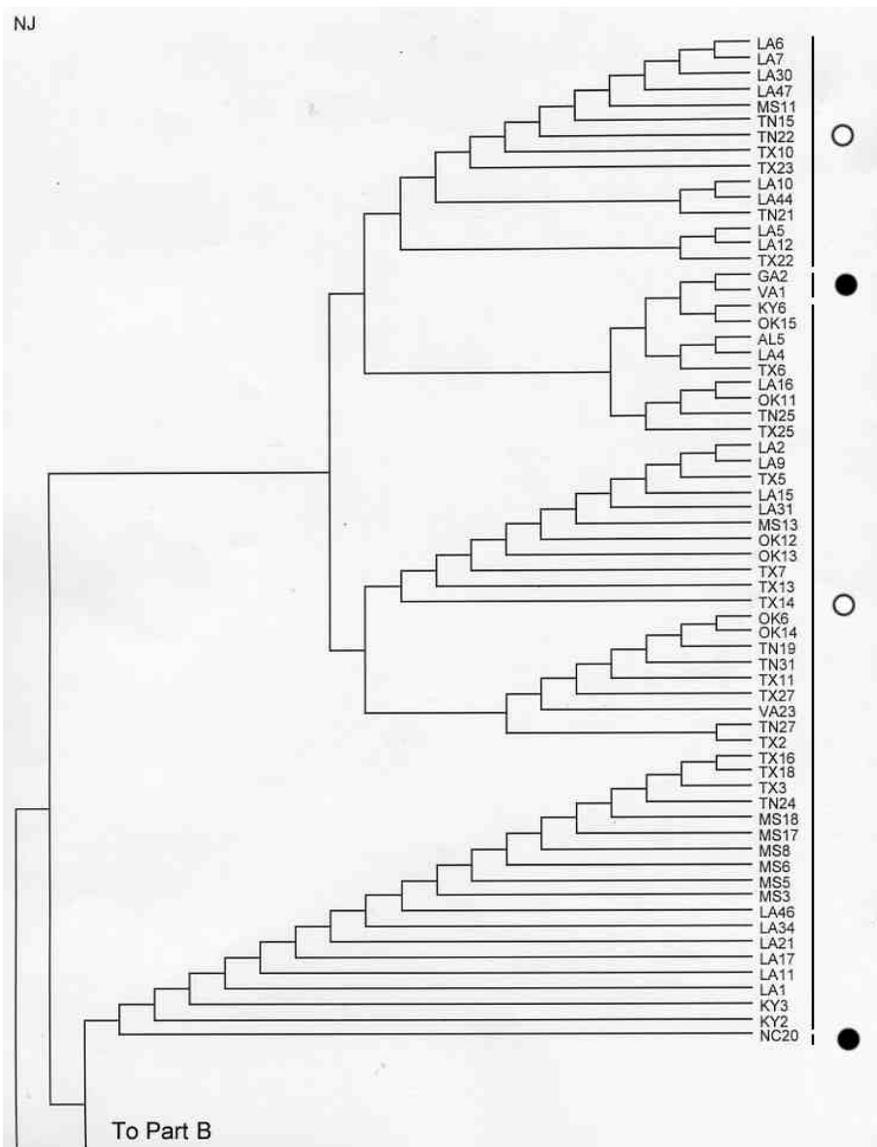


FIG. 4 (Part A). Midpoint-rooted neighbor-joining tree, based on five morphological characters. OTUs are individual specimens of *Gonolobus*. First two characters of alphanumeric code indicate state of origin by standard abbreviation. Second two characters are a unique, sequential number assigned to each specimen studied. Circles represent individuals with uniformly green corollas - either glabrous adaxially (open circle) or pubescent (closed circle). Squares represent individuals with multi-colored corollas - either glabrous adaxially (open square) or pubescent (closed square).

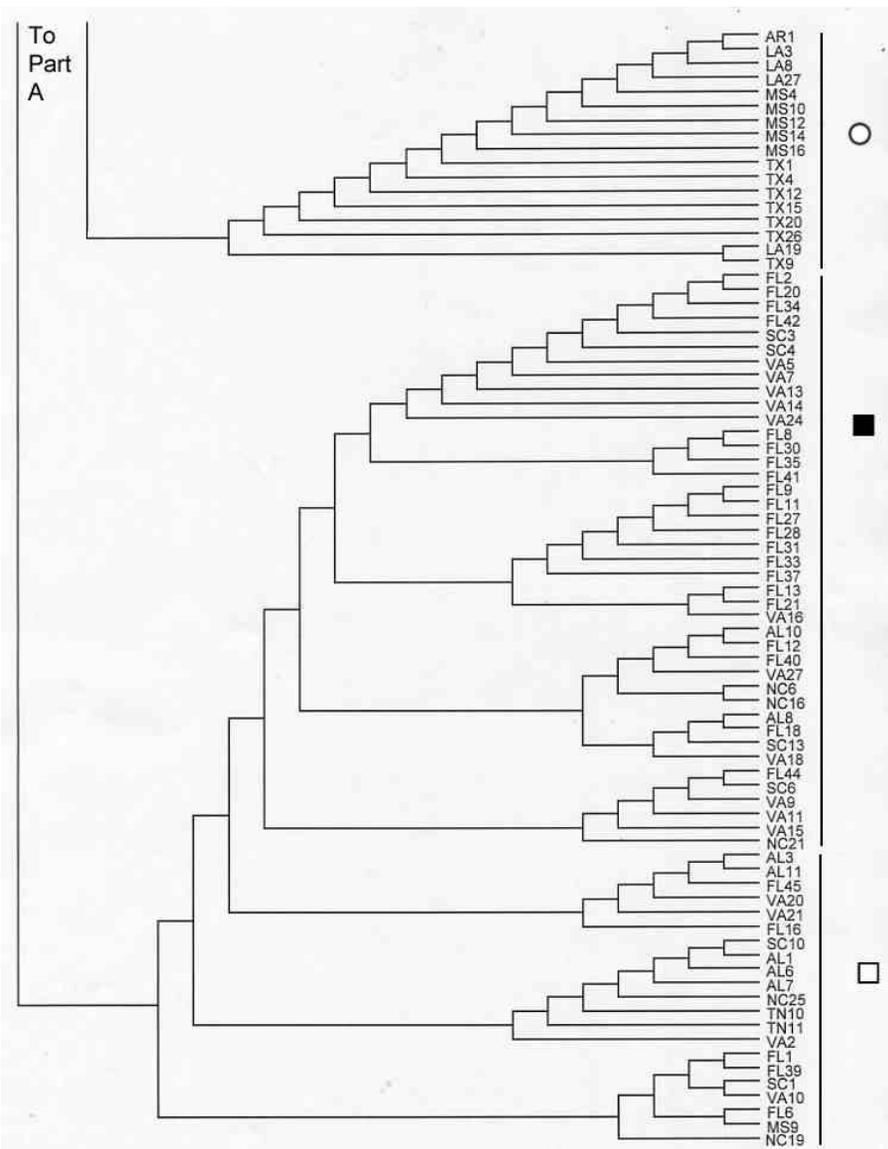
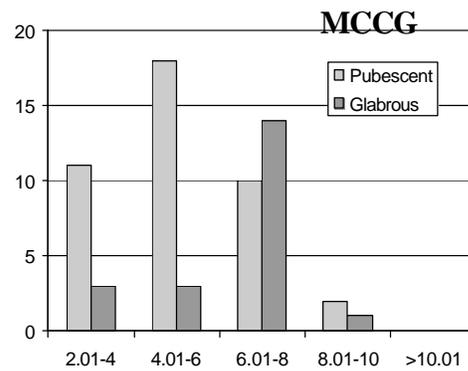
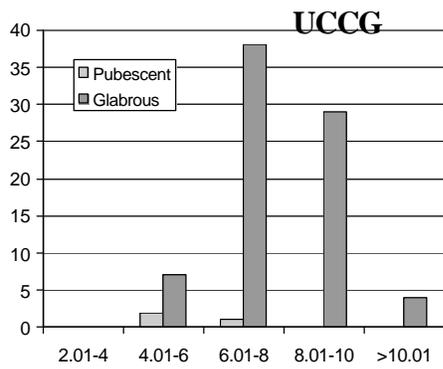
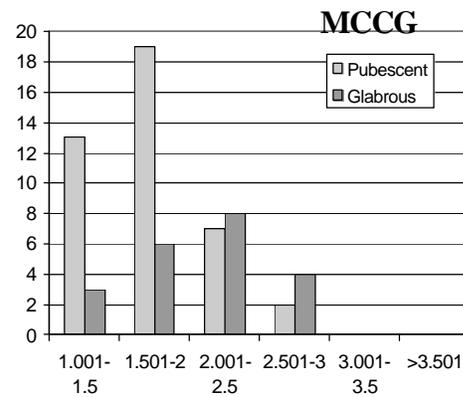
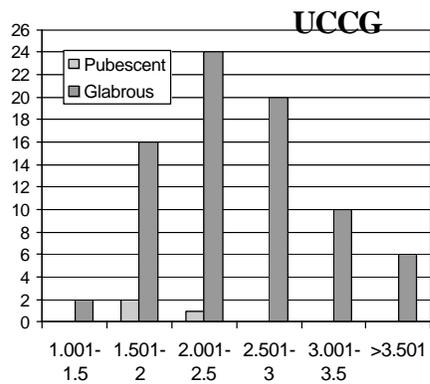


FIG. 4 (Part B).



**A**

**B**



**C**

**D**

FIG. 5. Frequency histograms for floral characteristics in the uniformly colored corolla group (UCCG) and the multi-colored corolla group (MCCG) of southeastern *Gonolobus* – Corolla lobe length in mm ranges (A: UCCG; B: MCCG) and ratio of corolla lobe length to sepal length (C: UCCG; D: MCCG). Y axes represent number of individuals and X axes respective character state ranges.

## Chapter II

### **Taxonomy of the *Gonolobus* complex (Apocynaceae: Asclepiadoideae) in the southeastern United States: ISSR evidence and parsimony analysis**

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Krings did all of the work reported in this paper, but Dr. Jenny Xiang provided scientific advice and guidance.

Running head: KRINGS AND XIANG, *GONOLOBUS* COMPLEX (APOCYNACEAE,  
ASCLEPIADOIDEAE)

TAXONOMY OF THE *GONOLOBUS* COMPLEX (APOCYNACEAE, ASCLEPIADOIDEAE) IN THE  
SOUTHEASTERN UNITED STATES: ISSR EVIDENCE AND PARSIMONY ANALYSIS

ALEXANDER KRINGS<sup>1</sup> AND (JENNY) QIU-YUN XIANG<sup>2</sup>

Footnotes start here-----

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Footnotes end here-----

**Abstract.** In a recent morphometric analysis of the *Gonolobus* complex (subgenus *Gonolobus*) in the southeastern United States, we found former specific concepts untenable as stated, as the diagnostic characters could not consistently assign individuals to one of two groups. However, our analysis showed a strong geographical component to the distribution of individuals delimited by uniformly and multicolored corollas, which we used as a basis for suggesting that two entities do appear to exist in the Southeast that may deserve recognition at some taxonomic rank. In the present study, we performed analysis of Inter-Simple Sequence Repeats (ISSR) to assess whether the two entities are genetically differentiated and, if so, to what level. We also conducted a cladistic analysis of morphological characters of the subgenus to determine whether the entities emerge as closest relatives. Our ISSR results showed substantial genetic differentiation at 18 loci between the two entities, although no fixed differences between them were detected. At 7 loci, the frequencies of band presence are significantly higher in the multicolored corolla group (MCCG) than in the uniformly colored corolla group (UCCG). At 11 loci they are significantly higher in the UCCG. Nineteen bands are unique to the MCCG, although at various frequencies (3.5--39.0%), whereas only a single band is unique to the UCCG, suggesting that the latter possesses a subset of the MCCG gene pool and is likely a derivative of it. Analysis of 61 parsimony-informative characters using Neighbor-Joining (NJ) and Unweighted Pair-Group Method using Arithmetic means (UPGMA) did not resolve the two groups, consistent with the view of a single species. In a parsimony analysis of morphological characters of 14 species of the subgenus, the two groups consistently appear as closest relatives. This evidence indicates that the complex represents a single evolutionary lineage with two incompletely differentiated morphological subgroups. On the basis of these results, we propose to treat the MCCG and UCCG as two varieties of *Gonolobus suberosus*. *Gonolobus granulatus* Scheele is neotypified in association with the required new combination for the UCCG variety. A key to the infraspecific taxa is provided.

**Keywords:** *Gonolobus*, Apocynaceae, Asclepiadoideae, southeastern United States

Whether more than one *Gonolobus* Michx. species (Apocynaceae---Asclepiadoideae) should be recognized for the southeastern United States has long occupied taxonomists and has been additionally complicated by the nomenclatural confusion surrounding *Gonolobus suberosus* (L.) R. Br. (see Drapalik, 1969; Reveal and Barrie, 1992). Small (1933) and later Perry (1938) recognized two species of *Gonolobus* in the Southeast based on corolla pubescence and the ratio of corolla lobe length to sepal length. Small (1933) referred the taxon with glabrous corollas and lobes more than twice as long as the sepals to *G. gonocarpos* (Walter) L. M. Perry (*Vincetoxicum gonocarpos sensu* Small), whereas the taxon with pubescent corollas and lobes twice as long or less than the sepals was referred to *G. suberosus* (*V. suberosum sensu* Small). Others following essentially similar concepts include Fernald (1950) and Gleason (1952). Drapalik (1969) recognized only a single species on the basis of evidence of overlapping character states. In a recent morphometric analysis of the complex, we found the specific concept of Small (1933) and others (Perry, 1938; Fernald, 1950; Gleason, 1952) untenable as stated as the diagnostic characters could not consistently assign individuals to one of two groups (Krings and Xiang, 2004). Our quantitative analysis of morphological characters also showed no clear separation of specimens. Instead, we found a strong correlation between geographical distribution and corolla morphology, which does suggest the existence of two entities in the Southeast that may deserve recognition at some taxonomic rank. As application of differential species concepts (e.g., quantitative/phenetic vs. phylogenetic) could recognize the entities at different ranks (i.e., species vs. subspecies/variety) (see Luckow, 1995), we cautiously accepted a single species until further evidence became available. The objectives of the present study were to (1) analyze southeastern *Gonolobus* using inter-simple sequence repeat (ISSR) fingerprinting to determine whether the two entities are also genetically differentiated, (2) perform a parsimony analysis of morphological features, including other *Gonolobus* species, to test whether the southeastern entities would emerge as sisters, and (3) evaluate the taxonomic implications from the new evidence.

## MATERIALS AND METHODS

### Sampling and ISSR Analysis

Fresh leaf material was obtained from fourteen *Gonolobus* populations from Alabama, Florida, Louisiana, North Carolina, South Carolina, Tennessee, and Texas (Fig. 1). These populations represent both the morphological extremes and intermediates as suggested by our morphometric analysis (Fig. 1; Krings and Xiang, 2004). Herbarium vouchers (Table 1) are deposited at NCSC and FLAS (abbreviations follow Holmgren et al., 1990). Leaf material was collected from 40 individuals and dried in silica gel. DNA was extracted using the Qiagen DNeasy® Plant Mini Kit and accompanying protocols (Qiagen, 2003). Ten primers were tested---801 [(AT)8-T], 802 [(AT)8-G], 807.1 [(AG)8-TG], 814.1 [(CT)8-TG], 844 [(CT)8-RC], 17898 [(CA)6-RY], 17902 [(GT)6-AY], AW3 [(GT)6-RG], M1 [CAA-(GA)5], and oligo7 [(CT)8-RG]. Primers 801, 802, and M1 were not successful with our material and showed no banding. Banding was observed for some individuals with oligo7 and 814.1; however, the results were too poor to be scored and were not included in the analysis. Amplification, electrophoresis conditions, and detection of ISSR-amplification products were as follows. Master mixes of each primer solution (i.e., including appropriate amounts of dH<sub>2</sub>O, 10x buffer, MgCl<sub>2</sub>, dNTPs, BSA, Primer, and taq) were created in dilution tubes (Table 2). Twenty-two µl of the master mixes were then added to an empty sample tube. Three µl of DNA were added to each of these sample tubes so that each represented 1 OTU. PCR reactions were run on a Stratagene Robocycler with the thermocycler program set at 2 min at 94 °C; 34 cycles of 40 sec at 94 °C, 45 sec at 45 °C, 1.5 min at 72 °C; 45 sec at 94 °C, 45 sec at 45 °C, 5 min at 72 °C, 6 °C soak. PCR products were run on a gel (size: 45 x 30 cm) composed of 0.7% agarose, 0.7% synergel (for improved clarity), and 330 ml 1x TAE buffer. All gels were run for 4 hr at 100 volts and then stained with Ethidium bromide for 20 min. Gels were de-stained in a dH<sub>2</sub>O bath for an additional 20 min and then imaged under ultraviolet light. For reproducibility, positive controls were run on each gel, and some gels were replicated. Bands on imaged gels were computer-labeled (using Kodak 1D 2.0.2. image analysis software), but selected by eye for inclusion in a presence/absence matrix. This judgment was necessary as bands did not always run

evenly. Only bands whose positional homology could be interpreted unambiguously were included. Band presence was scored as 1 and absence as 0. The binary data matrix was analyzed using Neighbor-Joining and UPGMA methods in PAUP 4.0\* (Swofford, 2003) to determine the relatedness of samples on the basis of genetic distance.

### **Morphological Analysis**

In the absence of comparable molecular data for other species of *Matelea* Aubl. and *Gonolobus*, we conducted a parsimony analysis based on morphological characters to test whether the *Gonolobus* entities of the southeastern United States would emerge as sisters. For the outgroup, we chose *Asclepias curassavica* L. and three species of *Matelea*, including the type of the genus---*Matelea palustris* Aubl. (Table 3). *Matelea* is closely related to *Gonolobus*---the two consistently resolve near each other in phylogenetic analyses (see Fishbein, 2001; Potgieter and Albert, 2001; Rapini et al., 2003)---and there has been disagreement over whether southeastern *Gonolobus* should instead be recognized in *Matelea* (see Krings and Xiang, 2004). *Matelea palustris* occurs in northern South America, whereas *Matelea maritima* (Jacq.) Woodson occurs in northern South America and the Caribbean, and *M. carolinensis* (Jacq.) Woodson in the southeastern United States. The chosen *Matelea* species represent three subgenera *sensu* Woodson (1941) (Table 3). The 12 additional *Gonolobus* taxa occur in geographic regions proximal to the Southeast (the Caribbean and Central America), belong to the same subgenus as the two southeastern entities (Table 3), and cover a spectrum of floral and foliar morphology. We estimate including at a minimum ca. 10% of subgeneric members as estimates of species numbers in *Gonolobus* vary from 100 to 150 (Mabberley, 1987; Rosatti, 1989; Stevens, 2001). Thirty morphological characters were selected for analysis (Table 4). Character states were determined by careful study of herbarium specimens and the literature (Woodson et al., 1975; Spellman, 1978; Stevens, 2001). The matrix (Table 5) was subjected to parsimony analysis in PAUP 4.0\* (Swofford 2003) with multistate characters treated as polymorphisms, characters equally weighted, and specified unordered. Heuristic search with TBR branch swapping was used to find the shortest trees.

## RESULTS

### ISSRs

Sixty polymorphic ISSR bands were scored (using the 5% rule) with a range of bands per OTU between 11 and 22. There is substantial genetic differentiation at 18 loci between the two entities, although no fixed differences between them were detected. At 7 loci, the frequencies of band presence are significantly higher in the multi-colored corolla group (MCCG) than in the uniformly colored corolla group (UCCG). At 11 loci they are significantly higher in the UCCG. A single band is unique to the UCCG at a 12.5% frequency (Fig. 2---AW3: 13), whereas 19 bands are unique to the MCCG at frequencies of 3.5--39%, (Fig. 2---AW3: 2, 3, 6, 10, 12, 15--17; 844: 1, 2, 6, 17; 807.1: 5; 17898: 1, 5, 9; 17902: 1, 3, 7)---suggesting that the former possesses a subset of the MCCG gene pool and is likely a derivative of it. For bands occurring in both groups, the frequencies were not significantly different ( $F = 0.005 < F_{crit} = 3.95$ ; Fig. 2).

The Neighbor-Joining (NJ) analysis found a tree with little bootstrap support, which is similarly suggested by the short branches for most internal nodes. The NJ tree indicates no separation of the two groups. The UCCG samples are nested among the MCCG samples (Fig. 3A). There is in general no good correlation between clusters and geographic distributions. Samples from the same state also do not form an exclusive single cluster. For instance, the 9 individuals (AL1--9) sampled from one population (Houston Co., Alabama) (Fig. 1, #10) appeared in several different clusters (Fig. 3A). The tree resulting from UPGMA analysis shows the same results except that the internal branches are longer and terminal branches are decreased (Fig. 3B). Furthermore, in the UPGMA tree all UCCG samples (except one) appear in a single cluster that also includes a few MCCG samples.

### Morphological Analysis

Parsimony analysis (using PAUP) of *Asclepias curassavica*, 3 *Matelea* taxa, and 14 *Gonolobus* taxa using 30 morphological characters resulted in 1498 most-parsimonious trees, each with a length of 73 (Fig. 3B). Seventeen characters were parsimony-informative. A total of 3,043,595 re-arrangements were tried. Although a strict consensus tree showed no resolution of

relationships among the *Gonolobus* species (Fig. 3A), a 50% majority-rule consensus tree resolved a sister relationship between the MCCG and UCCG in 98% of the trees. The *Gonolobus* species formed a monophyletic group.

#### DISCUSSION

The PCR-based ISSR method of fingerprinting has been used in a variety of applications from forensic DNA profiling to assessing hybridization in natural populations and to testing genomic instability (Wolfe et al., 1998; Kumar et al., 2001; Leroy et al., 2000). The method can also be applied to resolving phylogenetic questions below the species level or in rapidly radiating lineages (Kochieva et al. 2002; Mort et al. 2003; Treutlein et al. 2003). Closely related taxa, such as subspecies, can exhibit specific banding profiles that differ from members of the same species. ISSR analysis is relatively inexpensive, quick and more repeatable than using RAPDs (due to higher annealing temperatures in the polymerase chain reaction and use of longer primers). AFLPs have also been used to study taxonomic problems at the species level or below (Saarela et al., 2003; Dehmer and Hammer, 2004). To our knowledge, neither ISSRs nor AFLPs have previously been used in addressing taxonomic issues in Asclepiadoideae, although RAPDs have (Meve et al., 2001).

The ISSR banding profiles in our analysis reveal great genetic complexity among our 40 OTUs. Members of both the MCCG and UCCG exhibit similar frequencies in many of the scored ISSR bands but also some significant differences (Fig. 2), suggesting substantial genetic differentiation between the two groups. On the other hand, no separation of the two groups in the NJ and UPGMA trees suggest that the divergence of the two is incomplete (Fig. 4). Distribution and frequencies of bands in the two groups indicate that the UCCG possesses only a portion of the gene pool of the MCCG (Fig. 2), suggesting that the UCCG is probably an incompletely diverged derivative from the MCCG. Genetic relationships revealed from the NJ and UPGMA analyses are not in conflict with such a hypothesis (Fig. 4). Population aggregation analysis (Davis and Nixon, 1992) revealed that floral coloration is constant in the vast majority of populations at either extreme

of the range and that primarily populations in the zone of convergence (e.g., Harrison Bay SP, Tennessee) are polymorphic for the character. Davis and Nixon (1992) interpreted such a result as potential evidence of clinal variation, incomplete divergence, or zones of hybridization between once-distinct species (Fig. 1). The combined evidence supports our previous treatment based on quantitative morphometric and biogeographic analyses (Krings and Xiang, 2004) that recognized a single species and leads us to now propose to treat the MCCG and UCCG as two varieties within *Gonolobus suberosus*. Results of the parsimony analysis of morphological characters suggest that the two are sisters, in corroboration with this treatment. Given the evidence, this treatment is close to a strict application of the phylogenetic species concept (PSC) *sensu* Nixon and Wheeler (1990). Nixon and Wheeler (1990) indicated that the strictest application of the PSC would treat sister species showing extensive intergradation as a single species. The two varieties are diagnosable by a single, discrete morphological character (corolla color; see key below) and exhibit statistically significant differences in mean corolla length and ratio of mean corolla length:sepal length, and differences in frequency of adaxial corolla pubescence, as well as geographic coherence in distribution and some genetic differentiation (see also Krings and Xiang, 2004). However, we recognize that application of infraspecific ranks in classification has been anything but uniform.

In a review of the application of the ranks of subspecies, variety, and forma, Hamilton and Reichard (1992) concluded that past attempts to differentiate between the two have not produced any consensus regarding the basis of such differentiation and argued for the necessity of explicit statements regarding an individual author's philosophy when making infraspecific assignments. Although a comprehensive review of the various concepts is beyond the scope of this paper, we do present two concepts that have been followed by numerous workers and evaluate their application to our problem. Fernald (1940) considered the rank of subspecies appropriate for the subdivision of aggregate species, variety for recognizing geographic variations in ordinary species, and forma for recognizing morphological variations lacking geographical integrity. His distinction between aggregate and ordinary species is somewhat ambiguous, except that he regarded subspecies as worthy of recognition at the specific rank (Fosberg, 1942). Stuessy (1990) suggested the following

characteristics for distinguishing among the three ranks: subspecies---exhibiting several conspicuous morphological differences and displaying cohesive, largely allopatric or peripatric geographic patterns; varieties---exhibiting one to few conspicuous morphological differences and displaying cohesive, largely allopatric geographical patterns with some overlap; formae---exhibiting usually a single conspicuous morphological difference and displaying a sporadic, sympatric geographic pattern.

Application of Fernald's (1940) concept to the present study would result in the recognition of two subspecies (corresponding to the MCCG and UCCG). Subspecific rather than varietal rank for the MCCG and UCCG is warranted in applying Fernald, as the two entities would fit his concept of a species aggregate and in part have certainly been recognized as distinct species in the past (see Small, 1933; Perry, 1938; Fernald, 1950; Gleason, 1952). The application of Stuessy's (1990) concepts of infraspecific ranks to our entities would result in the recognition of two varieties, largely allopatrically distributed. We suggest that, in addition to personal conceptual differences among taxonomists, some of the difficulties with the consistent application of infraspecific ranks to plants are the intrinsically varied evolutionary histories of taxa, including rates and completeness of divergence, that defy strict application of uniform concepts across groups. As it better captures the morpho-geographical variation within our complex and is less ambiguous, we choose to follow Stuessy's (1990) concept in recognizing two varieties. The taxonomic treatment follows.

#### TAXONOMY

***Gonolobus suberosus*** (L.) R. Br., *Asclepiadeae*: 24. 1810.

Basionym: *Cynanchum suberosum* L., *Sp. pl.* 1: 212. 1753.

TYPE: illustration in Dillenius, *Hortus elthamensis* 308, t.229, f. 296. 1732.

Herbaceous perennial vines. Trichomes of three types: short, multicellular, erect or spreading, 0.05--0.20 mm long; long, multicellular, acicular, erect to spreading, 0.7--1.2 mm long; short, unicellular, flattened, ribbonlike, 0.05--0.40 mm (restricted to the adaxial corolla lobe surface). Stems to 6.5 m long, retrorsely pubescent to glabrate. Leaves opposite, simple, deltate to ovate-

elliptic, oblong, or suborbicular, to 24.5 cm long, to 17.5 cm wide, adaxially strigillose, spreading short-pubescent, or glabrate, abaxially strigillose to spreading pubescent, antrorsely pubescent along the midvein, apices acuminate or apiculate, bases cordate, margins entire, densely to very sparsely ciliolate; petioles 2.8--5.0 cm long, antrorsely pubescent to glabrate. Colleters 2--4, on the adaxial midvein base. Inflorescence axillary, corymbose, 2- to 29-flowered, pedicels 0.7--3.7 cm long. Calyx lobes green, lanceolate to ovate, 1.6--5.4 mm long, fused basally, adaxially glabrous, abaxially strigillose, ciliolate, or glabrate. Corolla lobes ovate to elongate-deltate, adaxially uniformly green to yellowish or multicolored with the bases dark maroon to brownish and the apices green to yellowish, rotate to reflexed, 2.6--11.0 mm long, fused basally, adaxially glabrous to asymmetrically pubescent, the trichomes unicellular, flattened, ribbon-like, 0.05 mm--0.40 mm long, abaxially glabrous. Coronas brown, black, green, or yellow, 5-lobed (very rarely 4-lobed), 3.5--4.9 mm diam., each lobe typically retuse or emarginate, rarely truncate, protruding upward and touching the dorsal anther appendages, the apices lower than the corpusculum apices. Faucal annulus present, glabrous. Gynostegia 2.9--3.7 mm diam. Dorsal anther appendages to 0.9 mm long and wide, the apices rounded to truncate. Pollinaria 5 (very rarely 4). Pollinia 610--762  $\mu\text{m}$  long (fide Drapalik, 1969). Follicles ovoid, green, smooth, 5-angled and winged, 8--15 cm xxx 1.5--2.8 cm. Seeds brown or brownish-black with brown margins, 38--299, 0.6--1.0 cm xxx 0.3--0.7 cm, apices rounded except with ca. 7--12 teeth or undulations, bases truncate, the coma whitish-translucent, to 4.5 cm long. Flowers June--August; fruits August--November.

Illustrations: Holmgren (1998), Krings (2003), Lipow and Wyatt (1998).

Some Robert Brown names have sometimes been incorrectly dated. In 1810, a preprint of his "On the Asclepiadeae, a Natural Order of Plants separated from the Apocinae of Jussieu" was made available. This same work later appeared in the first volume of the 1811 *Memoirs of the Wernerian Natural History Society* (Stearn, 1960; Stafleu and Cowan, 1976; Mabberley, 1985). Although sometimes incorrectly cited from the first reading of the paper in 1809, communication at public meetings does not constitute effective publication (Forster, 1991; Greuter et al., 2000).

Names should also not be ascribed to the 1811 appearance of the Memoirs of the Wernerian Natural History Society but rather to the preprint released in 1810. Thus the combination *Gonolobus suberosus* (L.) R. Br. should be cited as above, rather than in Mem. Wern. Nat. Hist. Soc. 1:35 (1810). As Brown's 1810 combination in Asclepiadeae is validly published (by definite association of the final epithet with the genus name), it takes priority over the Schultes combination in Systema Vegetabilium 6:59 (1820).

#### **DIAGNOSTIC KEY TO THE VARIETIES**

1a. Adaxial corolla lobes uniformly colored, green to yellowish ... *G. suberosus* (L.) R. Br. var. *granulatus* (Scheele) Krings & Q. Y. Xiang

1b. Adaxial corolla lobes multicolored, generally dark maroon to brownish near the base and green to yellowish near the tips ... *G. suberosus* (L.) R. Br. var. *suberosus*

#### *Varieties*

1. ***Gonolobus suberosus*** (L.) R. Br. var. ***granulatus*** (Scheele) Krings & Q. Y. Xiang, *comb. nov.*  
Basionym: *Gonolobus granulatus* Scheele, Linnaea 21: 759. 1848. TYPE: U.S.A. Texas: Comal Co., New Braunfels, Lindheimer s.n. (Neotype, here designated: BRIT).

Of the names described in the southeastern *Gonolobus* complex, *G. granulatus* Scheele is the only one based on the entity characterized by adaxially glabrous, uniformly colored corolla lobes. All other names (see below) can be referred to the entity with multicolored corollas---i.e., *G. suberosus* var. *suberosus* (Krings and Xiang, 2004). *Gonolobus granulatus* was described in 1848 on the basis of a collection gathered by Lindheimer along the Guadalupe River, Comal Co., Texas. Unfortunately, no duplicates of this collection have been located, despite searches of the main collections known to house Lindheimer material and Scheele types (i.e., BAYLU, BREM, CAS, GH, GOET, MO, NA, NY, REG, SMU [BRIT], TEX/LL). Scheele cited no additional collections. Thus, a neotype is here proposed. The proposed neotype may be the original material for this name; however, the level of uncertainty requires the cautious neotypification. The label data do not match

statements in the protologue, solely indicating New Braunfels as the locality and Lindheimer as the collector. No date is provided. The protologue, however, additionally notes: "Am Guadeloupe-Walde nördlich von Neubraunfels über hohes Gesträuch rankend. Oktober. Lindheim." Typification of *G. suberosus* var. *suberosus* is discussed in detail by Reveal and Barrie (1992).

**Distribution:** *Gonolobus suberosus* var. *granulatus* occurs from Texas to Mississippi, north to Oklahoma, Illinois, Kentucky, and Tennessee (see Fig. 1: circles).

2. ***Gonolobus suberosus*** (L.) R. Br. var. ***suberosus***, *Asclepiadeae*: 24. 1810.

Basionym: *Cynanchum suberosum* L., *Sp. Pl.* 1: 212. 1753. TYPE: illustration in Dillenius, *Hortus elthamensis* 308, t.229, f. 296. 1732.

*Matelea suberosa* (L.) Shinnery, *Field and Lab.* 18: 73. 1950.

Synonyms: *Vincetoxicum gonocarpos* Walter, *Fl. Carol.* 104. 1788. TYPE: U.S.A. South Carolina:

*Walter s.n.* (Holotype: BM!)

*Asclepias gonocarpos* (Walter) J. F. Gmelin, *Syst. Nat.* 2: 446. 1791.

*Gonolobus gonocarpos* (Walter) L. M. Perry, *Rhodora* 40: 284. 1938.

*Matelea gonocarpa* (Walter) Shinnery, *Field and Lab.* 18: 73. 1950.

*Gonolobus laevis* Michx. var. *macrophyllus* A. Gray, *Proc. Amer. Acad. Arts* 12: 76. 1877.

TYPE: U.S.A. Illinois: *Michaux s.n.* (Holotype: P, IDC #6211, 1:29!).

?*Gonolobus tiliifolius* Decne., in de Candolle, *Prodr.* 8: 596. 1844. TYPE: U.S.A. Kentucky:

Lexington, *Short s.n.* (Holotype: P!)

**Distribution:** var. *suberosus* occurs primarily in east coast states to Florida and west to Tennessee and Mississippi (see Fig. 1: squares).

A complete list of *exsiccatae* is being prepared for inclusion in *Vulpia* (<http://vulpia.ncsu.edu>). This list will at a minimum include basic label information, such as state, county, collector, and date, for all specimens of *Gonolobus suberosus* examined by the authors.

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TABLE 1. Voucher specimens from the southeastern *Gonolobus* complex for the ISSR analysis (deposited at NCSC and FLAS).

STATE	COUNTY OR PARISH	LOCALITY	COLLECTOR AND NOS.
Alabama	Houston	Chattahoochee SP	Krings AL1-9
Alabama	Barbour	Blue Springs SP	Krings AL10
Florida	Orange	Wekiwa Spring SP	Krings FL1-5
Florida	Hillsborough	Hillsborough River SP	Krings FL6-8
Florida	Alachua	Paynes Prairie Preserve SP	Krings FL9
Florida	Columbia	Ichetucknee SP	Krings FL10-11
Florida	Jackson	Three Rivers SP	Krings 13-14
Florida	Wakulla	Wakulla Springs SP	Krings FL15
Louisiana	Webster	Lake Bistineau SP	Krings LB1
Louisiana	Evangeline	Chicot SP	Krings LC1-5
North Carolina	Wake	Schenck Forest	Krings NC1-2
South Carolina	Lancaster	Andrew Jackson SP	Krings SC1-2
Tennessee	Hamilton	Harrison Bay SP	Krings TN1-4
Tennessee	Hamilton	Booker T. Washington SP	Krings TN-5
Texas	Comal	Landa RV Park and Campground	Krings L4

Note: SP = state park.

TABLE 2. Primer solution master mixes.

PRIMER (1?L)	DH <sub>2</sub> O	10XBUFFER	MgCL <sub>2</sub>	DNTPs	BSA	TAQ
AW3	12.5 µl	2.5 µl	2 µl	3 µl	0.8 µl	0.2 µl
844	12.5 µl	2.5 µl	2 µl	3 µl	0.8 µl	0.2 µl
807.1	11.5 µl	2.5 µl	3 µl	3 µl	0.8 µl	0.2 µl
17898	11.5 µl	2.5 µl	3 µl	3 µl	0.8 µl	0.2 µl
17902	11.5 µl	2.5 µl	3 µl	3 µl	0.8 µl	0.2 µl

TABLE 3. Taxa included in the parsimony analysis of morphological data.

SPECIES	SUBGENUS*	DISTRIBUTION
<i>Asclepias curassavica</i> L.	<i>Asclepias</i>	Cosmopolitan
<i>Gonolobus albomarginatus</i> (Pittier) Woodson	<i>Eugonolobus</i>	Western Colombia, Panama, Costa Rica
<i>Gonolobus barbatus</i> Kunth in H. B. K.	<i>Eugonolobus</i>	Costa Rica to Mexico
<i>Gonolobus calycosus</i> (Donn. Sm.) Woodson	<i>Eugonolobus</i>	Nicaragua to Guatemala
<i>Gonolobus cuajayote</i> W. D. Stevens	<i>Eugonolobus</i>	El Salvador and Nicaragua
<i>Gonolobus</i> entity 1 (MCCG)†	<i>Eugonolobus</i>	Southeastern United States
<i>Gonolobus</i> entity 2 (UCCG)†	<i>Eugonolobus</i>	Southeastern United States
<i>Gonolobus fuscoviolaceus</i> Woodson	<i>Eugonolobus</i>	Panama
<i>Gonolobus heterophyllus</i> (Hemsl.) W. D. Stevens	<i>Eugonolobus</i>	Panama to Nicaragua
<i>Gonolobus incerianus</i> W. D. Stevens & Montiel	<i>Eugonolobus</i>	Nicaragua to Mexico
<i>Gonolobus leianthus</i> Donn. Sm.	<i>Eugonolobus</i>	Nicaragua to Mexico
<i>Gonolobus macranthus</i> Kunze	<i>Eugonolobus</i>	Nicaragua to Mexico
<i>Gonolobus martinicensis</i> Decne.	<i>Eugonolobus</i>	Lesser Antilles
<i>Gonolobus stephanotrichus</i> Griseb.	<i>Eugonolobus</i>	Greater Antilles, except Jamaica
<i>Gonolobus taylorianus</i> W. D. Stevens & Montiel	<i>Eugonolobus</i>	Costa Rica to Honduras

TABLE 3 (CONTINUED).

SPECIES	SUBGENUS*	DISTRIBUTION
<i>Matelea carolinensis</i> (Jacq.) Woodson	<i>Chthmalia</i>	Southeastern United States
<i>Matelea maritima</i> (Jacq.) Woodson	<i>Ibatia</i>	Venezuela, Colombia, Panama, Greater and Lesser Antilles
<i>Matelea palustris</i> Aubl.	<i>Eumatelea</i>	Northern South America

\*Subgenera given strictly *sensu* Woodson (1941), although subgenus *Eumatelea* and *Eugonolobus* violate ICBN Art. 22.1 and should correctly be known as subg. *Matelea* and subg. *Gonolobus* (both contain the types for the respective genera).

†Southeastern *Gonolobus* entities 1 and 2 are identified respectively on the basis of multicolored corollas (MCCG) or uniformly colored corollas (UCCG).

TABLE 4. Morphological characters used in the parsimony analysis.

	CHARACTER	STATE
1.	Habit	0 = twining; 1 = non-twining
2.	Shoot bases	0 = woody; 1 = herbaceous
3.	Indumentum	0 = eglandular only; 1 = eglandular and glandular
4.	Petioles	0 = glabrous; 1 = pubescent
5.	Leaf bases	0 = cordate; 1 = rounded/truncate; 2 = cuneate; 3 = attenuate
6.	Inflorescence	0 = umbelliform; 1 = racemiform
7.	Aestivation	0 = valvate; 1 = imbricate
8.	Abaxial sepal vestiture	0 = glabrous; 1 = pubescent
9.	Corolla shape	0 = rotate; 1 = campanulate
10.	Corolla coloration	0 = uniformly colored; 1 = reticulate; 2 = center differently colored
11.	Corolla lobe shape	0 = ovate to suborbicular; 1 = oblong, triangular-deltate, or lanceolate
12.	Adaxial corolla lobes	0 = glabrous; 1 = pubescent or papillate
13.	Abaxial corolla lobes	0 = glabrous; 1 = pubescent
14.	Corolla margins	0 = indistinctly banded, if at all; 1 = brilliant white banded
15.	Corolla apices	0 = tapered, acute, or obtuse; 1 = broad and retuse
16.	Faucal annulus	0 = absent; 1 = present
17.	Faucal annulus indumentum	0 = annulus absent; 1 = glabrous; 2 = pubescent
18.	Corona of fused staminal and interstaminal parts ( <i>C(is) sensu</i> Kunze, 1995)	0 = absent; 1 = present

TABLE 4 (CONTINUED).

CHARACTER	STATE
19. Staminal corona segments (Cs <i>sensu</i> Kunze, 1995)	0 = absent or poorly developed; 1 = prostrate, well-developed; 1 = erect, well-developed
20. Erect Cs	0 = absent; 1 = free, except for base
21. Styler head appendage	0 = absent; 1 = present
22. Dorsal anther appendages (Cd <i>sensu</i> Kunze, 1995)	0 = absent; 1 = present
23. Dorsal anther appendages (Cd <i>sensu</i> Kunze, 1995)	0 = absent; 1 = rounded/truncate; 2 = emarginate, bilobed, or bifurcate
24. Pollinia	0 = +/- horizontal; 1 = descending
25. Pollinia	0 = uniformly fertile; 1 = sterile and excavated basally
26. Follicle texture	0 = smooth (no ribs); 1 = ribbed; 2 = winged; 3 = muricate; 4 = slender tuberculate
27. Follicle cross section	0 = rounded; 1 = 5-angled; 2 = 4-angled; 3 = 3-angled
28. Follicle vestiture	0 = glabrous; 1 = pubescent
29. Follicle wings	0 = absent; 1 = continuous; 2 = interrupted
30. Seed shape	0 = plano-convex; 1 = plane

TABLE 5. Matrix of morphological character states for *Asclepias*, *Gonolobus*, and *Matelea* taxa.

<i>Asclepias curassavica</i>	100130013011{01}00000210001010?00
<i>Gonolobus albomarginatus</i>	0111011100111101211001{12}0122111
<i>Gonolobus barbatus</i>	001101111{01}01100111100110121011
<i>Gonolobus calycosus</i>	011101110010001121100120121011
<i>Gonolobus cuajayote</i>	0011011{01}00001101{12}1?001101?????
<i>Gonolobus</i> entity 1 MCCG*	0011011{01}021{01}000111100110121011
<i>Gonolobus</i> entity 2 UCCG*	0011011{01}001{01}000111100110121011
<i>Gonolobus fuscoviolaceus</i>	0110{01}110000100012110011012?0??
<i>Gonolobus heterophyllus</i>	001101110010100111100120121011
<i>Gonolobus leianthus</i>	0011011{01}0011000121100120121011
<i>Gonolobus macranthus</i>	001101110{01}11100121100110121?1?
<i>Gonolobus martinicensis</i>	00110110001{01}000121100110121011
<i>Gonolobus incerianus</i>	001101110{01}01100121?001201230??
<i>Gonolobus stephanotrichus</i>	001101110{02}10100121100110121011
<i>Gonolobus taylorianus</i>	0011011{01}0011100121?001101{02}2011
<i>Matelea carolinensis</i>	011101110010100??1200000130101
<i>Matelea maritima</i>	001101110001100??1211001140100
<i>Matelea palustris</i>	101121110010000??1000000100001

\*The two southeastern *Gonolobus* entities are coded separately on the basis of multicolored (MCCG) or uniformly colored corollas (UCCG).

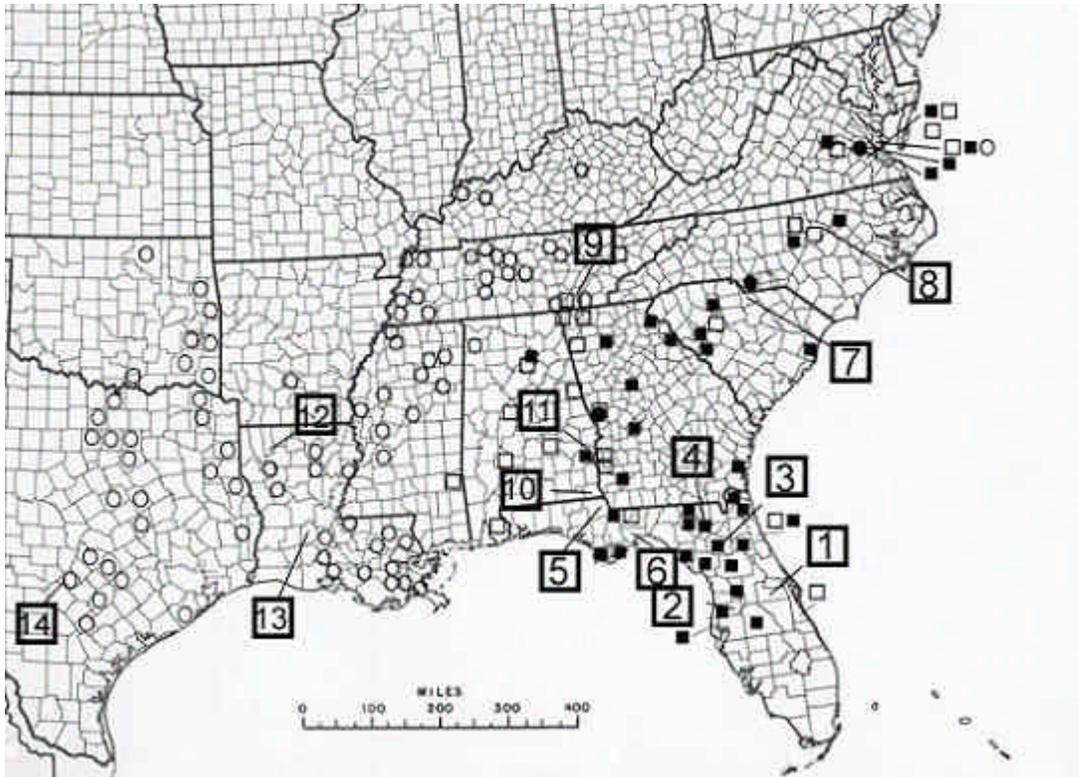


FIGURE 1. Collection localities for fresh *Gonolobus* material used in the ISSR analysis. 1 = Orange Co., Florida (FL1--5); 2 = Hillsborough Co., Florida (FL6--8); 3 = Alachua Co., Florida (FL9); 4 = Columbia Co., Florida (FL10--11); 5 = Jackson Co., Florida (FL13--14); 6 = Wakulla Co., Florida (FL15); 7 = Lancaster Co., South Carolina (SC1--2); 8 = Wake Co., North Carolina (NC1--2); 9 = Hamilton Co., Tennessee (2 sites, TN1--5); 10 = Houston Co., Alabama (AL1--9); 11 = Barbour Co., Alabama (AL10); 12 = Webster Parish, Louisiana (LB1); 13 = Evangeline Parish, Louisiana (LC1--5); 14 = Comal Co., Texas (L4). All vouchers deposited at NCSC. The underlying map shows the distribution of *Gonolobus* entities by flower color (from Krings and Xiang, 2004). Circles represent individuals with uniformly green corollas---either glabrous adaxially (open circle) or pubescent (closed circle). Squares represent individuals with multicolored corollas---either glabrous adaxially (open square) or pubescent (closed square).

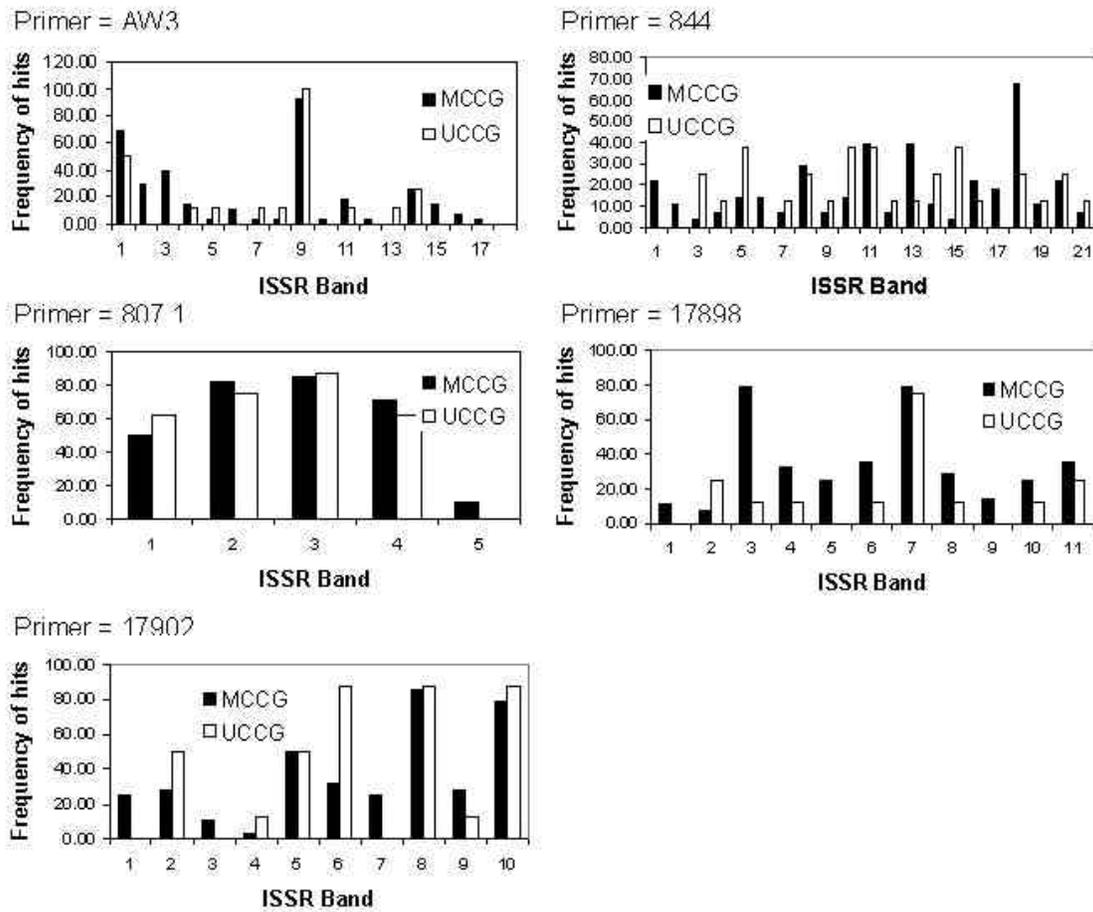


FIGURE 2. Frequency histograms of ISSR bands in the multicolor corolla group (MCCG) and uniformly colored corolla group (UCCG) of southeastern *Gonolobus* entities. Band numbers were assigned sequentially to scored bands. Frequency of hits refers to the percentage of OTUs exhibiting a particular band out of the total OTUs within each of the two groups (MCCG and UCCG).

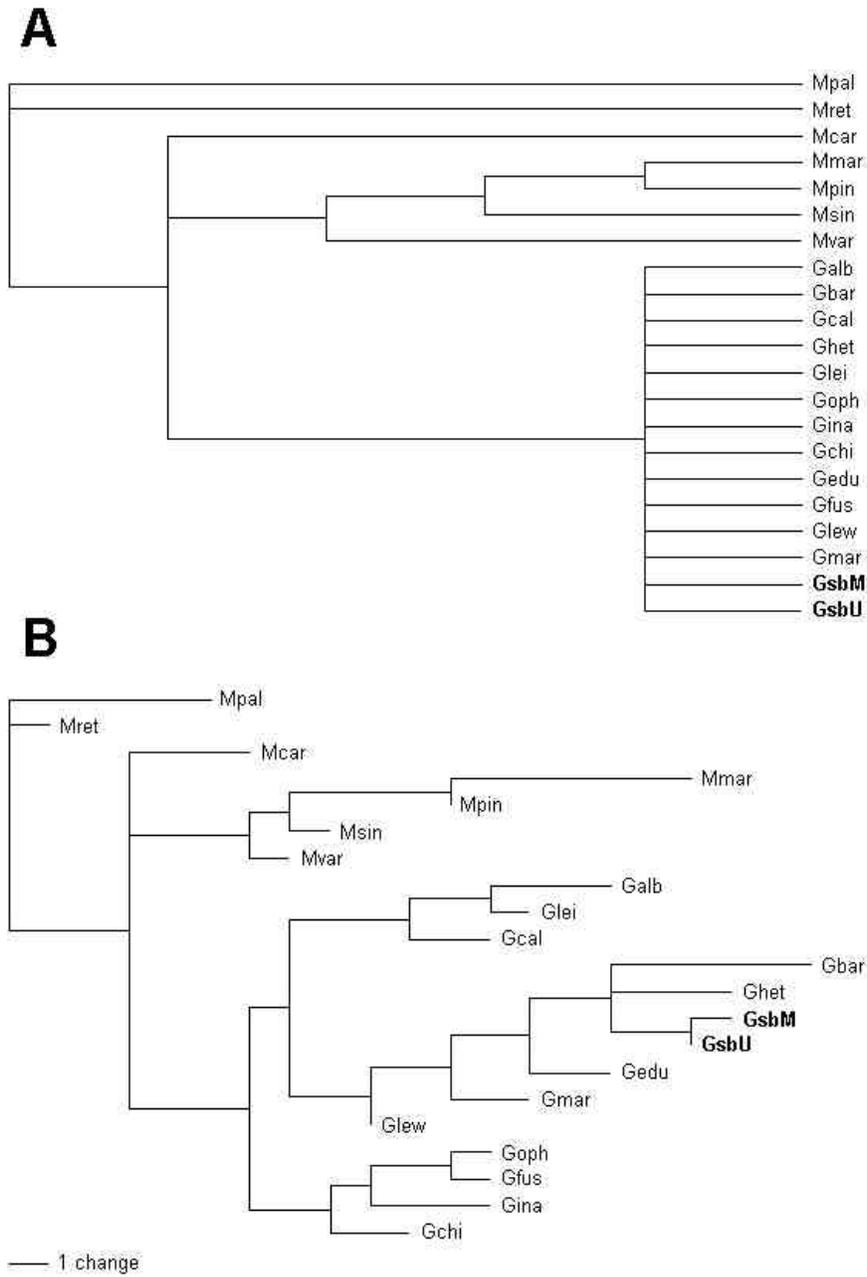


FIGURE 3. A, strict consensus; B, phylogram of one of 1498 most parsimonious trees (each with length 73) based on heuristic parsimony analysis of thirty morphological characters. Southeastern entities of *Gonolobus suberosus* in bold.

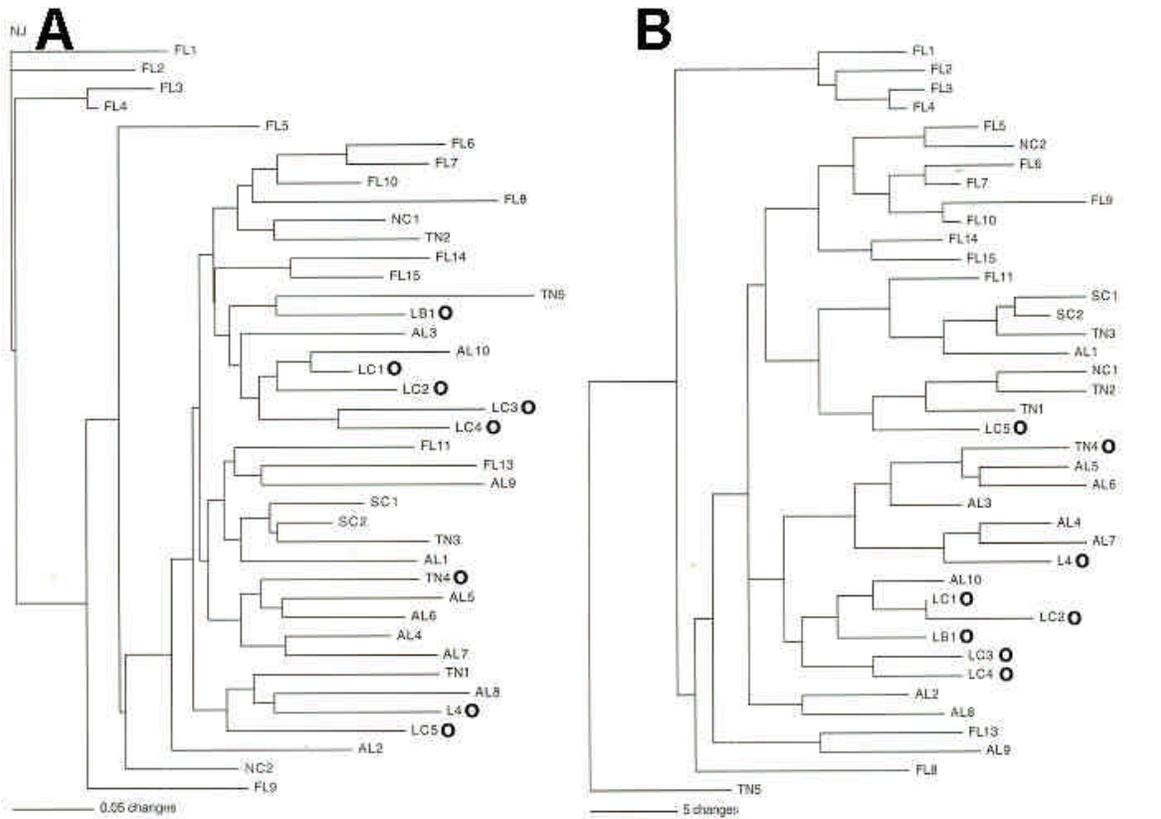


FIGURE 4. Neighbor-joining (A) and UPGMA (B) trees based on ISSR band profiles for 40 southeastern *Gonolobus* individuals. Open circles represent individuals with uniformly colored corollas (UCCG)---all others either were collected with multicolored corollas (MCCG) or occur in regions where only multicolored corollas have previously been known. AL1--9 = Houston Co., Alabama; AL10 = Barbour Co., Alabama; FL1--5 = Orange Co., Florida; FL6--8 = Hillsborough Co., Florida; FL9 = Alachua Co., Florida; FL10--11 = Columbia Co., Florida; FL13--14 = Jackson Co., Florida; FL15 = Wakulla Co., Florida; L4 = Comal Co., Texas; LB1 = Webster Parish, Louisiana; LC1--5 = Evangeline Parish, Louisiana; NC1--2 = Wake Co., North Carolina; SC1--2 = Lancaster Co., South Carolina; TN1--5 = Hamilton Co., Tennessee (2 sites).

## Chapter III

### Distribution and phenology of *Gonolobus suberosus* (Apocynaceae, Asclepiadoideae) and its varieties in North America

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## ABSTRACT

Recent morphological and molecular studies resulted in the recognition of two varieties of *Gonolobus suberosus* in the United States. The objectives of the present study were to (1) provide a list of exsiccatae and (2) present phenological data, as captured from herbarium specimens. Based on queries to sixty-seven herbaria, 578 herbarium specimens of *G. suberosus* from North America were examined, annotated, and catalogued. A critical re-evaluation of four apparently disjunct populations of var. *granulatus* in the East led to the hypothesis that eastern plants exhibiting uniformly colored corolla lobes represent mutants of var. *suberosus*, rather than true disjunctions of var. *granulatus*. This hypothesis is supported by similarities in the coloration and shape of laminar dorsal anther appendages as well as vestiture of the adaxial corolla lobes shared by putative mutant and wildtype var. *suberosus*, but not var. *granulatus*. There appears to be no separation of reproductive phenological activity between the two varieties. Over the period 1895 to 2005, in contrast to previous reports for other taxa, a positive correlation between year of collection and number of specimens with flowers was found for both varieties. The significance of the correlation suggests that collecting effort for flowering material has actually been increasing for both varieties over the past century. No significant correlation was found between year of collection and specimens with fruits. Differences in rates of flowering and fruiting collections may be the result not of collector preference or environmental factors, but of temporal differences in collecting activity coinciding with shifts from flowering to fruiting. Images and a key to the varieties are provided to facilitate identification.

Whether more than one *Gonolobus* Michx. species (Apocynaceae – Asclepiadoideae) should be recognized for the southeastern United States has long occupied taxonomists and has been additionally complicated by the nomenclatural confusion surrounding *Gonolobus suberosus* (L.) R. Br. (Drapalik 1969; Reveal & Barrie 1992; Krings & Xiang 2004, 2005). In a recent morphometric analysis of the *Gonolobus* complex in the southeastern United States, Krings & Xiang (2004) found former species concepts untenable as stated as the diagnostic characters could not consistently assign individuals to one of two groups. However, the analysis showed a strong geographic component to the distribution of individuals delimited by uniformly and multi-colored corollas, which was used as a basis for suggesting that two entities do appear to exist in the Southeast that may deserve recognition at some taxonomic rank. These entities were provisionally referred to as a uniformly-colored corolla group (UCCG) and a multi-colored corolla group (MCCG). Subsequently, Krings & Xiang (2005) analyzed Inter-Simple Sequence Repeats (ISSR) to assess if the two entities were genetically differentiated, and if so, to what level. The ISSR results showed genetic differentiation at several loci between the two entities, although no fixed differences between them were detected. Nineteen bands were unique to the MCCG, although at various frequencies 3.5–39%, while only a single band was unique to the UCCG, suggesting that the latter possesses a subset of the MCCG gene pool and is likely a derivative of it. In a parsimony analysis of morphological characters of fourteen species of the subgenus, the two southeastern entities consistently appeared as closest relatives (Krings & Xiang 2005). This evidence suggested that the complex represents a single evolutionary lineage with two incompletely differentiated morphological subgroups. Based

on these results, Krings & Xiang (2005) proposed to treat the MCCG and UCCG as two varieties of *Gonolobus suberosus* — var. *granulatus* (Scheele) Krings & Q.Y. Xiang and var. *suberosus*. The objective of the present work is to (1) provide a list of exsiccatae for specimens studied by Krings & Xiang (2004, 2005) and (2) present phenological data, as captured from herbarium specimens. Images and a key to the varieties are also provided to facilitate identification.

## METHODS

Based on queries to sixty-seven herbaria, 578 herbarium specimens of *Gonolobus suberosus* from North America were examined. All vouchers cited have been studied and annotated. With the exception of Florida, label data presented here includes state, county, directions to locality, date, collector(s) and number, and herbaria of deposit. Detailed locality data is not provided for Florida specimens as *G. suberosus* is State listed as threatened in Florida under its synonym *Matelea gonocarpos* (Walter) Shinnery (Florida Administrative Code Ch. 5B-40.0055). Occurrences were mapped at the county level using DIVA-GIS (<http://www.diva-gis.org>) and ESRI ArcView GIS 3.3 (<http://www.esri.com>). County shape files and centroid latitude and longitude data were obtained from the United States Census Bureau (<http://www.census.gov>).

## RESULTS & DISCUSSION

Four collections of entities with uniformly green adaxial corolla lobes (putative var. *granulatus*) appeared disjunct and well inside the range of var. *suberosus*: (1) Harris Co., Georgia (*S.B. Jones* 22079, FLAS, USF), (2) Union Co., North Carolina (*H.E. Ahles* 31482,

USF), (3) Surry Co., Virginia (*B. Mikula* 2838, WILLI), and (4) City of Newport News, Virginia (*P. Baldwin* 95, WILLI) (Krings & Xiang 2004). Disjunctions of entities with multi-colored adaxial corolla lobes (var. *suberosus*) in the primary area of var. *granulatus* have not been recorded. However, additional examination of the putative UCCG/var. *granulatus* disjunctions in Virginia, as well as a mixed population in Tennessee during Summer 2006, revealed subtle floral characters missed in earlier studies by Krings & Xiang (2004, 2005). At least in Huntington Park (Newport News, Virginia) and Harrison Bay State Park (Hamilton Co., Tennessee), populations of *G. suberosus* include individuals with both multi-colored and uniformly colored corollas. However, closer inspection led to the hypothesis that the individuals with uniformly colored corollas in these mixed populations are more likely mutants of the eastern multi-colored var. *suberosus*, rather than representatives of the western uniformly colored var. *granulatus*. Consistent with wildtype var. *suberosus*, the putative var. *suberosus* mutants exhibit a dark-colored, frequently purplish, laminar dorsal anther appendage (Cd sensu Kunze 1995) with strongly developed lateral edges providing a bilobed or emarginate appearance. The Cd of individuals of var. *granulatus* tend to be uniformly yellow (frequently brightly so) and bear a much weaker development of lateral edges and thus an apex that appears rounded to truncate, but not bilobed. The putative mutants also share adaxially pubescent corolla lobes with wildtype var. *suberosus* (Fig. 1b-d), a character state otherwise not observed in var. *granulatus* (Fig. 1a). In addition, the color of the adaxial corolla surface tends to be yellow-green or nearly neon green, in contrast to the olive green of var. *granulatus* (Fig. 1). Although there is a limitation to how well rehydration can restore exact shapes of the Cd, until additional data can be brought to bear on the issue, I continue to recognize two varieties in *G. suberosus*,

provisionally treating eastern, uniformly-colored individuals as color mutants of var. *suberosus*.

Thus circumscribed, *Gonolobus suberosus* is endemic to the United States and occurs from south-central Texas to south Florida, and north to Kansas, Illinois, Indiana, Kentucky, and Virginia (Fig. 2). Its two varieties display a largely allopatric distribution, with a zone of contact or overlap that extends from southern Mississippi north to northwestern Alabama and eastern Tennessee. More collections are needed from this area to better understand contact zone populations. Based on the distribution pattern provided by specimens with flowers, specimens that are sterile or only bear fruits can be assigned to a variety with reasonable confidence in most states (Fig. 2).

There appears to be no separation of reproductive phenological activity between the two varieties (Fig. 3). Flowering in both varieties generally begins in April and ceases sometime in August through September. Both varieties start producing fruits within a month or two of the commencement of flowering. The largest number of fruiting specimens in both varieties was collected in the months of September and October (Fig. 3). Excluding specimens that could not be confidently referred to either variety, a similar percentage of specimens in fruit was found for both varieties: 17.1 % (45/263) var. *granulatus* and 17.3% (51/295) var. *suberosus*.

For the present *Gonolobus* data set, over the years 1920–2005, no significant correlation was found between year and number of fruit collections for either variety (Table 1).

Examining specimens collected over the period from 1895–2005, a positive correlation between year of collection and number of specimens with flowers was found for both var. *granulatus* ( $r^2 = 0.2302$ , p value =  $9.94\text{E-}8$ ) and var. *suberosus* ( $r^2 = 0.2966$ , p value =  $6.45\text{E-}10$ ) (Table 2, Fig. 4). The regression remains significantly positive for var. *suberosus* ( $r^2 = 0.085213$ ;  $F_{0.05, df=20} = 1.7698 > F_{crit} = 0.1991$ ), even if calculated based only on the past twenty years. The significance of the correlation suggests that collecting effort for flowering material has actually been increasing for both varieties over the past century. This finding is inconsistent with prior work using a much larger data set (but one that excluded milkweeds) that showed herbarium collections to be on the decline, especially over the last two decades (Prather et al. 2004). That a decline is not apparent for a less than showy taxon, such as *Gonolobus suberosus*, is surprising.

The disparity between significantly increasing flowering collections vis-à-vis constant fruiting collections could be explained by several scenarios. Differential preference by collectors for specimens with flowers versus fruits could result in the differences in correlations between year and numbers of collections for flowering and fruiting material—especially in light of the fact that taxonomic treatments have relied on flowers for distinguishing among the taxa (Krings & Xiang 2004, 2005). An alternative explanation could be that fruiting is actually declining among members of this species (perhaps due to climatic or pollinator shifts), as increased collection effort for flowering material could be expected to result in concomitant increases in fruiting material. Given the “novelty” of the winged follicles, it seems unlikely that a collector would choose not to collect a follicle if it was present along with flowers. However, the peaks for flowering and fruiting of both

varieties appear quite separated temporally. The number of flowering collections for both varieties peak in June/July (var. *suberosus*: 85/74; var. *granulatus*: 79/71). Fruiting collections of both varieties peak in September/October (var. *suberosus*: 10/15; var. *granulatus*: 7/6). During these peak months of fruiting, only a single flowering specimen has been collected (Fig. 3). In fact, at least based on collections, flowering appears to start declining in July, drops significantly in August, and then precipitously in September. Conversely, during the June peak of flowering in both varieties, only a single fruiting collection has been taken (Fig. 3). The collection of fruits increases in August, but at this point flowering is already in precipitous decline. Thus, evident differences in rates of flowering and fruiting collections may be the result not of collector preference or environmental factors, but of temporal differences in collecting activity coinciding with shifts from flowering to fruiting. Fewer fruiting collections are likely reflective of fewer *total* collections made in the autumn months of peak fruiting activity, whereas increases in flowering collections the result of increasing collector activity in summer months. As the majority of collections have been made by persons associated with universities (either faculty or students), the autumnal drop in collections could be largely explained by return to classes and university commitments. However, this is not to say that changes in pollination success or fruiting behavior have not occurred or are presently occurring. Severely limited pollination visitation and fruit-set rates have been documented in *G. suberosus*, as well as in other climbing milkweeds and the further exploration of long-term trends are necessary to address questions of both conservation and evolutionary biology

(Liede 1994; Lipow & Wyatt 1998; Krings 1999; see also ASCLEPOL<sup>1</sup> and references therein). In fact, much of the basic biology, including pollinators, of this species—as of so many in the Southeast—remains unknown. Drapalik (1969) captured small dipterans (all Chloropidae) on flowers of *G. suberosus*, but it remains unclear whether they are effective pollinators due to their size (1.5–3 mm) and lack of pollinaria on capture. Lipow & Wyatt (1998) also attempted to determine pollinators for the species, but were unsuccessful despite daily and nightly searches. Pollinators have not been documented (or at least not reported in mainstream publications) for any other species of *Gonolobus*<sup>2</sup>—a genus including 100–150 species.

Although long-term phenological shifts in fruiting behavior could not be determined using the present dataset, the utility of exsiccatae and herbarium databases to explore whether long-term floristic and phenological changes have occurred will only increase as more collections go online and become networked. With the assumption of equal collecting effort over a given period (or with an understanding of its trend through data exploration), herbarium specimens can provide a means to assess whether taxa are exhibiting statistically significant differences in rates of fruit set and whether such differences are correlated with environmental parameters. When collecting effort is shown to be increasing, a negative

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<sup>1</sup> ASCLEPOL is a compilation of pollinator records for the former Asclepiadaceae. It currently resides at: [http://www.uni-bayreuth.de/departments/planta2/research\\_wgl/pollina/as\\_pol\\_t.html](http://www.uni-bayreuth.de/departments/planta2/research_wgl/pollina/as_pol_t.html). For more information, see Ollerton & Liede (1997).

<sup>2</sup> Although the ASCLEPOL database currently lists pollinators for *G. argentinensis* (1 sp. of Calliphoridae, Diptera), the latter has most recently been recognized in *Matelea*.

correlation between fruit production and year of collection, over a given period, can be a significant finding that needs to be seriously explored.

A key and exsiccatae follow that seek to document previous work by Krings & Xiang (2004, 2005) and facilitate future studies of the species as well.

### **Key to the varieties of *Gonolobus suberosus***

1. Adaxial corolla lobes uniformly-colored, olive green on anthesis, glabrous; laminar dorsal anther appendages (Cd) yellow, apex rounded or truncate.....  
.....*G. suberosus* var. *granulatus* (Fig. 1a), p. 4
- 1'. Adaxial corolla lobes multi-colored, generally dark maroon to brownish near the base and green to yellowish near the tips on anthesis (or uniformly yellowish-green to neon green in rare mutants), pubescent or glabrous; laminar dorsal anther appendages (Cd) darkly purplish or maroon tinted, apex bilobed to emarginate.....  
.....*G. suberosus* var. *suberosus* (Fig. 1b–d), p. 12

### **List of exsiccatae**

The following abbreviations for the phenological condition of specimens are used in the list of exsiccatae: fl=flowering; fr=fruiting; imm=immature; st=sterile.

*Gonolobus suberosus* (L.) R.Br. var. *granulatus* (Scheele) Krings & Q.Y. Xiang, Harvard Papers in Botany 10: 157. 2005.

ALABAMA. *Specimens with flowers or both flowers and fruits.* **Franklin:** Speck cedar glade, ca. 1 mi E of Waco on S side of Al. 24 at jct. with 83, 20 Jun 1980 (fl), *S. McDaniel* 23965 (FSU, UNA). **Pickens:** 6.3 mi NW of Pickensville, 13 Jun 1967 (fl), *S. McDaniel* 9214 (FSU).

ARKANSAS. *Specimens with flowers or both flowers and fruits.* Central Arkansas, Jul 1883 (fl), *F.L. Harvey s.n.* (F); Central Arkansas, Jul 1884 (fl), *F.L. Harvey s.n.* (F). **Benton:** Gravette, 21 Jul 1995 (fl), *R.L. Walker 6478* (NEMO). **Dallas:** Dalark, elev. 240 ft., 18 Jun 1970 (fl), *D. Demaree 62244* (WILLI). **Desha:** 15 mi NE of Dumas, 1 mi S of Arkansas River, 12 Aug 1988 (fl), *E. Sundell 8613 with A. Van Horn, J. Black, D. Etheridge* (KANU); 3 mi N of Arkansas City on Mississippi River at McCallie Access, 8 Aug 1995 (fl), *E. Sundell 11704 with Dale Thomas and Carl Amason* (KANU). **Garland:** Hot Springs, 21 Jul 1879 (fl), *G.W. Letterman s.n.* (F). **Independence:** Near Ark. 106 at Spring Creek, 2 mi W of Batesville, S13 T13N R7W, 26 Jun 1968 (fl), *R.D. Thomas 9290* (SIU); Bluffs beside White river and Missouri Pacific RR tracks, between Lock 3 and Lafferty Creek, S26 T14N R8W, 6 Jul 1968 (fl), *R.D. Thomas 10108* (KANU, UMO). **Jackson:** Beside Ark. 18 at Village Creek, 1 mi E of US 67, S29&32 T12N R2W, 8 Jul 1968 (fl), *R.D. Thomas 10271 with Bio. 451* (SIU). **Montgomery:** Ouachita National Forest, above Caddo River at Caddo Gap, 7 mi NW on Ark. Hwy 27 from Glenwood, elev. 600-1000 ft, 18 Jun 1954 (fl), *H.H. Iltis 5118* (F). **Newton:** Lost Valley State Park, 28 Jun 1974 (fl), *R.L. Thompson 552* (SMS). **Randolph:** Washington Road, off Rte. 166, beside Big Creek, 18 Jun 1976 (fl), *O. Ohmart 1061* (SEMO). **Sebastian:** Vache Grass Creek at S boundary

road, S31 T7N R30W, 8 Jul 1989 (fl), *R.A. Thompson, R. Rudman, and F.L. Johnson*  
C0776 (KANU). **Washington:** Devil's Den State Park, 5 Jun 1964 (fl), *P.L. Redfearn, Jr.*  
14852 (FSU).

GEORGIA. *Specimens with flowers or both flowers and fruits.* **Harris:** Blackmar place, just  
S of Ossahatchie Creek, ca 2 mi N of Cataula, 10 Jun 1972 (fl), *S.B. Jones* 22079 (FLAS,  
USF).

ILLINOIS. *Specimens with flowers or both flowers and fruits.* **Alexander:** Along the Cache  
River, near Unity, 4 Jul 1948 (fl), *G.S. Winterringer* 1151 (ILL); Along Lake Creek at  
Horseshoe Lake Conservation Area, S12 T16S R2W, 19 Jun 1993 (fl), *M.A. Basinger* 5751  
(ILLS); Il. Rte. 3, 0.2 mi SE of jct. Il. 127, W side of Cache River, S12 T16S R2W, 22 Jun  
1999 (fl), *S.R. Hill* 31740 (ILLS); Shawnee National Forest, S21 T14S R2W, 23 Jun 1994  
(fl), *L.R. Phillipe* 24835 (ILLS). **Hardin:** Rocky wooded bluff, 5 mi E of Cave in Rock, 15  
Jul 1954 (fl, fr-imm), *R.A. Evers* 44990 (ILLS – 2 sheets). **Johnson:** Wildcat Bluff, along  
two-track, just W of parking area, S24 T13S R3E, Jun 1994 (fl), *C.A. Morse* 65 (KANU).  
**Massac:** Devils washboard woods, 3 mi S of Unionville, 25 Jun 1966 (fl), *R.H. Maxwell*  
623 (JEF). **Pulaski:** Il. Rte. 3, 0.3 mi SE of Il. Rte. 127, bridge over Cache River, elev. 305  
ft., 22 Jun 1999 (fl), *S.R. Hill* 31733 (ILLS). **Union:** Atwood Ridge Research Natural Area,  
Jonesboro 7.5 min topographic map, S4 T13S R2W, 6 Jun 1991 (fl), *L.R. Phillipe, E.*  
*Ulaszek, and P.E. Phillipe* 19115 (ILLS).

*Specimens with fruits only or sterile, but most likely var. granulatus based on distribution*  
*of flowering specimens (see Fig. 2).* **Alexander:** Horseshoe Lake, 28 Oct 1973 (st), *K. Wilson*

2352 (SIU); Low ground, near Gale, 27 Jun 1956 (st), *F.B. Buser 6036* (ILLS); Shawnee National Forest, S34 T14S R3W, 25 Aug 1994 (fr), *L.R. Phillipe 25460* (ILLS). **Hardin:** 3 mi E of Rosiclare, along Ohio River, 6 Oct 1949 (fr), *G.S. Winterringer 2284* (ILL, ISM); S side of Il. Rte. 146, just W of Hum Wve [sic], 26 Aug 1988 (st, but label mentions strongly angled fruits), *J.B. Taft 521* (ILLS); 3 mi E of Rosiclare, 6 Oct 1949 (fr), *G.S. Winterringer 2284* (IMS). **Johnson:** Lowland woods S of Heron Pond, 16 Aug 1968 (st), *J. White 389* (SIU); 3 mi S of Vienna, Heron Pond Area, 22 Jun 1969 (st), *J. White 1285* (SIU). **Massac:** Open field, 3 mi E of Joppa, S28 T15S R4E, 25 Oct 1973 (fr), *J.E. Ebinger 14341* (EIU); Wooded ravine, E of Joppa, 12 Sep 1961 (st), *R.A. Evers 71287* (ILLS); Floodplain of Ohio River, 6 mi N of Metropolis, near Rocky Branch, 17 Oct 1973 (fr), *W. McClain 773* (EIU). **Pulaski:** Route 3, 0.3 mi SE of Il. Rte. 127, E end of bridge at S side of Cache River, S12 T16S R2W, elev. 305 ft., 30 Aug 2001 (fr), *S.R. Hill 34290 with J.A. Koontz* (ILLS). **Union:** Atwood Ridge Research Natural Area, Jonesboro 7.5 min topographic map, S8 T13S R2W, 10 Jul 1991 (fr), *L.R. Phillipe 19210* (ILLS).

INDIANA. *Specimens with flowers or both flowers and fruits.* **Clark:** Indiana Army Ammunition Plant, Charlestown, Fourteen Mile Creek Area, 1 Aug 1997 (fl), *R.H. Maxwell 3151* (JEF).

*Specimens with fruits only or sterile, but most likely var. granulatus based on distribution of flowering specimens (see Fig. 2).* **Harrison:** Slope of Ohio River, below Tobacco Landing, 1 Sep 1945 (fr), *R.C. Friesner 19534* (BUT). **Gibson:** Near Skelton, 10 Oct 1939 (st), *R.M. Kriebel 7010* (PUL [22660]). **Knox:** Little Cypress Swamp, 14 mi SW of Decker,

2 Sep 1939 (st), *R.M. Kriebel 8433* (PUL – 2 sheets [14736 & 21924]). **Posey:** Edge of swamp, 4 mi W of Mt. Vernon, S3 T7S R14W, 27 Sep 1980 (st), *J. Ebinger 20351* (EIU).

KANSAS. *Specimens with flowers or both flowers and fruits.* **Cherokee:** 1.5 mi S of Galena, 16 Jul 1969 (fl), *K.L. Johnson 2239* (KANU); Rocky wooded bluff, 5 mi N of Galena, 16 Jul 1960 (fl), *R.L. McGregor 15809* (KANU); 5 mi E Baxter Springs, 16 Jul 1947 (fl), *R.L. McGregor and W.H. Horr s.n.* (KANU); Schermerhorn Park, 2 mi S of Galena, 11 Jun 1965 (fl), *S. Stephens 2454* (KANU).

*Specimens with fruits only or sterile, but most likely var. granulatus based on distribution of flowering specimens (see Fig. 2).* **Cherokee:** 1.5 mi S of Galena, 17 Jul 1970 (fr), *J.E. Bare 2527* (KANU); Galena, 1 mi S Schermerhorn Park and immediate vicinity, S35 T34S R25E, elev. 820-900 ft., 21 Oct 1994 (st), *C.C. Freeman 6827* (KANU); 3 mi E of Crestline, roadside park at Spring River, 22 Sep 1962 (st, fr), *S. Stephens 1294* (KSTC – 2 sheets).

KENTUCKY. *Specimens with flowers or both flowers and fruits.* **Ballard:** Woods NW of Wicklife 1 mi, 27 Jun 1962 (fl), *D. O'Dell and D. Windler 827* (SIU). **Jefferson:** Louisville, [no date given] (fl), *F.H. Snow s.n.* (KANU). **Jessamine:** Hill-top E of Hickman Creek at Ky. River, elev. 800 ft., 28 Jul 1962 (fl), *D. Pittillo 2398* (KY [2 sheets]). **McLean:** River bottoms 3 mi upstream from Calhoun, 13 Jul 1970 (fl), *J. Conrad 1365* (KY). **Mercer:** Side of road at Shakers Bend, 14 Jul 1951 (fl – heavy insect damage), *B.B. McInteer 1122* (KY). **Union:** Near Rockford Bridge, 6 Jul 1936 (fl), *H.T. Shacklette 405*

(KY). **Woodford**: 2 mi beyond Versailles on road to Sublet's Ferry, Jul [no year indicated] (fl, fr), *C.W. Short s.n.* (KY).

*Specimens with fruits only or sterile, but most likely var. granulatus based on distribution of flowering specimens (see Fig. 2).* **Caldwell**: Hunter Bluff area, 9 Sep 1992 (st), *J. Campbell s.n.* (KY). **Madison**: Fort Boonesborough State Park, 19 Aug 1992 (fr-imm), *J.R. Abbott 4125 with R.L. Mears* (FLAS).

LOUISIANA. *Specimens with flowers or both flowers and fruits.* **Assumption**: McDermott Fabrication Corp. off Hwy 90, 17 Aug 1978 (fl), *E. Sundell 2122* (NO). **Caldwell**: Ravine, 4 mi W of Columbia, 18 Jun 1956 (fl), *J.A. Moore 6800* (BRIT, NO, USF); W of Horseshoe Lake, NW of Columbia, Sec. 23, T14N, R3E, 4 Aug 1987 (fl), *R.D. Thomas 101125 and Dendrology Class* (BRIT, USCH, WILLI). **Evangeline**: Lake Chicot State Park, 10 Jul 2003 (fl), *Krings LC-1* (NCSC); Lake Chicot State Park, 10 Jul 2003 (fl), *Krings LC-5* (NCSC). **Iberia**: Weeks Island, 1 Jun 1963 (fl), *J.W. Thieret 15985* (BRIT). **Jefferson**: Edge of Jeff Parish landfill, 28 Jun 1979 (fl), *E. Sundell 2148* (NO); Jeaf Lafitte National Historical Park, 4 Jun 1982 (fl), *S. Darwin 2257* (NO). **Lafayette**: Edge of swamp, 1 mi SE of Broussard, 6 Jul 1938 (fl), *D.S. Correll and H.B. Correll 9381* (DUKE); Along Vermillion River, S side of Lafayette, 23 May 1963 (fl), *R. Kral 17147* (FLAS). **Lafourche**: Hunting preserve, La. 307, 5.6 mi N of Rte. 90, just S of Kraemer, 19 Jul 1987 (fl), *S.R. Hill 18201* (USF). **Livingston**: Springfield, along McCarroll Rd near Hwy 22, 21 Aug 1998 (fl), *G. Montz 8962* (NO). **Morehouse**: Swamp W of US 165 and S of La. 834, S21 T23N R8E, 17 Jun 1992 (fl), *R.D. Thomas 130029 and Aquatic Plants Class* (KANU). **Natchitoches**: Lime Kiln Rd, 2 mi S of La. 6, W of Natchitoches, S6 T8N R7W, 29 May

1989 (fl), *R.D. Thomas 110262* (FLAS). **Orleans:** New Orleans, Apr 1897 (fl), *R.S. Cocks s.n.* (NO). **Ouachita:** Along Illinois Central Railroad, 0.3 mi N of Cypress School Rd. on Ted Williams Rd., S34-35 T16N R2E, 26 Aug 1983 (fl), *D.D. Taylor, B.E. Dutton, and G. Varney 5181* (USF); Ca. 4 mi SW of Luna along hwy to Vixen, 20 Jul 1969 (fl), *J.W. Thieret 31744* (BRIT). **Plaquemines:** Tulane Univ. Riverside Campus, Road B, bunker A-21, 10 Jul 1978 (fl), *N.F. Fleming 258* (NO); Tulane Univ. Riverside Research Laboratories, Road B, on signposts between bunkers A-22 and A-21, 20 Jul 1978 (fl), *N.F. Fleming 305* (NO); Tulane Univ. Riverside Campus, Roads B and first, 25 Aug 1978 (fl), *N.F. Fleming 362* (NO, WILLI). **Rapides:** Vicinity of Alexandria, 2 Jun 1899 (fl), *C.R. Ball 529* (F). **Red River:** Grand Bayou and Coney Branch, beside La. 155, 2 mi NE of Coushatta, S4 T21N R9W, 13 Jul 1975 (fl), *R.D. Thomas 45494* (BRIT). **Richland:** Holly Ridge, 21 Aug '83 [1883?] (fl), *Anonymous s.n.* (F). **St. Charles:** Bonnet Carre Spillway, 1 mi N of Airline Hwy near E guide levee, 20 Aug 1973 (fl), *G. Montz 2745* (NO); 1 mi N of Airline Hwy near E guide levee, 5 Aug 1975 (fl), *G. Montz 3429* (NO); Spoilbank along Cypress Bayou, ca. 3 mi S of Boutte, 13 Jun 1979 (fl), *G. Montz 4823* (NO); St. Charles Borromea Church cemetery, 18 May 1981 (fl), *G. Montz 5224* (NO). **St. Landry:** Along Hwy 190, ca. 3 mi W of Eunice, 25 Jul 1975 (fl), *C.M. Allen 6671* (DUKE, FLAS, WVA). **St. Martin:** Des Ourses Swamp, Happytown Oil Field, Atchafalaya National Wildlife Refuge, S120 T7S R8E, 30°25'36" N 91°38'38"W, 19 May 1994 (fl), *R. Burckhalter 2572* (BRIT). **St. Tammany:** Bayou Cane access W of Lemieux Blvd., S48 T8S R12E, 28 Apr 2000 (fl), *J.Joyner 1301 with D.J. Rosen* (NO). **Tangipahoa:** Along ridge of Lake Pontchartrain, 2 Aug 1973 (fl), *G. Montz 2671 with L. Cutrer* (NO). **Tensas:** Tensas River bottomlands W of Somerset, 13 Jun 1957(fl), *J. Ewan 19150* (NO); 5 mi WNW of Church

Hill, Kings Point E of Miss River, 21 Jun 1967 (fl), *S.B. Jones 13417 with B. Noble, C. Hudson* (MISS). **Union:** Along Corney Bayou, ca. 6.25 mi E of Bernice, 5 Jun 1967 (fl), *J.W. Thieret 26437* (DUKE, FSU). **Webster:** Lake Bistineau State Park, 10 Jul 2003 (fl), *Krings LB-1* (NCSC, FLAS). **West Feliciana:** Woods, Jul 1914 (fl), *R. Cocks s.n.* (NO); Hwy 66, between St. Francisville and Angola, 11 Aug 1978 (fl), *S. Darwin and E. Sundell 777* (NO); Old Tunica Rd, 11 Aug 1978 (fl), *S. Darwin and E. Sundell 821* (NO).

*Specimens with fruits only or sterile, but most likely var. granulatus based on distribution of flowering specimens (see Fig. 2).* **Beauregard:** On road to Sabine River, 0.5 mi S of Bayou Amacoco, 7 Oct 1960 (fr), *J. Ewan 20122* (NO). **Evangeline:** Lake Chicot State Park, 10 Jul 2003 (st), *Krings LC-2* (NCSC); Lake Chicot State Park, 10 Jul 2003 (st), *Krings LC-4* (NCSC). **Jefferson:** Jean Lafitte National Historical Park, 29 Oct 1980 (st), *T.F. Dowling 294* (NO); Jean Lafitte Park, 23 Nov 1980 (fr), *A.S. Bradburn 1459* (NO). **Orleans:** Little Oak Island, 21 Jul 1981 (st), *L.M. McCook 904* (NO). **Plaquemines:** Delta Wildlife Refuge, 21-22 Nov 1947 (fr), *J. Ewan 17471* (NO); Belle Chasse, Tulane Univ. Riverside Research Laboratories, 30 Sep 1979 (st), *R.D. Suttkus 79-24-06* (NO). **St. Charles:** Hwy 90 near Boutte, 29 Sep 1979 (fr), *E. Sundell 2160* (NO). **St. Martin:** E side of Bayou Teché road to Parks, N edge of St. Martinville, 14 Oct 1956 (st), *J. Ewan 18850* (NO). **St. Tammany:** Military Rd NE of Slidell, 16 Jun 1956 (st), *J. Ewan 18782A* (NO). **Terre Bonne:** Point Barre, ca. 15 mi SE of Houma, Jun-Sep 1960 (st), *A. Fischer 111* (NO); Vicinity of Houma, ca. 1975 (st), *M.C. Hermann 23* (NO).

MISSISSIPPI. *Specimens with flowers or both flowers and fruits.* **Amite:** Homochitto National Forest, at edge of clearcut on USFS gravel road, W of Nub Road, S32 T4N R3E,

29 May 1998 (fl), *M.H. Alford 972* (DUKE); S Greensburg Road at the E Fork Amite River, S of Liberty, S27 T1N R4E, 31°01'N 90°47.5'W, 3 Jun 1998 (fl), *M.H. Alford 1052* (DUKE); Swamp Road at the E Fork Amite River, S10 T2N R5E, 13 May 1999 (fl), *M.H. Alford* (DUKE); Trask Road, near tributary to Stafford Creek, 2 mi N of Coppell Road, Clyde Well's property, S25 NW/4 NW4 T1N R2E, 14 May 1999 (fl), *M.H. Alford 1993* (DUKE – 2 sheets); **Attala**: Big Black River area on Hwy 19, just E of West at Holmes-Attala Co. line, 21 Jul 1968 (fl), *L.C. Temple 10076* (MISS). **Calhoun**: 0.7 mi S of Calhoun City, Hwy 9, 10 Jul 1964 (fl), *T.M. Pullen 64903* (MISS, NCU). **Chickasaw**: Tombigbee National Forest, Goodfood Lake, S6 T12S R4E, 3 Aug 1997 (fl), *J.R. MacDonald 10903b* (DUKE). **Clay**: Tibbee Creek bottoms, ca. 3.8 mi S of West Point, Hwy 45 W, 22 Jul 1969 (fl), *T.M. Pullen 69829* (MISS). **Copiah**: Ca. 1 mi S of Turkey Creek, S2 T1N R3W, 13 Jun 1978 (fl), *K.E. Rogers 45241* (WVA). **DeSoto**: Ca. 0.3 mi S of DeSoto-Shelby County line, 21 Jun 1969 (fl), *R.V. Ferrari 295* (MISS). **Hinds**: Lake Garaway, Clinton, 28 Jun 1964 (fl), *T.M. Pullen 64652* (MISS). **Lee**: 0.25 mi SW of Tupelo city limits off West Rd, 29 May 1982 (fl), *C.T. Bryson 3382* (UNA); Alongside Hwy 6, 5.5 mi W of Tupelo, 16 Jun 1964 (fl), *T.M. Pullen 64393* (MISS, NCU). **Leflore**: NW of Sidon, between Sidon cut-off and old Yazoo Rer run [sic], S19 T18N R1E, 8 Jul 1997 (fl), *C.T. Bryson 16040* (MISS); NW of Sidon, between Sidon cutt-off [sic] and old Yazoo River run, S19 T18N R1E, 4 Jun 1999 (fl), *C.T. Bryson 17190* (MISS); NW of Sidon between Sidon cutt-off [sic] and old Yazoo River, S19 T18N R1E, 9 Jul 2001 (fl), *C.T. Bryson 18790 with B. Coleman, J.P. Goodlett* (DOV). **Panola**: Loess bluffs, 2.8 mi W of Pleasant Grove, Hwy 315, 11 Jul 1967 (fl, fr), *L.C. Temple 5888* (MISS). **Pontotoc**: Trace State Park, 28 May 1993 (fl), *M.B. Honeycutt and M. Floyd s.n.* (MISS). **Sharkey**: Delta National Forest, 20 Jul 1984 (fl), *E.*

*Sundell and D. Evans 6470* (MUHW). **Tate:** Roadside and adjacent low woods, 4.5 mi W of Strayhorn, Hwy 4, 6 Jul 1967 (fl), *T.M. Pullen 67550* (MISS). **Washington:** E edge of section 28, ca. 2 mi SW of US82 at Leland, S28 T18N R7W, 5-12 Aug 1975 (fl), *C.R. Gunn 10915* (MISS); Bottomland hardwood forest, E of US 61 and 3.5 mi E of Helm on county road 380, 12 Jun 1992 (fl), *R.D. Thomas, C. Bryson, and C. Allen 129898* (KANU, UMO). **Yazoo:** Creek bridge, 5.2 mi W of Pickens, Hwy 432, 30 Jun 1969 (fl), *T.M. Pullen 69592* (MISS).

*Specimens with fruits only or sterile, but most likely var. granulatus based on distribution of flowering specimens (see Fig. 2).* **Lafayette:** Side of Rte. 7 where hwy crosses Yocona River, 23 Aug 2000 (fr), *B.A. Connolly 174* (MISS).

MISSOURI. *Specimens with flowers or both flowers and fruits.* **Butler:** Floodplain of Mud Creek and the S branch tributary W of state Hwy T and Sec 21 just on E side of Hwy T, 36°53'N 90°19'W, elev. 430 ft., 12 Jul 1994 (fl), *A.E. Brant 2999* (UMO). **Dunklin:** Campbell, 25 Jul 1895 (fl), *B.F. Bush 266* (KSC, WVA); Cardwell, 3 Jul 1934 (fl), *J.W. Cunningham s.n.* (UMO). **Jasper:** Near Waco, 24 Jul 1920 (fl), *E.J. Palmer 18472* (ILL, UMO); Near Waco, 24 Jul 1920 (fl), *E.J. Palmer 18472a* (ILL); Near Carthage, 19 Jun 1923 (fl), *E.J. Palmer 23405* (UMO). **McDonald:** N bank of Elk Creek, just W of Mo. 43, ca. 2.5 mi SE of Tiff City, S22 T22N R34W, 10 Jun 1962 (fl), *P.L. Redfearn 10236* (FSU, SMS). **New Madrid:** W side of slough NE of Hubbard Lake, 7 mi E of New Madrid, S34 T23N R15E, 4 Jul 1952 (fl), *J.A. Steyermark 73629* (F). **Pemiscot:** Smith-Ellis Cemetery, ca. 0.5 mi W of County Road T on county gravel road 201, just W of Portageville, 9 Jun 1998 (fl), *B. Summers, G. Yatskievych, and J. Sullivan 8650* (UMO). **Scott:** Hwy 61, N jct.

77 and S Benton, 7 Jul 1972 (fl), *R. Clinard and T.E. Brooks 118* (SEMO); Along 77, just S of Benton on fence, 7 Jul 1972 (fl), *T. Brooks 6629* (KANU). **Stone:** Near Baxter, 22 Aug 1935 (fl), *J.A. Steyermark 19521* (UMO).

*Specimens with fruits only or sterile, but most likely var. granulatus based on distribution of flowering specimens (see Fig. 2).* **Pemiscot:** Alluvial woods around Robinson Lake, E of Big Lake, S16 T19N R13E, 18 Sep 1938 (fr), *J.A. Steyermark 6702* (F). **Stone:** E end of Edwards Bluff, along James River, E of Buttermilk Springs, S34 T23N R24 W, 14 Jul 1956 (fr), *J.A. Steyermark 81963* (UMO – 2 sheets).

OKLAHOMA. *Specimens with flowers or both flowers and fruits.* **Cherokee:** Keyough Bluffs, 2 mi E of Ft. Gibson, 28 Jun 1957 (fl), *C.S. Wallis 4344* (OK); 1 mi E and 1 N of Tahlequah, 17 Jun 1967 (fl), *U.T. Waterfall 17268* (OK). **Latimer:** Valley of Gaines Creek, 7 mi SW of Wilburton, 30 Jun 1968 (fl), *F.H. Means, Jr. 3692* (OK). **Le Flore:** Below Wisteria Dam on Poteau River, 1 mi S of Wister, 15 Jun 1965 (fl), *F.H. Means, Jr. 1555* (OK). **Marshall:** 1 mi N of Univ. of Oklahoma Biological Station, Lake Texoma, 2 Jul 1957 (fl), *G.J. Goodman 6477* (BRIT); 4 mi N, 0.5 mi NW of Willis, 20 Jun 1965 (fl), *R. Pearce 1889* (OK - 2 sheets). **McCurtain:** Glades, 16 May 1936 (fl), *Garvin s.n.* (BRIT). **Murray:** Chickasaw National Recreation Area, 21 Jun 1994 (fl, fr), *M.D. Proctor, G.E. Brown, and J. Nellesen 0243* (BRIT). **Oklahoma:** Oklahoma City, W side of May Ave., between Reno and 10th, 20 Jul 1941 (fl), *U.T. Waterfall 3031* (OK). **Osage:** Tallgrass Prairie Preserve, The Nature Conservancy, S29 T27N R9E, 2 Jul 1997 (fl), *M.W. Palmer 2174* (OK). **Pushmataha:** 1 mi NE of Kiamichi, 19 Jun 1937 (fl), *U.T. Waterfall 721* (OK).

**Sequoyah:** Cookson Hills, 11 mi NE of Vian, 30 Jun 1950 (fl, fr -BRIT), *U.T. Waterfall* 9532 (BRIT, BUT, KANU).

*Specimens with fruits only or sterile, but most likely var. granulatus based on distribution of flowering specimens (see Fig. 2).* **Marshall:** Woods N of Univ. of Oklahoma Biol. Station, 29 Jun 1954, *G.J. Goodman* 5887 (BUT--st, peduncle remnant, ILL--fl).

**Oklahoma:** Oklahoma City, W side of May Ave., between Reno and 10th, 1 Sep 1941 (fr), *U.T. Waterfall* 3555 (OK). **Pontotoc:** 9 mi S of Ada, 19 Oct 1945 (fr), *R. Stratton* 6206 (OK). **Sequoyah:** 5.4 mi NE of Gore on State 100, 8 Oct 1957 (fr), *C.S. Wallis* 6133 (BRIT).

TENNESSEE. *Specimens with flowers or both flowers and fruits.* **Anderson:** 2 mi E of Lake City, 14 Jul 1940 (fl), *R.M. Kriebel* 8875 (PUL [14737]). **Carroll:** Site #1, Milan Ammo. plant, 8 Jul 1993 (fl), *H.R. DeSelm s.n.* (TENN). **Cheatham:** Ashland City, 25 Jun 1962 (fl), *D. Demaree* 45769 (BRIT). **Davidson:** Nashville, [no date] (fl), *Gattinger s.n.* (F – 2 sheets); Nashville, 18 mi S on Old Hickory Blvd., 21 Jun 1947 (fl), *E. Quarterman* 3002 (DUKE); S of Couchville, 19 Jun 1948 (fl), *S. Fairchild, E. Clebsch, and A.J. Sharp* 7570 (TENN); Bluffs of Cumberland by Railroad, ca. 1 mi W of Scotsboro, 17 Jun 1969 (fl), *K.E. Blum* 3817 (FSU). **DeKalb:** Dry Creek, 13 Jun 1985 (fl), *M. Guthrie* 546 (TENN). **Dickson:** SE of Burns, near Fitzgerald farm, 11 Jul 1947 (fl), *A.J. Sharp, E. Clebsch, and A. Clebsch* 47-434 (TENN). **Franklin:** Vicinity of Lost Cove and Lost Cove Creek, “7/8/49” (fl), *P.H.W. Webb and students* 175 (TENN). **Hardeman:** Edge of Hatchie River swamps between Pocahontas and Bolivar, 9 Jul 1947 (fl), *A.J. Sharp, E. Clebsch, and A. Clebsch* (TENN). **Hamilton:** Harrison Bay State Park, 23 Jul 2003 (fl), *Krings TN-4*

(NCSC). **Haywood:** Roadside W of Shaw, 8 Aug 1983 (fl), *P. Lewis 1203* (TENN).

**Hickman:** Hwy 100, 0.1 mi NE of Mill Creek crossing, 8 mi NE of jct with Hwy 48 at Fairfield, 3 Jul 1981 (fl), *G. Nesom 4249* (TENN). **Houston:** Near Ellis Mills, 13 Jul 1952 (fl), *A. Clebsch s.n.* (TENN). **Jackson:** Woods along Flynn Creek Road, ca. 9 mi W of Rte. 56, 11 Jun 1992 (fl), *V.E. McNeilus 92-458* (TENN). **Knox:** Knoxville, Jun 1896 (fl), *A. Ruth s.n.* (TENN); Knoxville, Aug 1896 (fl), *A. Ruth s.n.* (ILL). **Lake:** Walnut log, Jun 1932 (fl), *C.E. Moore H540* (TENN); Field N of Donaldson Ditch, S of Eagle Hacking Area, 11 Jun 1986 (fl), *M. Guthrie 1077* (TENN). **Lewis:** Little Swan Creek Road, 17 Jun 1987 (fl), *M. Guthrie 1849* (TENN). **Marion:** Near Sequatchie River, Jasper, 14 Jul 1934 (fl, fr-imm), *Underwood and Sharp 2581* (TENN). **Montgomery:** Long Pond swamp S of Dotsonville Rd, 18 Jun 1970 (fl), *E.W. Chester 2345* (BRIT); Lock B area on the Cumberland River, Hickory Point side, 9 Jul 1979 (fl, fr), *E.W. Chester 4097* (TENN); Haynes Slough, Ross Farm, Palmyra, 8 Jul 1982 (fl), *P. Somers et al.* [additional collectors not identified on label] *s.n.*(TENN); E side of Cumberland River, across from old Lock B, between Muddy Branch and Midnight Hollow, along TC railroad tracks, 10 Aug 1967 (fl), *E. Wofford and E.W. Chester 1794* (NCU). **Obion:** Grassy Island near Walnut Log, 16 Jun 1942 (fl), *D.E. Eyles and M.S. Eyles 8392* (NCSC); S of Walnut log on Reelfoot Lake Rd, 2 Jun 1970 (fl), *K.E. Rogers and F.D. Bowers 45131* (BRIT, TENN). **Putnam:** Bluff of Rock Springs Branch, ca. 1 mi from Caney Fork River, 28 Jun 1976 (fl), *E. Wofford, D. Webb, L. Rader, R. Phillippe, and D. Smith 51808* (TENN). **Rutherford:** S of Northfield Blvd., 12 Jun 1985 (fl), *M. Guthrie 542* (TENN). **Shelby:** W of Arlington, roadside, 30 Jun 1948 (fl), *S. Fairchild, E. Clebsch, and A.J. Sharp 8187* (TENN). **Smith:** Bluffs along Caney Fork River, 8.1 mi W of Smithville exit off I-40, 9 Jul 1972 (fl), *R. Kral 47439* (NCU – 2

sheets); Plunkett Road slope, ca. 1 mi S of Rauls Creek Road jct, 7 Jul 1995 (fl), *H.R. DeSelm s.n.* (TENN). **Tipton:** Hwy 51, 4 mi S of Covington, 16 Jun 1965 (fl), *K.E. Rogers 33731* (NCU, TENN). **Van Buren:** Limestone slope, W of Spencer, 11 Jun 1958 (fl-imm), *A.J. Sharp 23745* (TENN). **White:** Near Big Dollar Tobacco Warehouse, ca. 2 mi S of Hamptons Crossroads, W side of Hwy 42, 28 Jun 1976 (fl), *R. Phillips, E. Wofford, D. Webb, L. Rader, and D. Smith 51782* (TENN). **Williamson:** Jct of Crockett Rd. and Wilson Pike in NE part of county, in and around Crockett and Own cemeteries, 14 Jun 1987 (fl), *L. Kelly 737* (TENN).

*Specimens with fruits only or sterile, but most likely var. granulatus based on distribution of flowering specimens (see Fig. 2).* **Decatur:** Along Lick Creek near Cozette, 13 Oct 1949 (st), *F.W. Woods, R.E. Shanks, and E.H. Cooley 14968* (TENN). **Giles:** Between Bethel and Minor Hill, 12 Sep 1949 (st), *R.E. Shanks, F.W. Woods, and E.H. Cooley 9175* (TENN). **Lawrence:** Near Fall River, along E Fork of Sugar Creek, 12 Jul 1948 (st), *A.J. Sharp, E. Clebsch, and A. Clebsch 9732* (TENN). **Monroe:** Near Union Grove, 8 Oct 1961 (st), *A.J. Sharp, W. Ellis, J. Drumke, J.S. Pringle, and G. Ramsey 29674* (TENN). **Obion:** Walnut Log, bank of Bayou de Chieh, 14 Aug 1947 (fr), *A.J. Sharp, E. Clebsch, and A. Clebsch 6193* (TENN). **Roane:** Clinch River Breeder Reactor Site, 15 Aug 1974 (fr), *S.F. Hale and F.E. Williams 48581* (TENN). **Shelby:** Edge of Cow Island, SW of Memphis, 20 Aug 1951 (fr), *F.H. Norris and A.J. Sharp 16319* (TENN). **Wilson:** At intersection of Hwys 109 and US70, 14 Oct 1968 (fr), *K.E. Rogers 42868* (TENN); Cedars of Lebanon State Park, May 1941 (fr), *A.J. Sharp 1568-a* (TENN); Cedars of Lebanon State Park, 27 Jul 1950 (fr), *A.J. Sharp 15323* (TENN).

TEXAS. *Specimens with flowers or both flowers and fruits.* **Austin:** Industry, Jul 1844 (fl), *F. Lindheimer and E. Dapprich 7234* (BRIT). **Bastrop:** Smithville, 14 Jun 1926 (fl), *E.R. Bogusch 1987* (ILL); Buescher State Park, 5 Jul 1957 (fl), *D.S. Correll and I.M. Johnston 17461* (LL); Bastrop State Park, 9 May 1974 (fl), *T. Patterson s.n.* (BRIT). **Brazoria:** Varner-Hogg State Park, West Columbia, 11 Jul 1974 (fl, fr), *R.J. Fleetwood 11093* (BRIT); S side of Kitchel Woods, 29 Aug 1968 (fl), *R.J. Fleetwood 9288* (LL); San Bernard NWR, 28 Jul 1970 (fl), *R.J. Fleetwood 9894* (TEX). **Brazos:** College Station, “6-7-47” (fl), *H.B. Parks s.n.* (TEX). **Comal:** New Braunfels, [no date given] (fl, fr), *F. Lindheimer s.n.* (neotype: BRIT); New Braunfels, about 100 yds S of Landa Park on Comal Creek, 23 Jun 1996 (fl), *M. Enquist 3090* (TEX); New Braunfels, Landa RV Park and Campground (across Comal River from Landa Falls), 9 Jul 2003 (fl), *Krings L-4* (NCSC, NY). **Cooke:** 8 mi N of Gainesville, on small creek W of Hwy 77 at Red River, 24 May 1946 (fl), *E. Whitehouse 15786* (BRIT). **Dallas:** May 1877 (fl), *J. Reverchon s.n.* (F); Reunion, Jun 1876 (fl), *J. Reverchon s.n.* (F); Below White Rock Lake Dam, 5 Jun 1940 (fl), *C.L. Lundell and A.A. Lundell 9288* (BRIT, LL); Dallas, [no date given] (fl, fr), *E. Dapprich 7233* (BRIT); Dallas, 10 Jun 1901 (fl), *J. Reverchon 2556* (BRIT). **Ellis:** Along White Rock Creek, 11 mi S of Italy, 4 Jul 1957 (fl), *D.S. Correll and I.M. Johnston 17365* (LL). **Fayette:** Hwy 71, 6-8 mi E of La Grange, Jun 1966 (fl), *Strother s.n.* (TEX). **Gonzales:** Ottine, “8-7-26” (fl), *B.C. Tharp s.n.* (TEX). **Harrison:** Caddo Lake State Park, 9 Jul 1975 (fl), *L.N. Lodwick 319* (BRIT); Caddo Lake State Park, 30 Jul 1975 (fl), *R.J. Fleetwood 11771* (BRIT). **Hockley:** [no locality], [no date] (fl), *J.M. Coulter s.n.* (F). **Jasper:** At little roadside park along Hwy 96, ca. 1-2 mi S of Jasper, 13 Jun 1972 (fl), *P.A. Amerson 1221* (BRIT). **Karnes:** San Antonio River bank, 5 mi NE of Karnes City, 13 Jun

1954 (fl), *J.C. Johnson 1582* (BRIT, TEX). **Kendall:** Edge Falls S of Kendalia on Curry Creek, 1 Jul 1984 (fl), *B. Ertter 5475 with L. Hamilton* (TEX). **Limestone:** Fort Parker State Park, Jul 1993 (fl), *J. Singhurst, L. Jones, and K. Blair 1298* (BRIT). **McLennan:** Battle Lake, 5 mi W of Mart, 31 May 1965 (fl), *J. Massey 938* (BRIT); Battle Lake, 0.5 mi W of Battle, 16 Jun 1968 (fl), *J. Massey 2127* (BRIT). **Parker:** Weatherford, 6 Jun 1902 (fl), *S.M. Tracy 7977* (F, TEX). **Red River:** Lennox Woods Nature Preserve, 10 mi N of Clarksville on SH 37, 15 Jun 1993 (fl), *R.W. Sanders 1965* (BRIT). **Robertson:** 2.6 mi SW of Old Salter Farm, tributary to the Little Brazos River, 22 May 1982 (fl), *T. Starbuck 2143* (BRIT). **Rusk:** 7 mi N of Mt. Enterprise, along Rt. 259, 3 Jun 1965 (fl), *D.S. Correll and H.B. Correll 31098* (LL). **Shelby:** 2 mi S of Strong, 18 May 1970 (fl), *D.S. Correll and H.B. Correll 38736* (LL). **Tarrant:** Along the Trinity, 25 Aug 1914 (fl, fr), *A. Ruth 563* (ILL); Between Irving and Arlington, 10 Jun 1944 (fl), *C.L. Lundell and A.A. Lundell 12903* (LL); Boaz Park, Benbrook, 25 May 1948 (fl), *V.L. Cory 54544* (BRIT, KANU, NCSC, LL). **Titus:** SE of West Midway, open improved pasture along stream, 33° 7' 40" 95° 4' 40", 7 Aug 1971 (fl), *J.D. Smith 404* (BRIT); Along Blundell Creek, NE of Monticello community, 15 Jul 1971 (fl, fr), *P.A. Amerson 901* (BRIT). **Travis:** Watkins Ranch in N.W. Travis Co. above Cow Creek on Lake Travis, 2 Jun 1951 (fl), *B.C. Tharp et al.* [other collectors not named on label] *51-969* (BRIT, KANU, TEX); Along Barton Creek, 5 mi N of Oak Hill, 29 May 1949 (fl), *G.L. Webster and N.S. Webster 121* (KANU, TEX); Valley of Barton Creek, ca. 2 mi upstream from Barton Springs in Zilker Park, Austin, 31 May 1989 (fl), *S.L. Orzell and E.L. Bridges 10150* (TEX); S bank of Bull Creek, ca. 50 ft E of dam, ca. 300 ft W of Spicewood Springs Road from low water crossing, ca 2.2 road mi N of jct with Loop 360, 30°24'17"N, 97°47'25" W, elev. 660 ft., 30 Jul 1995

(fl), *W.R. Carr 14779 with P. McNeal, P. Turner* (TEX). **Waller:** Hempstead, 12 Jun 1872  
(fl), *E. Hall 523* (F). **Wise:** Denton Creek, 11 mi E of Decatur, 18 May 1967 (fl), *D.S. Correll and H.B. Correll 34204* (LL).

*Specimens with fruits only or sterile, but most likely var. granulatus based on distribution of flowering specimens (see Fig. 2).* **Dallas:** Cedar Hill State Park, 15 Aug 1996 (st), *B. Baldon 323* (BRIT); S of Elam, Trinity River bottoms, 17 Sep 1942 (fr), *C.L. Lundell and A.A. Lundell 11983* (BRIT). **Fayette:** Kreische Brewery State Historical Site, La Grange, 31 May 1991 (st, but peduncle persistent), *Bro. D. Lynch with E. Kutac 7693* (TEX). **Hill:** Cobb Creek, SW of Hillsboro, 9 Sep 1972 (fr), *W.F. Mahler 6986 with J.M. Flock* (BRIT). **Limestone:** Fort Parker State Park, Jul 1993 (fr), *J. Singhurst, L. Jones, and K. Blair 1297* (BRIT). **Tarrant:** Moist sand, “1926 or 27” (fr), *Killian s.n.* (TEX). **Travis:** Austin, 19 Jul 1940 (fr), *B.C. Tharp s.n.* (TEX - 2 sheets); Lake Austin, 17 Aug 1923 (fr), *R.H. Painter s.n.* (TEX).

VIRGINIA. *Specimens with flowers or both flowers and fruits.* City of Newport News, Huntington Park, 26 Sep 1989 (fl), *P. Baldwin 95* (WILLI). **Surry:** 2 mi SE of Claremont, 16 Jul 1949 (fl), *B. Mikula 2838* (WILLI - 2 sheets).

***Gonolobus suberosus*** (L.) R.Br. var. *suberosus*, Asclepiadeae: 24. 1810.

ALABAMA. *Specimens with flowers or both flowers and fruits.* [no location given beside state], [no date] (fl), *Anonymous s.n.* (ex herb. A.S. Hitchcock) (KSC). **Baldwin:** Spanish Fort, 22 May 1975 (fl), *R. Kral 55728* (TEX). **Barbour:** Vicinity of Comer, 26 May 1998

(fl), *J.R. MacDonald 11270* (UNA). **Bibb:** Ca. 9.4 mi NE of Centreville, ca. 0.5 mi W of Bulldog Bend Bridge, 7 Jun 1998 (fl), *J.R. Allison 10898* (UNA). **Blount:** 2 air mi NNW of Altoona, SW side of Co. Rd. 41, just S of jct with Co. Rd. 42, 34°3'8"N 86°20'21"W, S28 T11S R3E, 17 Jul 1998 (fl), *B.R. Keener 1257* (UNA); 1 air mi S of Summit, on NE side of lake, on SE side of 231, 34°11'35"N 86°29'35" W, S1 T10S R1E, 8 Jun 1998 (fl), *B.R. Keener 934* (UNA). **Etowah:** Gadsden, Jul 1878 (fl, fr-imm), *G.R. Vasey s.n.* (F). **Greene:** 8 air mi S of Sawyerville, 30 Jun 1966 (fl), *J.L. Thomas 832* (UNA). **Houston:** Chattahoochee State Park, near fishing pond, 5 Jun 1972 (fl), *R. Kral 47233* (FSU, USCH); Chattahoochee State Park, 31 Jul 2003 (fl), *Krings AL-1* (NCSC); Chattahoochee State Park, 31 Jul 2003 (fl), *Krings AL-7* (NCSC). **Marengo:** 10 mi S of Demopolis, S14 T16N R2E, 30 May 1992 (fl), *D.H. Burk 106* (UNA). **Montgomery:** Hwy 30, 0.3 mi S of Sandy Creek, S 22 T14N R19E, 16 May 2001 (fl), *A.R. Diamond 12445* (MISS). **Randolph:** E bank of Tallapoosa River, S5 T18S R10E, 2 Aug 1986 (fl), *C.F. Nixon 3561 with R.D. Whetstone, C.L. Lawler* (UNA); Along Co. Rd 33, above Cornhouse Creek, S8 T21S R11E, 28 Jul 1988 (fl, considerable insect damage), *C.F. Nixon 4151 and G.D. Bryant* (UNA). **Wilcox:** Prairie Bluff on W shore of Alabama River, near Prairie Mission, S32 T14N R7E, 23 Jun 1982 (fl), *S.C. Gunn 842* (UNA).

*Specimens with fruits only or sterile, but most likely var. suberosus based on distribution of flowering specimens (see Fig. 2).* **Barbour:** Blue Springs State Park, 31 Jul 2003 (st), *Krings AL-10* (NCSC). **Houston:** Chattahoochee State Park, 31 Jul 2003 (st), *Krings AL-2* (NCSC); Chattahoochee State Park, 31 Jul 2003 (st), *Krings AL-3* (NCSC); Chattahoochee State Park, 31 Jul 2003 (st), *Krings AL-4* (NCSC); Chattahoochee State Park, 31 Jul 2003 (st), *Krings AL-5* (NCSC); Chattahoochee State Park, 31 Jul 2003 (st), *Krings AL-6*

(NCSC); Chattahoochee State Park, 31 Jul 2003 (st), *Krings AL-8* (NCSC); Chattahoochee State Park, 31 Jul 2003 (st), *Krings AL-9* (NCSC). **St. Clair:** Along Little Canoe Creek, E of Lake Sumatanga, 6 Oct 1962 (fr), *P.E. Bostick 253-12* (NCU).

FLORIDA. *Specimens with flowers or both flowers and fruits.* Mosquito Inlet, June (fl), *A.H. Curtiss 2308* (F, KANU, LL, ND-G [040257], NY). **Alachua:** 22 Jun 1986 (fl), *C. Easley 367b* (FLAS); 25 Jul 1935 (fl, fr), *G.F. Weber s.n.* (FLAS); 18 Jun 1936 (fl), *O. Evers and E. West* (FLAS); *Krings FL-9* (NCSC). **Brevard:** 15 Jun 1928 (fl), *Rhoades and West s.n.* (FLAS). **Columbia:** 16 May 1992 (fl), *B. Herring 739 with D. Herring* (FLAS); 10 May 1990 (fl), *B. Tan 620* (FLAS). **Dixie:** 12 Jun 1960 (fl), *R. West and E. West s.n.* (FLAS, NCU). **Duval:** 18 Jun 1993 (fl), *R. Stalter 13* (USF). **Franklin:** 26 Jul 1985 (fl), *L.C. Anderson 8648* (FLAS, FSU). **Gadsden:** 18 Jun 1973 (fl), *A. Gholson s.n.* (FSU); 3 Aug 1983 (fl, fr), *J.B. Nelson 2758 with G.R. Knight* (FSU); 13 Jul 1897 (fl), *A.H. Curtiss 5948* (DOV, FLAS, ILL, KSC, USF); 22 Jun 1975 (fl), *D.B. Ward 8861* (FLAS, WILLI); 1 Jul 1965 (fl, fr-imm (FSU)), *S. McDaniel 6446* (FLAS, FSU, NY, UNA); 22 May 1959 (fl), *R.K. Godfrey 58650* (FSU). **Gulf:** 18 Jul 1986 (fl, fr-imm (FSU)), *L.C. Anderson 9802* (FSU, USF); 7 Jun 1990 (fl), *L.C. Anderson 12868* (FSU). **Hamilton:** 16 Jun 1983 (fl), *D.W. Hall 1231 with B. Simons* (USF). **Jefferson:** 8 Jun 1974 (fl), *R.K. Godfrey 73629* (FSU). **Hernando:** May 1928 (fl), *J.K. Small s.n.* (USF). **Lake:** 16-30 Jun 1895 (fl), *G.V. Nash 1986* (F, ND-G [040255]); 1-10 Jul 1895 (fl), *G.V. Nash 2133* (DOV, F, ND-G [040254]). **Levy:** Jun 1876 (fl), *A.P. Garber s.n.* (FLAS); 11 Aug 1937 (fl), *E. West and L.E. Arnold* (FLAS); 9 Jul 1996 (fl), *J.R. Abbott 9184 with H. Mitchell, N. Makruski* (FLAS, TEX); 18 Jul 1993 (fl), *R. Moranz 3 with L. Fink* (FLAS); 21 Jun 1994 (fl), *W.S.*

*Judd 7024* (FLAS). **Leon:** 5 Jun 1996 (fl), *L.C. Anderson 16540* (FSU). **Liberty:** 4 Jul 1972 (fl), *R.K. Godfrey 71489* (FSU); 24 Apr 1982 (fl, fr), *S.W. Leonard 7747* (FSU). **Marion:** 27 May 1941 (fl), *West and Arnold s.n.* (FLAS). **Nassau:** 4 Jul 1951 (fl), *S.C. Hood s.n.* (FLAS). **Pasco:** 8 May 1986 (fl), *T. Rochow s.n.* (USF). **Pinellas:** 3 Jun 1973 (fl), *P. Genelle and G. Fleming 1679* (USF). **Polk:** 8 Jul 1979 (fl), *D. Rhodes et al.* [additional collectors not specified on label] *s.n.* (USF). **Putnam:** 22 Jul 1941 (fl), *A.M. Laessle s.n.* (FLAS). **St. Johns:** 22 May 1904 (fl), *J.K. Small and P. Wilson s.n.* (F); 14 May 1994 (fl), *J. Harrison 685 with L. Harrison* (FLAS); 6 Jul 1940 (fl), *West and Arnold s.n.* (FLAS). **Sumter:** 24 Apr 1992 (fl), *C. vanHoek 261* (holotype: USF). **Suwannee:** 18 Jul 1967 (fl), *S. McDaniel 9449* (FLAS, FSU). **Volusia:** 13 Jun 1941 (fl), *E.L. Brasol s.n.* (FLAS). **Washington:** 13 Jul 1969 (fl), *R.K. Godfrey 68758* (FSU); 24 May 1990 (fl), *L.C. Anderson 12760* (FSU).

*Specimens with fruits only or sterile, but most likely var. suberosus based on distribution of flowering specimens (see Fig. 2).* **Alachua:** 17 Apr 1986 (st), *W.S. Judd 5093* (FLAS). **Calhoun:** 9 Sep 1958 (fr), *R.K. Godfrey 57724* (FSU). **Columbia:** 29 Jul 2003 (st), *Krings Fl-10* (NCSC); 29 Jul 2003 (st), *Krings Fl-11* (FLAS). **Dixie:** 18 Sep 1960 (st), *D.W. Ward and A.A. Will 2208* (FSU). **Duval:** 15 Sep 1992 (st, but peduncle persistent), *C. Easley 1192* (FLAS). **Gadsden:** “11-6-87” (fr, no lvs), *P.W. Alcorn 366* (FLAS); 15 Oct 1972 (st), *D.B. Ward 8410 with D.W. Hall, N.E. Lee* (FLAS); 15 Oct 1972 (st), *D.B. Ward 8453* (FLAS). **Glades:** 27 Jan 1962 (st), *D.W. Ward 2428 with T. Myint, R.R. Smith* (FLAS). **Hernando:** 18 May 1965 (st), *D.B. Ward 4706 with J. Beckner* (FLAS). **Hillsborough:** 28 Jul 2003 (st), *Krings FL-6* (NCSC); 28 Jul 2003 (st), *Krings FL-7* (FLAS); 28 Jul 2003 (st), *Krings FL-8* (FLAS). **Jackson:** 25 Jun 1960 (st), *R.S. Mitchell 338* (FSU); 29 Jul 1960 (st),

*R.S. Mitchell 463* (FSU); 23 Jun 1975 (st), *D.B. Ward 8928* (FLAS); 1 Aug 2003 (st), *Krings FL-13* (NCSC); 1 Aug 2003 (st), *Krings FL-14* (FLAS). **Lee**: Jun-Jul 1898 (st), *A.S. Hitchcock s.n.* (F). **Liberty**: 17 Jul 2001 (fr), *L.C. Anderson 19833* (FSU). **Marion**: 24 Sep 1941 (fr), *West and Arnold s.n.* (FLAS). **Orange**: 27 Jul 2003 (st), *Krings FL-1* (NCSC); 27 Jul 2003 (st), *Krings FL-2* (NCSC); 27 Jul 2003 (st), *Krings FL-3* (NCSC); 27 Jul 2003 (st), *Krings FL-4* (FLAS); 27 Jul 2003 (st), *Krings FL-5* (FLAS). **Polk**: 24 Dec 1965 (st), *H.S. Conard s.n.* (FLAS). **Seminole**: 16 Feb 1965 (st), *D.B. Ward 4382 with J. Beckner* (FLAS). **Wakulla**: 1 Aug 2003 (st), *Krings FL-15* (NCSC); 1 Aug 2003 (st), *Krings FL-16* (FLAS).

GEORGIA. *Specimens with flowers or both flowers and fruits.* [no locality], [no date] (fl), *Anonymous s.n.* (F). **Baker**: Ichauway (former plantation, maintained as a natural ecosystem SW of Newton, ca. 28 mi SW of Albany), 18 May 1996 (fl), *L.C. Anderson 16407* (FSU, GA); Along west bluffs of Flint River near jct with Ichawaynochawa Creek, 26 Jul 1946 (fl), *W.H. Duncan 6640* (GA); Along Flint River near its jct with Ichawaynochaway Creek, 30 Jul 1947 (fl), *R.F. Thorne 5806* (FSU). **Bryan**: Fort Stewart Military Reservation, Training Area C16, 4 Jun 1992 (fl), *T.M. Zebryk 0350 with M. Moore, D. Giannasi* (GA). **Butts**: SE of Jackson, off Ga. Hwy 42, 4 Jul 1988 (fl), *C.L. Howel 1531* (GA, KANU). **Cherokee**: Little River Area, 14 Jul 1988 (fl), *S.B. Jones 24980 with C. Jones, L. Foote, G. Foote* (GA). **Clay**: Chattahoochee River bluff, Fort Gaines, 31 May 1947 (fl), *R.F. Thorne 4334* (F); Ca. 3 mi SSE of Fort Gaines, 29 May 1988 (fl), *J.R. Allison 3203* (GA). **Columbia**: Bank of Savannah River, Germain's Island, 7 Jun 1902 (fl), *R.M. Harper 1298* (F). **Dade**: Lower end of Sitton's Gulch, 6 Jun 1942 (fl, fr), *W.H. Duncan 5446* (GA). **Decatur**: Ca. 100 m SE of the workshop at Jim Woodruff Dam N of

Chattahoochee, Florida, 5 Jun 1964 (fl), *D. Drapalik M454* (NCU). **Elbert**: Richard B. Russell Dam and Lake Area, 20 Jun 1979 (fl), *W.C. Credle 935* (GA). **Floyd**: Hillside on S side of Catoona River, ca. 3 mi SW of Rome, 26 Jun 1948 (fl, fr), *W.H. Duncan 8448* (GA); SW of Rome, along Coosa River, 12 Jul 1984 (fl), *S.B. Jones 24340 with N.C. Coile* (USCH). **Glynn**: St. Simon's Island, 16 Jun 1970 (fl), *R. B. McGhee 36* (GA). **Gordon**: New Echota Historic Site, 14 Jun 1998 (fl – heavy insect damage), *C.L. Howel 2210* (GA). **Harris**: Along Mulberry Creek, 1.5 mi SSE of Mountain High School toward Mulberry Grove on Mt. Hill Road, 12 Jun 1972 (fl), *S.B. Jones 22109 with V. Jones* (GA). **Johnson**: Harrison property, 11 Jun 1994 (fl – heavy insect damage), *J.O. Harrison 154-B* (GA). **McDuffie**: Clark Hill Wildlife Management Area, 4 Jun 1982 (fl – imm), *N.C. Coile 2853 with L. Kay, K. Boring* (UMO). **Macon**: Above E bank of Flint River, N of public boat ramp at W end of Co. Rte. 267, 11 Jun 1988 (fl), *J.R. Allison 3244 with T.S. Patrick* (GA); Slopes above Beaver Creek, 100 ft N of owerline [sic], 1000 ft E of Glorious Hope Cemetery, 17 May 1990 (fl), *L.G. Chafin 2001* (GA). **Quitman**: Ca. 1.5 mi NNE of Georgetown, 30 May 1988 (fl), *J.R. Allison 3207* (GA). **Stephens**: By Panther Creek, 22 Jun 1962 (fl), *C.H. Fitzgerald s.n.* (GA). **Thomas**: Greenwood Plantation youth camp, just E of Ochlockonee River, off hwy 84 at Old Cassidy Road, 4 mi W of Thomasville, 21 May 1977 (fl), *L.C. Anderson 4456* (FSU). **Whitfield**: Creek on E side of W. Chickamauga Creek, 3.1 mi W 11°N of Ft. Oglethorpe, elev. 670 ft., 18 Aug 1951 (fl), *W.H. Duncan 13043 with H. Venard* (GA). **Wilkes**: Anthony Shoals on the Broad River, 11.5 mi NE of Tignall, 8 Jul 1973 (fl), *S.B. Jones 22475 with O. Bounds, L. Bounds, C. Jones* (DUKE).

*Specimens with fruits only or sterile, but most likely var. suberosus based on distribution of flowering specimens (see Fig. 2).* **Baker**: Bank of Flint River, 4 mi E of Field Station, 14

Oct 1947 (st), *R.F. Thorne 7238a* (GA). **Cherokee:** Allatoona Lake shore, 7 Sep 1988 (fr), *L. Foote s.n.* (GA). **Glynn:** 0.3 mi thru [sic] swamp NNE of end of Point Road (Union Camp) off Prick Road, 13 Oct 1992 (st), *C. Nordman s.n.* (GA); Union Camp, Brunswick, 24 Aug 1992 (st), *C. Nordman s.n.* (GA). **Harris:** Callaway Gardens, 15 Jul 1999 (fl – heavy insect damage), *Crook 436 with D.E. Giannasi* (GA); Callaway Gardens, 21 Oct 1998 (fr), *D. Giannasi 1998-99 with M. Zimmerman* (GA). **Lincoln:** SW side of Savannah River, ca. 3 mi above jct with Little River and just opposite lower end of Price's Island, 29 Jun 1949 (fr-imm), *W.H. Duncan 9825* (GA). **Long:** S side of Carters Island, near Altamaha River, "6/4/93" (st), *C. Nordman and K. Tassin s.n.* (GA). **Monroe:** High Falls State Park, 27 Jun 1987 (st), *C.L. Howel 0421* (GA).

KENTUCKY. *Specimens with flowers or both flowers and fruits.* **Jessamine:** Dug from High Bridge, 230 m N of the dance hall in High Bridge Park, transplanted to Botanical Garden plots at the Univ. North Carolina, Orange Co., NC, 19 Jun 1963 (fl), *D.J. Drapalik M315* (FLAS).

LOUISIANA. *Specimens with flowers or both flowers and fruits.* **Orleans:** Swamps, New Orleans, May [no year on label] (fl), *R.S. Cocks s.n.* (NO).

MISSISSIPPI. *Specimens with flowers or both flowers and fruits.* **Wayne:** Bluff of Chickasawhay River, ca. 2.5 mi NW of Waynesboro, S35 T6N R9W, 13 Jun 1969 (fl), *S.B. Jones 16348* (MISS).

NORTH CAROLINA. *Specimens with flowers or both flowers and fruits.* **Alamance:** Riverbottom along Haw River, ca. 5 mi SE of Saxapahaw, 17 Jul 1956 (fl), *C.R. Bell 4080* (NCU); Austin Quarter, along small stream about 500 m W of confluence of Orange County's Cane Creek and Haw River, 35° 54' 46" N, 79° 16' 26" W, 30 Jul 2005 (fl), *C.A. McCormick 150 with M. Peifer* (NCU – 3 sheets). **Anson:** Blewett Falls on Pee Dee River, 30 Jun 1956 (fl), *A.E. Radford 13383* (NCU). **Beaufort:** Indian Island, 9 Jun 1966 (fl), *A.E. Blair 538* (NCSC). **Carteret:** Lenox Point, 3 mi E of Beaufort, 27 Jul 1954 (fl, fr), *R.K. Godfrey s.n.* (DUKE); 1 mi W of Atlantic Beach, top of front dune, 15 Jun 1947 (fl), *L.A. Whitford s.n.* (NCSC). **Chatham:** Low cleared area just W of Cumnock bridge, 5 Jul 1955 (fl), *D.F. Houck 328* (NCU); W bank of Haw River at Co. Rte. 1545 bridge, 27 Jul 1971 (fl), *S.W. Leonard 4926* (DOV, FLAS, KANU, PUL [52408], SMS, SIU, TEX, WILLI, WNC [6612], WVA); White Pines Natural Area, Rocky River floodplain, 25 Jun 1988 (fl), *E.C. Swab 334* (USCH). **Davidson:** Stream side, 2.8 mi NW of Snider, 26 Aug 1962 (fl), *H.E. Ahles 57441* (NCU). **Granville:** Northside Diabase area, SW of Will Suit Road, 13 Jun 2004 (fl), *A. Walker s.n.* (NCSC). **Durham:** Along Norfolk and Western tracks by Eno River, ca. 6 mi NW of Durham, 21 Jun 1968 (fl), *R.L. Wilbur 10434* (DUKE). **Guilford:** Near Conoho Creek, off Co. Rd. 125 (1417?), ca. 4.5 mi NW of Williamston (SE of bridge), 7 Feb 1960 (fl), *C.R. Bell 17051* (NCU). **Halifax:** 2 mi N of Thelma along Roanoke River, 19 Jul 1956 (fl), *H.E. Ahles 17000 with R.S. Leisner* (NCU). **Johnston:** Middle Creek, 2.3 mi WNW of Edmundson, 19 Jun 1957 (fl), *A.E. Radford 25381* (NCU). **Jones:** Island Creek, 5 mi NE of Pollocksville, 6 Jun 1965 (fl), *M.N. Sears C274* (NCU); Island Creek, E of jct of Trent River and Island Creek, 5 mi NE of Pollocksville, 6 Jun 1965 (fl), *M.N. Sears C315* (NCU). **Jones/Onslow:** Croatan National Forest, Jun 1979 (fl),

*C. Stone 243* (NY). **Lee:** 1 mi W Moncure at US Hwy 1 bridge on Deep River, 28 Jul 1955 (fl), *L.S. Beard 1059* (NCU). **Lenoir:** Neuse River, 2.5 mi E of Seven Springs, 22 Jun 1957 (fl), *A.E. Radford 25712* (FSU, NCU). **Mecklenburg:** 7 mi W of Huntersville, along Catawba River, 6 Aug 1958 (fl), *H.E. Ahles 48676 with J.A. Duke* (NCU); 2.7 mi SE of Davidson on NC 73, 6 Aug 1958 (fl), *H.E. Ahles 48688 with J.A. Duke* (NCU); NC 73 at Davidson Branch of W Fork of Rocky River, a short distance SE of jct with Co. Rd. 2420, Westmoreland farm, 15 Jul 1967 (fl), *T. Daggly 4069* (DUKE). **Montgomery:** Little River near NC 27, E of Troy, 24 Jun 1956 (fl), *A.E. Radford 13294* (NCU). **Nash:** Tar River, 0.8 mi N of Strickland Cross Roads, 12 Jul 1956 (fl), *H.E. Ahles 16673 with C.R. Bell* (NCU, FSU, USF). **Onslow:** Bear Island or Hammock Beach State Park, 29 Jun 1961 (fl), *R.L. Wilbur and E.O. Beal 6456* (DUKE); NC 210 N of Surf City, 29 Jun 1963 (fl), *A. McCrary 548 with H. Ahles, T. Bradley* (NCU). **Orange:** near Cates' on the Eno River, 12 Aug 1972 (fl), *L.F. Conder 180 with C.R. Broome, R. Foster, M.F. Conde* (DUKE). **Pender:** Ca. 2 mi NE of Annandale, off US 17, 30 Jun 1963 (fl), *T. Bradley 1013 with Ahles, McCrary* (NCU). **Richmond:** Mountain Creek near Pee Dee River, NW of Rockingham, 24 Jul 1956 (fl), *A.E. Radford 14479* (NCU). **Robeson:** Dry river slope 1 mi SE of Lumberton along US 74 and Lumber River, 21 Jun 1958 (fl), *R.F. Britt 2135* (NCU). **Union:** Alluvial woods, 3.6 mi S of New Salem on NC 205 along Richardson Creek, 14 Jul 1957 (fl), *H.E. Ahles 31460 with J. Haesloop* (NCU); Rocky River on NC 205, N of New Salem, 14 Jul 1957 (fl), *H.E. Ahles 31482 with J. Haesloop* (NCU, USF). **Wake:** Raleigh, Lake Johnson, 13 Jul 1938 (fl), *R.K. Godfrey 5015* (NCSC); Raleigh, Schenck Forest, Jul 2001 (fl), *A. Krings 416* (NCSC); Raleigh, Schenck Forest, 6 Oct 2001 (fr), *A. Krings 418* (NCSC).

*Specimens with fruits only or sterile, but most likely var. suberosus based on distribution of flowering specimens (see Fig. 2).* **Alamance:** E side of first small creek upstream of the confluence of Orange County's Cane Creek and the Haw River, 30 Jul 2005 (st), C.A. McCormick 149 with M. Peifer (NCU). **Bertie:** NNE of Williamston, US 13 and 17, 30 Sep 1966 (fr), D.R. Windler 1839 (SIU); N of Williamston, along the Roanoke River, 30 Sep 1966 (st), D.M. Dumond 495 (NCSC). **Carteret:** Lennox Point, 3 mi E of Beaufort, 29 Jul 1952 (st), H.L. Blomquist 15566 (DUKE). **Chatham:** N side of the Haw River on NC 15 and 501, 29 Oct 1956 (fr), G.S. Ramseur 2826 with A.E. Hammond (NCU). **Craven:** Trent River, opposite New Bern, 19 Oct 1952 (fr), E.D. Cappel and W.B. Fox 472 (NCSC). **Hyde:** Woods beside Pungo River, 9 Oct 1965 (st), E.G. Batts s.n. (NCU). **Lee:** 1 mi W Moncure at US Hwy 1 bridge on Deep River, 7 Jul 1955 (st), L.S. Beard 761 (NCU). **Madison:** 3.1 mi NW of Hot Springs, on N side of French Broad River, 8 Oct 1958 (fr), H.E. Ahles 50647 with J.A. Duke (NCU). **Mecklenburg:** 2.7 mi SE of Davidson on NC 73, 6 Aug 1958 (fr), H.E. Ahles 48688 with J.A. Duke (NCU). **Moore:** By McLendons Creek, 11 Mar 1956 (fr - remnant), D.F. Houck 880 (NCU). **Northampton:** 3.1 mi W of Boones Crossroads, vic. of Roanoke River, 30 Oct 1958 (fr), H.E. Ahles 52470 with J.G. Haesloop (NCU). **Onslow:** Bear Island or Hammock Beach State Park, 5 Sep 1962 (fr), R.L. Wilbur and E.O. Beal 6519 (DUKE). **Orange:** Swamp of New Hope Creek, 1 Aug 1937 (fr), H.R. Totten s.n. (NCU); Mason Farm Biological Reserve, 1 Oct 1991 (fr), J. Larke 2172 (NCU). **Stanly:** 2.2 mi W of Aquadale on Long Creek, 24 Sep 1956 (fr), H.E. Ahles 19926 with R.S. Leisner (NCU). **Wake:** Neuse River, near Bayleaf, Barton's Creek Township, 4 Aug 1944 (fr), M.F. Buell 44019 (NCSC).

SOUTH CAROLINA. *Specimens with flowers or both flowers and fruits.* **Aiken:** N Augusta along the Savannah River, 10 Jun 1962 (fl), *H.E. Ahles 56873 with R. Baird* (NCU).

**Beaufort:** Bluffton, [no date] (fl), *Mellichamp s.n.* (F); [No locality provided], 1882 (fl), *Mellichamp s.n.* (DOV, F); Bluffton, Jul 1877 (fl), *Mellichamp s.n.* (NCU); Airfields, Bluffton, 1878 (fl), *Mellichamp s.n.* (NCSC); Bluffton, 1887 (fl), *Mellichamp s.n.* (ND-G [040256]); 0.4 mi WNW of Old Hilton Head Ferry landing on Co. Rt. 39, E of Bluffton, 28 Jun 1956 (fl, st), *H.E. Ahles 15633 with C.R. Bell* (NCU – 2 sheets); Sea Pines, 5 Jun 1993 (fl), *R. Stalter 7* (USF). **Berkeley:** Francis Marion National Forest, 24 May 1974 (fl), *L.R. Phillippe 2832* (EIU); Old Santee Canal State Park, 2 Jun 1988 (fl), *D. Soblo 1835* (USCH). **Edgefield:** Sumter National Forest, 20 Jun 1993 (fl), *S.R. Hill 25130 with B. Dorsey* (USF); Sumter National Forest, Compartment 322, Stand 2, elev. ca. 250 ft, 30 May 1997 (fl), *J.B. Nelson 18333* (USCH). **Fairfield:** Near railroad station, Strother, 20 Jun 1956 (fl), *O.M. Freeman 56367* (NCU); Roadside thicket at Shelton, 21 Jun 1956 (fl), *O.M. Freeman 56412* (NCU); Ca. 3.5 mi SE of Jenkinsville, 34.2236°N, 81.2438°W, elev. 330 ft., 26 Jun 2002 (fl), *J.B. Nelson 22832* (NCSC); Ca. 900 m ESE of main reactor, V.C. Summer Nuclear Station, NW side of Jenkinsville off SC 215, UTM 17 471672E 3794415N, elev. ca. 370 ft., 31 May 2002 (fl), *J.B. Nelson with S. Summer, M. Whitten* (NCSC). **Georgetown:** Tom Yawkey Wildlife Center, just W of ‘Five Points,’ South Island, 23 May 1991 (fl), *J.B. Nelson 10483 with D.E. Kennemore* (FLAS, NCU, USCH); Prince George Tract, just S of Pawley’s Island, ca. 7 mi NE of Georgetown, 14 Jun 1996 (fl), *B. Seckinger 169* (USCH). **Greenwood:** Henley Creek, near SC 248, 2.6 mi S of Ninety Six, 1 Jul 1957 (fl, fr-imm), *A.E. Radford 26569* (NCU); Wilson Creek, near SC 246, 1.5 mi N of Ninety Six, 7 Jul 1957 (fl), *A.E. Radford 26588* (NCU); SC 248, just S of

Ninety Six Creek crossing, Ninety Six, 24 Jun 1987 (fl), *S.R. Hill 18134 with C.N. Horn* (NCU, NY, USF - 2 sheets); Sumter National Forest, E side of Hard Labor Cr, about a mile downstream from Cunning Ford Cr, 27 Jun 1989 (fl), *J.B. Nelson 8088 with S. Bennett* (USCH). **Hampton:** Hamilton ridge, floodplain of the Savannah River, 1 Jun 2000 (fl), *A.B. Pittman 06010015 and A.R. Darr 590* (USCH); Hamilton ridge, floodplain of the Savannah River, 1 Jun 2000 (fl), *A.B. Pittman 06010024 and A.R. Darr 589* (USCH).

**Horry:** Low woods near Myrtle Beach, 13 Jul 1932 (fl), *W.C. Coker and H.R. Totten s.n.* (NCU). **Kershaw:** Near Miller Bridge over Lynches River, 11 mi NE of Kershaw, 4 Jun 1957 (fl), *A.E. Radford 23665* (NCU). **Lancaster:** Near Rocky Creek, 3 mi S of jct. SC 97 and Co. 20 on SC 97 (SW corner of county), 6 Jun 1957 (fl), *H.E. Ahles 27370 with J.G. Haesloop* (NCU); Flat Creek, ca. 8 mi NE of Kershaw, 16 Jul 1961 (fl), *B.F. Williamson 1398* (NCU). **Laurens:** SC 56 at Enoree River, ca. 12 mi NE of Laurens, 2 Jul 1988 (fl), *C.N. Horn 2814* (USCH). **Lexington:** 31 May 1891 (fl), *Anonymous s.n.* (NCU).

**Marlboro:** Pee Dee River, 9 mi SW of Bennettsville, 10 Aug 1956 (fl), *A.E. Radford 15492* (NCU); Boat landing next to bridge, US 15 just N of Great Pee Dee River, 22 Jul 1989 (fl), *C.N. Horn 3527* (USCH). **McCormick:** SC 823 at Little River, ca. 13 mi NW of McCormick, 17 Jul 1993 (fl), *C.N. Horn 7219* (USCH); Sumter National Forest, edge of clearcut on E side of Persimmon Br, 34.0199 N 82.3764 W, elev. 370 ft, 8 Jun 2000 (fl), *J.B. Nelson 21297* (USCH). **Newberry:** County Rt 28, 0.5 mi S SC 213 at creek and railroad tressel, ca. 16 mi E of Newberry, 2 Jun 1987 (fl), *C.N. Horn 1848* (USCH); Newberry County 403 at tributary to Camping Creek, 2 Jul 1987 (fl), *C.N. Horn 2116* (USCH); Lynch's Woods Park, E of downtown Newberry, 25 Jun 1989 (fl), *C.N. Horn 3459* (USCH); Forest Service Compartment 173, S of Sumter National Forest Road 380 at

Joshuas Branch, 26 Jun 1993 (fl), *C.N. Horn 6993* (USCH). **Saluda:** Big Creek, near SC 194, 6.5 mi NE of Saluda, 8 Jul 1957 (fl), *A.E. Radford 26930* (NCU). **Union:** At bridge over Fair Forest Creek, SW of Jonesville, 5 Jun 1957 (fl), *C.R. Bell 8525* (NCU); Sumter National Forest, 7 Jul 1994 (fl), *S.R. Hill 25893* (NY); Sumter National Forest, Rosehill Boat Ramp, 18 Jul 1992 (fl), *C.N. Horn 5393* (USCH); Forest Service Compartment 101, ca. 15 mi S of Union, 12 Jul 1993 (fl), *C.N. Horn 7155* (USCH); Headwaters of John's Cr S of S-18, about 2 mi W of downtown Sedalia, 22 Jun 1989 (fl), *J.B. Nelson 8044 with O. Stuart, A. Schkenck* (USCH). **York:** Kings Mountain State Park, Lake York camping area near the dam, elev. 675 ft, 8 Jun 1993 (fl), *D.E. Kennemore, Jr. 531* (USCH); Woods at terminus of Hemlock Rd off Porter Rd, S side of Rock Hill, 23 Jun 1988 (fl), *J.B. Nelson 6727* (DUKE, USCH); near edge of Stony Fork Cr, on N side of SC 324, 29 Jul 1988 (st), *J.B. Nelson 6809 with R. Greenburg* (USCH).

*Specimens with fruits only or sterile, but most likely var. suberosus based on distribution of flowering specimens (see Fig. 2).* **Aiken:** N Augusta near Savannah River, 27 Oct 1961 (fr), *H.E. Ahles 55121 with P.J. Crutchfield* (NCU – 3 sheets). **Allendale:** Savannah River, 1.4 mi SW of jct. Co. Rt. 60 and 41, 11 Sep 1956 (fr), *H.E. Ahles 18446 with C.R. Bell* (NCU). **Beaufort:** Beaufort District, [no date] (st), *Mellichamp s.n.* (F). **Charleston:** 3.8 mi SW of Hollywood on SC 162, 21 Jul 1957 (st, peduncles persistent), *H.E. Ahles 32055 with R.S. Leisner* (NCU). **Cherokee:** 1 mi N of jct. SC 18 and Co. 98 along Broad River (NW of Blackburg), 11 Jul 1957 (fr), *H.A. Ahles 30953 with J.G. Haesloop* (NCU). **Darlington:** Woods at Lauther's Lake, 23 Jul 1939 (fr), *B.E. Smith 1155* (NCU); Woods near Lauther's Lake, 25 Aug 1941 (st), *B.E. Smith 2040* (NCU). **Georgetown:** Tom Yawkey Wildlife Center, South Island, 3 Oct 1990 (fr), *J.B. Nelson 9805* (USCH). **Lancaster:** Andrew

Jackson State Park, 22 Jul 2003 (st), *Krings SC-1* (NCSC). Andrew Jackson State Park, 22 Jul 2003 (st), *Krings SC-2* (NCSC). **Newberry**: 1.3 mi W of Chappells, 16 Sep 1957 (fr), *C.R. Bell 9846* (NCU). **Oconee**: Chauga River, ca. 0.25 mi downstream from the junction of forest service route 748-D with the Chauga River, 17 Oct 1986 (fr), *J.D. Tobe 1442* (ILL). **Richland**: Congaree Swamp National Monument, 2.1 river mi downstream from boat landing at upstream boundary of CSNM, elev. ca. 100 ft, 26 Oct 1998 (fr), *J.B. Nelson 20224 with J.E. Cely, A. Thompson, H. Steele* (USCH); Old pasture on W side of S.C. 215, at Cedar Creek, 13 Aug 1979 (fr), *J.B. Nelson 1290* (FSU). **York**: Bullocks Creek on SC 907 (SW of Sharon), 19 Sep 1957 (fr), *H.E. Ahles 34604* (NCU).

TENNESSEE. *Specimens with flowers or both flowers and fruits.* **DeKalb**: Edgar Evins State Park, 36°03'53.3"N 85°47'18.2"W, 1 Jul 2002 (fl), *L.R. Phillipe 34311* (ILLS). **Hamilton**: Harrison Bay State Park, 23 Jul 2003 (fl), *Krings TN-1* (NCSC); Harrison Bay State Park, 23 Jul 2003 (fl, fr), *Krings TN-2* (NCSC); Harrison Bay State Park, 23 Jul 2003 (fl), *Krings TN-3* (NCSC); Harrison Bay State Park, 23 Jul 2003 (fl), *Krings TN-5* (FLAS, NCSC). **Knox**: Tennessee River bank, Cherokee farm, 12 Jul 1922 (fl), *A.R. Bechtel 10970* (NY); Along Northshore Dr., ca. 0.4 mi W of Ebenezer Road, 30 Jun 1989 (fl), *V.E. McNeilus 89-439* (TENN); Old Sevierville Pike, 20 Jun 1938 (fl), *A.J. Sharp 236* (TENN); Between Hardin Valley and Clinch River, 1 Jul 1958 (fl), *A.J. Sharp 24903* (TENN); Limestone barrens near Mascot, 11 Jul 1958 (fl), *A.J. Sharp 24927* (TENN); Limestone barrens near Mascot, 11 Jul 1958 (fl), *A.J. Sharp 24929* (TENN). **Marion**: Along river below Hales Bar Dam, 16 Jun 1948 (fl), *S. Fairchild, E. Clebsch, and A.J. Sharp 48-74* (TENN).

VIRGINIA. *Specimens with flowers or both flowers and fruits.* **City of Hampton:** Langley Research & Development Park, 5 Jul 1994 (fl), *P. Baldwin 601* (WILLI). **Charles City:** Bank of Chickahominy River, S of bridge, 5 Jul 1949 (fl), *B. Mikula 2303* (FLAS, WILLI). **Chesterfield:** Presquile, 24 Jun 1970 (fl), *M.F. Johnson 3375* (WILLI). **Gloucester:** “Catbird” Creek, off Carter’s Creek, on Rosewell property, 2 Jul 1975 (fl), *J.M. Greaves 486 with P.H. Wilson* (FLAS, WILLI); Kenney Building at Botetourt Elementary School in Gloucester GH, 17 Jun 1977 (fl), *J.M. Greaves 1816* (WILLI); Along Rt. 602, just N of James Store P.O., 9 Jul 1975 (fl), *J.M. Greaves 555* (WILLI). **Greensville:** 1 mi NW of Dahlia, 15 Jul 1949 (fl), *B. Mikula 2766* (WILLI); Ca. 1 mi N of St. Rt. 621 and 3.25 mi W of Skippers, elev. 140 ft., 27 Jun 1984 (fl), *T.F. Wieboldt 5135 with A. Wieboldt* (WILLI, WVA). **James City:** Jamestown Island, 14 Jul 1969 (fl), *L.E. Loetterle 188* (WILLI). **Powhatan:** 0.25 mi S of the James River, 1 mi E of Fine Creek, 28 Jun 1976 (fl), *C.M. Corcoran 744 with G.M. Diggs, Jr.* (WILLI). **Surry:** Hog Island Waterfowl Refuge, 3 Aug 1974 (fl), *D.M. Eggers Ware 5662a* (WILLI). **Sussex:** Along Nottoway River, SW of Homeville, 18 and 19 Jun 1939 (fl), *M.L. Fernald and B. Long 10399* (F). **York:** Ca. 0.25 mi S of Bellfield Plantation site, on S side of Yorktown Colonial Pkwy, 20 Jul 1971 (fl), *E.D. Sallé 432* (WILLI); Ca. 0.5 mi E of entrance to Ringfield picnic area, on S side of Yorktown Colonial Pkwy, 26 Jul 1971 (fl), *E.D. Sallé 465* (WILLI); Ca. 0.5 mi E of Bellfield Plantation site, on S side of Yorktown Colonial Pkwy, 28 Jul 1971 (fl, fr), *E.D. Sallé 485* (WILLI); Cheatham Annex Naval Supply Center, across from Cabin 261 near Cheatham Pond, 8 Jul 1975 (fl), *K. Kirkman 268* (FLAS, WILLI).

*Specimens with fruits only or sterile, but most likely var. suberosus based on distribution of flowering specimens (see Fig. 2).* **Albemarle:** Monticello, elev. 830 ft., “12-8-80” (fr),

*T.F. Wieboldt M-702* (WILLI). **Charles City**: Old Neck, Co. Rt. 627, NE of Mt. Airy, 31 Mar 1971 (fr), *D.M. Eggers Ware 3485* (WILLI). **Gloucester**: Rosewell site, 3 Oct 199? (fr), *J.H. Brown 821* (WILLI). **Goochland**: On Rt. 6, near Manakin, 24 Oct 1969 (fr), *M.F. Johnson 3041* (WILLI). **Isle of Wight**: Mogarts Beach, 18 Sep 1979 (fr), *L.L. Whitmarsh and D.M.E. Ware 669* (WILLI). **James City**: Jamestown Island, 5 Nov 1969 (fr), *L.E. Loetterle 594* (WILLI). **Prince Edward**: Buffalo River, W of Farmville on US 460, 16 Oct 1965 (fr), *H.E. Ahles 62973 with F. James* (NCU). **York**: Cheatham Annex Naval Supply Center, near Patrol Rd 1, 24 Oct 1975 (fr), *K. Kirkman 839 with G. Roe* (WILLI).

**Specimens sterile, with immature flowers, or only with fruits that could not be confidently referred to variety based on morphological characters or locality**

MISSISSIPPI. **Jackson**: Along Pascagoula River at Long Point, 15 Nov 1952 (fr), *R.L. Diener 781* (ILL). **Perry**: Ragland Hills, 15 Jul 1970 (fr – imm), *K.E. Rogers 3756 with R. Watson* (NCU); Pearces Creek, SE of Forest Service Road 311, opposite Road 311A in Camp Shelby Training Area 24, S4 T2N R11W, 22 Jul 1996 (fr), *S.W. Leonard 9577* (NCU – 2 sheets).

TENNESSEE. **Anderson**: Melton Hill Reservoir, 28 Jun 1961 (fl-imm), *W.H. Ellis 28829* (TENN). **Blount**: Great Smokey Mountains National Park, Tabcat Creek Watershed, 35.52097°N –83.98019°W, 7 Oct 2002 (fr), *D.T. Busemeyer, C. Carrol, M.A. Feist, R.L. Larimore, P.B. Marcum, L.R. Phillipe, and G. Spireas 1167* (ILLS); Beside US129, 5 mi N of Talassee, 17 Sep 1964 (fr), *R.D. Thomas s.n.* (TENN); Beside US129, 5 mi N of

Talassee, 17 Sep 1964 (fr), *R.D. Thomas 33258* (TENN). **Hamilton:** Behind the Tennessee Welcome Center along I-75, 26 Sep 1996 (fr), *V.E. McNeilus 96-1041* (TENN). **Knox:** Bank Tennessee River, near asylum, 17 Aug 1921 (fr), *A.R. Bechtel 10971*(NY); Melton Hill Reservoir, 2 Aug 1961 (st), *W.H. Ellis 28894* (TENN); West Knoxville, 3 Nov 1941 (fr), *A.J. Sharp 1696* (TENN - 2 sheets); Near Little Creek, 11 Nov 1962 (fr), *A.J. Sharp 30914* (TENN). **Marion:** Road up Big Fiery Gizzard Cove, 21 Aug “19380” (fr), *T.S. Patrick and M.E. Medley 1399* (TENN). **Washington:** Near Nolichucky River, Lamar community, 10 Oct 1953 (fr), *R.L. James 18244* (TENN).

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Environment and Conservation - Division of Natural Heritage, New Braunfels Department  
of Parks and Recreation (Texas).

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TABLE 1. Correlation between number of collections in fruit and year for the two varieties of *Gonolobus suberosus* (L.) R.Br. over the period 1920–2005.

var. *granulatus* ( $r^2 = 0.00001529$ )

ANOVA

	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>F</i>	<i>P value</i>
Regression	1	0.810689	0.810689	0.001285	0.971490095
Residual	84	52996.69	630.913		
Total	85	52997.5			

var. *suberosus* ( $r^2 = 0.009045$ )

ANOVA

	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>F</i>	<i>P value</i>
Regression	1	479.373	479.373	0.766732	0.383726965
Residual	84	52518.13	625.2158		
Total	85	52997.5			

TABLE 2. Correlation between number of collections with flowers and year for the two varieties of *Gonolobus suberosus* (L.) R.Br. over the period 1895–2005.

var. *granulatus* ( $r^2 = 0.230178$ )

ANOVA

	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>F</i>	<i>P value</i>
Regression	1	26231.13	26231.13	32.59125	9.94E-08
Residual	109	87728.87	804.852		
Total	110	113960			

var. *suberosus* ( $r^2 = 0.296614$ )

ANOVA

	<i>df</i>	<i>SS</i>	<i>MS</i>	<i>F</i>	<i>P value</i>
Regression	1	33802.17	33802.17	45.96476	6.45E-10
Residual	109	80157.83	735.393		
Total	110	113960			

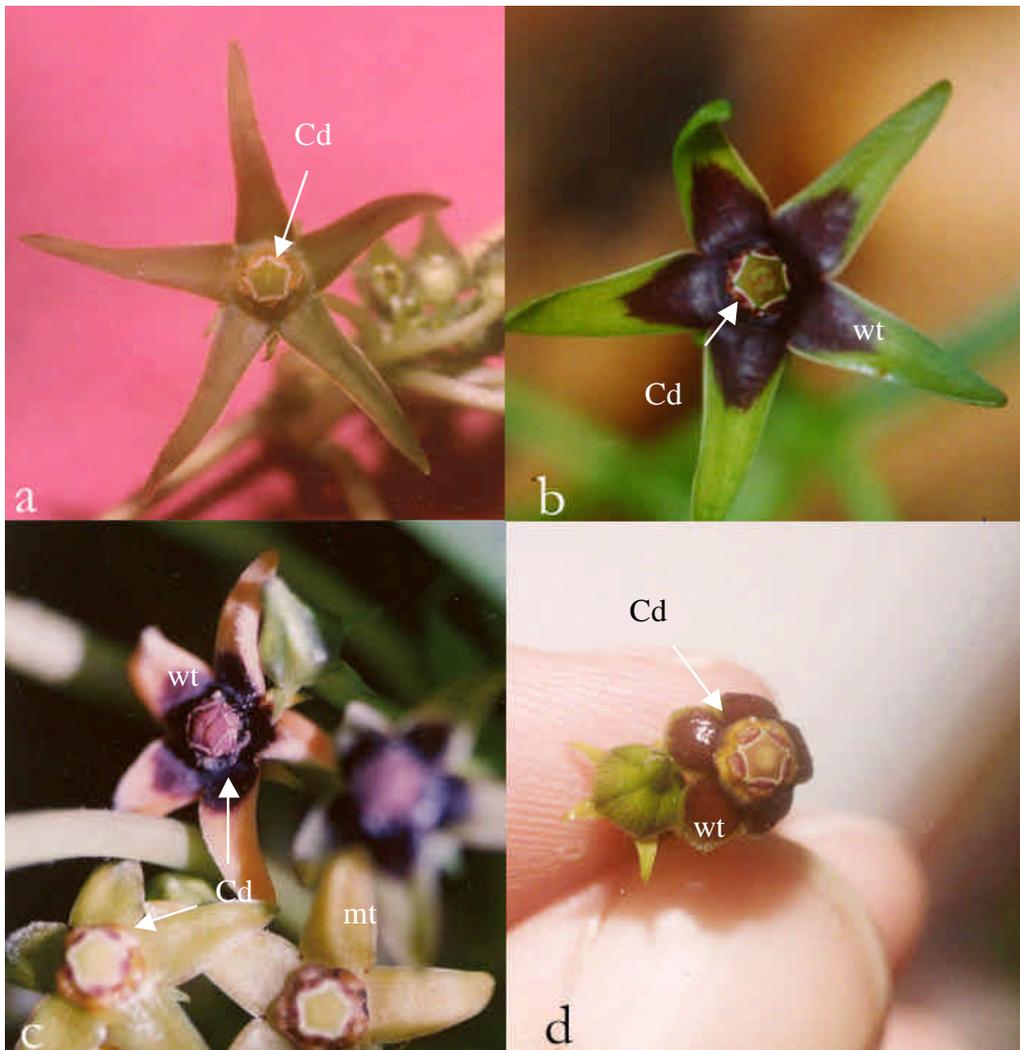


FIG. 1. Flowers of the varieties of *Gonolobus suberosus* (L.) R.Br.: a, var. *granulatus* (Comal Co., Texas); b, var. *suberosus* (Wake Co., North Carolina); c, var. *suberosus* (Newport News, Virginia); d, var. *suberosus* (Alachua Co., Florida). Note the dark purplish laminar dorsal anther appendage (Cd) of putative mutant (mt) and wildtype (wt) var. *suberosus* (b–c, arrowed) versus the yellow Cd of var. *granulatus* (a, arrowed). Putative mutant and wildtype flowers do not co-occur on the same individual vine. The orangish corolla lobes of the multi-colored flower in c is not unusual for a senescing flower.

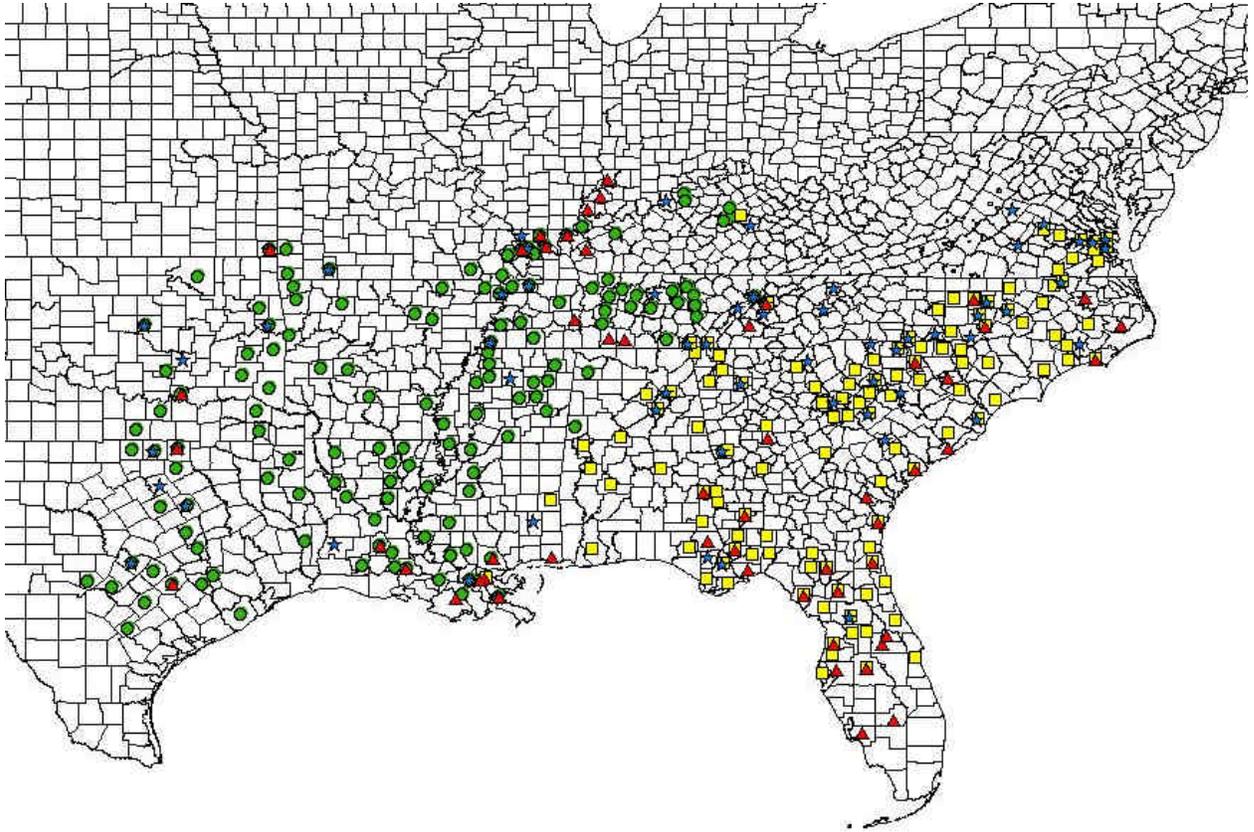
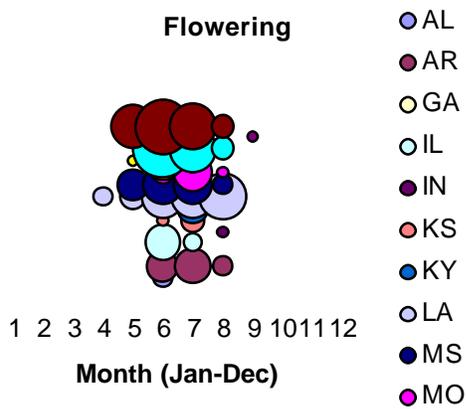
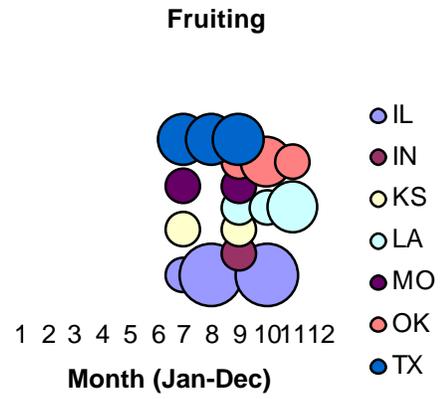


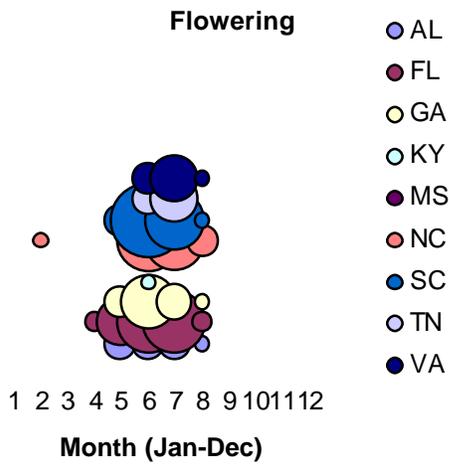
FIG. 2. Distribution of the varieties of *Gonolobus suberosus* (L.) R.Br. in North America. Specimens with flowers: green circles = var. *granulatus*; yellow squares = var. *suberosus*. Specimens lacking flowers: blue stars = specimens with follicles; red triangles = specimens sterile.



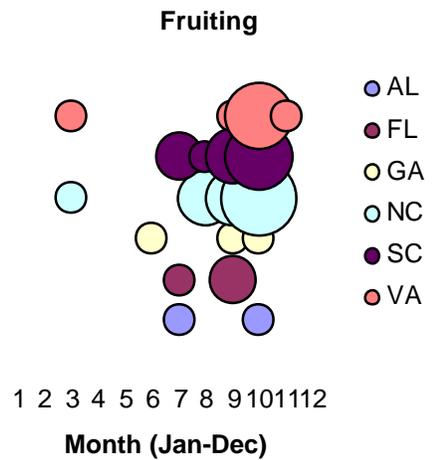
**Ai**



**Aii**



**Bi**



**Bii**

FIG. 3. Flowering and fruiting phenology of the varieties of *Gonolobus suberosus* (L.) R.Br. by state: Ai–ii, var. *granulatus*; Bi–ii, var. *suberosus*. The size of individual bubbles reflects the number of specimens collected in a particular month.

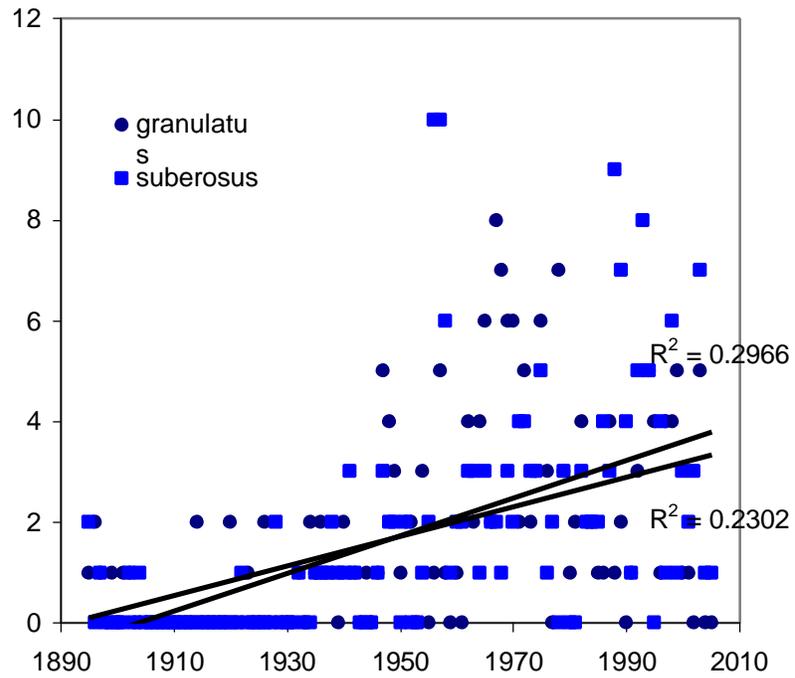


FIG. 4. Number of herbarium specimens with flowers (y-axis) versus year of collection (x-axis) over the period of 1895–2005 for the two varieties of *Gonolobus suberosus* (L.) R.Br.

## **Chapter IV**

### **Novelties in *Gonolobus* (Apocynaceae: Asclepiadoideae)**

#### **from the Lesser Antilles**

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**ABSTRACT.** Five new species of *Gonolobus* (Apocynaceae: Asclepiadoideae) are described from the Lesser Antilles: *G. absalonensis*, *G. dussii*, *G. iyanolensis*, *G. waitukubuliensis*, and *G. youroumaynensis*. The species exhibit distinct differences in floral characters, including the structure of corolline and gynostegial coronas. *Gonolobus martinicensis* is lectotypified. A key to *Gonolobus* in the Lesser Antilles is provided.

*Gonolobus* Michx. (Apocynaceae: Asclepiadoideae) is a New World genus comprising an estimated 100–150 species (Rosatti 1989; Mabberley 1997; Stevens 2001). The genus was erected by Michaux in 1803, based on a taxon from the southeastern United States – *Gonolobus suberosus* (L.) R.Br. Reveal and Barrie (1992) reviewed the complicated nomenclatural history of the type species and Krings and Xiang (2004, 2005) its taxonomy. The degree of variation in estimated species numbers in *Gonolobus* is largely the result of still poorly known tropical taxa and differences regarding generic limits. Woodson (1941) considered that the genus *Gonolobus* should contain plants characterized by only long, eglandular trichomes, laminar dorsal anther appendages (Cd sensu Kunze 1995), and smooth, angled or winged follicles, whereas *Matelea* Aubl. should contain plants characterized by glandular and eglandular trichomes, anthers lacking dorsal appendages, and muriculate follicles. Unconvinced that laminar dorsal anther appendages should serve as a generic character and citing examples of smooth [but not angled or winged] fruits in *Matelea*, Shinnery (1950) argued against Woodson's generic concept and later included twelve of Woodson's (1941) *Gonolobus* combinations in *Matelea* (Shinnery 1950, 1964). Taking a broader geographical perspective of generic morphology, Rosatti (1989) argued for renewed circumscription of *Gonolobus* based on the presence of laminar dorsal anther appendages. Most recently the concept of *Gonolobus* as characterized by short, capitate-glandular, short acicular, and long acicular trichomes, laminar dorsal anther appendages (typically), and smooth, winged follicles has been used by Stevens (2001, 2005). However, glandular hairs, although thought characteristic of *Matelea* by Woodson (1941), appear without circumscriptional value in the *Gonolobus-Matelea* question, being present in both the type of *Gonolobus* (i.e., *G. suberosus*) and numerous species lacking dorsal anther

appendages (Rosatti 1989; Krings, pers. obs.). The utility of the follicle character (primarily winged in *Gonolobus* vs. primarily muricate in *Matelea*) is also problematic. With greater collections since Woodson (1941), it has become clear that several taxa apparently lacking dorsal anther appendages bear winged instead of muricate follicles. Examples of such taxa include Bahaman *Matelea correllii* Spellman, Cuban *M. bayatensis* (Urb.) Woodson, *M. tigrina* (Griseb.) Woodson, *M. nipensis* (Urb.) Woodson, and *M. oblongata* (Griseb.) Woodson, and Hispaniolan *M. pauciflora* (Spreng.) Woodson (see also Krings 2005). Although fruit collections are not known, based on floral and vegetative morphology, putative sister species of some of these taxa, such as Cuban *M. acuminata* (Griseb.) Woodson (sister to *M. oblongata*?) and Jamaican *M. rhamnifolia* (Griseb.) Krings (sister to *M. nipensis*?) likely also bear smooth, winged follicles. Some of these taxa, such as *M. bayatensis*, *M. correllii*, *M. nipensis*, and *M. tigrina*, do not bear an erect staminal gynostegial corona (Cs sensu Kunze 1995), whereas others, such as *M. acuminata* and *M. oblongata* bear an intricate and very well-developed Cs. None share the prostrate gynostegial corona present in the type of *Gonolobus*, as well as many, though not all, species presently referred to the genus. The evolution of characters historically used to delimit genera in Gonolobinae, such as laminar dorsal anther appendages and various follicle morphologies, remains unknown and cannot be understood outside of a phylogenetic framework. However, the absence of a robust phylogeny should not prevent the description of new taxa that are morphologically distinct. Until additional data can suggest a better course of action, the presence of laminar dorsal anther appendages should continue to be used to delimit *Gonolobus* from *Matelea*. Such application is consistent

with numerous historic, as well as recent treatments (e.g., Rosatti 1989; Stevens 2001, 2005).

Howard (1989) provided the most recent treatment of *Gonolobus* for the Lesser Antillean flora and recognized two species—*G. denticulatus* (Vahl) W.D. Stevens and *G. martinicensis* Decne.—unfortunately reversing them in key and description (though not in illustration).

The generic placement of *G. denticulatus* has been uncertain and recent authors have placed the species within *Matelea* (Fontella and Schwarz 1981; Stevens 2001). This position is followed here as well. The taxon appears to lack laminar dorsal anther appendages, but bears winged follicles. The corollas of *M. denticulata* (Vahl) Fontella & E.A. Schwarz are quite different from other Lesser (and Greater) Antillean species bearing laminar dorsal anther appendages in being distinctly reticulate (at least when dried) and bearing a very fine pubescence on the adaxial surface. This pubescence is much coarser in the species referred to *Gonolobus* in the Antilles (which agree much more with the generic type: *Gonolobus suberosus*). The corolla lobes of *M. denticulata* are ovate to oblong-ovate and 5–11.2 mm wide (vs. lanceolate or narrowly lanceolate and 1.8–3.7 mm wide in Lesser Antillean *Gonolobus*). In the West Indies, *Matelea denticulata* is known only from Grenada (and perhaps St. Thomas—*Finlay 1841, P!*—although there may have been a label mix-up). Additional evidence from molecular data is needed to clarify its generic placement.

*Gonolobus martinicensis* was originally described by Decaisne based on specimens from Martinique. Subsequent workers recognized the species as occurring also in Dominica, Guadeloupe, and St. Vincent (Urban 1919; Howard 1989; Fournet 2002). However, recent

study revealed that *G. martinicensis* of prior authors actually includes six distinct entities, treated here as species. A revised key to *Gonolobus* in the Lesser Antilles is provided below and the five novelties are described. *Gonolobus martinicensis* is lectotypified. The position of the species within *Gonolobus* and their closest relatives in South America remain unknown, pending additional molecular studies.

#### KEY TO *GONOLOBUS* IN THE LESSER ANTILLES

Corona terminology (e.g., Ca, Cd, Ci, Cs) follows Liede and Kunze (1993) and Kunze (1995).

1. Faucal annulus of corolla (corolline corona or Ca) a conspicuously raised (to 0.5 mm tall), uninterrupted ring, pubescent along the entire rim or only opposite each corolla lobe sinus; gynostegial corona appearing densely folded apically, basally fused into a ring, obscured from view by the faucal annulus; gynostegial stipe 1–1.5 mm tall; Cd emarginate; Dominica..... *G. waitukubuliensis*
1. Faucal annulus of corolla (corolline corona or Ca) reduced to an interrupted ridge, distinct only opposite each corolla lobe sinus, tufted pubescent to glabrate or, if uninterrupted, then very shallow, mostly 0.08 mm tall, and glabrous, except to 0.16 mm tall and tufted pubescent opposite each corolla lobe sinus; gynostegial corona neither apically densely folded nor basally obscured by a faucal annulus; gynostegial stipe = 1 mm tall; Cd rounded or truncate (emarginate in *G. absalonensis*) .....2.
2. Interstaminal gynostegial corona double (i.e., a narrower upper ligulate corona lobe occurring on top of the broader lower corona) .....3.

2. Interstaminal gynostegial corona single .....4.
3. Corolla robust, base of corolla tube subcampanulate, as broad as long or broader than long; sepals 6.1–6.7 mm x 1.6–1.8 mm; corolla lobes 10.2–17.3 mm x 2.7–4.8 mm; horizontal length of lower interstaminal gynostegial corona (Ci) from base of stipe to lobe apex 1.1–1.4 mm, narrow upper ligulate corona lobe of the Ci abruptly ending in a scooped out depression before reaching the stipe base, dorsally ridged; St. Lucia .....*G. iyanolensis*
3. Corolla slender, base of corolla tube elongate-campanulate, distinctly longer than broad; sepals 4.3–6.7 mm x 1–1.2 mm; corolla lobes 9.7–11.4 mm x 2–3.5 mm; horizontal length of interstaminal gynostegial corona (Ci) from base of stipe to lobe apex = 0.7 mm, narrow upper ligulate corona lobe of the Ci ending essentially at the stipe base, dorsally plane or sometimes slightly raised into a shallow bump; Martinique ..... *G. martinicensis*
4. Gynostegial stipe with a single tooth ca. 0.2 mm long below each anther; St. Vincent....  
.....*G. youroumaynensis*
4. Gynostegial stipe edentate .....5.
5. Corolla lobes to 6.7 mm long, abaxial surface glabrous; interstaminal gynostegial corona (Ci) smooth, lacking raised bumps; laminar dorsal anther appendages (Cd) emarginate; Martinique.....*G. absalonensis*
5. Corolla lobes = 10 mm long, abaxial surface coarsely pubescent; interstaminal gynostegial corona (Ci) with two distinctly raised and rounded mounds; laminar dorsal anther appendages (Cd) truncate or rounded.....*G. dussii*

*Gonolobus absalonensis* Krings, sp. nov. (Fig. 1).—TYPE: MARTINIQUE. Absalon, Pres la cascade, Mai 1910 (fl), Herb. d'Alleizette *s.n.* [4801?] (holotype: L!).

Species nova *Gonolobus* differt a *G. dussii* Krings, *G. iyanolensis* Krings, *Gonolobus martinicensis* Decne., *G. youroumaynensis* Krings et *G. waitukubuliensis* Krings floribus parvis, tumulis interstaminealis deficiens, corona interiora dorso antherarum adnata emarginata.

Herbaceous perennial vines. *Stems* glabrate to very sparsely pubescent, both short, capitate-glandular, and longer, sharp, eglandular trichomes present, the latter retrorse immediately below the nodes or antrorse-appressed along an indistinct, horizontal ridge between two opposite petioles and/or just above the node, to 0.5 mm long; nodes sparsely pubescent, gland field apparently absent. *Leaf* blades ovate to oblong-ovate, (3.4)6.6–8.6 cm x (1.3)3.4–4.5 cm, adaxial surface sparsely strigose, abaxial surface more densely strigose with sharp, eglandular trichomes scattered along the major and minor veins, glandular emergences from the surface absent or very sparse, apices abruptly acuminate with the acumen narrowly obtuse, to 0.7 cm long, bases deeply or shallowly cordate, margins entire; petioles 3.6–5.7 cm long, glabrous or very sparsely pubescent on all sides, capitate trichomes to 0.1 mm long, sharp, eglandular trichomes ca. 0.3 mm long, antrorsely-appressed or -ascending; colleters 2, 0.5–0.9 mm long. *Inflorescences* racemiform, peduncles 4.1–5.4 cm long, glabrate to very sparsely pubescent, capitate, as well as sharp, eglandular trichomes present, the latter antrorsely-appressed or -ascending, found primarily

at the apex, ca. 0.3 mm long; pedicels 1.5–1.7 cm long, more pubescent at the apex than at the base, capitate-glandular trichomes ca. 0.05 mm long, longer, sharp, eglandular trichomes antrorsely-appressed or –ascending, ca. 0.13 mm long. *Calyx* lobes 5, lanceolate, 1.95 mm x 1 mm, pubescent mostly at the base, sharp, eglandular trichomes, antrorsely-ascending or -appressed, to 0.25 mm long, apices narrowly obtuse or acute, margins glabrous; colleters 1 per sinus. *Corolla* lobes 5, lance-ovate, 4.8–6.7 mm x 2.5–2.8 mm, slightly lobed at the base, a glandular swelling frequently present in the sinus, adaxial glabrous, abaxial surface glabrous; faucal annulus (corolline corona or Ca) a shallow, uninterrupted ring, ca. 2.5 mm diam, ca. 0.08 mm tall, glabrous except where raised opposite each corolla lobe sinus, then to ca. 0.16 mm tall and short hispid; gynostegial corona of fused staminal (Cs) and interstaminal parts (Ci), single, 5-lobed, erect- or prostrate-undulating, 0.4–0.6 mm tall; gynostegial head ca. 3.2 mm diam, stipe 0.3–0.5 mm long, not toothed, anther guiderails without appendages, laminar dorsal anther appendages (Cd) 0.48–0.7 mm x 0.5–0.8 mm, emarginate; corpuscula ca. 0.18 mm long, pollinaria borne horizontally, ovate, ca. 0.9 mm x 0.3 mm. *Follicles* unknown.

***Distribution and Habitat.*** *Gonolobus absalonensis* is apparently endemic to Martinique (Fig. 2). Its habitat is poorly known, but likely primarily middle elevation rainforest based on the requirements of congeners in the Lesser Antilles. The type was apparently collected near a waterfall.

***Etymology.*** The epithet is derived from the locality of the type collection—Absalon, Martinique.

***Observations.*** *Gonolobus absalonensis* is the smallest-flowered Lesser Antillean *Gonolobus* species (corolla lobes reaching only to 6.7 mm) and one of three *Gonolobus*

species apparently endemic to Martinique. It can be distinguished from other *Gonolobus* species on Martinique by the following key:

1. Corolla lobes to 6.7 mm long, both surfaces glabrous; interstaminal gynostegial corona (Ci) single, smooth, lacking raised bumps; laminar dorsal anther appendages (Cd) emarginate  
..... *G. absalonensis*
1. Corolla lobes > 9.5 mm long, either or both surfaces pubescent; interstaminal gynostegial corona (Ci) double or if single, then with defined raised bumps medially; laminar dorsal anther appendages (Cd) rounded or truncate..... 2.
2. Interstaminal gynostegial corona double (i.e., a narrower upper ligulate corona lobe occurring on top of the broader lower corona)..... *G. martinicensis*
2. Interstaminal gynostegial corona single ..... *G. dussii*

*Gonolobus dussii* Krings, sp. nov. (Fig. 3).—TYPE: GUADELOUPE. Chemin de la Soufriere, alt. 500 m, *Quentin* 732 (holotype: P!-fl; isotype: GH!-fl)

Species nova *Gonolobus* haec ab *Gonolobus martinicensis* Decne. differt floribus rotatis vel subcampaniformis, corona simplici et a *G. youroumaynensis* Krings tumulis interstaminealis praesentia.

Herbaceous perennial vines. *Stems* glabrate to very sparsely pubescent, both short, capitate-glandular, and longer, sharp, eglandular trichomes present, the latter retrorse

immediately below the nodes or antrorse-appressed along an indistinct, horizontal ridge between two opposing petioles and/or just above the node, to 0.5 mm long; nodes pubescent or glabrous, gland field apparently absent. *Leaf* blades ovate to oblong-ovate, (3.3–)5.7–10.7 cm x (0.9–)2.5–6.1 cm, adaxial surface glabrate or sparsely strigose, abaxial surface glabrate or more densely strigose with sharp, eglandular trichomes scattered along the major and minor veins, glandular emergences from the surface absent or very sparse, apices gradually acuminate with the acumen narrowly obtuse, to 2 cm long, bases deeply or shallowly cordate, margins entire; petioles (1.3–)2.1–5.5 cm long, glabrous or sparsely pubescent on all sides, capitate trichomes to 0.09 mm long, sharp, eglandular trichomes 0.3–0.4 mm long, mostly antrorsely appressed or ascending (some spreading and a very few retrorse); colleters 2–3, 0.4–0.6 mm long. *Inflorescences* racemiform, peduncles 0.7–2.3 cm long, glabrate to very sparsely pubescent, capitate, as well as sharp, eglandular trichomes present, the latter antrorsely-appressed or -ascending, found primarily at the apex, ca. 0.3 mm long; pedicels 1.8–2.2 cm long, more pubescent at the apex than at the base, capitate-glandular trichomes ca. 0.08 mm long, longer sharp, eglandular trichomes antrorsely-appressed or -ascending, ca. 0.3 mm long. *Calyx* lobes 5, sublanceolate to elongate triangular (widest at or just above the base), 3.9–5.8 mm x 1–1.5 mm, coarsely pubescent at the base and variously toward the apex, trichomes antrorsely-appressed or -ascending, to 0.5 mm long, apices obtuse to narrowly rounded, margins glabrous; colleters 1 per sinus. *Corolla* lobes 5, narrowly lanceolate to elongate triangular, (10–)12–17 mm x 3.2–3.7 mm, slightly overlapping at the base, a glandular swelling frequently present in the sinus, adaxial surface glabrous, abaxial surface with coarse, sharp, eglandular trichomes, antrorsely-appressed or -ascending, particularly at the base and variously toward the apex,

ca. 0.36 mm long; faucal annulus (corolline corona or Ca) interrupted, a distinctly raised ridge opposite each corolla lobe sinus, short-hispid or glabrate; gynostegial corona of fused staminal (Cs) and interstaminal parts (Ci), single, erect-undulating, two distinctly raised and rounded mounds borne in the interstaminal position; gynostegial head 2.3–2.4 mm diam, stipe ca. 0.45 mm long, not toothed, anther guiderails without appendages, laminar dorsal anther appendages (Cd) ca. 0.8 mm wide, rounded or emarginate; corpuscula 0.18–0.3 mm long, pollinaria borne horizontally, ovate, ca. 0.5–1 mm x 0.25–0.35 mm. Follicles unknown.

***Distribution and Habitat.*** *Gonolobus dussii* occurs in Guadeloupe and Martinique (Fig. 2). Its habitat is not well known, but it appears to have been collected from riversides and at mid-elevations (480–500 m).

***Etymology.*** The specific epithet honors Pere Duss, whose collections of the species are at once the oldest and broadest geographically.

***Additional Specimens Examined.*** GUADELOUPE. Bord de la riviere Noire, 29 Jun 1895 (fl), *Pere Duss* 3775 (MO!-fragment, NY!); Porrite-Noire, 20 Oct 1895 (fl), *Pere Duss* 3714 (NY!-2 sheets). MARTINIQUE. Environs a St. Pierre, 1884 (fl), *Pere Duss* “1862, 4565” (NY!); Porrite (sp?)-Fine, pres de la riviere Calabre, April 1900 (fl), *Pere Duss* 4565 (NY!).

***Observations.*** The numbering of *Duss* “1862, 4565” (NY) would seem to indicate mixed material, however the elements mounted on the sheet clearly belong to a single gathering from a single location. Although two segments of stem and associated leaves and flowers are present, they are naturally intertwined and not disparate. Intertwining of multiple stems is not infrequent among ramets of *Gonolobus* species, as well as other vines. Interestingly,

*Duss 4565* (NY) is comprised of two separately mounted elements, which makes one wonder whether the labels for the specimens at NY currently labelled *Duss “1862, 4564”* and *Duss 4565* were mixed up. However, *Duss “1862, 4565”* (NY) also contains seeds of unknown provenance in its fragment pocket, which may be the material originally associated with *1862*.

*Gonolobus dussii* can be distinguished from *G. youroumaynensis* of St. Vincent by the short pedicel trichomes, the edentate stipe, and the adaxially glabrous corolla lobes. The gynostegial coronas of the *G. absalonensis*, *G. dussii*, and *G. youroumaynensis* are most similar to each other among Lesser Antillean *Gonolobus* species, but *G. dussii* uniquely exhibits two distinctly raised and rounded mounds in the interstaminal position (Fig. 3). The mounds appear very close and near ridge-like in Martinique specimens, as well as *Duss 3775* of Guadeloupe. Additional collections are needed to determine the extent of variation in the coronas and to evaluate whether additional taxa are represented.

*Gonolobus iyanolensis* Krings, sp. nov. (Fig. 4).—TYPE: ST. LUCIA. Gros Piton, “9/8/76” (fl), *Roger Graveson 107* (holotype: GH!).

Species nova *Gonolobus* distinguibili a *Gonolobus martinicensis* Decne. floribus robustis, basibus subcampaniformis, tubis brevibus, sepalis longioribus.

Herbaceous perennial vines. *Stems* glabrous or glabrate, both short, capitate-glandular, and longer, sharp, eglandular trichomes present, the latter particularly at nodes and to 1.2 mm long, mostly retrorse or spreading, but antrorse-appressed along an indistinct,

horizontal ridge between two opposing petioles; nodes pubescent or glabrous in age, gland field sometimes present. *Leaf* blades ovate to oblong-ovate, to 8 cm x 5.4 cm, adaxial surface glabrous, abaxial surface glabrous or with sharp, eglandular trichomes scattered along the major veins, glandular emergences from the surface present, apices obtuse or short-acuminate with the acumen obtuse, bases cordate, margins entire; petioles to 6.2 cm long, glabrous or glabrate, capitate-glandular trichomes very sparse if present, sharp, eglandular trichomes near apex if present, to 0.9 mm long; colleters 2–4, 0.37–0.65 mm long. *Inflorescences* racemiform, peduncles 2.1–2.8 cm long, glabrous or glabrate, sharp, eglandular hairs antrorsely-appressed or -ascending, most pronounced near apex, ca. 0.7 mm long; pedicels 2.8–3.1 cm long, glabrate, capitate-glandular trichomes scattered throughout or only near the apex, ca. 0.09 mm long, longer, sharp, eglandular hairs antrorsely- appressed or -ascending, occurring only near the apex, 0.3–0.9 mm long. *Calyx* lobes 5, lanceolate (widest distinctly above the base, ca. 1.5–2 mm above base), 6.1–6.6 mm x 1.6–1.8 mm, glabrous or glabrate with the few trichomes present, coarse, antrorsely-ascending or -appressed, to 0.4 mm long, apices obtuse, margins glabrous; colleters 1 per sinus. *Corolla* lobes 5, lanceolate, 10.2–17.3 mm x 2.7–4.8 mm, slightly lobed at the base, a glandular swelling frequently present in the sinus, adaxial surface pubescent along the right half, trichomes flat, ribbon-like, 0.18–0.26 mm long, abaxial surface glabrous; faucal annulus (corolline corona or Ca) interrupted, a distinctly raised ridge, opposite each corolla lobe sinus, short hispid; gynostegial corona of fused staminal (Cs) and interstaminal parts (Ci), double, 5-lobed, prostrate, narrow upper ligulate corona lobe of the Ci appressed to the lower, dorsally ridged; gynostegial head ca. 2.5 mm diam, stipe ca. 0.23 mm long, not toothed, anther guiderails apparently without appendages, laminar dorsal anther appendages

(Cd) 0.5–0.6 mm wide, rounded or truncate; corpuscula 0.16–0.18 mm long, polliniaria borne horizontally, ovate, ca. 0.5–0.7 mm x 0.25–0.35 mm. *Follicles* ovoid, 10–11.6 cm x 3.3–4 cm, 5-winged, appearing glabrous, but with minute papillae or capitate trichomes evident at high magnification; seeds pyriform, compressed, not plano-convex, 9–9.4 mm x 4.2–5.8 mm, glabrous, margins dentate, coma to 3.7 mm long.

***Distribution and Habitat.*** *Gonolobus iyanolensis* is apparently endemic to St. Lucia (Fig. 2). An established population occurs on Gros Piton. Roger Graveson (pers. comm.) noted having seen vines away from the Pitons, but that they have not established themselves well. Woodland boundaries and recent forest openings appear to be the preferred habitat.

***Etymology.*** The epithet is derived from Iyanola (eye-a-NO-la), an Arawak name for St. Lucia (Winer, pers. comm.).

***Additional Material Examined.*** ST. LUCIA. Chassin, edge of clearing, alt. 600 ft, 7 Jan 1987 (fr), *Slane 1056* (GH!); Soufriere, Gros Piton summit, facing Soufriere, semi-open, sunny, rocky spot, climbing on shrubs, elev. ca. 750 m, 13° 48.612' N 61° 04.527' W, herbaceous vine (3 m), green flowers, white latex, 5 Jul 2005 (fl), *Johnny 57 with Samuel and Sealys* (UPRRP!); Soufriere, Gros Piton summit, facing Soufriere, on shrubs in open, sunny spot, elev. ca. 800 m, 13° 48.689' N 61° 03.439' W, herbaceous vine (3 m), greenish petals, white latex, 13 Sep 2005 (fl), *Graveson 1248 with Smith* (UPRRP!); Gros Piton, seasonal deciduous woods, elev. ca. 1300 ft., 11 Mar 2006 (fl), *Krings 1373 with Graveson and Smith* (NCSC!).

***Observations.*** Roger Graveson (pers. comm.) noted that the collection date is incorrect on the label of *Graveson 107* (GH) and should instead be 9 Aug 1996. *Gonolobus iyanolensis*

is immediately recognizable among Lesser Antillean *Gonolobus* species by its double interstaminal gynostegial corona (Ci). The only other species that shares this corona type in the area is *G. martinicensis*. (Fig. 5). In contrast to the robust-flowered *G. iyanolensis*, *G. martinicensis* exhibits distinctly more slender flowers with elongate-campanulate bases (ca. 2 mm long) that are longer than wide (as wide as long or wider than long in *G. iyanolensis*) and a narrower gynostegial corona (see key). The distinct dorsal ridge of the narrow upper ligulate corona lobe of the Ci in *G. iyanolensis* has also not been seen in *G. martinicensis*, which is either plane in the homologous position or exhibits a slightly raised bump.

***Gonolobus waitukubuliensis*** Krings, sp. nov. (Fig. 6).—TYPE: DOMINICA. In sylvis ad Laudat, Mai 1882 (fl), *Eggers 728* (holotype: HBG! – 2 sheets; isotypes: FR!, G!, GH!, JE!, M!, P!, W!, Z!)

Species nova *Gonolobus* differt a *G. absalonensis* Krings, *G. dussii* Krings, *G. iyanolensis* Krings, *Gonolobus martinicensis* Decne. et *G. youroumaynensis* Krings annulis faucetibus completis, stipite gynostegio longiore.

Herbaceous perennial vines. *Stems* glabrous or glabrate, both short, capitate-glandular, and longer, sharp, eglandular trichomes present, the latter particularly at nodes and to 0.64 mm long, mostly retrorse or spreading, but antrorse-appressed along an indistinct, horizontal ridge between two opposing petioles and/or just above the node; nodes pubescent or glabrous in age, gland field sometimes present. *Leaf* blades ovate to oblong-

ovate, (2.1–)6.7–10.4 cm x (0.9–)3.2–5.7 cm, adaxial surface glabrate or sparsely strigose, abaxial surface glabrate or more densely strigose with sharp, eglandular trichomes scattered along the major and minor veins, glandular emergences from the surface present (less common in specimens from Martinique), apices gradually or abruptly acuminate with the acumens acute, to 1.8 cm long, bases deeply or shallowly cordate (rarely rounded, but then other leaves present with cordate bases), margins entire; petioles (0.9–)2.2–5.4 cm long, glabrate or sparsely pubescent primarily along the adaxial side and near the apex on the abaxial side, trichomes mostly capitate, to 0.09 mm long, with some short, sharp, eglandular trichomes mixed in, 0.2–0.4 mm long; colleters 2, (0.4–)0.7–0.9 mm long.

*Inflorescences* racemiform, peduncles 4.1–5.2 cm long, glabrous or very sparsely pubescent with both capitate and sharp, eglandular hairs present, the latter antrorsely-appressed or –ascending, most pronounced near apex, ca. 0.3 mm long; pedicels 1.4–3.4 cm long, pubescence pronounced at apex and essentially absent elsewhere or sparsely to densely, relatively evenly pubescent from apex to base, capitate-glandular trichomes ca. 0.08 mm long, longer, sharp, eglandular hairs antrorsely- appressed or -ascending, ca. 0.3 mm long.

*Calyx* lobes 5, sublanceolate to elongate triangular (widest at or just above the base), 2.2–5.3 mm x 0.8–1.4 mm, glabrous or pubescent primarily at the base and variously toward the apex, trichomes, if present, antrorsely-ascending or -appressed, to 0.27 mm long, apices obtuse to narrowly rounded, margins glabrous; colleters 1 per sinus. *Corolla* lobes 5, narrowly lanceolate to elongate triangular, 4.2–11.2 mm x 1.8–3.4(–3.7) mm, slightly lobed at the base, a glandular swelling frequently present in the sinus, adaxial surface glabrous, abaxial surface glabrous; faucal annulus (corolline corona or Ca) a distinctly raised ring, ca. 0.5 mm high, short-hispid along the entire rim or only opposite each corolla lobe sinus;

gynostegial corona of fused staminal (Cs) and interstaminal (Ci) parts, single, fused at the base into an erect ring, 5-lobed, lobes appearing strongly folded; gynostegial head 2.8–3.14 mm diam, stipe 1–1.5 mm long, not toothed, anther guiderails apparently without appendages, laminar dorsal anther appendages (Cd) 0.6–0.9 mm wide, emarginate or truncate; corpuscula 0.14–2 mm long, pollinaria borne horizontally, ovate, ca. 0.6–0.85 mm x 0.3–0.38 mm. *Follicles* unknown.

***Distribution and habitat.*** *Gonolobus waitukubuliensis* is apparently endemic to Dominica (Fig. 2). It has been found primarily in middle elevation rainforests (ca. 609–1067 m; 2000–3500 ft). On a recent expedition, it was not found in the high elevation *Clusia* dominated communities around Boeri Lake or Freshwater Lake and only rarely in a *Clusia* transitional community on Morne Diablotins. It was not found along the trail to Middleham Falls, Titou Gorge, or Emerald Pool. The seasonal deciduous, lower elevation forests on Dominica's lee appear too dry. Like most West Indian *Gonolobus* taxa, *G. waitukubuliensis* appears to require small gaps in mature forests. It does not appear to be able to compete in large gaps or roadside edges in which other vines quickly become dominant. It is rather infrequent to rare, especially in mature forests with few gaps.

***Etymology.*** The epithet is derived from Waitukubuli (why-too-KOO-boo-lee), a Carib name for Dominica.

***Additional Specimens Examined.*** DOMINICA. Mar 1882 (fl), *Eggers s.n.* (US!); July 1882 (fl), *Eggers 1100* (K!); May 1882 (fl), *Eggers 1700* (MO!); *Imray 263* (K!-fl); St. John/St. Peter, Hiking trail to Morne Diablotins, ca. 2000–2500 ft elev., forest rather open and marked by large diameter trees, 3 May 2006 (st), *Krings 1375, 1376, 1377* (NCSC!); St. John/St. Peter, Syndicate hiking trail, trailside at edge of small gap in mature forest of

large diam *Sloanea* spp., climbing to 1.5 m, 3 May 2006 (st), *Krings 1378* (NCSC!); St. John/St. Peter, Hiking trail to Morne Diablotins, ca. 2000–2500 ft elev., in small gap, climbing on *Miconia* sp., to 2 m, about 10 seedlings observed in gap, rainforest of 60–80 ft tall trees, 4 May 2006 (st), *Krings 1380* (NCSC!); St. John/St. Peter, Hiking trail to Morne Diablotins, ca. 2000–2500 ft elev., in small gap (same as *Krings 1380*), climbing to 20 ft, twining around 10 cm dbh liana, rainforest of 60–80 ft tall trees, 4 May 2006 (st), *Krings 1381* (NCSC!); St. John/St. Peter, Hiking trail to Morne Diablotins, small gap in small stature forest, below the *Clusia* dominated zone, but with an occasional *Clusia* present, 4 May 2006 (st), *Krings 1382, 1383, 1384* (NCSC!); St. John/St. Peter, Hiking trail to Morne Diablotins, *Clusia* dominated, low stature forest, at opening in trail with westward vista of Portsmouth and Cabrits, 4 May 2006 (st), *Krings 1385* (NCSC!); St. John/St. Peter, Hiking trail to Morne Diablotins, right side of trail (when facing uphill), just below *Clusia* dominated zone, canopy ca. 20 ft tall, vine climbing into canopy, 4 May 2006 (st), *Krings 1386* (NCSC!); St. Joseph, En Haut Jean, alt. 2750 ft., 24 Jun 1965 (fl), *G.L. Webster 13505* (BM!, US!).

**Observations.** *Gonolobus waitukubuliensis* is immediately recognizable among Lesser Antillean *Gonolobus* species by the combination of a distinctly raised, completely circular faucal annulus (ca. 0.5 mm tall), an erect gynostegial corona that appears quite folded apically, and a relatively tall gynostegial stipe (1–1.5 mm). It shares with *G. absalonensis*, *G. iyanolensis*, and sometimes *G. martinicensis*, the absence of hairs from the abaxial corolla lobe surface. The trichomes of the pedicel are fine and not as long (ca. 0.3 mm) as in *G. iyanolensis* (0.3–0.9 mm).

*Gonolobus youroumaynensis* Krings, sp. nov. (Fig. 7).—TYPE: ST. VINCENT. Orange Hill Estate, roadbank in banana and pigeon pea plantations, uphill from fork in road to the C.W.S.A. water intake site, Kiss-me, 14 Mar 2006 (fl), *Krings 1374 with Springer* (holotype: NCSC!; isotypes: GH!, K!, NY!, US!, P!).

Species nova *Gonolobus corona* *G. dussii* Krings similis, differt stipitibus dentatis.

Herbaceous perennial vines. *Stems* glabrate to pubescent, both short, capitate-glandular, and longer, sharp, eglandular trichomes present, the latter throughout, spreading, or retrorse immediately below the nodes and to 1.2 mm long, or antrorse-appressed along an indistinct, horizontal ridge between two opposing petioles and/or just above the node; nodes pubescent, gland field apparently absent. *Leaf* blades ovate to oblong-ovate, (3.0–)5.4–9.6 cm x (1.2–)2.4–6.3 cm, adaxial surface glabrate or sparsely strigose, abaxial surface glabrate or more densely strigose with sharp, eglandular trichomes scattered along the major and minor veins, glandular emergences from the surface present, apices gradually or abruptly acuminate with the acumen narrowly obtuse, to 1.5 cm long, bases deeply or shallowly cordate, margins entire; petioles (1.2–)2.7–5.3 cm long, spreading pubescent on all sides, some trichomes capitate, to 0.09 mm long, but mostly sharp, eglandular, 1–1.2 mm long; colleters 2–4, 0.35–1 mm long. *Inflorescences* racemiform, peduncles 0.7–3.1 cm long, capitate, as well as sharp, eglandular trichomes present, the latter mostly spreading, but also some antrorsely-appressed or -ascending, distributed throughout, 0.7–0.9 mm long; pedicels 1.3–1.8 cm long, relatively evenly pubescent from apex to base, capitate-glandular trichomes ca 0.08 mm long, longer, sharp, eglandular trichomes mostly

spreading, but some antrorsely-appressed or -ascending, ca. 0.9 mm long. *Calyx* lobes 5, sublanceolate to elongate triangular (widest at or just above the base), 3.8–5.8 mm x 1–1.3 mm, densely and coarsely pubescent at the base and variously toward the apex, trichomes spreading and antrorsely appressed or -ascending, to 0.8 mm long, apices obtuse to narrowly rounded, margins ciliate or glabrate; colleters 1 per sinus. *Corolla* lobes 5, narrowly lanceolate to elongate triangular, (7.5–)8.7–10.1 mm x 1.9–3.1 mm, slightly lobed at the base, a glandular swelling frequently present in the sinus, adaxial surface pubescent on the right half, trichomes capitate, ca. 0.1 mm long, abaxial surface pubescent with coarse, sharp, eglandular, antrorsely-appressed or -ascending trichomes, particularly at the base and variously toward the apex, 0.36–0.5 mm long; faucal annulus (corolline corona or Ca) interrupted, a raised bump or indistinct ridge opposite each corolla lobe sinus, pubescent or glabrous; gynostegial corona of fused staminal (Cs) and interstaminal (Ci) parts, prostrate-undulating, single, a small bump borne near the base in the interstaminal position; gynostegial head 2.8–3.95 mm diam, stipe 0.48–0.7 mm long, bearing a single tooth ca. 0.2 mm long below each anther, anther guiderails without appendages, laminar dorsal anther appendages (Cd) ca. 0.5 mm wide, rounded or truncate; corpuscula 0.2–0.23 mm long, pollinaria borne horizontally, ovate, 0.6–0.9 mm x 0.32–0.45 mm. Follicles unknown.

***Distribution and habitat.*** *Gonolobus youroumaynensis* is apparently endemic to St. Vincent (Fig. 2). It occurs on the windward side of the island at the foot of La Soufriere in the Orange Hill Estate area. Vines were found growing along the road to the water intake amidst banana and pigeon pea plantations. Vines were not found along the trail to the

crater of La Soufriere. However, only a half day was spent searching this trail and they could have been overlooked.

**Etymology.** The epithet is derived from Youroumayn (YOO-roo-MAYN), a Kalina name for St. Vincent (Divonne 1998; Winer, pers. comm.).

**Additional Specimens Examined.** ST. VINCENT. Mar 1890 (fl), *H.H. and G.W. Smith* 382 (BM!, E!, GH!, K!, NY!); Orange Hill Estate, 10 Feb 1980 (fl), *R.A. Howard 19584* (BM!, GH!, NY!, US!).

**Observations.** *Gonolobus youroumaynensis* is immediately recognizable among Lesser Antillean *Gonolobus* species by the combination of a single, prostrate-undulating gynostegial corona exhibiting a small bump towards the base of the Ci, a toothed stipe, and long, spreading trichomes (to 0.9 mm) found on stems, peduncles, and pedicels.

#### LECTOTYPIFICATION

Lectotypification of *Gonolobus martinicensis* Decne. (Prodromus Systematis Naturalis Regni Vegetabili 8: 595. 1844.) is necessary as Decaisne did not designate a holotype. From Decaisne's syntypes, *Pleé s.n.* (P!-fl, Martinique) is here designated lectotype, as *Plum. et Surian 821* was not found at P. Additional specimens of *G. martinicensis* seen include: MARTINIQUE. L.C. Rich. Herb. Guyanensi-Antillanum (P!-fl, 2 specimens [*G. caribaeus* Rich., nom. sched.]); *Lieber s.n.* (M!-fl).

#### A NOTE ON RANKS

Some authors have preferred recognizing morphologically similar entities occurring in close proximity but on different islands as subspecies or varieties, rather than species, to

highlight the morphological and assumed phylogenetic proximity of the taxa (e.g., Darwin 1872; Wiggins and Porter 1971; Lammers 1988). Intraspecific ranks however, remain controversial and anything but universally defined or accepted (Fernald 1940; Fosberg 1942; Stuessy 1990; Hamilton and Reichard 1992; Krings and Xiang 2005). Lammers (1988) defined subspecies as “a morphologically distinguishable group of conspecific populations, which show geographic integrity.” Although Lammers (1988) goes on to define geographic integrity—populations either allopatric or with restricted, marginal distributions (essentially the same concept as Stuessy 1990 except without the stress on populations *largely* allopatric or peripatric)—he did not define how conspecificity would be evaluated. Of course, addressing conspecificity necessarily requires a definition of species, which is demonstrably controversial itself (see Luckow 1995 for a review). Krings and Xiang (2005) suggested that, in addition to personal conceptual differences among taxonomists, some of the difficulties with the consistent application of infraspecific ranks to plants are the intrinsically varied evolutionary histories of taxa, including rates and completeness of divergence, that defy strict application of uniform concepts across groups. In the present author’s opinion, the rank of subspecies (or variety) should be used to convey more than mere phylogenetic proximity, but additional properties about the populations themselves, such as incompleteness of divergence and continued genetic interaction (usually in zones of contact). For example, Krings and Xiang (2005) recognized two varieties of *Gonolobus suberosus* (L.) R. Br. in the southeastern United States after finding that populations cohesively distributed east and west of a zone of contact or overlap were (1) consistently diagnosable by a single, discrete morphological character (corolla color), (2) exhibited statistically significant differences in mean corolla length and ratio of mean

corolla length:sepal length, (3) exhibited differences in frequency of adaxial corolla pubescence, and (4) exhibited incomplete genetic differentiation. Recognition at a rank below species seemed warranted due to the extreme morphological similarity (no structural differences were apparent), yet cohesive geographic distribution of populations exhibiting minor floral differences. Subspecific entities are here interpreted in part as incompletely differentiated conspecific populations. A zone of contact or overlap is frequently critical in evaluating the appropriateness of recognition at the subspecific rank. The recognition of two entities at the subspecific rank does not seem appropriate when populations of the two show several distinct morphological differences (especially structural ones), are clearly allopatric, and lack intermediate forms or are essentially no longer genetically influenced by one another. Admittedly, the latter is infrequently known, but can be hypothesized based on the maintenance of distinct morphologies in populations of the two (see Stuessy 1990 for more on this point). In a classification, the phylogenetic proximity of the taxa could be better articulated using one of the subgeneric ranks, rather than a subspecific rank, as this would not imply that their evolutionary trajectory remains intertwined. In the case of the Lesser Antillean *Gonolobus* entities described above, the taxa exhibit structural morphological differences that are consistent with the historical recognition of species in the genus. The maintenance of the distinct morphologies associated with allopatric distributions argue for recognition of the taxa at the rank of species.

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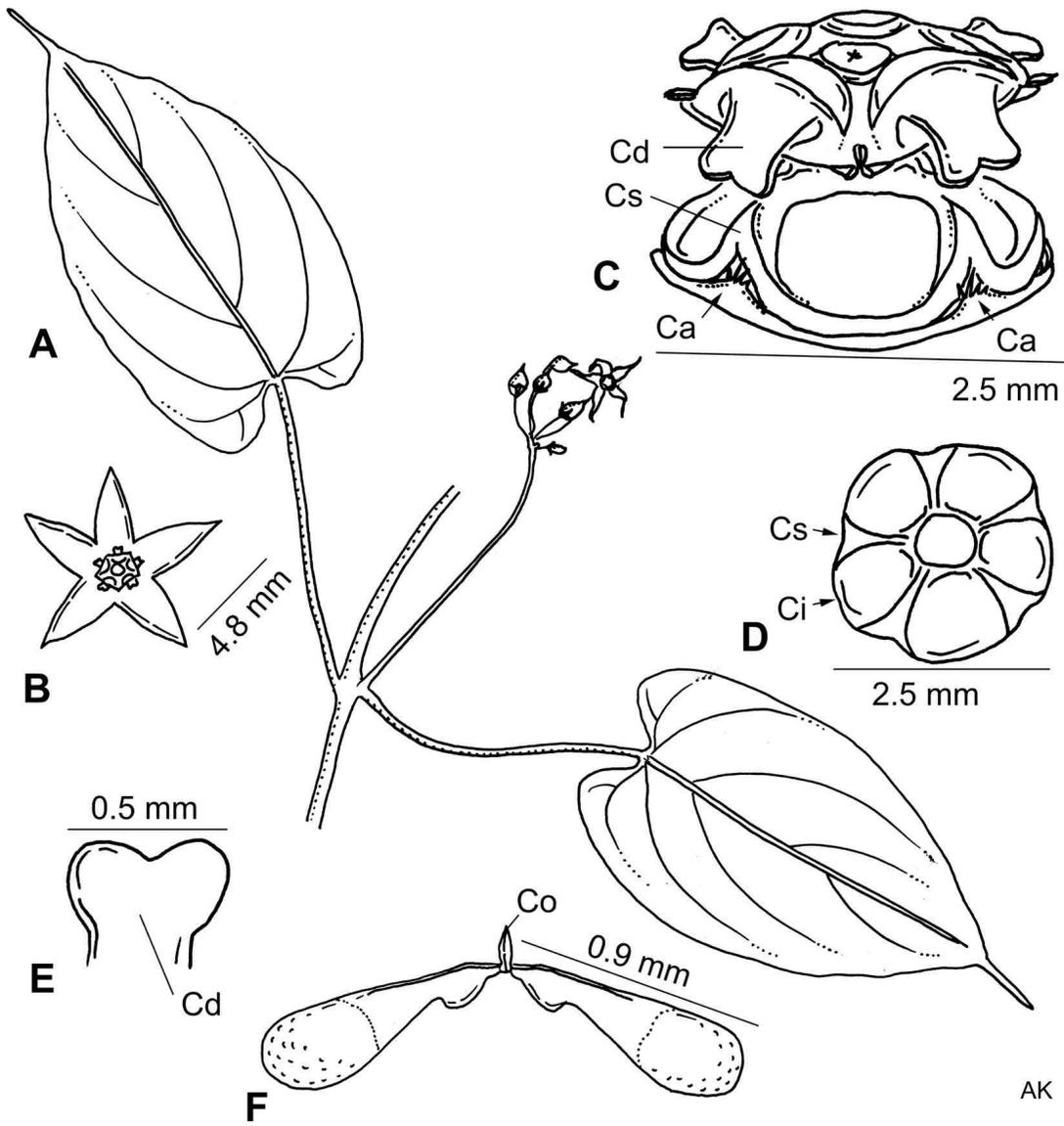
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FIG. 1. *Gonolobus absalonensis*. A. Leaves and inflorescence. B. Open flower. C. Faucal annulus of the corolla (Ca), gynostegial corona, and gynostegial head. D. Gynostegial corona of fused staminal (Cs) and interstaminal (Ci) segments (gynostegial head removed). E. Laminar dorsal anther appendage (Cd). F. Pollinarium. Based on Herb. d'Alleizette *s.n.* [4801?] (L). Ca = Faucal annulus of corolla; Ci = interstaminal gynostegial corona segment; Cd = laminar dorsal anther appendage; Co = Corpusculum; Cs = staminal gynostegial corona segment.



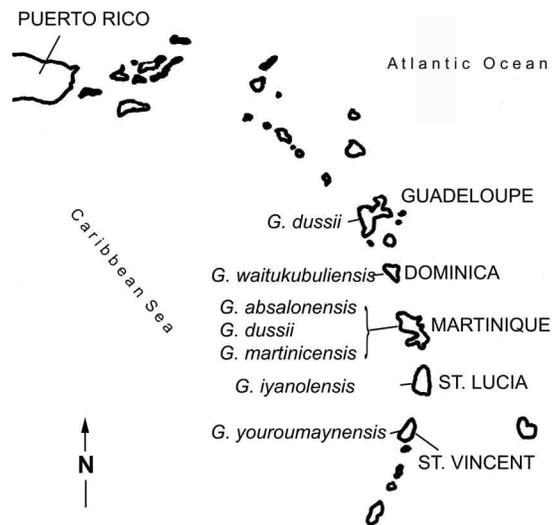


FIG. 2. Distribution of *Gonolobus* in the Lesser Antilles. Based on an outline map provided courtesy of [www.worldatlas.com](http://www.worldatlas.com).

FIG. 3. *Gonolobus dussii*. A. Leaves and inflorescence. B. Flower showing coarse abaxial pubescence of the corolla lobes. C. Faucal annulus of the corolla (Ca), gynostegial corona, and gynostegial head. D. Gynostegial corona of fused staminal (Cs) and interstaminal (Ci) segments (gynostegial head removed). E. Laminar dorsal anther appendage (Cd). F. Pollinarium. A–B based on *Duss 3775* (NY). C and E–F based on *Duss 4565* (NY). D based on *Quentin 732* (P). Ca = Faucal annulus of corolla; Ci = interstaminal gynostegial corona segment; Cd = laminar dorsal anther appendage; Co = Corpusculum; Cs = staminal gynostegial corona segment.

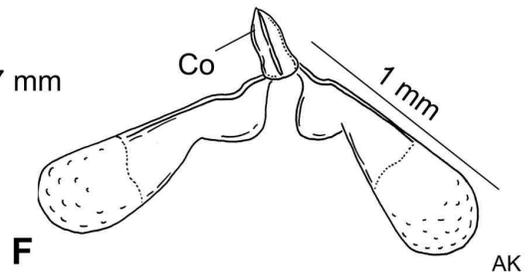
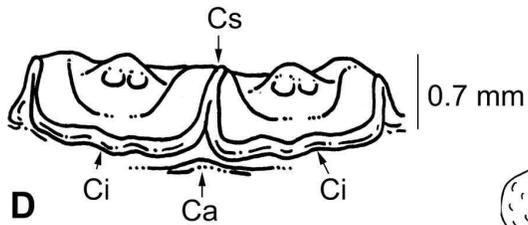
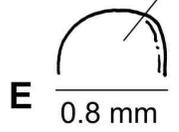
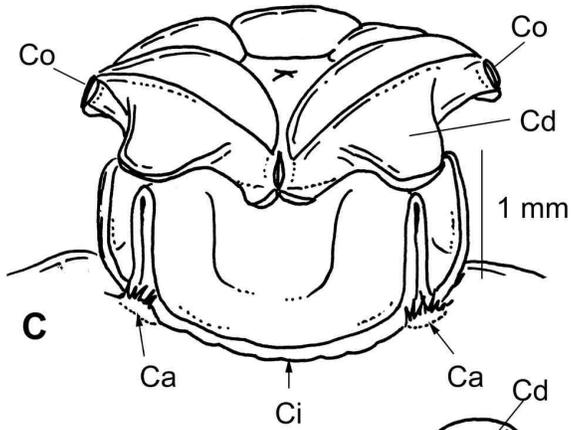
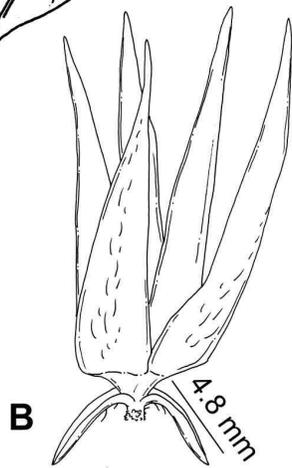


FIG. 4. *Gonolobus iyanolensis*. A. Leaves and inflorescence. B. Open flower. C. Flower showing adaxial pubescence of the corolla lobes. D. Faucal annulus of the corolla (Ca), gynostegial corona, and gynostegial head. E. Gynostegial corona of fused staminal (Cs) and interstaminal (Ci) segments (gynostegial head removed), showing dorsal ridge of upper ligulate corona lobe of the Ci. F. Top view of gynostegial corona (gynostegial head removed). G. Cross-section of corolla tube showing position of corollar and gynostegial corona elements. H. Pollinarium. I. Follicle. J. Seed. A–B based on *Johnny 57 et al.* (UPRRP). C and E based on *Graveson 107* (GH). D and F–H based on *Krings 1373 et al.* (NCSC). I–J based on *Graveson s.n.* (NCSC). Ca = Faucal annulus of corolla; Ci = interstaminal gynostegial corona segment; Cd = laminar dorsal anther appendage; Co = Corpusculum; Cs = staminal gynostegial corona segment.

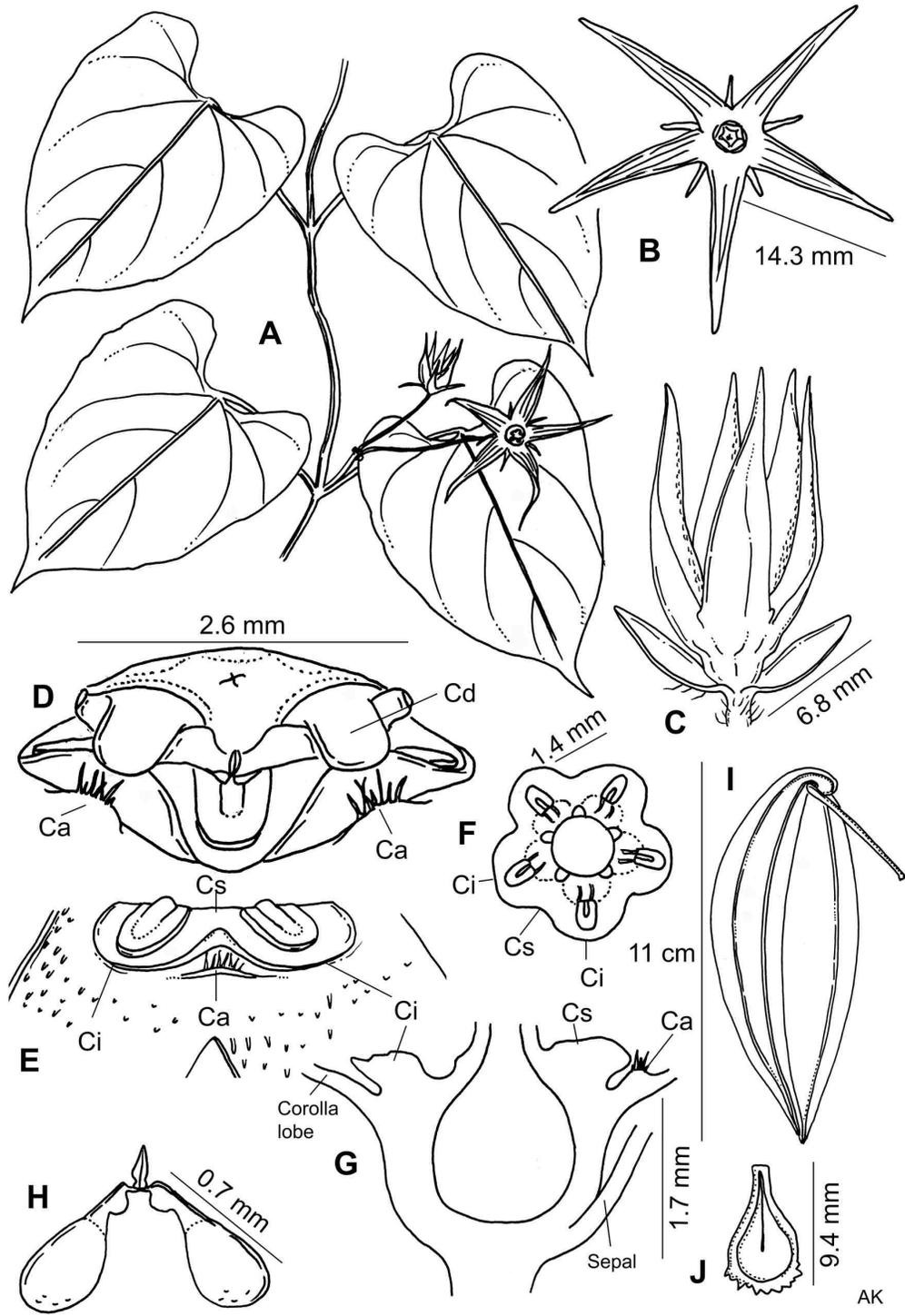


FIG. 5. *Gonolobus martinicensis*. A. Leaves and inflorescence. B. Flower showing narrow corolla tube. C. Faucal annulus (Ca), gynostegial corona, and gynostegial head. D. Top view of gynostegial corona (gynostegial head removed). E. Gynostegial corona of fused staminal (Cs) and interstaminal (Ci) segments (gynostegial head removed), showing upper ligulate corona lobe of the Ci. F. Laminar dorsal anther appendage (Cd). G. Pollinarium. A based on Herb. Mart. Suppl. Nr. 63 (MO). B and E–F based on *Lieber s.n.* (M). C–D and G based on L.C. Rich. Herb. Guyanensi-Antillanum (P). Ca = Faucal annulus of corolla; Ci = interstaminal gynostegial corona segment; Cd = laminar dorsal anther appendage; Co = Corpusculum; Cs = staminal gynostegial corona segment.

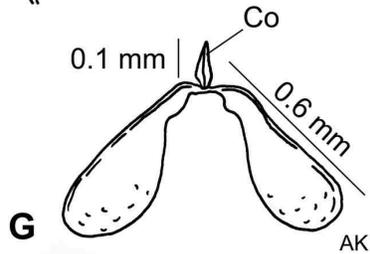
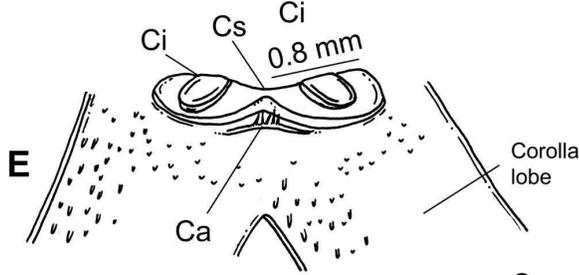
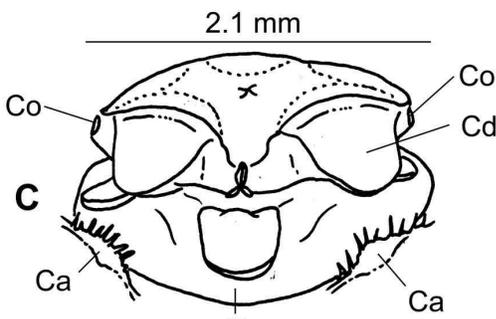
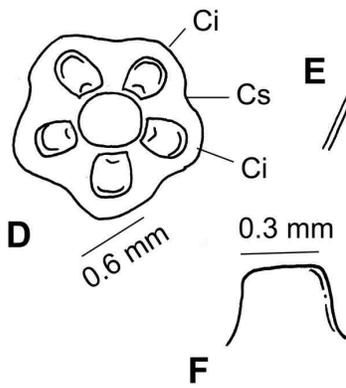
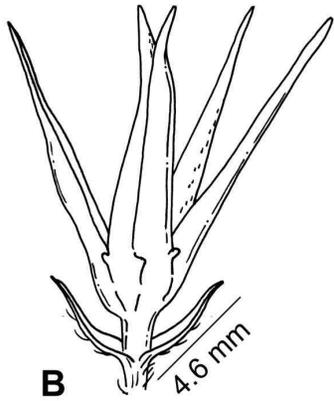
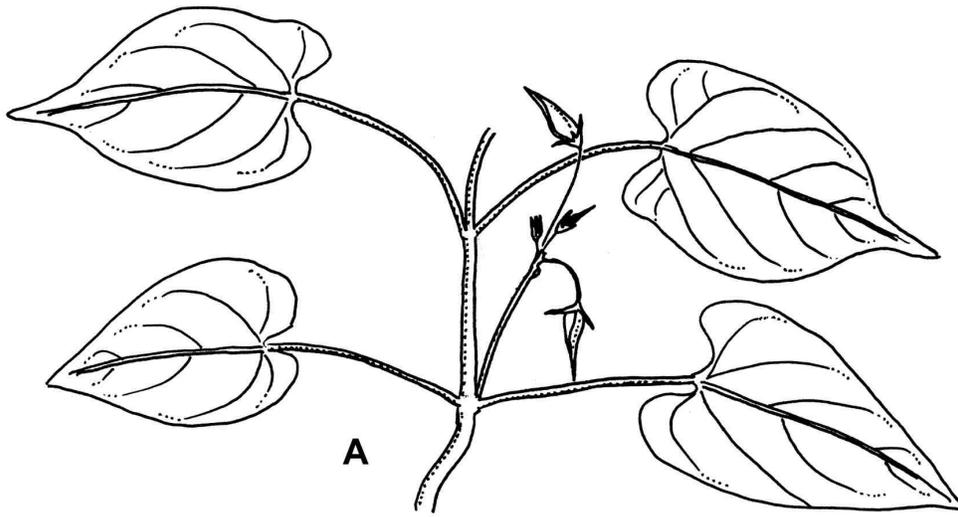


FIG. 6. *Gonolobus waitukubuliensis*. A. Leaves and inflorescence. B. Flower. C. Raised and completely circular faucal annulus of the corolla (Ca) and gynostegial head (gynostegial corona obscured behind the Ca). D. Gynostegial corona of fused staminal (Cs) and interstaminal (Ci) segments (gynostegial head removed). E. Top view of gynostegial corona (gynostegial head removed). F. Cross-section of corolla tube showing position of corollar and gynostegial corona elements. G. Laminar dorsal anther appendage (Cd). H. Pollinarium. A and C based on *Eggers 728 (M)*. B and D–H based on *Webster 13505 (US)*. Ca = Faucal annulus of corolla; Ci = interstaminal gynostegial corona segment; Cd = laminar dorsal anther appendage; Co = Corpusculum; Cs = staminal gynostegial corona segment.

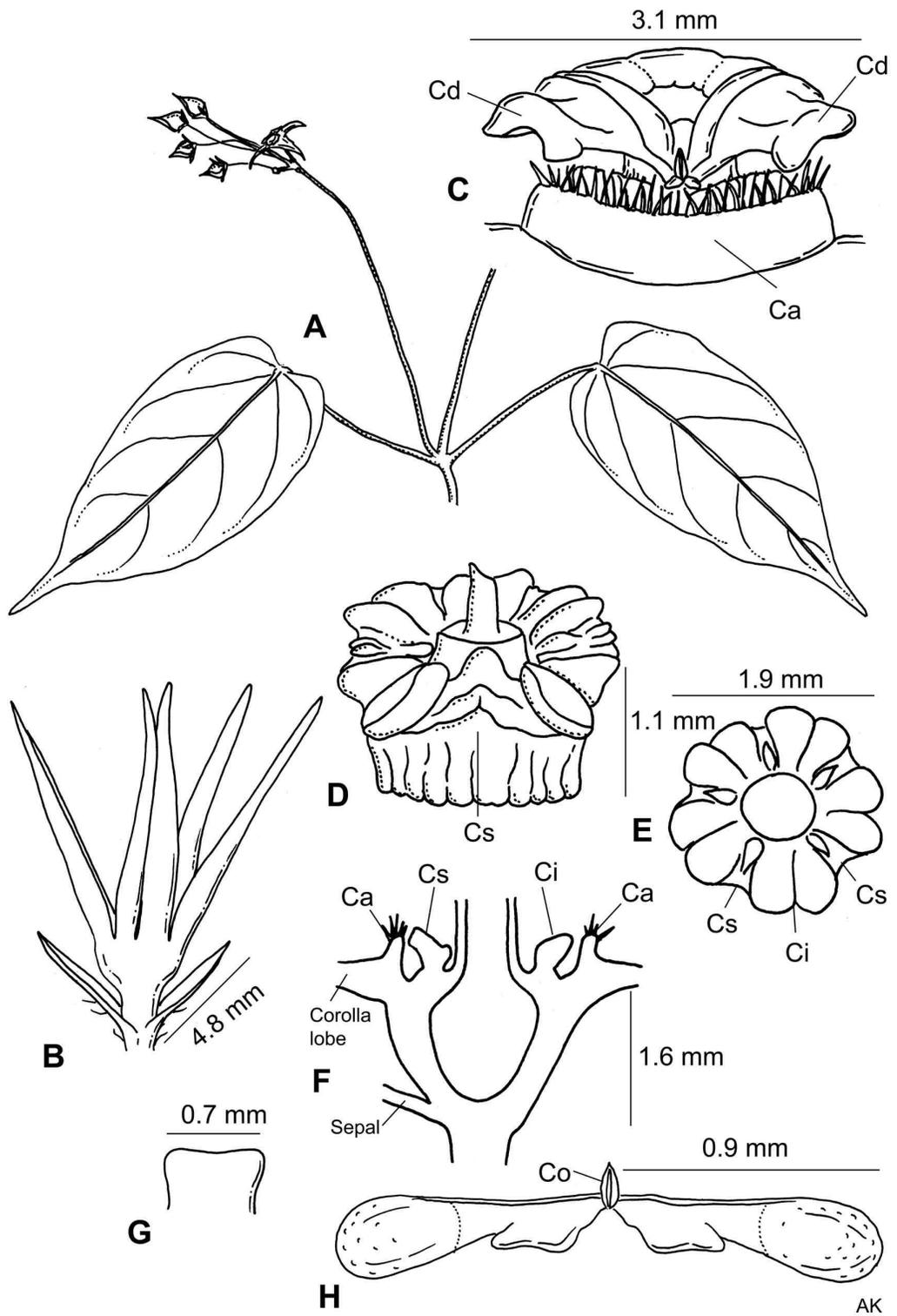
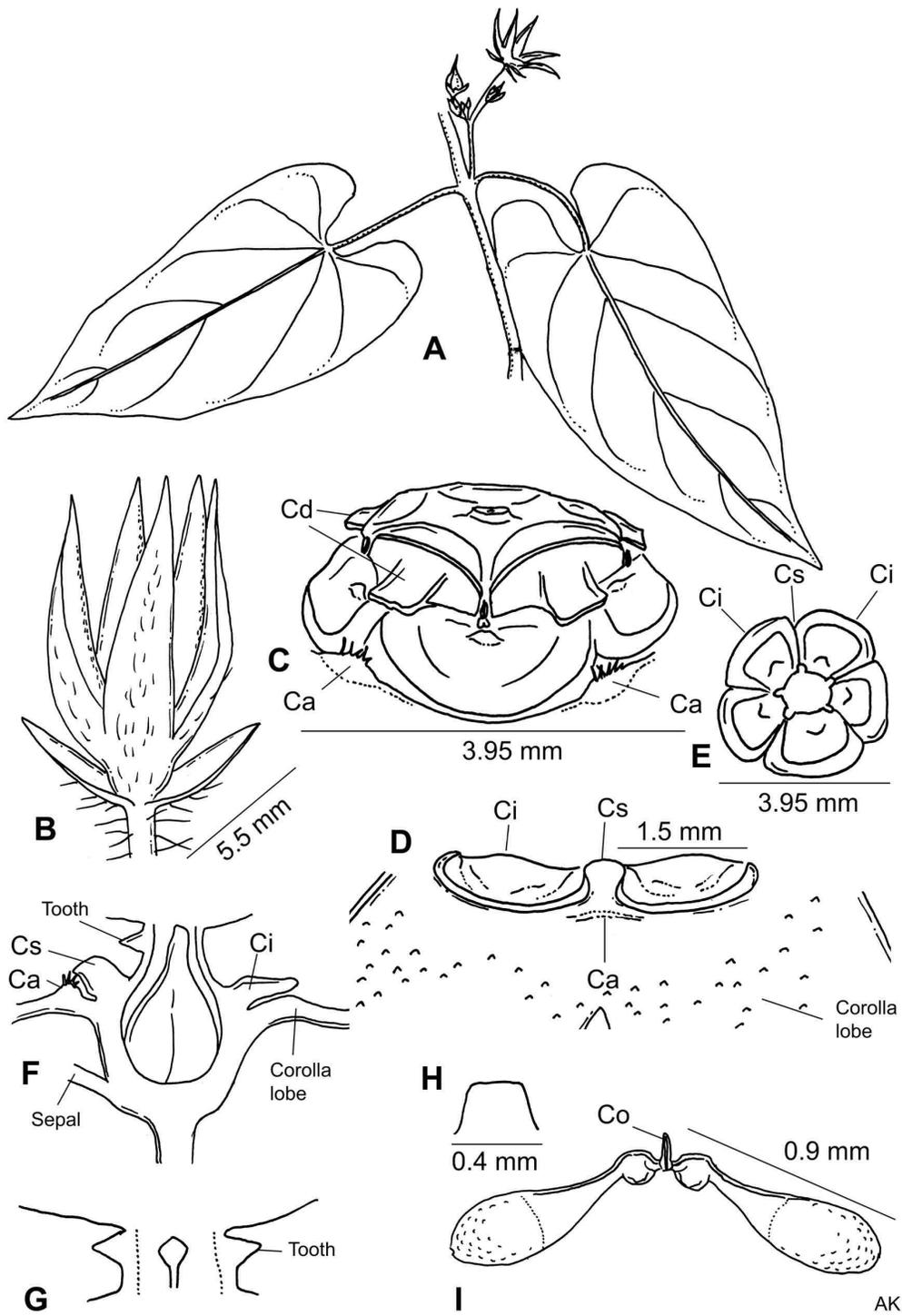


FIG. 7. *Gonolobus youroumaynensis*. A. Leaves and inflorescence. B. Flower showing coarse abaxial corolla lobe pubescence. C. Faucal annulus of the corolla (Ca), gynostegial corona, and gynostegial head. D. Gynostegial corona of fused staminal (Cs) and interstaminal segments (Ci) (gynostegial head removed). E. Top view of gynostegial corona (gynostegial head removed). F. Cross-section of corolla tube showing position of corollar and gynostegial corona elements. G. Detail of teeth of the gynostegial stipe. H. Laminar dorsal anther appendage (Cd). I. Pollinarium. A–B and D based on *Howard 19584* (GH, NY, US). C and E–I based on *Krings 1374 with Springer* (NCSC). Ca = Faucal annulus of corolla; Ci = interstaminal gynostegial corona segment; Cd = laminar dorsal anther appendage; Co = Corpusculum; Cs = staminal gynostegial corona segment.



## Chapter V

### **On the generic circumscription of *Gonolobus* (Apocynaceae: Asclepiadoideae): Evidence from molecules and morphology**

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ABSTRACT. *Gonolobus* Michx. (Apocynaceae, Asclepiadoideae) is a New World genus comprising an estimated 100–150 species. The degree of variation in estimated species numbers is largely the result of still poorly known tropical taxa and differences regarding generic limits. Characters historically used to delimit genera such as *Gonolobus* within Gonolobinae—such as laminar dorsal anther appendages and various follicle morphologies—have been controversial and their evolution remains unknown, not having been explored in a phylogenetic framework. The primary objectives of the current study were to (1) test the monophyly of *Gonolobus* sensu Woodson in the context of a phylogeny of New World Asclepiadeae and (2) explore the evolution of laminar dorsal anther appendages and winged follicles with respect to their potential utility in generic circumscription. Chloroplast (*trnL-F*, *rps16*) data are newly presented for sixty-five taxa of Gonolobinae, representing an increased sampling of the subtribe from a maximum of seven taxa in prior studies. These data were combined with a previously published dataset to form a 180 taxa matrix of New World Asclepiadeae. Nuclear (*Leafy*) data were newly generated for forty-nine taxa of Gonolobinae. Evidence from parsimony and Bayesian analyses of chloroplast and nuclear data presented here supports the monophyly of both the subtribe and the genus *Gonolobus* in a narrow or broad sense. Laminar dorsal anther appendages are restricted to *Gonolobus* s.l. or s.s., although parsimony remains equivocal on whether they evolved once or twice. A transversion in the *trnL-F* spacer is shown synapomorphic for *Gonolobus* s.s. Two indels in *Leafy*, as well as winged follicles, are shown synapomorphic for *Gonolobus* s.l.

KEYWORDS: Gonolobinae, delimitation, dorsal anther appendages, winged follicles

*Gonolobus* Michx. (Apocynaceae, Asclepiadoideae) is a New World genus comprising an estimated 100–150 species (Rosatti 1989; Mabberley 1997; Stevens 2001). The genus was erected by Michaux in 1803, based on a taxon from the southeastern United States—*Gonolobus suberosus* (L.) R.Br. Reveal and Barrie (1992) reviewed the complicated nomenclatural history of the type species and Krings and Xiang (2004, 2005) its taxonomy. The degree of variation in estimated species numbers in *Gonolobus* is largely the result of still poorly known tropical taxa and differences regarding generic limits. *Gonolobus* has most recently been accepted as a member of subtribe Gonolobinae (Liede-Schumann et al. 2005). Evidence from the chloroplast genome supports the monophyly of the subtribe, although the sample size has not exceeded seven species and about half of the species in each study have been *Gonolobus* (Rapini et al. 2003; Liede-Schumann et al. 2005; Rapini et al. 2006). Other genera referred to the subtribe include *Amphorella* Brandegee, *Callaeolepium* H. Karst., *Cyclodon* Small, *Chthamalia* Decne., *Dictyanthus* Decne., *Edisonia* Small, *Fischeria* DC., *Heliostemma* Woodson, *Himantostemma* A. Gray, *Hostea* Willd., *Hypolobus* E. Fourn., *Ibatia* Decne., *Jacaima* Rendle, *Labidostelma* Schltr., *Macroscepis* Kunth, *Matelea* Aubl., *Metalepis* Griseb., *Microdactylon* Brandegee, *Odontostephana* Alexander *Pachystelma* Brandegee, *Peckoltia* E. Fourn., *Pherotrichis* Decne., *Poicilla* Griseb., *Poicillopsis* Schltr., *Polystemma* Decne., *Prosthecidiscus* Donn. Sm., *Ptycanthera* Decne., *Rothrockia* A. Gray, *Rytidoloma* Turcz., *Schubertia* Mart., *Stelmagonum* Baill., *Tetracustelma* Baill. *Trichosacme* Zucc., *Tympananthe* Hassk., *Urostephanus* B.L. Rob. & Greenm., and *Vincetoxicum* of North American authors (Fontella and Schwarz 1981a; Vethacke 1994; Kunze 1995; Liede 1997; Morillo 1997; Rapini et al. 2003; Liede-Schumann et al. 2005; Rapini et al. 2006). Woodson (1941) recognized only *Fischeria*, *Gonolobus*, and *Matelea* in

Gonolobeae, submerging twenty-nine of the above genera, many of them monotypic, into a broadly circumscribed *Matelea* that is in large part still followed today (Stevens 2001). A few genera, such as *Dictyanthus* (16 spp.), *Labidostelma* (monotypic), *Polystemma* (2 spp.), and *Prosthecidiscus* (monotypic) have been resurrected in recent syntheses and floras (Vethacke 1994; Stevens 2001), but without accompanying phylogenetic analyses. Subtribal position has been perhaps most controversial for *Metalepis*, which some workers have also placed among *Cynanchum* L. in the Metastelmatinae (Woodson 1941; Spellman 1975; Sundell 1981). Most authors have generally agreed on the placement of the remaining Gonolobinae genera, although generic circumscriptions in this group remain poorly defined. One controversy has been the circumscriptions of *Gonolobus* and *Matelea*. Woodson (1941) considered that the genus *Gonolobus* should contain plants characterized by only long, eglandular trichomes, laminar dorsal anther appendages (Cd sensu Kunze 1995), and smooth, angled or winged follicles, whereas *Matelea* should contain plants characterized by glandular and eglandular trichomes, anthers lacking dorsal appendages, and muricate follicles. Unconvinced that laminar dorsal anther appendages should serve as a generic character and citing examples of smooth—but not angled or winged—fruits in *Matelea*, Shinnery (1950) argued against Woodson's generic concept and later included twelve of Woodson's (1941) *Gonolobus* combinations in *Matelea* (Shinnery 1950, 1964). Drapalik (1969) essentially followed Shinnery by maintaining the type of *Gonolobus* (i.e., *G. suberosus* (L.) R.Br., syn. *G. gonocarpos* (Walter) L.M. Perry) in *Matelea*, although noting its morphological distinctness vis-à-vis other subtribal members in the southeastern United States. Some more recent flora authors have also continued to recognize the type in *Matelea* (Wunderlin 1998; MacRoberts and MacRoberts 2006). Taking a broader

geographical perspective of generic morphology, Rosatti (1989) argued for renewed circumscription of *Gonolobus* based on the presence of laminar dorsal anther appendages. Most recently the concept of *Gonolobus* as characterized by short, capitate-glandular, short acicular, and long acicular trichomes, laminar dorsal anther appendages (typically), and smooth, winged follicles has been used by Stevens (2001, 2005). However, glandular hairs, although thought characteristic of *Matelea* by Woodson (1941), appear without circumscriptional value in the *Gonolobus-Matelea* question, being present in both the type of *Gonolobus* (i.e., *G. suberosus*) and numerous species lacking dorsal anther appendages (Rosatti 1989; Krings, pers. obs.). The utility of the follicle character (primarily winged in *Gonolobus* vs. primarily muricate in *Matelea*) is also problematic. With greater collections since Woodson (1941), it has become clear that several taxa apparently lacking dorsal anther appendages bear winged instead of muricate follicles. Examples of such taxa include Bahaman *Matelea correllii* Spellman, Cuban *M. bayatensis* (Urb.) Woodson, *M. tigrina* (Griseb.) Woodson, *M. nipensis* (Urb.) Woodson, and *M. oblongata* (Griseb.) Woodson, Hispaniolan *M. linearipetala* Alain, and the broadly distributed *M. denticulata* (Vahl) Fontella & E.A. Schwarz (see also Krings 2005, 2006). Although fruit collections are not known, based on floral and vegetative morphology, putative sister species of some of these taxa, such as Cuban *M. acuminata* (Griseb.) Woodson (sister to *M. oblongata*?) and Jamaican *M. rhamnifolia* (Griseb.) Krings (sister to *M. nipensis*?) likely also bear smooth, winged follicles. Some of these taxa, such as *M. bayatensis*, *M. correllii*, *M. nipensis*, and *M. tigrina*, do not bear an erect staminal gynostegial corona (Cs sensu Kunze 1995), whereas others, such as *M. acuminata* and *M. oblongata* bear an intricate and very well-developed Cs. The evolution of characters historically used to delimit genera in Gonolobinae,

such as laminar dorsal anther appendages and various follicle morphologies, remains unknown and cannot be understood outside of a phylogenetic framework. The objectives of this paper are to (1) test the monophyly of *Gonolobus* as circumscribed by Woodson (1941) in the context of a phylogeny of New World Asclepiadeae and (2) explore the evolution of laminar dorsal anther appendages and winged follicles with respect to their potential utility in generic circumscription.

## METHODS

**Sampling.** Sixty-five taxa were sampled from throughout the range of Gonolobinae (i.e., South America, Mesoamerica, North America, and the West Indies) representing ca. 19% of the subtribe sensu Mabberley (1997), up from a maximum of 2% of prior studies (Rapini et al. 2003; Liede-Schumann et al. 2005; Rapini et al. 2006). Sampled taxa include type species for sixteen genera of Gonolobinae (twelve of which had been submerged into *Matelea* by Woodson 1941), five of thirteen species transferred from Woodson combinations in *Gonolobus* to *Matelea* by Shinnery (1950, 1964), as well as a breadth of morphological lineages. Type species for both *Gonolobus* (*G. suberosus*) and *Matelea* (*M. palustris*) were included. The broad sampling was designed to test whether species assigned to *Gonolobus* by Woodson (1941) are para- or polyphyletic as implied by Shinnery (1950). Emergence of *Gonolobus* species sensu Woodson (1941) in different clades containing as well members of *Matelea* sensu Woodson, would support Shinnery (1950). Emergence of *Gonolobus* sensu Woodson as a single monophyletic clade would support Woodson (1941) in contrast to Shinnery (1950, 1964). To obtain fresh material, field collections were undertaken by the senior author and local botanists (see

Acknowledgments) in Cuba, Dominica, Jamaica, Puerto Rico, St. Lucia, St. Vincent, and the southeastern United States. Additional silica-dried material was obtained courtesy of Mark Fishbein (Portland State University) for *G. arizonicus*, *G. fraternus*, *G. gonoloboides*, *G. grandiflorus*, *G. jaliscensis*, *G. uniflorus*. Herbarium specimens chosen for sampling were representative recent material as determined by study of loans from sixty-five institutions (see Acknowledgments). Herbarium vouchers are provided in Appendix A.

**DNA Extraction and PCR.** Total DNA was isolated from silica-dried young leaves or from herbarium specimens using the DNeasy Plant Mini Kit (Qiagen).

#### *trnL-F* AND *rps16*

In order to build on the framework established by prior studies of New World Asclepiadeae (e.g., Liede-Schumann et al. 2005), the two chloroplast regions *trnL-F* and *rps16* were sequenced for sixty-five additional taxa of Gonolobinae. For each PCR reaction, approximately 100ng of total DNA was included in a 50µl reaction. Primers follow Taberlet et al. (1991) for *trnL-F* and Lee and Downie (2000) for *rps16*. Two µl of DNA template were added to a solution containing 26.3 µl dH<sub>2</sub>O, 5 µl of 10x Mg free buffer, 1.5 µl BSA (10mg/ml), 6 µl of MgCl<sub>2</sub> (25mM), 8 µl of dNTPs (2.5mM), 0.2 µl *Taq* (5U/µl), and 0.5 µl of the respective primers for each amplified region: *trnL* (5'AAAATCGTGAGGG TTGAAGTC) and *trnF* (5'GATTTGAACTGGTGACAC GAG); *rpsF* (5'GTGGTAGAAAGCAACGTGCGACTT) and *rpsR2* (5'TCGGGATCGAACATC AATTGCAAC)(all 20µM). Thirty-one (*trnL-F*) or thirty-five (*rps16*) cycles of three-step PCR followed with a final extension at 72° C for 4 min (*trnL-F*) or 5 min (*rps16*): denaturation at 94°

C for 1 min, primer annealing at 52° C, and primer extension at 72° C for 1 min (*trnL-F*) or 1.5 min (*rps16*).

### *LEAFY*

*Leafy* is a homeotic gene regulating the establishment of floral meristem identity and flowering time in *Arabidopsis* (Blázquez et al. 1997). It is present in a single copy in diploid angiosperms (Frohlich and Meyerowitz 1997; Frohlich and Parker 2000). Its structure—three exons and two introns—is well conserved across seed plants (Frohlich and Meyerowitz 1997). Universal degenerate primers can be used to amplify the second intron, located between the highly conserved second and third exon (Oh and Potter 2003). The length of the second intron can range in size from 88 bp in *Peperomia* (Piperaceae) to 7946 bp in *Platanus* (Platanaceae) (Frohlich and Meyerowitz 1997). Livshultz (2003) found length variation in *Dischidia* R.Br. (Asclepiadoideae, Marsdenieae) to range from 658 to 744 bp. Unfortunately, the specific primers developed by Livshultz (2003) for *Dischidia* did not work with our material.

Consequently, we sought to develop specific primers by first cloning portions of the second and third exon and the intervening intron using the degenerate primers LFsxL-3 and LFtxr of Frohlich and Meyerowitz (1997). Degenerate primers proved successful only with eleven taxa, most collected in the past five years. PCR products were excised from agarose gels, purified with the QIAquick Gel Extraction Kit (Qiagen), and cloned using the TOPO TA Cloning Kit (Invitrogen). Using T3 (5'ATTAACC TTCACTAAAGGGA) and T7 (5'TAATACGACTCA CTATAGGG) primers, multiple attempts were made to sequence eight to ten colonies (three for *G. suberosus*) for these eleven taxa. However, useable sequences were obtained for only nine of

the eleven and these varied from one to seven per accession. The useable sequences were subsequently compared to existing *Leafy* sequences in GenBank and to the yet unpublished *Dischidia* sequences (Livshultz 2003) to verify their *Leafy* identity. Specific primers LfyF1 (5'GAGCAATGTCGCGAGTTCTT) and LfyR (5'CTTGCTCCTGCTTTC TTTGC) were then developed based on the cloned sequences and used to amplify sequences for additional taxa (see (3) below). As the reagent concentrations and PCR protocols of Livshultz (2003) also proved unsuccessful with our material, we optimized a successful procedure through trial and error. PCR protocol was most successful following Oh and Potter (2003). For each PCR reaction, about 100ng of total DNA was included in a 50 $\mu$ l reaction. Two  $\mu$ l of DNA template were added to a solution containing 25.85  $\mu$ l dH<sub>2</sub>O, 5  $\mu$ l of 10x Mg free buffer, 1.5  $\mu$ l BSA (10mg/ml), 6  $\mu$ l of MgCl<sub>2</sub> (2.5mM), 8  $\mu$ l of dNTPs (2.5mM), 0.7  $\mu$ l each of primers LFsxl-3 and LFtxr (20 $\mu$ M), and 0.25  $\mu$ l HotStart *Taq* (5U/ $\mu$ l). Thirty-five cycles of three-step PCR followed with a final extension at 72° C for 5 min: denaturation at 94° C for 1 min, primer annealing at 55° C for 1 min, and primer extension at 72° C for 1.5 min. Even with the designed primers, direct PCR frequently failed to yield a single band. In these cases, gel excised PCR products were gel-purified with the QIAquick gel extraction kit (Qiagen) and then direct sequenced. Future efforts may seek to focus on designing primers around the last 22 bp of the second exon, which appear highly conserved not just in Gonolobinae, but more distant members of Gentianales (see Livshultz 2003; Smith and Baum 2006).

***Phylogenetic analyses.*** Three matrices, as described below, were analyzed. All are available from TreeBASE. Indels were simple gap coded using GapCoder (Young and Healy 2003).

Optimal models of nucleotide substitution were determined for gene partitions using the Akaike Information Criterion (Posada and Buckley 2004) with the aid of Modeltest 3.7 (Posada 2005). The first matrix was developed to test the monophyly of *Gonolobus* in the context of a phylogeny of New World Asclepiadeae. This matrix is based exclusively on chloroplast data (*trnL-F*, *rps16*). Although analyses of this matrix showed a monophyletic Gonolobinae (see Results), we considered that resolution of *Gonolobus* taxa might be improved with the addition of characters from the nuclear gene *Leafy*. Our *Leafy* clone matrix (2<sup>nd</sup> matrix below) is included here to demonstrate that there are no paralogous genes compromising the phylogenetic utility of the gene sequence. This matrix is based exclusively on sequences derived from degenerate primers (see DNA extraction and PCR above) and, because the latter were successful only with limited material, includes only nine taxa. The third matrix presented below—Gonolobinae matrix—incorporates both chloroplast (*trnL-F*, *rps16*) and nuclear data (*Leafy*) for forty-nine species. *Leafy* data in this matrix were obtained using specific primers (see DNA extraction and PCR above), except for the few taxa which had previously been cloned. Each matrix is described in greater detail below.

(1) New World Asclepiadeae matrix (*trnL-F* and *rps16*)—This matrix comprises sequence data from the chloroplast *trnL-F* and *rps16* regions for 180 taxa, of which 115 are derived from Liede-Schumann et al. (2005). Sequences of sixty-five taxa were newly generated in this study. These sixty-five taxa have previously been referred to Gonolobeae or Gonolobinae (Woodson 1941; Rosatti 1989; Vethacke 1994; Swarupanandan et al. 1996; Liede 1997). Sequences were manually added to the aligned matrix of Liede-Schumann et al. (2005).

(2) *Leafy* clone matrix—This matrix comprises *Leafy* sequence data for one to seven clones for nine Gonolobinae species from the West Indies and the southeastern United States (34 accession total). Contigs were assembled using CodonCode Aligner (Codoncode Corp. 2006) and manually corrected in MacClade 4.06 (Maddison and Maddison 2003). Because of difficulties in alignment only 558 bp of the ca. 800 bp sequences were used in the analyses. Included were 86 bp of the end of the second exon of *Leafy* and 472 bp of the second intron. The boundary of the second exon and the second intron was identified based on comparison with *Leafy* sequences in GenBank and other published and unpublished sequences (Frohlich and Meyerowitz 1997; Livshultz 2003).

(3) Gonolobinae matrix (*trnL-F*, *rps16*, and *Leafy*)—This matrix comprises chloroplast and nuclear sequence data for 49 species of Gonolobinae from throughout Meso- and North America and the West Indies (Woodson 1941; Rosatti 1989; Vethacke 1994; Swarupanandan et al. 1996; Liede 1997). Contigs of *Leafy* sequences (all new to this study) were assembled using CodonCode Aligner and manually corrected in MacClade 4.06. Because of *Leafy* alignment difficulties, only 170 bp from the 5' end (including a portion of the second exon and adjoining second intron) and a 17 bp intron indel were incorporated into the matrix. Sequences were joined with *trnL-F* and *rps16* sequences already assembled as noted above.

Maximum parsimony analyses were run using PAUP 4.0\* (Swofford 2003) and Bayesian analyses using MrBayes 3.1.2 (Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck

2003). Single gene partitions in the *trnL-F/rps16* and combined *trnL-F/rps16/Lfy* matrices were analyzed with and without indels simple gap coded.

For the parsimony analyses, phylogenetic trees were generated using heuristic searches with 1000 replicates, random addition, MulTrees off, and tree-bisection-reconnection (TBR) branch-swapping. The resulting trees were subsequently used as starting trees for a second round of tree searching with TBR and MulTrees on. When searches did not complete due to computer memory limitations, they were stopped at 200,000 trees and subsequently summarized in strict consensus trees. This search strategy followed Liede-Schumann et al. (2005) and attempts to find as many tree islands as possible. Bootstrap support was calculated as a measure of clade support using the fast heuristic option in PAUP and 1000 replicates for the New World Asclepiadeae (*trnL-F/rps16*) matrix and 50,000 replicates for the *Leafy* clone and Gonolobinae (*trnL-F/rps16/Leafy*) matrices.

Heterogeneous Bayesian analyses were conducted using MrBayes 3.1.2 with a substitution model specified for each region (Table 1). Bayesian analyses were conducted with four independent runs, each with 2,000,000–8,000,000 generations, using default, uniform priors. Model parameters including trees were sampled every 100 generations. Burnin was estimated by inspection of a plot of likelihood scores at each sampling point using Tracer (Rambaut and Drummond 2004). Burnin trees were excluded from the tree set. Remaining trees from each run were combined to constitute the full sample assumed representative of the posterior probability distribution.

Partition homogeneity tests, or incongruence length-difference tests (Farris et al. 1995), were run in PAUP 4.0\* to test the congruence of the phylogenetic signal from the separate gene regions. These tests were chosen as they outperformed both Templeton and Rodridgo tests in identifying instances in which combining gene partitions would increase phylogenetic accuracy (Cunningham 1997). For the partition homogeneity tests, heuristic searches were run using 100 replicates with the starting sequence random, addition sequence replicates numbering 1000, and MulTrees turned off—an approach following Levin and Miller (2005). Subsequently, partitions were respectively combined in the New World Asclepiadeae and Gonolobinae data matrices. Each matrix was then submitted to Bayesian analysis, as well as parsimony analysis, using the same tree searching strategy as outlined above for the single gene analyses.

## RESULTS

Single gene maximum parsimony and Bayesian analyses, with and without indels scored, resulted in poorly resolved trees compared to those obtained through the maximum parsimony or Bayesian analyses of the combined data. As partition homogeneity tests showed no significant incongruence between the signal from the various gene regions (see below), the single gene analyses are not discussed further here, with the following exception. Despite numerous experiments with several herbarium specimens and combining or concentrating PCR products, only the *trnL-F* sequence could be obtained for *Matelea palustris* (type for *Matelea*). Fresh material was unavailable for this species. Consequently, it was excluded from the combined gene analyses. Whereas all *Gonolobus* species, except *G. stenosepalus*, emerged as a

monophyletic clade in the strict consensus of a parsimony analysis on *trnL-F* alone, *M. palustris* emerged in a polytomy of *Matelea* species that also included *G. stenosepalus*.

***New World Asclepiadeae chloroplast matrix.*** The combined alignment (available from TreeBASE) comprises 180 taxa and 1734 characters (*trnL-F*: 489 bp; *rps16*: 1032 bp; indels: 213; unknown cells: 1901 or 0.6%). Sixty-five of the taxa have been previously referred to Gonolobeae or Gonolobinae. With indels not coded (i.e., all binary data generated from simple gap coding excluded), 65.2% (N=991) characters were constant, 16.3% (N=248) were autapomorphic, and 18.5% (N=282) were informative. With indels coded, 57.2% (N=992) characters were constant, 20.4% (N=353) were autapomorphic, and 22.4% (N=389) were informative. Partition homogeneity tests resulted in a p-value of 0.49, well above the threshold at which phylogenetic accuracy has been shown to suffer by combining gene partitions (i.e.,  $P < 0.001$ ; Cunningham 1997). Optimal models of nucleotide substitution for the two gene partitions are provided in Table 1. Topologies resulting from inclusion and exclusion of indels did not differ significantly and clade structure largely followed the results of Liede-Schumann et al. (2005). The Metastelmatinae-Oxypetalinae-Gonolobinae (MOG) clade, which resolved with 99% bootstrap (BS) support in Liede-Schumann et al. (2005), resolved with moderate to strong BS support (indels coded: 79%; indels not coded: 83%) and strong posterior probability (PP) support (indels coded or not: 100%; Fig. 1). Relationships among subtribes were not as clearly resolved as in Liede-Schumann et al. (2005), although two of four subtribes—discussed below—were well to strongly supported by BS. The Metastelmatinae clade resolved with strong BS (indels coded: 99%; indels not coded: 100%) and strong PP support (indels coded or not: 100%).

The Orthosiinae did not resolve as a clade in the parsimony analysis with indels not coded and did so with only weak support (54%) with indels coded. However, this clade received strong PP support in the Bayesian analysis (indels coded or not: 100%). The subtribe received moderate BS support in Liede-Schumann et al. (2005). The Oxypetalinae s.l. did not resolve as a clade, although the Oxypetalinae “core group” of Liede-Schumann et al. (2005) formed a clade well- to strongly supported by BS (indels coded: 83%; indels not coded: 87%) and PP (indels coded or not: 100%). The Gonolobinae was resolved well-supported by BS (indels coded: 82%; indels not coded: 77%) and strongly supported by PP (indels coded or not: 100%), but its relationship to other taxa remain unclear. A very sparsely sampled Gonolobinae (N=7 spp.) had previously emerged in a polytomy that also included Oxypetalinae with 100% BS support (Liede-Schumann et al. 2005).

In general, there was little resolution among the sixty-five Gonolobinae species based on the present chloroplast data (Fig. 1A–B). However, strong BS and PP support was found for a number of small clades, including species with divergent floral morphology (Fig. 1B) such as the sympatric island endemic species pairs *M. variifolia*-*M. sintenisii* (Puerto Rico) and *M. bicolor*-*M. ekmanii* (Sierra Maestra, Cuba). Hispaniolan *Matelea viridivenia* emerged as sister to the Cuban *M. bicolor*-*M. ekmanii* pair with moderate to moderately-strong BS support (indels coded: 88%; indels not coded: 70%) and strong PP support (indels coded or not: 100%). The sister relationship of *Matelea maritima* (*Ibatia*) and *M. rubra* (*Omphalophthalma*) also received strong BS support (indels coded: 96%; indels not coded: 95%) and strong PP support (indels coded or not: 100%). This is consistent with general floral and fructal morphology although there are

some striking differences between the two in the development of the gynostegial corona, stipe, and stylar head ornamentation (Krings and Saville, in review). Both taxa had been placed in Woodson's (1941) *Matelea* subgenus *Ibatia*. *Matelea cordifolia* (*Rothrockia*) was also referred to the subgenus by Woodson (1941), based presumably on pollinarium morphology and the shared terminal appendage of the stylar head. However, it emerged in a clade strongly supported by BS (indels coded: 92%; indels not coded: 94%) and PP values (indels coded or not: 100%), that included as well the types of several other submerged genera, including *Labidostelma* and *Polystemma* (Fig. 1A). *Matelea prosthecidiscus* (*Prosthecidiscus*) was referred to subg. *Ibatia* as well (Woodson 1941), but its placement was not well-resolved here. A group of mostly West Indian ocellate flowered taxa—*M. acuminata* (E Cuba), *M. correllii* (Bahamas), *M. nipensis* (E Cuba), *M. oblongata* (W Cuba), *M. phainops* (Hispaniola), and *M. pusilliflora* (Yucatan Peninsula)—form a monophyletic clade with weak BS support, but very strong support PP support (indels coded: 100%; indels not coded: 99%; Fig. 1B). Some species pairs in this group—notably *M. pauciflora*-*M. phainops* and *M. correllii*-*M. oblongata*—were highly supported by both BS and PP values. The latter putative sister relationship is surprising, as the east Cuban *M. acuminata* and west Cuban *M. oblongata* are more similar to each other morphologically (both in flower and leaf shape), than either is to *M. correllii* (see also Krings 2005). Although ocellate, *Matelea correllii* bears much larger flowers and lacks the well-developed, intricate Cs found in both *M. oblongata* and *M. acuminata*. *Matelea acuminata* emerged as sister to sympatric *M. nipensis*, albeit with weak support from both bootstrap and posterior probabilities. The strongly supported sister relationship of Hispaniolan *M. pauciflora* and *M. phainops* is also noteworthy, as the two differ strikingly in the structure of both the

gynostegial corona and the gynostegium (Krings 2006). Nonetheless, their vegetative morphology remains much more similar to one another than to any other species in the putative clade. A clade of *Gonolobus* species minus *G. stenosepalus* (*Gonolobus* s.s. from here on) emerged in both the Bayesian analyses and the strict consensus trees of the parsimony analyses, whether indels were coded or not. The clade received weak BS support (indels coded: 53%; indels not coded: 55%), but strong PP support (indels coded or not: 100%). This clade is further supported by a synapomorphic transversion (T to G) at aligned position 279 in the *trnL-F* sequences. All members of *Gonolobus* s.s. share a guanine at this position, whereas all other species in the matrix share a thymine. There is no other site in the combined dataset that is as tightly correlated with a morphological character as is the guanine in position 279 with laminar dorsal anther appendages. *Gonolobus stenosepalus* is the only included species exhibiting laminar dorsal anther appendages, but lacking a guanine at position 279. Interestingly, it did not emerge within the *Gonolobus* s.s. clade, but in a clade sister to *Gonolobus* s.s. The clade of *G. stenosepalus*-*M. denticulata* as sister to *Gonolobus* s.s. received no BS support, but strong PP support (indels coded: 99%; indels not coded: 100%). Anther appendages in *G. stenosepalus*—and its morphological relatives such as *G. calycosus* (Donn. Sm.) Woodson, and *G. fimbriatiflorus* (Morillo) W.D. Stevens (neither sampled here)—are unusual in that they are strongly laterally and basally developed, frequently lacking a strong medial component as seen in the only other *Gonolobus* s.s. species that remotely approach this morphology, such as *G. pectinatus*, *G. barbatus*, and *G. bibrabatus*. The vast majority of members of *Gonolobus* s.s. tend to exhibit laminar dorsal anther appendages that are more radially, rather than basally developed. *Gonolobus stenosepalus* and relatives also exhibit a pronounced, tubular elongation

of the Ca not observed to a similar extent in other *Gonolobus* s.s. species in this study. They have been treated as a small, separate genus—*Fimbristemma*—in the past (ca. 5 spp.).

***Leafy clones matrix.*** Cloning of *Leafy* was undertaken primarily to facilitate the development of specific primers, but served as well to demonstrate that there are no paralogous genes compromising the phylogenetic utility of the gene sequence. The alignment of cloned sequences (available from TreeBASE) comprises thirty-five accessions and nine species. Of a total of 558 characters, 75.5% (N=421) were constant, 12.5% (N=70) were autapomorphic, and 12% (N=67) were informative. Optimal models of nucleotide substitution for the exon and intron partitions are provided in Table 1. With uninformative characters removed, parsimony analysis of the matrix found 47168 equally most parsimonious trees from 961 islands (Length=166 steps; CI=0.934; RI=0.954) (Fig. 2). With the exception of the moderate BS support for *Gonolobus stapelioides* clones (74%), all other cloned sequences grouped by species with strong BS support (BS 92–100%; Fig. 2) for each clade. All species-clone clades received 100% PP values. Relationships between species were essentially unresolved, although a clade of the two included *Gonolobus* s.s. species received 98% PP support.

***Gonolobinae chloroplast and nuclear matrix.*** The alignment (available from TreeBASE) comprises forty-nine species of Gonolobinae and 1904 characters (*trnL-F*: 489 bp; *rps16*: 1032 bp; *Leafy*: 190 bp; gap characters: 193; unknown cells: 763 or 0.8%). Partition homogeneity tests resulted in p-values of 0.31 for *trnL-F/Leafy*, 0.01 for *rps16/Leafy*, and 0.02 for *trnL-F/rps16*. All p-values were above the threshold at which phylogenetic accuracy has been shown

to suffer by combining gene partitions (i.e.,  $P < 0.001$ ; Cunningham 1997). The number of parsimony informative characters, constant characters, autapomorphic characters, as well as the optimal model of nucleotide substitution for each of the three data partitions is provided in Table 1. Inclusion of indels in the maximum parsimony analysis resulted in 1559 most parsimonious trees from 209 islands (Length = 294 steps; CI=0.527; RI=0.731). Of 1904 total characters, 79.4% (N=1511) were constant, 13.3% (N=254) were autapomorphic, and 7.3% (N=139) were parsimony informative. Exclusion of indels in the maximum parsimony analysis resulted in 116,084 most parsimonious trees from 552 islands (Length = 178 steps; CI=0.607; RI=0.768). Of 1711 total characters, 85.2% (N=1457) were constant, 9.5% (N=162) autapomorphic, and 5.4% (N=92) parsimony informative. Consensus topologies resulting from inclusion and exclusion of indels in the parsimony and Bayesian analyses did not differ significantly, although inclusion of indels generally contributed to increased support of clades. A phylogram of one of 1559 most parsimonious trees resulting from the parsimony analysis with indels scored is provided in Figure 3. Superimposed on the topology are support values from parsimony and Bayesian analyses for indels respectively scored or not. Clades supported by both BS and PP values in the analyses of the 180 taxa New World Asclepiadeae chloroplast matrix continued to be supported by BS and PP values in the analysis of the *Gonolobinae trnL-F/rps16/Leafy* matrix. Of particular note however, is the improved support for the (*G. stenosepalus*-*M. denticulata* (*Gonolobus* s.s.)) clade. With indels coded, this clade emerged well-supported by BS (76%) and PP values (100%; Fig. 3), previously receiving weak BS support (<50%) in the parsimony analysis of the 180 taxa New World Asclepiadeae chloroplast matrix. Also of note is the improved BS support for a *Gonolobus* s.s. clade vis-à-vis the New World Asclepiadeae analysis

(indels coded: 67% vs. 53%; indels not coded: 58% vs. 55%). This clade also continued to receive strong support from PP values (indels coded or not: 100%; Fig. 3). Removal of *G. stenosepalus* from the clade, increased BS values for the *Gonolobus* s.s. clade to 78% with indels coded. Removal of *M. denticulata* from the clade had essentially no effect on the BS support for the *Gonolobus* s.s. clade (indels coded: 66%). Particularly noteworthy features of the *Leafy* sequences related to these clades are two significant indels (chs 1817: 82 bp and 1891: 17 bp; Table 2) shared by all members of *Gonolobus* s.s., as well as *G. stenosepalus* and *M. denticulata*. Based on the present analyses, these indels can be considered synapomorphic for the clade containing these taxa. Despite resolving with *M. inconspicua*, *M. prosthecidiscus* (*Prosthecidiscus*) may instead belong to the (*G. stenosepalus*-*M. denticulata* (*Gonolobus* s.s.)) clade, sharing at least the shorter of the two indels (i.e., ch. 1891). The event resulting in the longer indel may have occurred in a common ancestor, as the *M. prosthecidiscus* indel differs only in exhibiting a single additional tandem repeat at the indel beginning (i.e., an extra cytosine-adenine). This additional tandem repeat is lacking in members of the (*G. stenosepalus*-*M. denticulata* (*Gonolobus* s.s.)) clade. All other included taxa, including those of the putative ocellate clade, lack both indels.

## DISCUSSION

**Clade support.** The disparity between low BS and high PP support at some internodes in the analyses is not surprising given the data sets. A great majority of characters in all matrices analyzed were constant or autapomorphic. In the *Gonolobinae* matrix, only 5.4–7.3% of

characters were parsimony informative, depending on whether indels were included in the analyses or not. In addition, most internodes exhibiting low BS/high PP support were short. It is well-known that Bayesian analyses may sometimes assign high PP values to nodes otherwise receiving low BS support (Susuki et al. 2002; Wilcox et al. 2002; Erixon et al. 2003). While some have interpreted this behavior as over-credibility and subsequently cautioned against use of Bayesian PP values for this reason (e.g., Simmons et al. 2004), others have considered the behavior as rather attractive (Alfaro et al. 2003). However, a price to be paid may be the tendency for the latter to assign high confidence to incorrect internodes (Alfaro et al. 2003). On the other hand, the conservative behavior of the BS is also well-known (Alfaro et al. 2003). Some have even suggested interpreting BS and PP values as lower and upper limits respectively (Douady et al. 2003). Discerning signal from noise becomes a particularly acute problem when numbers of informative characters are few. Data exploration seems particularly useful in these cases. In the case of *Gonolobus* s.s., the high correlation of floral morphology with several characteristics of the chloroplast and nuclear genomes described above (i.e., transversion in position 279 of *trnL-F*, 82 bp indel in *Leafy* (ch. 1817), 17 bp indel in *Leafy* (ch. 1891)) seems to us particularly compelling evidence that the high PP values assigned particularly to this clade are accurate reflections of phylogeny.

**Character evolution.** The Gonolobinae comprise at least two major lineages based on two indels in the *Leafy* genome (chs. 1817 and 1892 as discussed in Results; Table 2; Fig. 3: Evolution of Gonolobinae figure). The lineage lacking the two indels includes *Fischeria* and a diverse array of taxa largely synonymized into *Matelea* by Woodson (1941), including *Chthamalia*,

*Dictyanthus*, *Edisonia*, *Heliostemma*, *Labidostelma*, *Microdactylon*, *Omphalophthalma*, *Pachystelma*, *Poicilla*, *Polystemma*, *Ptycanthera*, *Rytidoloma*, *Trichosacme*, and *Urostephanus*. This lineage exhibits a dazzling array of floral variation (Fig. 4A–C) that makes one appreciate the advantages of Woodson’s (1941) broad concept of *Matelea*. The synorganization of androecium and gynoecium appears to have facilitated such a myriad of gynostegial structural variation in this group that it is very difficult to discern morphological synapomorphies. Increased sampling is necessary to better resolve relationships in this lineage, as well as to better understand evolution of floral morphological characters and thus generic or subgeneric circumscriptions. Particularly intriguing is the potentially sympatric evolution of endemic Puerto Rican sisters *M. sintenisii*-*M. variifolia* and endemic Cuban sisters *M. bicolor*-*M. ekmanii*. Both species pairs received very strong support in all analyses (Fig. 3), but each species exhibits a rather divergent floral morphology from the others (Fig. 4B u, v, x, y). Interesting as well is the apparently parallel evolution of a “reduced” gynostegial corona associated with reticulate corolla lobes. This morphology is exhibited by taxa such as *M. correllii* (Fig. 4B q), *M. denticulata* (Fig. 4B aa), *M. nipensis* (Fig. 4B s), and *M. reticulata* (Fig. 4A j). Taxa with ocellate, reticulate corollas, such as *M. correllii* and *M. nipensis*, emerged within the same clade, however *M. denticulata* clearly belongs to the second Gonolobinae lineage (discussed below), and the placement of *M. reticulata* remains unclear. Both *Matelea denticulata* and *M. oblongata* (an ocellate species emerging in a well-supported clade with *M. correllii*) exhibit winged follicles, whereas *M. reticulata* exhibits muricate follicles. *Matelea variifolia* also exhibits reticulate coronas, but clearly does not belong with any of these taxa. Nonetheless, it exhibits a gynostegial corona that intriguingly appears to mimic a “reduced” corona (Fig. 4B y).

The second major Gonolobinae lineage, characterized by the presence of the two indels (chs. 1817 and 1892), includes *Gonolobus* s.s., *G. stenosepalus*, *M. denticulata*, and perhaps *M. prosthucidiscus* (see Results). It remains unclear whether laminar dorsal anther appendages have evolved once or twice in Asclepiadeae (Fig. 3). Parsimony is equivocal on the issue. Based on the recovered topology, placing the evolution of the appendages immediately ancestral to the (*Gonolobus* s.s. (*G. stenosepalus*-*M. denticulata*)) clade, would require two evolutionary steps: one origin and one loss (in *M. denticulata*). If the appendages evolved independently in *Gonolobus* s.s. and *G. stenosepalus*, two steps are likewise required. Neither an independent origin nor a subsequent derivation of the appendages seem unrealistic considering the apparent lability of corona elements in Gonolobinae in general. The *Fimbristemma* group to which *G. stenosepalus* belongs is distinct in a number of additional ways. Members—such *G. calycosus* and *G. fimbriatiflorus*—exhibit a very well-developed faucal annulus that is conspicuously vertically elongate and tubular (Fig. 4B bb–dd). Completely annular faucal annuli with vertical development are also seen in other *Gonolobus* s.s. species, such as *G. jamaicensis* and *G. waitukubuliensis* (Fig. 4C jj, ll). However, in none of the included taxa is the Ca as vertically elongate as in the *Fimbristemma* group. *Gonolobus fimbriatiflorus* lacks medial development of the laminar dorsal anther appendages, although swellings are evident in the basal and lateral positions (Fig. 4B cc).

To the extent known and with a few exceptions (such as *G. niger*), taxa in the (*Gonolobus* s.s. (*G. stenosepalus*-*M. denticulata*)) clade exhibit smooth, winged follicles (Fig. 3; Fig. 5 a–c).

When slight murications are present, they appear in addition to wings. Smooth, winged follicles are also exhibited by members of the ocellate clade that includes *M. correllii* and *M. oblongata* (Fig. 5 d). In all fruits examined to date of members of both clades, the bases become curved so that the angle between peduncle and central follicle axis is 90° or greater (Fig. 5 a–d). This stands in contrast to the lack of twisting exhibited by the type of *Matelea* and numerous other Gonolobinae species such as *M. cyclophylla*, *M. decaisnei*, *M. palustris*, *M. prosthecidiscus*, and *M. pubiflora* (Fig. 5 e–k). Based on the recovered topology (Fig. 3), smooth, winged follicles appear to have arisen twice independently in Gonolobinae—once in *Gonolobus* s.l. and once in the ocellate clade. An independent origin is reconstructed regardless of whether the character is optimized using ACCTRAN or DELTRAN.

**Circumscription.** Based on current evidence, strict cladistic recognition of a broadly delimited *Gonolobus* that includes *Gonolobus* s.s. and the *Fimbristemma* group (e.g., Stevens 2001), requires the inclusion of *M. denticulata* (contra Fontella and Schwarz 1981b and Stevens 2001) if monophyly is to be maintained (Figs. 1 & 3). *Gonolobus* sensu Woodson (1941)—i.e., *Gonolobus* s.s. + *Fimbristemma*—is paraphyletic. However, Shinnery's (1950, 1964) approach (i.e., submerging the type of *Gonolobus* into *Matelea*) clearly represents an unnecessary swelling of *Matelea*, given that the monophyly of *Gonolobus* (s.l. or s.s.) is well-supported. Although a broad concept of *Matelea* has its advantages, especially given the great floral morphological diversity (Fig. 4), it is in the end only poorly predictive and scientifically unsatisfying. Most certainly a broad concept of *Matelea* should not include the type for *Gonolobus* as proposed by Shinnery (1950), and followed by subsequent North American authors (e.g., Drapalik 1969;

Wunderlin 1998). In contrast to members of the *Gonolobus* s.s. clade, the type for *Matelea* exhibits the plesiomorphic thymine in position 279 of the *trnL-F* sequence (Krings, unpubl.) and lacks (1) a faucal annulus, (2) laminar dorsal anther appendages, and (3) winged follicles (Figs. 4B p & 5 i). It also differs in habit, having been described most frequently as a shrub in collections and rarely as a vine. Its leaf blades are uniformly cuneate at the base, a character state very rare in *Gonolobus* s.s. or s.l., the more common being cordate. In the strict consensus tree of a parsimony analysis of *trnL-F* alone (data not presented), the type for *Matelea* emerged in a polytomy of species referred to *Matelea* rather than in the recovered monophyletic *Gonolobus* s.s. Thus, although neither *rps16* nor nuclear sequence data could be obtained for the species, it is well-supported as distinct from *Gonolobus* s.s., contrary to Shinnars (1950, 1964) and Drapalik (1969). Furthermore, all of the sampled species of *Gonolobus* sensu Woodson (1941) that Shinnars (1950, 1964) referred to *Matelea* emerged in the *Gonolobus* s.s. or s.l. clades—consistent with the concept of *Gonolobus* of the former.

Two *Leafy* indels (chs 1817 & 1891) can be considered synapomorphies for *Gonolobus* s.l. (Fig. 6). However, macromorphological synapomorphies of *Gonolobus* s.l. are difficult to define and few at best. Smooth, winged follicles appear to be synapomorphic for the clade. Laminar dorsal anther appendages may be synapomorphic for the clade, but as discussed above, parsimony is equivocal on the issue. Strict cladistic recognition of *Gonolobus* s.s. to the exclusion of the *Fimbristemma* group and the *M. denticulata* complex, must recognize the latter two as either separate genera or as a single heterogeneous genus. The former option seems preferable considering the morphological distinctions between the *Fimbristemma* group and the *M.*

*denticulata* complex. Under this scenario, *Gonolobus* s.s. could be recognized at least in part by the synapomorphic guanine in position 279 of *trnL-F* (Fig. 6). Laminar dorsal anther appendages would be an additional synapomorphy, should their origin be shown independent of the structures exhibited by the *Fimbristemma* group. An independent origin of anther appendages would also allow their use as a synapomorphy for *Fimbristemma*, along with the presence of a vertically elongate, tubular Ca.

An alternative to a strictly cladistic classification is an eclectic classification that maintains *Gonolobus* s.s. and the *Fimbristemma* group in a paraphyletic *Gonolobus*, and *M. denticulata* in a segregate genus. This classification is essentially what is currently followed in practice by other asclepiad workers (e.g., Fontella and Schwarz 1981b; Stevens 2001) and consistent with Woodson (1941). Advantages to such a classification are the recognition of all taxa with any sort of laminar dorsal anther appendages, whether radially or basio-laterally developed, in a single genus. *Matelea denticulata* is quite distinct morphologically from *Gonolobus* s.s. and the *Fimbristemma* group, and its segregate recognition has a certain aesthetic appeal.

Regardless of whether one accepts a narrow or broad *Gonolobus*, a strict cladistic or an eclectic classification, current evidence supports the monophyly of entities bearing laminar dorsal anther appendages with strong radial and medial development in a clade that includes the type of *Gonolobus* (Fig. 3, 6). This clade can be considered the “core *Gonolobus*” clade and encompasses the vast majority of species with laminar dorsal anther appendages (likely > 100–130 spp.). Taxa belonging to *Fimbristemma* or the *M. denticulata* complex doubtfully number

more than fifteen. To date, only five names have been described in the former genus and only a few additional combinations would be required should it be resurrected. Thus, the description of new taxa exhibiting laminar dorsal anther appendages with strong radial and medial development in *Gonolobus* is unlikely to prove ephemeral. This stands in contrast to the current practice of describing taxa not readily placed in one of Woodson's (1941) other accepted gonolobinoid genera in *Matelea*.

Some additional observations on generic and subgeneric circumscriptions in *Matelea* can also be offered based on the present analyses (Fig. 3). Several of Woodson's (1941) informal subgeneric concepts appear not to be monophyletic. These include subgenera *Ptycanthera*, *Pachystelma*, and *Ibatia*. *Matelea ekmanii* (subg. *Ptycanthera*) was strongly supported in all analyses as sister to sympatric *M. bicolor* (subg. *Pachystelma*) in a clade that likely includes *M. viridivenia*, whereas other members of subg. *Ptycanthera* (e.g., *M. oblongata*, *M. nipensis*) resolved as an independent clade. Woodson (1941) placed *M. maritima* (*Ibatia*), *M. rubra* (*Omphalophthalma*), *M. prosthecidiscus* (*Prosthecidiscus*), *M. cordifolia* (*Rothrockia*), and *M. gonoloboides* (*Urostephanus*) in subgenus *Ibatia*. However, *M. prosthecidiscus* (*Prosthecidiscus*) exhibits an indel structure in the *Leafy* genome not shared by other members of subg. *Ibatia* (Table 2). *Matelea rubra* (*Omphalophthalma*) is strongly supported as sister to *M. maritima* (*Ibatia*), but distant to the remaining taxa based on evidence from chloroplast and nuclear genomes. In the analysis of New World Asclepiadeae chloroplast matrix, *M. cordifolia* (*Rothrockia*) emerged in a strongly BS supported clade of *Labidostelma*, *Polystemma*, and *Microdactylon* taxa (indels coded: 92%; indels not coded: 94%), whereas *M. gonoloboides* (*Urostephanus*) emerged in a

strongly BS supported clade of *Dictyanthus* taxa (indels coded: 94%; indels not coded: 91%).

Increased sampling is necessary to address most additional problems in *Matelea* sensu Woodson (1941), but it is hoped that the present study provides a framework on which to build.

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TABLE 1. Optimal substitution models, total number of nucleotides included in the phylogenetic analyses, number of constant and variable sites for each of the various data partitions used in the heterogeneous Bayesian analysis of the three specified data sets.

New World Asclepiadeae chloroplast matrix

<i>Region</i>	<i>Model</i>	<i>Nucleotides</i>	<i>Constant</i>	<i>Autapomorphic</i>	<i>Informative</i>
<i>trnL-F</i>	GTR+G	489	315	83	91
<i>rps16</i>	TVMef+G	1032	676	165	191

Leafy clones matrix

<i>Region</i>	<i>Model</i>	<i>Nucleotides</i>	<i>Constant</i>	<i>Autapomorphic</i>	<i>Informative</i>
2 <sup>nd</sup> Exon	K80+G	86	73	10	3
2 <sup>nd</sup> Intron	K81vf+G	472	348	60	64

Gonolobinae matrix

<i>Region</i>	<i>Model</i>	<i>Nucleotides</i>	<i>Constant</i>	<i>Autapomorphic</i>	<i>Informative</i>
<i>trnL-F</i>	TVM	489	437	39	13
<i>rps16</i>	TVM+I+G	1032	904	70	58
<i>leafy</i>	HKY+I	190	116	53	21

TABLE 2. Noteworthy indels in the *Leafy* genome of sampled Gonolobinae species. When a species serves as generic type, the respective genus is provided in parentheses following the species name. - = gap; ?/N= nucleotide ambiguous; F=*Fischeria*; G=*Gonolobus*; M.=*Matelea*.

	Indel 1 (ch. 1817; 82bp)	Indel 2 (ch. 1891; 17bp)
	*-<-start	end->*      *-<-start      end->*
<i>F. scandens</i> ( <i>Fischeria</i> )	CACACACACTCACACTCACACACACACA--TATATATATATATATAT?GAGAGT?T??AAA?A?A?-----A?AAAAA----CG?GTT	CGA-GA-CCT-----C
<i>F. panamensis</i>	CACACACACTCACA--CACACA-----T?TATATATATATAT--?GA?AGATTATAA?AA--G?AAGGAAAAAAA?G?A??AGAT	NNNNNNNNNNNNNNNNNNNN
<i>M. bicolor</i>	CACACACACA-----TATATATTGACAGTTTAAAAAAAAG---AAAAAAAAGTA-ATAGTT	CAA-GA-C-T-A--C-T-C
<i>M. cordata</i> ( <i>Microdactylon</i> )	CACACACACA-----TATATATTGACAGATTGTAATAAGATAAAAGAGAAAAAAGTA-ATAGTT	CGA-GA---TYW--C-T-C
<i>M. cordifolia</i> ( <i>Rothrockia</i> )	CACACACACACACAC-----ATGTATTGACAGTTGAAAAATAAAG---AAAAAAAAGTA-ATAGTT	CAA-GA---TTA--C-T?C
<i>M. correllii</i>	CACACACACA-----TACACACA-----TATATTGACAGTTTAAAAATAAAG---AAAAAATGTA-----	CAA-GA-C-T-A--C-T-C
<i>M. cyclophylla</i>	CACACACACACACA-----TTGACAGTTTAAAAA-----TA-AT-G-T	CA--GC-C-G-C--C-T-C
<i>M. decaisnii</i> ( <i>Polystemma</i> )	C?C?C?---TC-----TAC-TAC-----	CTA-GT-T-TT---C-T-C
<i>M. denticulata</i>	CACA-----TT	C-----C
<i>M. dictyantha</i> ( <i>Rytidoloma</i> )	CACACACACA?A-----TATATATTGACAGTTCAAAAAGT---AAAGAAAAAAAAG-AAATAGTT	CANAG----TTAAACCT-C
<i>M. ekmanii</i>	CACACACACA-----TATATATTGACAGTTTAAAAAAAAG---AAAAAAAAGTA-ATAGTT	CAA-GA-C-T-A--C-T-C
<i>M. gonoloboides</i> ( <i>Urostephanus</i> )	CACAC---TCACACACA?A-----	CAAAGA-C-T-A--C-T-C
<i>M. hemsleyana</i>	CACACACACACACACACA-----TATATATTGACAGTTCAAAAAGTAAAG---AAAAAAAAGTA-ATAGTT	CAA???????????????
<i>M. inconspicua</i>	CACA?A-----TATATTATTACTATATTGACAGTTTAAAAATAAAGAAAAA-----TAGTT	CGA-GA-C-T-A--C-T-C
<i>M. lanata</i> ( <i>Trichosacme</i> )	CACACACACACACACACACA-----GATATTGACATTTTAAAAAGTAAAG---AAAAAAAAGTA-ATAGTT	CAA-GA-C-T-A--C-T-C
<i>M. nipensis</i>	CACACACACA-----TACAC-----?GACA?ATTGACAG-TTAAAA?AAAGGAAA?A-----?GTA--TATAT	CAA-GA-C-A-A--C-T-C
<i>M. oblongata</i>	CACACACACACA-----TACACACA-----TATATTGACAGTTTAAAAATAAAG---AAAAAATGTA-ATA--T	CAA-GA-C-T-A--C-T-C
<i>M. phainops</i>	CACACACACACACACACACACA-----TATATATTGACAGTTTAAAAA?AAA?---AAAAAAAAG?-----T	CA--GA-G-T-A--C-T-C



TABLE 2 (continued).

	Indel 1 (ch. 1817; 82bp)	Indel 2 (ch. 1891; 17bp)
<i>G. niger</i>	CACA-----TT	C-----C
<i>G. pectinatus</i>	CACA-----TT	C-----C
<i>G. stapelioides</i>	CACA-----TT	C-----C
<i>G. stenosepalus</i>	CACA-----TT	????????????????
<i>G. suberosus (Gonolobus)</i>	CACA-----TT	C-----C
<i>G. stephanotrichus</i>	CACA-----TT	C-----C
<i>G. uniflorus</i>	CACA-----TT	C-----C
<i>G. waitukubuliensis</i>	CACA-----TT	C-----C
<i>G. youroumaynensis</i>	CACA-----TT	C-----C

APPENDIX A. Herbarium voucher specimens for newly generated sequences. See Liede-Schumann et al. (2005) for species not represented below.

*Fischeria panamensis* Spellman, *Folsom 9364* (DUKE); *Fischeria scandens* DC., *Krings s.n.* (NCSC); *Gonolobus albomarginatus* (Pittier) Woodson, *Taylor & Skotak 4455* (DUKE); *G. arizonicus* (A. Gray) Woodson, *van Devender 2004-893* (ARIZ); *G. barbatus* Kunth, *Taylor 2227* (DUKE); *G. bibarbatus* W.D. Stevens, *Cowan 5620* (TEX); *G. breedlovei* L.O. Williams, *King 2778* (TEX); *G. chloranthus* Schltldl., *Cowan 5513* (TEX); *G. croceus* W.D. Stevens, *Cowan 4785* (TEX); *G. fraternus* Schltldl., *Fishbein 5164* (ARIZ); *G. fuscoviolaceus* Woodson, *Taylor 3882* (DUKE); *G. gonoloboides* (Greenm.) Woodson, *Reina 2003-884* (ARIZ); *G. grandiflorus* (Cav.) Schult., *Fishbein 5114* (ARIZ); *G. iyanolensis* Krings, *Krings SL1* (NCSC); *G. jaliscensis* B.L. Rob. & Greenm., *Fishbein 5121* (ARIZ); *G. jamaicensis* Rendle, *Krings J3* (NCSC); *G. niger* (Cav.) Schult., *Mayfield et al. 860* (TEX); *G. pectinatus* Brandegee, *Prinzie & Lozada 202* (TEX); *G. rostratus* (Vahl) Schult., *Morreau 30645* (TRIN); *G. stapelioides* Desv. ex Ham., *Krings J1* (NCSC); *G. stenosepalus* (Donn. Sm.) Woodson, *Taylor 2536* (DUKE); *G. stephanotrichus* Griseb., *Krings et al. s.n.* (NCSC); *G. suberosus* (L.) R.Br. var. *granulatus* (Scheele) Krings & Q.-Y. Xiang, *Krings LC1* (NCSC); *G. suberosus* (L.) R.Br. var. *suberosus*, *Krings FL9* (NCSC); *G. taylorianus* W.D. Stevens & Montiel, *Saunders 872* (TEX); *G. uniflorus* Kunth, *van Devender 2003-1323* (ARIZ); *G. waitukubuliensis* Krings, *Krings D12* (NCSC); *G. youroumaynensis* Krings, *Krings SV4* (NCSC); *Matelea acuminata* (Griseb.) Woodson, *Krings Mac1* (NCSC); *M. alabamensis* (Vail) Woodson, *Allison 3159* (GA); *M. angustiloba* (B.L. Rob. & Greenm.) W.D. Stevens, *Soto 1037* (TEX); *M. bicolor* (Britton & P. Wilson) Woodson, *Krings Mbi1* (NCSC); *M. chrysantha* (Greenm.) Woodson, *Taylor 2384* (DUKE); *M. cordata*

(Brandege) Woodson, *Tenorio 11556* (TEX); *M. cordifolia* (A. Gray) Woodson, *Stevens 1517* (MSC); *M. correllii* Spellman, *Correll 48157* (DUKE); *M. cyclophylla* (Standl.) Woodson, *Stevens et al. 2299* (MSC); *M. decaisnei* Woodson, *Tucker 2766* (DUKE); *M. denticulata* (Vahl) Fontella & E.A. Schwarz, *Hammel 9304* (DUKE); *M. dictyantha* Woodson, *Stevens et al. 2311* (MSC); *M. ekmanii* (Urb.) Woodson, *Krings Mek1* (NCSC); *M. gonoloboides* (B.L. Rob. & Greenm.) Woodson, *Stevens 1349* (MSC); *M. hemsleyana* Woodson, *Stevens 1399* (MSC); *M. inconspicua* (Brandege) Woodson, *Panero 5804* (TEX); *M. lanata* (Zucc.) Woodson, *Hinton et al. 23755* (TEX); *M. lanceolata* (Decne.) Woodson, *Toriz 627 et al.* (TEX); *M. maritima* (Jacq.) Woodson, *Goldman 1941* (BH); *M. nipensis* (Urb.) Woodson, *Krings Woodfred* (NCSC); *M. oblongata* (Griseb.) Woodson, *Krings Mob1* (NCSC); *M. palustris* Aubl., *Hequet 576* (NY); *M. pauciflora* (Spreng.) Woodson, *Lavastre 2290* (NY); *M. phainops* Krings, *Liogier 16617* (NY); *M. prosthecidiscus* Woodson, *Stevens & Fairhurst 1811* (DUKE); *M. pubiflora* (Decne.) Woodson, *Orzell & Bridges 20226* (USCH); *M. pusilliflora* L.O. Williams, *Martinez 14847* (TEX); *M. quirosii* (Standl.) Woodson, *Steinmann 1084* (NY); *M. reticulata* (Engelm. ex A. Gray) Woodson, *Krings L3* (NCSC); *M. rubra* (H. Karst.) Spellman & Morillo, *Proosdij et al. 667* (NY); *M. sintenisii* (Schltr.) Woodson, *Krings 1405* (NCSC); *M. tamnifolia* (Griseb.) Woodson, *Krings Mtam1* (NCSC); *M. trachyantha* (Greenm.) W.D. Stevens, *Stevens et al. 2300* (DUKE); *M. variifolia* (Schltr.) Woodson, *Krings 1397* (NCSC); *M. viridivenia* Alain, *Veloz et al. 836* (JBSD); *Schubertia* sp., *Hennen & Hennen 84-228* (PUR); *Schubertia* sp., *Murphy & Parra 730* (DUKE).

FIG. 1A. Strict consensus of 200,000 most parsimonious trees resulting from parsimony analysis of *trnL-F* and *rps16* regions of New World Asclepiadeae (Length = 1078; CI = 0.464; RI = 0.793). For members of Gonolobinae, if a species is the type for a genus, the latter is indicated in bold following the scientific name. Support values are provided based on analysis with indels simple gap coded/indels not coded. Bootstrap support (BS) is given above branches and Bayesian posterior probabilities (PP) are given below branches. To save space, not all taxa are shown for the Metastelmatinae, Core Oxypetalinae, and Orthosiinae clades (inverted triangles), although the number of taxa in each that was included in the analyses is provided in parentheses. - = less than 65% BS or less than 95% PP; \* = 95–99% BS/PP; ! = 100% BS/PP. M. = *Matelea*; MOG = Metastelmatinae-Oxypetalinae-Gonolobinae group sensu Liede-Schumann et al. (2005).

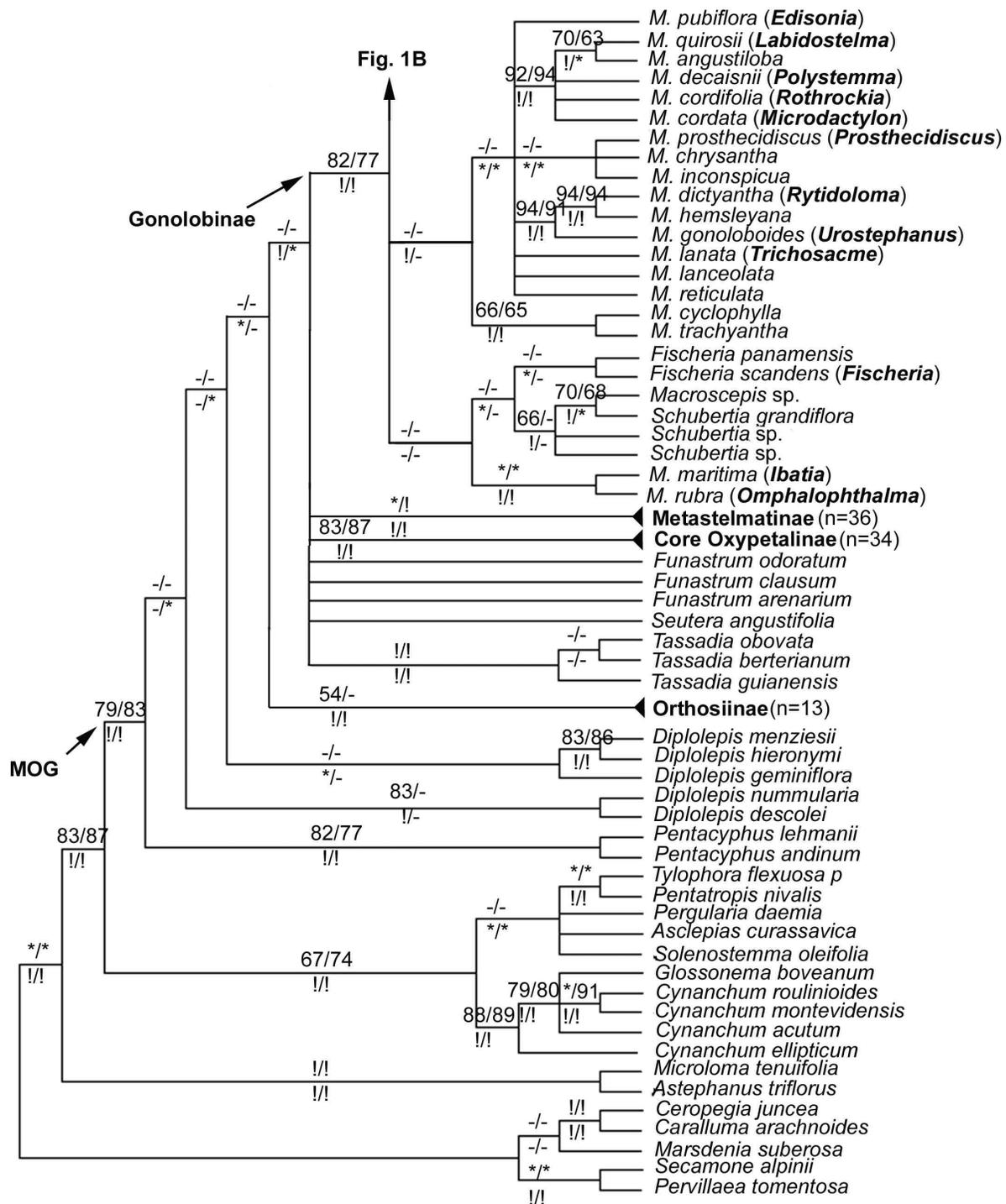


FIG. 1B. Strict consensus of 200,000 most parsimonious trees resulting from parsimony analysis of *trnL-F* and *rps16* regions of New World Asclepiadeae (Length = 1078; CI = 0.464; RI = 0.793). For members of Gonolobinae, if a species is the type for a genus, the latter is indicated in bold following the scientific name. Support values are provided based on analysis with indels simple gap coded/indels not coded. Bootstrap support (BS) is given above branches and Bayesian posterior probabilities (PP) are given below branches. - = less than 65% BS or less than 95% PP; \* = 95–99% BS/PP; ! = 100% BS or PP; G. = *Gonolobus*; M. = *Matelea*.

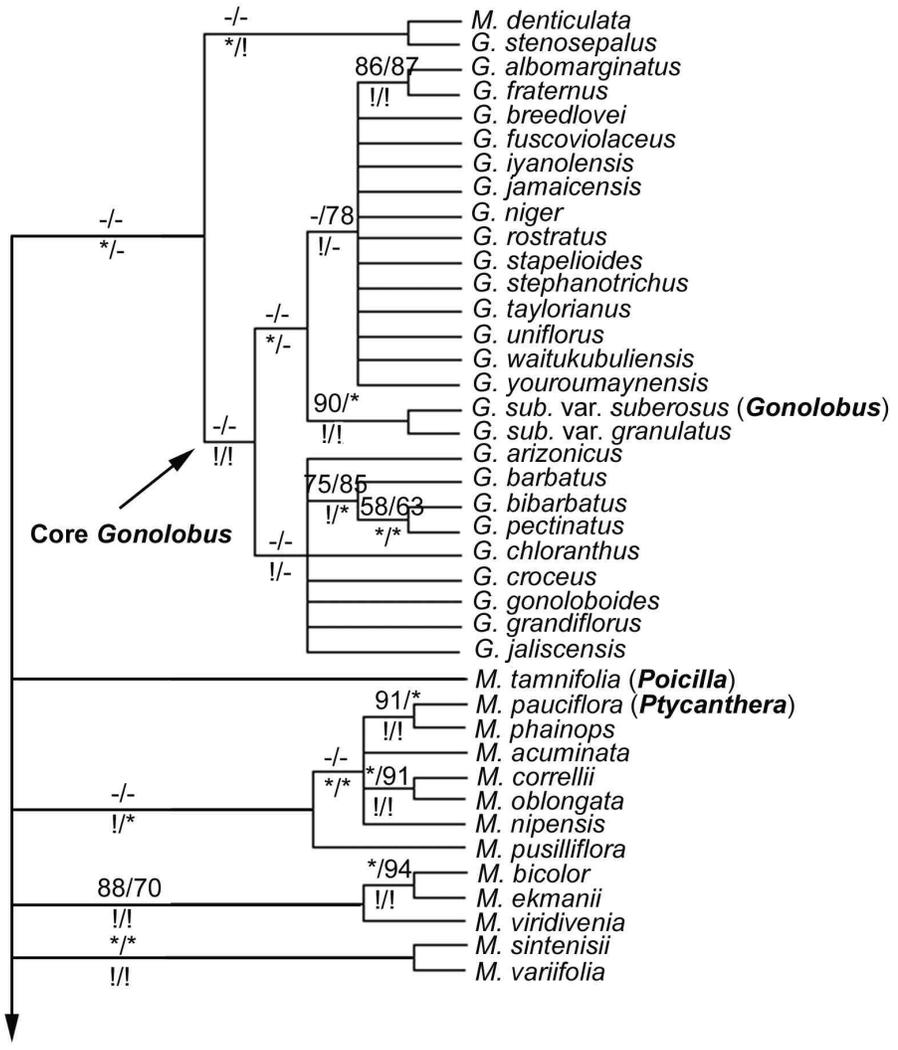


Fig. 1A

FIG. 2. Strict consensus of 47,168 most parsimonious trees recovered from parsimony analysis of *Leafy* clones for nine species of Gonolobinae (Length = 166; CI = 0.934; RI = 0.954).

Bootstrap support values (BS) given above branches. Bayesian posterior probabilities (PP) given below branches. - = less than 50% BS or less than 95% PP. al = *Matelea alabamensis*; bic = *Matelea bicolor*; ek = *Matelea ekmanii*; obl = *Matelea oblongata*; sint = *Matelea sintenisii*; stap = *Gonolobus stapelioides*; subsub = *Gonolobus suberosus* var. *suberosus*; tamni = *Matelea tamnifolia*; varii = *Matelea variifolia*.

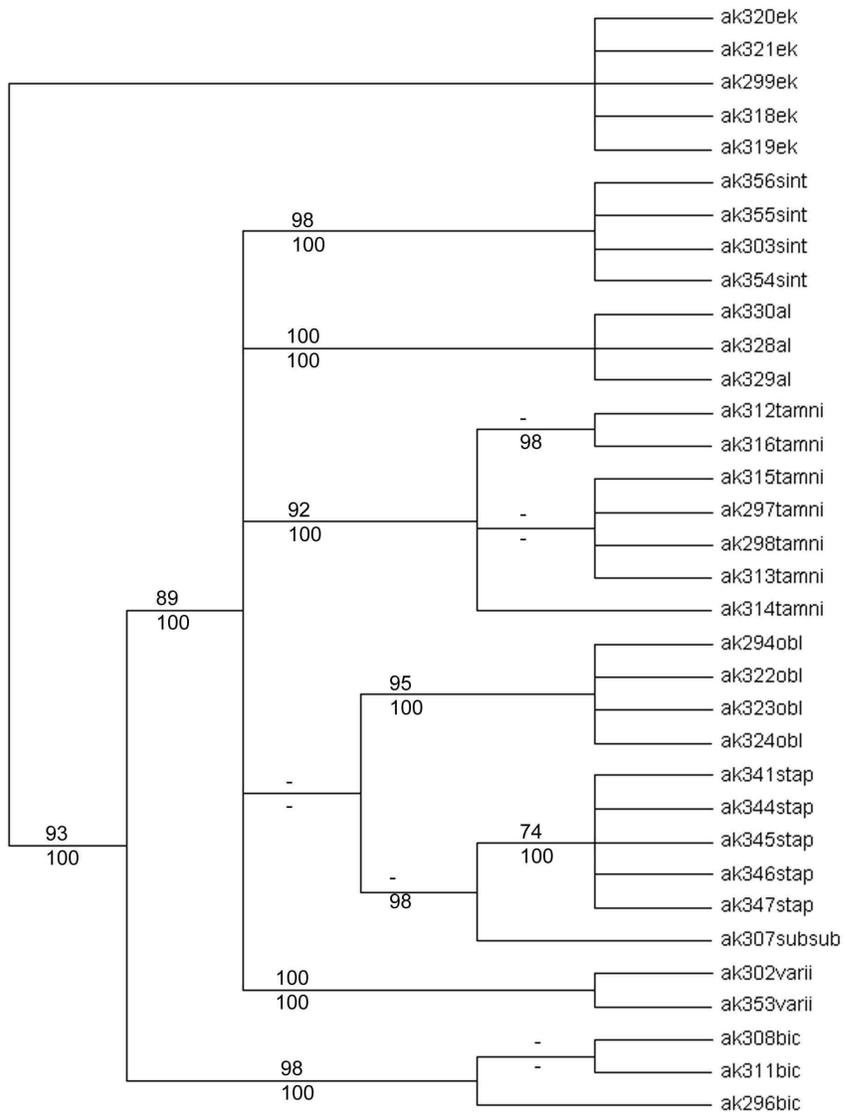
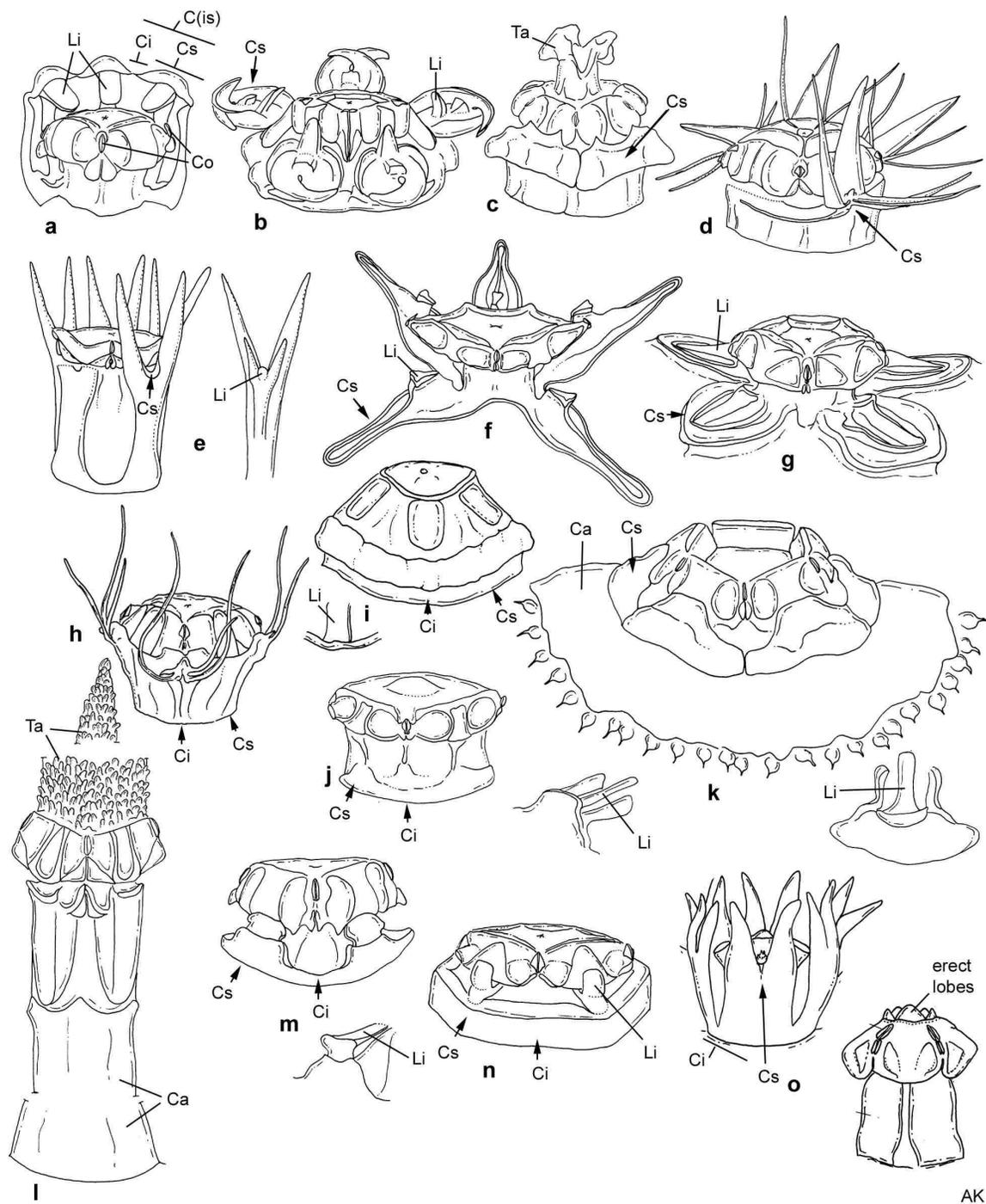


FIG. 3. Phylogram of one of 1559 most parsimonious trees based on analysis of *trnL-F*, *rps16*, and *Leafy* for Gonolobinae taxa. Nodes collapsing in the parsimony strict consensus tree (Length=294; CI=0.527; RI=0.731) are indicated by dashed lines. Support values are provided based on analysis with indels simple gap coded/indels not coded. Bootstrap support (BS) is given above branches and Bayesian posterior probabilities (PP) are given below branches. Branches receiving > 95 PP are bolded. If a taxon is a type for a genus, the latter is indicated in bold following the scientific name. Scientific names are also followed by a two-letter abbreviation for subgenus, then, if applicable, an abbreviation in italics for genus assigned to by Shinnery (1950, 1964), then a bracketed reference to an illustration in Figure 4. *Leafy* indels (cha. 1817 and 1892) arrowed. - = less than 65% BS or less than 95% PP; \* = 95-99% BS/PP; ! = 100% BS/PP; Cd = dorsal anther appendage; Ch = subg. *Chthamalia*; Di = subg. *Dictyanthus*; Em = subg. *Eumatelea*; Eu = subg. *Eugonolobus*; F. = *Fischeria* sensu Woodson (1941); G. = *Gonolobus* sensu Woodson (1941); He = subg. *Heliostemma*; Ib = subg. *Ibatia*; La = subg. *Labidostelma*; M. = *Matelea* sensu Woodson (1941); Mat-S = *Matelea* sensu Shinnery (1950, 1964); Mi = subg. *Microdactylon*; Pa= subg. *Pachystelma*; Pc = subg. *Poicilla*; Po = subg. *Polystemma*; Pr = subg. *Pterolobus*; Ps = subg. *Pseudolachnostoma*; Pt = subg. *Ptycanthera*; Tr = subg. *Trichosacme*.



FIG. 4A. Gynostegia and gynostegial coronas in Gonolobinae: a–o, *Matelea* sensu Woodson (1941). Gynostegia shown with corpusculum (Co) facing reader, except for *M. rubra* (o). Gynostegial corona terminology follows Liede and Kunze (1993) and Kunze (1995). Staminal and interstaminal coronas are regions corresponding to their position (see **a**), but for convenience are arrowed in the remaining illustrations. All depicted taxa share a C(is), but this is only lettered in **a**. Tubular Ca and elongate Ta of *M. prosthecidiscus* (l) are interrupted in illustration to fit on page. Ca are only present in taxa when lettered. **a**, *M. pubiflora* (*Edisonia*; Orzell & Bridges 20226, USCH); **b**, *M. quirosii* (*Labidostelma*; Steinmann 1084 & Variela, NY); **c**, *M. cordifolia* (*Rothrockia*; Stevens 1517, MSC); **d**, *M. decaisnei* (*Polystemma*; Hinton 8522, US); **e**, *M. cordata* (*Microdactylon*; Tenorio 11745 et al., MSC); **f**, *M. dictyantha* (*Rytidoloma*; Stevens 1346, MSC); **g**, *M. hemsleyana* (Sántiz C. 741, TEX); **h**, *M. gonoloboides* (*Urostephanus*; Stevens 1423, MSC); **i**, *M. lanata* (*Trichosacme*; Hinton 23755, TEX); **j**, *M. reticulata* (Krings 327, NCSC); **k**, *M. inconspicua* (Panero 8504 et al., TEX); **l**, *M. prosthecidiscus* (*Prosthecidiscus*; Koch et al. 87198, TEX); **m**, *M. cyclophylla* (Hinton 8041, US); **n**, *M. trachyantha* (Stevens et al. 2300, MSC); **o**, *M. rubra* (*Omphalophthalma*; Howard 20294, A, NY). Ca = faucal annulus; Ci = interstaminal gynostegial corona; C(is) = fused gynostegial corona of staminal and interstaminal parts; Co = corpusculum; Cs = staminal gynostegial corona; Li = ligule; Ta = terminal appendage of stylar head.



AK

FIG. 4B. Gynostegia and gynostegial coronas in Gonolobinae: p–cc, *Matelea* and *Gonolobus* sensu Woodson (1941). Gynostegia shown with corpusculum (Co) facing reader. Staminal and interstaminal coronas are regions corresponding to their position (see **p**), but for convenience are arrowed in the remaining illustrations. Ca are only present in taxa when lettered. **p**, *M. palustris* (*Matelea*; Prance & Boeke 28102, NY); **q**, *M. correllii* (Correll 49112, FTG); **r**, *M. oblongata* (*Krings obl*, NCSC); **s**, *M. nipensis* (Webster 3813, GH); **t**, *M. phainops* (Liogier 16617, GH); **u**, *M. bicolor* (*Krings bil*, NCSC); **v**, *M. ekmanii* (*Krings ek1*, NCSC); **w**, *M. viridivenia* (Veloz et al. 881, JBSD); **x**, *M. sintenisii* (*Krings P15*, NCSC); **y**, *M. variifolia* (*Krings P2*, NCSC); **z**, *M. tamnifolia* (*Poicilla*; *Krings tam1*, NCSC); **aa**, *M. denticulata* (Dodson & Dodson 15450, NY); **bb**, *G. stenosepalus* (Taylor 2536, DUKE); **cc**, *G. fimbriatiflorus* (McDade 552, DUKE); **dd**, *G. calycosus* (Williams et al. 24759, LL). Ca = faucal annulus; Cd = dorsal anther appendages; Ci = interstaminal gynostegial corona; C(is) = fused gynostegial corona of staminal and interstaminal parts; Co = corpusculum; Cs = staminal gynostegial corona; Li = ligule.

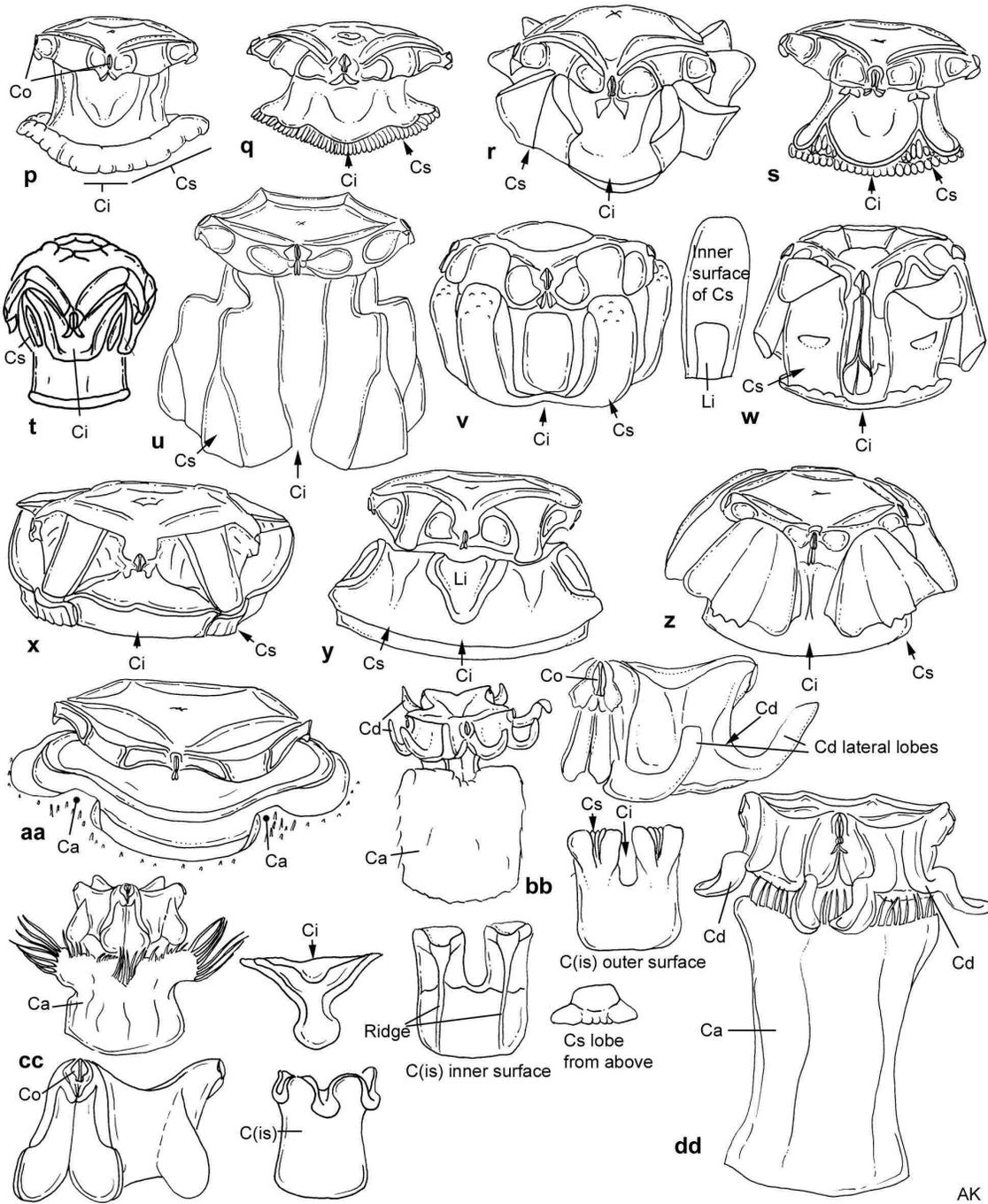
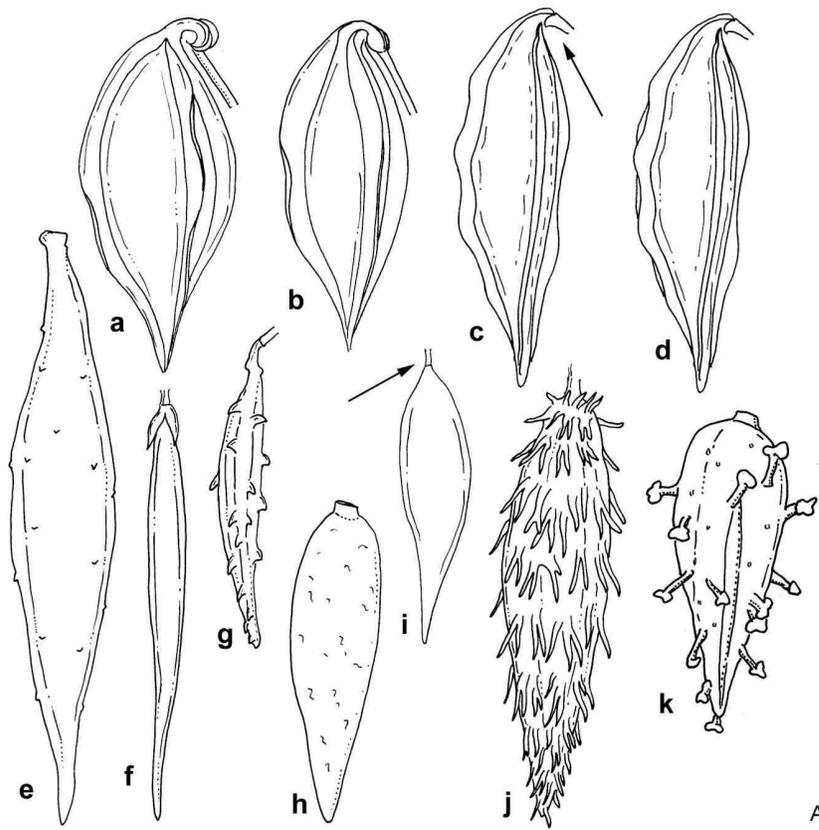


FIG. 4C. Gynostegia and gynostegial coronas in Gonolobinae: ee–vv, *Gonolobus* sensu Woodson (1941). Gynostegia shown with corpusculum (Co) facing reader. Ca are present in all taxa. **ee**, *G. albomarginatus* (Folsom 9953, TEX); **ff**, *G. fraternus* (Fryxell 3776, TEX); **gg**, *G. breedlovei* (King 2778, TEX); **hh**, *G. niger* (Alcorn 1759, TEX); **ii**, *G. iyanolensis* (Kring 1373 et al., NCSC); **jj**, *G. waitukubuliensis* (Eggers 728, M; Webster 13505, US); **kk**, *G. youroumaynensis* (Kring 1374 with Springer, NCSC); **ll**, *G. jamaicensis* (Kelly et al. 10207, TCD); **mm**, *G. uniflorus* (Pringle 6389, MSC); **nn**, *G. stapelioides* (Kring 2394, NCSC); **oo**, *G. stephanotrichus* (Acevedo-Rodríguez 10596, US); **pp**, *G. suberosus* var. *suberosus* (*Gonolobus*; Walker s.n., NCSC); **qq**, *G. barbatus* (Stevens 2909, LL); **rr**, *G. bibarbatulus* (Cowan 5620 et al., TEX); **ss**, *G. pectinatus* (Prinz & Lozada 202, TEX); **tt**, *G. jaliscensis* (Torres C. 6712 & Garcia M., TEX); **uu**, *G. chloranthus* (Panero 6641 et al., TEX); **vv**, *G. grandiflorus* (Barkley et al. 7656, TEX). Ca = faucal annulus; Cd = dorsal anther appendages; Ci = interstaminal gynostegial corona; C(is) = fused gynostegial corona of staminal and interstaminal parts; Co = corpusculum; Cs = staminal gynostegial corona; Li = ligule; N<sup>2</sup> = secondary nectary.

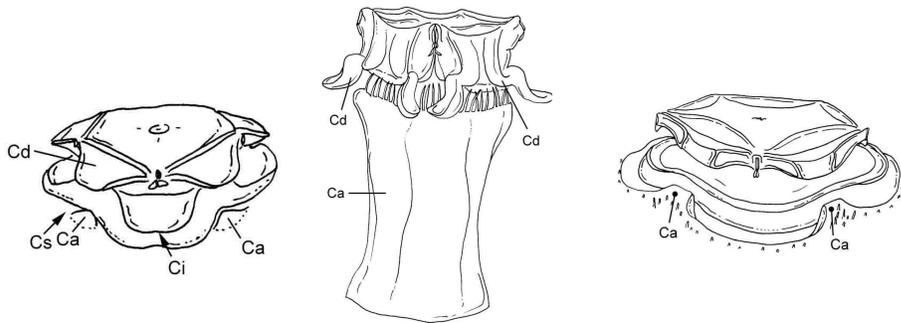


FIG. 5. Sample variation in follicle morphology in *Gonolobus* and *Matelea*, including types of the genera. Genus indicated in parentheses following species name when species is generic type. Note angle of peduncle attachment particularly in types of *Gonolobus* and *Matelea* (arrowed). **a**, *G. barbatus* (Stevens 13596, LL); **b**, *G. chloranthus* (Vega 240 et al., TEX); **c**, *G. suberosus* (*Gonolobus*; Krings 418, NCSC); **d**, *M. correllii* (Correll 48157, MO); **e**, *M. cyclophylla* (Stevens 1815, MSC); **f**, *M. decaisnei* (*Polystemma*); **g**, *M. dictyantha* (Stevens 1311, MSC); **h**, *M. lanata* (*Trichosacme*; von Rozynski 210, US); **i**, *M. palustris* (*Matelea*; Billiet & Jadin 1251, NY); **j**, *M. prosthecidiscus* (*Prosthecidiscus*; Koch et al. 87198, TEX); **k**, *M. rubra* (*Omphalophthalma*; Howard 20294, A, NY).



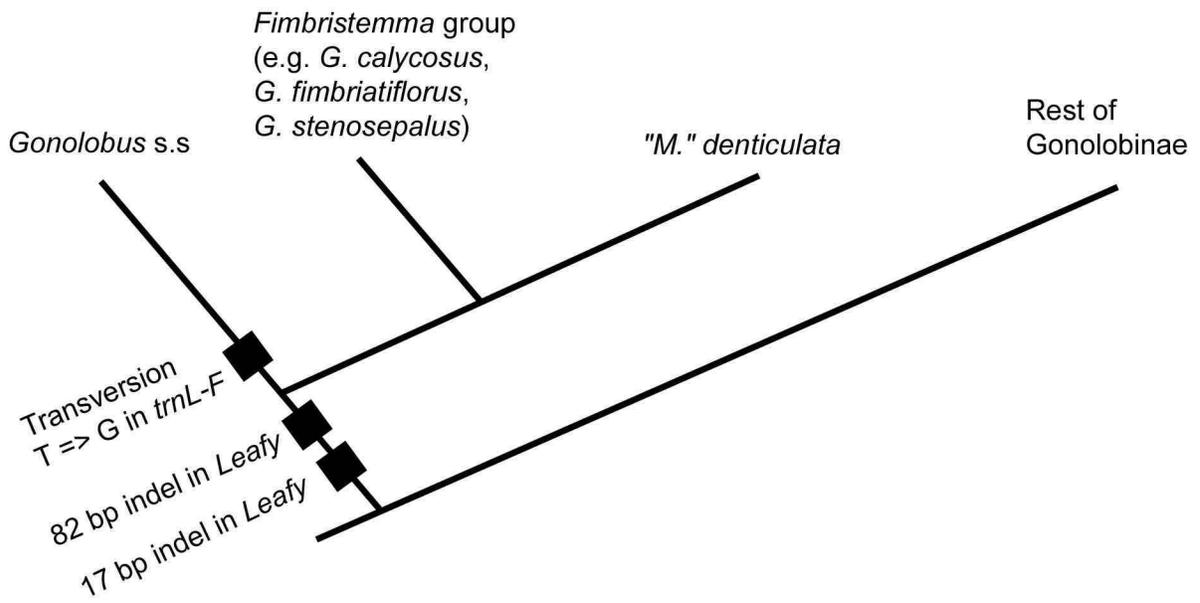
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FIG. 6. Model of evolution of *Gonolobus* s.l. based on current evidence, with molecular synapomorphies mapped on branches. The T>G synapomorphy in *trnL-F* occurs is position 279 of the aligned sequence matrix. The indel synapomorphies in *Leafy* are characters 1817 and 1891 in the Gonolobinae *trnL-F/rps16/Leafy* matrix. Cd = dorsal anther appendages. G. = *Gonolobus*; M. = *Matelea*.



Cd laminar

Cd absent



## **Chapter VI**

### **Revision of *Gonolobus* (Apocynaceae: Asclepiadoideae) in the West Indies**

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ABSTRACT. A revision to Gonolobus s.s. (Apocynaceae, Asclepiadoideae, Gonolobinae) in the West Indies is provided based on recent evidence of support for the monophyly of the genus from molecular and morphological data. Twelve species are treated (nine endemic to a single island each). Keys, descriptions, illustrations, and an index to exsiccatae are provided for all twelve species. The conservation status of each species is provisionally assessed using IUCN and NatureServe criteria. Two new combinations are made in Matelea: M. dictyopetala and M. pubescens.

## INTRODUCTION

Subtribe Gonolobinae (Apocynaceae, Asclepiadoideae) comprises about fifty species in the West Indies (here considered to include the Greater and Lesser Antilles, the Bahamas, Trinidad and Tobago, Aruba and the Netherland Antilles, and the Cayman Islands). Evidence from the chloroplast (Rapini et al. 2003; Liede-Schumann et al. 2005; Rapini et al. 2006; Krings et al., in review) and nuclear genomes (Krings et al., in review) supports the monophyly of the subtribe. Genera referred to the subtribe with representation in the region include Fischeria DC., Gonolobus Michx., Matelea Aubl. (incl. Ibatia Decne., Jacaima Rendle, Poicilla Griseb., Poicillopsis Schltr., Ptycanthera Decne.), Macroscepis Kunth, and Metalepis Griseb. (Fontella & Schwarz 1981a; Kunze 1995; Liede 1997; Morillo 1997; Rapini et al. 2003; Liede-Schumann et al. 2005; Rapini et al. 2006). Subtribal position has been most controversial for Metalepis, which some workers have also placed among Cynanchum L. in the Metastelmatinae (Woodson 1941; Spellman 1975; Sundell 1981). The last regional treatment of Gonolobinae is now over 100 years old (Schlechter 1899) and a number of new species have recently been described

(Krings 2005b, 2006, 2007). Most members of the subtribe have never been monographed (Rapini et al. 2003) and generic circumscriptions of most genera remain poorly defined. The Gonolobus-Matelea complex in particular is in desperate need of taxonomic revision. However, the size of the complex (ca. 200–350 spp.) requires an approach focusing on smaller, more tractable subgroups. Considering the support for a monophyletic Gonolobus s.s. based on recent evidence from chloroplast (trnL-F, rps16) and nuclear (Leafy) data (Krings et al., in review), recent taxonomic changes in West Indian taxa (Krings 2005a–d), and that several species have been published from the area since the last comprehensive treatment over a hundred years ago (Schlechter 1899; Krings 2006, 2007), a revision of the genus in the West Indies seemed appropriate. This revision treats all twelve West Indian Gonolobinae species referable to Gonolobus s.s. (i.e., characterized by the presence of laminar, dorsal anther appendages, winged follicles, and a synapomorphic guanine; Krings et al., in review). In addition, two new combinations are made in Matelea: M. dictyopetala and M. pubescens (see Doubtful and excluded names).

## METHODS

This treatment is based on critical study of ca. 250 specimens of the fifty some known species in West Indian Gonolobinae, obtained in part through: (1) loan requests from ninety herbaria—of which sixty-five responded with either loans, digital images, or negative search results (see Acknowledgements), (2) visits to BM, BSC, DUKE, HAC, HAJB, IJ, K, UCWI, UPRRP, US, and P, and (3) forty-eight days of field work by the author in the Bahamas (Long Island), Cuba, Dominica, Jamaica, Puerto Rico, St. Lucia, and St. Vincent. The treatment is also informed by

analyses of sequences of portions of the chloroplast (trnL-F, rps16) and nuclear genomes (Leafy) of selected accessions (see Krings et al., in review). The species concept employed is an amalgam of the Phylogenetic Species Concept (PSC) of Nixon and Wheeler (1990) and the Evolutionary Species Concept (ESC) as modified by Wiley (1978), namely that: a species is a lineage of ancestral-descendent populations, which have maintained their identity from other such lineages, and which are diagnosable by a unique combination of character states in comparable individuals. Although the PSC has been critiqued as a non-historical concept—and thus potentially failing to identify instances of phenotypic homoplasy (Baum & Donoghue 1995)—this critique has not been accepted universally (Luckow 1995). The concept has been useful both as theoretical definition and operational delimitation criterion. However, as the application of the PSC, and its discovery method Population Aggregation Analysis (PAA; Davis & Nixon 1992), requires study of populations, its application is limited when entities are known uniquely from a population, or worse, from a single collection (e.g., G. absalonensis). In the absence of complete, multi-population accessions for extant and historical species, the provisional approach taken here is to rely on observable patterns of differentiation, with the general phytomonographic assumption that these patterns are due to a variety of biological processes underlying the morphological and historical integrity of species (McDade 1995). As a result, character states of each lone populational representative were assumed fixed and together used to form a population profile for PAA. Specimens representing each distinct aggregated population profile were considered to belong to distinct species, even if represented by only single collections, if they exhibited unique, qualitative morphological character states, unknown

from other population profiles. As with any hypothesis, concepts of these species are open to modification and reinterpretation in light of any new collections.

The conservation status of treated species was provisionally evaluated by applying the criteria articulated in version 3.1 of the International Union for Conservation of Nature and Natural Resources (IUCN) Red List Categories and Criteria (IUCN 2001) and version 6.1 of the NatureServe Conservation Status Ranks (NatureServe 2006).

## RESULTS

Twelve species of Gonolobus are recognized from the West Indies, here defined to include the Bahamas, the Greater Antilles, and the Lesser Antilles (incl. Aruba, Bonaire, Curaçao, Trinidad, and Tobago; Fig. 1). Descriptions of the species are provided following a discussion of morphology and keys to the species. Species are arranged alphabetically. Synonymy is limited to names applied in the West Indies. This restriction treats the vast majority of names, as eleven of twelve species are endemic to the area. Extra-West Indian synonymy for G. rostratus (Vahl) Schultes is not provided as the conspecificity of South American and West Indian collections referred to this name remains to be verified. IUCN criteria justifying an assigned conservation category are listed following each category. Taxon concept mapping is provided to facilitate databasing. The operators <, =, and > are used to indicate whether a given taxon concept is respectively narrower than, equal to, or broader than a previously published concept. The symbol ? is used to indicate the misapplication of a name to a concept. Herbarium abbreviations follow Index Herbariorum (Holmgren & Holmgren 1998–present). Book abbreviations follow TL-2 and journal abbreviations BPH. Author abbreviations follow Brummitt and Powell (1992).

## TAXONOMIC HISTORY

The genus Gonolobus was erected by Michaux in 1803 based on a taxon from the southeastern United States—Gonolobus suberosus (L.) R.Br. Reveal and Barrie (1992) reviewed the complicated nomenclatural history of the type species and Krings and Xiang (2004, 2005) its taxonomy. Estimates of species numbers of Gonolobus vary from 100 to 150 (Rosatti 1989; Mabberley 1997; Stevens 2001). About 318 names have been published in the genus. The degree of variation is largely the result of still poorly known tropical taxa and differences regarding generic limits. Woodson (1941) considered that the genus Gonolobus should contain plants characterized by only long, eglandular trichomes, laminar dorsal anther appendages, and smooth, angled or winged follicles, whereas Matelea should contain plants characterized by glandular and eglandular trichomes, anthers lacking laminar dorsal appendages, and muricate follicles. Unconvinced that laminar dorsal anther appendages should serve as a generic character and citing examples of smooth [but not angled or winged] fruits in Matelea, Shinnery (1950) argued against Woodson's generic concept and later included twelve of Woodson's (1941) Gonolobus combinations in Matelea (Shinnery 1950, 1964). Drapalik (1969) essentially followed Shinnery by maintaining the type of Gonolobus (i.e., G. suberosus, syn. G. gonocarpos (Walter) L.M. Perry) in Matelea, although noting its morphological distinctness vis-à-vis other subtribal members in the southeastern United States. Taking a broader geographical perspective of generic morphology, Rosatti (1989) argued for renewed circumscription of Gonolobus based on the presence of laminar dorsal anther appendages. Most recently the concept of Gonolobus as characterized by short, capitate-glandular, short acicular, and long acicular trichomes, laminar

dorsal anther appendages (typically), and smooth, winged follicles has been used by Stevens (2001). However, glandular hairs, although thought characteristic of Matelea by Woodson (1941), also appear without circumscriptional value in the Gonolobus-Matelea question, being present in both the type of Gonolobus and numerous species lacking dorsal anther appendages (Rosatti 1989). Nonetheless, the monophyly of Gonolobus, whether narrowly or broadly circumscribed, was supported in a recent analysis of chloroplast and nuclear data (Krings et al., in review). Although parsimony is equivocal on whether laminar dorsal anther appendages evolved once in the most recent common ancestor of Gonolobus s.l., or once in Gonolobus s.s. and once in the Fimbristemma Turcz. group within Gonolobus s.l. (Fig. 2), the character remains restricted to the Gonolobus s.l. clade within Gonolobinae. Interestingly, winged follicles appear to have arisen twice independently and can be considered synapomorphic for both Gonolobus s.l. (Krings et al., in review), as well as for a mostly West Indian ocellate-petaled complex that likely includes Matelea acuminata (Griseb.) Woodson, M. bayatensis (Urb.) Woodson, M. correllii Spellman, M. costata (Urb.) Morillo, M. nipensis (Urb.) Woodson, M. oblongata (Griseb.) Woodson, M. pusilliflora L.O. Williams, M. rhamnifolia (Griseb.) Krings, and M. tigrina (Griseb.) Woodson. None of these latter taxa exhibit laminar dorsal anther appendages. This putative complex did not evolve within the Gonolobus s.l. clade and may deserve independent generic recognition. Members of the complex tend to share morphological characters apparently rare in Gonolobus s.l., such as reticulate, ocellate corollas.

A monophyletic Gonolobus s.l. can be characterized by the presence of two synapomorphic indels in Leafy, as well as winged follicles (Krings et al., in review). A monophyletic Gonolobus s.s. can be characterized by a synapomorphic transversion in trnL-F (thymine to guanine). The

former circumscription (i.e., Gonolobus s.l.) essentially agrees with that of Woodson (1941), Rosatti (1989), and Stevens (2001), and stands in contrast to that of Shoiners (1950) and Drapalik (1969). To remain monophyletic however, Gonolobus s.l. must include the Matelea denticulata (Vahl) Fontella & E.A. Schwarz complex. Considering the morphological and molecular distinctions, between the three lineages in the Gonolobus s.l. clade (Fig. 2), recognition of three separate genera currently seems preferable to me.

## MORPHOLOGY

A discussion of the morphology of species of West Indian Gonolobus s.s. (hereafter simply Gonolobus, unless otherwise specified) is provided below. The discussion concentrates on West Indian Gonolobus species, but when possible provides a broader context of variation within West Indian Gonolobinae.

**GROWTH FORM.** Species of West Indian Gonolobus are twining vines, as are all currently known members of West Indian Gonolobinae (Fig. 3A). Older stems may become somewhat woody, but no collection or live plant has been seen by the author that approached 1 cm or greater in diameter. Individuals may climb as high as a few meters in gaps and openings.

**LATEX.** Latex is known for the following species: Gonolobus iyanolensis Krings, G. jamaicensis Rendle, G. stapelioides Desv. ex Ham., G. stellatus Griseb., G. stephanotrichus Griseb., G. waitukubuliensis Krings, and G. youroumaynensis Krings. It has been primarily described as either milky or white, observations confirmed by the author in the field for G. iyanolensis, G.

jamaicensis, G. stapelioides, G. stephanotrichus, G. waitukubuliensis, and G. youroumaynensis.

Latex was described as watery in a single instance—a Puerto Rican collection of a young sterile vine referred to G. stephanotrichus (Acevedo-Rodríguez & Axelrod 7785, US!). Published studies of latex chemistry in Gonolobinae are unknown to the author, although such inquiry would likely yield interesting results based on studies of other members of Asclepiadoideae (see Uses). Latex chemistry has been applied to solving taxonomic problems in Cynanchinae (Liede et al. 1993; Liede & Kunze 2002).

PUBESCENCE. Most members of subtribe Gonolobinae, exhibit at least two distinct trichome types, but frequently more. West Indian species of Gonolobus exhibit four types: (1) multi-cellular, sharp, eglandular, (2) uni-cellular, sharp, eglandular, (3) uni(?) -cellular, glandular-capitate, and (4) papillate (Fig. 3B). Papillae appear to be restricted to the adaxial surface of the corolla lobes—typically borne only on the right side of the lobes. The remaining trichome types may be found anywhere else on the stem, leaves, inflorescences, or flowers, usually in combination. Multi-cellular, sharp, eglandular trichomes found on stems are primarily retrorse to retrorse-spreading internodally, but may be appressed-ascending along a narrow ridge connecting opposite petioles. In contrast to some other members of West Indian Gonolobinae (e.g., M. corynephora Krings, M. linearipetala Alain, M. phainops Krings, M. rhynchocephala Krings, M. torulosa Krings), stem trichomes in West Indian Gonolobus are not borne in two distinct lines.

LEAVES. In general, species of Gonolobus exhibit simple, opposite, membranous, cordate leaves, although a few taxa, such as the Jamaican G. stellatus, G. jamaicensis, and G. stapelioides, exhibit truncate to cuneate leaf bases (Fig. 3A & C). The leaves of G. jamaicensis and G. stapelioides tend to be coriaceous. Leaf apices vary from acute to acuminate. Leaf size and shape may be influenced by position on the stem (e.g., sun vs. shade leaves) and habitat (e.g., edge vs. forest interior) (Krings, pers. obs.).

LAMINAR COLLETTERS. In West Indian Gonolobus species, as in all West Indian Gonolobinae, two or more colleters are borne on the adaxial midrib near the junction of the leaf base and the petiole apex (Fig. 3D). Colleters vary from deltoid to lanceoloid.

STIPULAR COLLETTERS. In West Indian Gonolobus species, a single colleter is borne on each side of the petiole at its extreme base (Fig. 3E). Colleters vary from deltoid to lanceoloid. Inter-petiole (borne along a ridge or line between two opposing petioles at a node) colleters are rare and infra-petiole (borne within the width of a petiole at its base) are apparently absent. Stipular colleters in other West Indian Gonolobinae vary in position, but frequently appear to be associated with the stem rather than the petiole.

INFLORESCENCES. Inflorescences of most West Indian Gonolobinae species, including all Gonolobus species in the area, are extra-axillary and racemose (umbelliform inflorescences appear to be restricted to Haitian Matelea crispiflora (Urb.) Jiménez). Inflorescences can be borne at nodes with immature leaves as short as 1–3 cm long. The inflorescence is indeterminate

and a series of flowers are produced on lateral pedicels from a single axis, the oldest at the base and the youngest at the apex (Fig. 3F). The axis is frequently significantly contracted and may not measure more than 1 cm in some species. In West Indian Gonolobus, bracts are frequently borne at pedicel bases, although they tend to be small and caducous in most species. An exception is G. tobagensis, which exhibits significantly longer and apparently more persistent bracts. For additional information on inflorescence structure in other members of Asclepiadoideae, readers may be interested in the review by Liede and Weberling (1995).

Based on specimens of West Indian Gonolobus seen in the course of the present study, one to three flowers may be open at a time. No phenological studies in West Indian Gonolobus have been undertaken and the life span of individual flowers remains unknown. Based on prior studies in Gonolobinae (see Lipow & Wyatt 1998; Krings 1999) and informal observation, it is unlikely that individual flowers last much longer than a week. In Gonolobus suberosus of the southeastern United States, individual flowers were open (2–) 4.61 (–10) days (N = 175; s.d. = 1.53) and inflorescences had open flowers for (2–) 8.96 (–23) days (N = 57; s.d. = 4.63)(Lipow & Wyatt 1998).

**AESTIVATION.** The flowers of West Indian Gonolobus species are imbricate and dextrorse in bud (Fig. 3G). Imbricate aestivation is seen also in other members of West Indian Gonolobinae, but not all other genera exhibit dextrorse buds.

**CALYCES.** Calyces of Gonolobus species consist of five, green sepals (Fig. 3H). Apices are generally narrowly obtuse to rounded. Adaxial surfaces are uniformly glabrous. Abaxially

surfaces vary from pubescent to glabrous. Frequently, the distal pedicel pubescence (when present) creeps onto the calyx base.

CALYCINE COLLETTERS. West Indian Gonolobus species, as most members of West Indian Gonolobinae, bear 1–2 colleters in each sepal sinus (Fig. 3I). The colleters are deltoid to lanceoloid.

COROLLAS. Corollas of West Indian Gonolobinae, including all Gonolobus species in the area, are 5-parted (Fig. 3J). Corollas are generally subcampanulate to campanulate at the base with lobes spreading to reflexed. The corolla lobes of most species are plane. An exception is Jamaican G. stapelioides, which exhibits wavy and recurved corolla lobes. Corolla lobes of Gonolobus in the area slightly overlap at the base and frequently bear a minute glandular emergence in the sinus. Adaxial corolla coloration of West Indian Gonolobus species varies from uniformly green (most taxa) to burgundy tinged (G. stephanotrichus) to maroon (G. jamaicensis). Pubescence of the adaxial surfaces, when present, is limited to the faucal annulus and surrounding corolla lobe bases, and the right side of the corolla lobes.

FAUCAL ANNULI. Faucal annuli—Ca sensu Liede and Kunze (1993), non sensu Woodson and Moore 1938 (see Kunze 1990, 1995)—are secondary annular thickenings of the tubular portion of the corolla (Fig. 3Ki–iii, L). Endress and Bruyns (2000) considered the Ca and Cc (corolline corolla) of Liede and Kunze (1993) homologous, although Fishbein (2001) and Kunze (2005) explicitly rejected this hypothesis. Kunze (2005) noted that early ontogenetic stages of even taxa such as G. lasiostemma (Hemsl.) Woodson, which exhibits a Ca of five large fleshy lobes

interstaminally (similar to Jamaican G. stapelioides), show a closed annular meristem at the initial stage. Faucal annuli (Ca) are distinctive in West Indian Gonolobus species and generally much more developed in members of this genus than in other West Indian Gonolobinae. Kunze (1995) found faucal annuli present in continental Gonolobus spp., as well as Matelea lanata (Zucc.) Woodson, and Matelea dictyantha Woodson, and absent in Matelea argentinensis (T. Mey.) Pontir. and Fischeria spp. (all Gonolobinae). He also noted that outside Gonolobinae, faucal annuli were found mainly in some Stapelieae. The faucal annulus occurs immediately to the outside of the gynostegial corona (i.e., closer to the corolla lobes than the center of the flower). Annuli may be “interrupted” and reduced to a ridge opposite each corolla lobe sinus (e.g., G. martinicensis Decne.; Fig. 3L) or “uninterrupted” and well-developed (e.g., G. jamaicensis; Fig. 3Kiii). They are frequently pubescent, but not always, in contrast to the always glabrous, adjacent gynostegial coronas.

**GYNSTEGIAL CORONAS.** Gynostegial coronas are quite varied in West Indian Gonolobinae (Fig. 3Ki–iii, L). In West Indian Gonolobus species, the gynostegial coronas can be described conveniently in terms of staminal (Cs) and interstaminal (Ci) segments. The coronas have been interpreted as a “fusion” between the Cs and Ci (Liede & Kunze 1993), although it remains unclear whether the combined structure in fact represents a true fusion of disparate elements (see Endress & Bruyns 2000). The Cs region typically is raised and ridge-like, often meeting the lower portion of the laminar dorsal anther appendages (Cd). There are no instances of free, ligulate Cs segments as seen in other West Indian Gonolobinae taxa, such as M. ovatifolia (Griseb.) Woodson or M. pentactina Krings, or three-dimensionally complex Cs segments as

seen in M. tamnifolia (Griseb.) Woodson and M. oblongata. Ci segments are single and cup-like in most species, and double (i.e., ligulate) only in G. iyanolensis and G. martinicensis (Fig. 3L). The interstaminal ligules of the double coronas of the latter two species are not positionally homologous with the staminal ligules seen in numerous species of Matelea, such as West Indian M. ovatifolia and M. pentactina, or continental M. pubiflora (Decne.) Woodson. However, some Matelea species, such as M. maritima (Jacq.) Woodson, also exhibit interstaminal ligules. In the Asclepiadoideae in general and West Indian Gonolobus in particular, the Ci region appears to serve as a holding cup for nectar secreted from a primary nectary on the flanks of the filaments inside the guide rail and in the stigmatic chamber (Christ & Schnepf 1985, 1988). Among West Indian Gonolobus species, defined secondary nectaries are evident—at least as far as can be determined from herbarium specimens—only in a few species (e.g., G. dussii Krings). Kunze (1995, 1999) also found defined secondary nectaries in continental G. chloranthus Schltldl. and G. fraternus Schltldl., as well as the gonolobinoid Matelea reticulata (Engelm. ex A. Gray) Woodson and M. argentinensis. Secondary nectaries are epithelial, consisting of enlarged epidermal cells enriched with cytoplasm (Kunze 1995). Epithelial nectaries on the filament flanks appear to be widespread in Asclepiadoideae (Christ & Schnepf 1985; Kunze 1991; Kunze 1995).

The gynostegial stipe is generally edentate, although G. jamaicensis, G. stephanotrichus, and G. youroumaynensis have distinct teeth or “notches”. The stipe teeth or “notches” of all three species are distinct in shape and occur in different locations. Their homology is unclear.

LAMINAR DORSAL ANTHER APPENDAGES. Laminar dorsal anther appendages (Cd sensu Kunze 1995; Fig. 3Ki–ii, L–M) are restricted to Gonolobus s.l. or s.s., although it remains unclear whether they evolved once in the most recent common ancestor of the former, or once in the ancestor of the latter and in the ancestor of the Fimbristemma group within Gonolobus s.l. (Krings et al., in review). Parsimony is equivocal on the question (Krings et al., in review). The only other genus exhibiting dorsal anther appendages within Gonolobinae (and Asclepiadoideae, fide Kunze 1995) is Fischeria, but the appendages are vesicular rather than laminar (Murphy 1986; Vethacke 1994; Kunze 1995). Laminar dorsal appendages vary in shape from truncate to rounded to strongly, divergently bi-lobed. They tend to be spreading, but are conspicuously (and spectacularly) erect in mature flowers of G. stapelioides (Fig. 3Ki).

STYLAR HEADS. Stylar heads vary conspicuously in West Indian Gonolobinae, but tend to be essentially plane (varying from somewhat convex to somewhat concave) in Gonolobus species in the area (Fig. 3Kii, L). West Indian Gonolobus species also lack terminal styler head appendages, in contrast to other West Indian Gonolobinae species such as Matelea maritima, M. corynephora, M. rhynchocephala, and M. torulosa (see Krings 2006).

POLLINARIA. Pollinaria in Asclepiadoideae consist of a secreted corpusculum and two connected pollinia (pollen sacs; Kunze 1994). The two pollen sacs are the result of a reduction in anther locules from four in the more primitive Secamonoideae to two in the more derived Asclepiadoideae (Kunze 1996; Rapini et al. 2003; Liede-Schumann et al. 2005; Rapini et al. 2006). The pollinia are borne essentially horizontally in West Indian Gonolobus species—as they are in most members of the Gonolobinae—and should be considered broad, rather than long

(Kunze 1995; Endress & Bruyns 2000; Fig. 3N). Only a portion of each pollinium is fertile and hyaline, sterile portions are easily visible. The corpusculum in the Gonolobinae (based on studies of Matelea reticulata and M. argentinensis) consists of solid side walls and a thick, three-layered floor (Kunze 1994). Kunze (1994) suggested that the formation of the side-walls originates in two primarily separated strands of secretion which eventually merge into one compact wall. Caudicles are present (Fig. 3N), but Kunze (1994) noted it was difficult to determine whether they are extensions of the outer flanks or new additions. He suggested the latter, based on the lack of staining with either hematoxylin or safranin, although noting that caudicle initiation in the two Matelea species occurs very early in ontogeny and directly from the corpusculum, rather than apart from it.

FOLLICLES. Follicles in West Indian Gonolobus species (as in most continental Gonolobus spp. fide Stevens 2001), when known, are 5-winged (Fig. 3O), although small murications may be seen between the wings of some taxa (e.g., G. stellatus). Some continental species of Gonolobus also exhibit 4-winged (G. albomarginatus (Pittier) Woodson) or apparently 3-winged (G. incerianus W.D. Stevens & Montiel) follicles (Stevens 2001). Winged follicles are also exhibited by other members of West Indian Gonolobinae, such as M. linearipetala, and the putative members of an ocellate complex M. acuminata, M. bayatensis, M. correllii, M. nipensis, M. oblongata, M. rhamnifolia, and M. tigrina.

SEEDS. Seeds of West Indian Gonolobus species, as of most West Indian Gonolobinae, are essentially plane and pyriform in outline (distinctly plano-convex in Matelea maritima and M.

rubra (H. Karst.) Spellman & Morillo). Distal margins vary from entire to dentate or crenate (Fig. 3P). Comas are translucent.

### HABITAT

In general, West Indian Gonolobus species occur in small gaps or openings in mid-elevation, moist or wet forests on limestone derived soils. They are absent from high-elevation Dwarf Forests, coastal thickets, mangroves, marshes, or dry forests. Occurrences are infrequent to rare and likely limited by available habitat. Small gaps in minimally disturbed forests appear vital to seedling germination as vines are rarely encountered elsewhere. Changes in gap dynamics or forest condition, thus could have profound impacts on the maintenance of Gonolobus populations. With the exception of G. rostratus and G. youroumaynensis, the species have not been found along roadside edges, where other vines (particularly Ipomoea L. spp. and Dioscorea L. spp.) are generally superior competitors and quickly form thick, tangled thickets. Gonolobus youroumaynensis was found along a roadside patch of vegetation in St. Vincent, although it remains unclear whether the population is competitive there or merely persistent following a colonization event. A population of Gonolobus iyanolensis persists on top of Gros Piton in St. Lucia among boulders.

### POLLINATION

As there have been no pollination biology studies on West Indian Gonolobus species, their pollinators remain unknown. In fact, pollinators appear to be documented for only two species

of Gonolobus range wide: G. fraternus (Mexico and Central America) and G. suberosus (United States).

Kunze (1999) studied the pollination ecology of G. chloranthus and G. fraternus, but was able to observe pollinators only on the latter. Pollinarium uptake was confirmed for two diptera species (Calliphoridae, Tachinidae), a bee (Apidae), and a wasp (Vespidae) (Kunze 1999). Other observed visitors included Apis mellifera Linnaeus (Apidae) and unidentified butterflies (Lepidoptera) (Kunze 1999). However, pollinarium removal for these could not be verified. Corpuscula were removed by the wasp and bee by their legs, and by the bee and the flies by their probosces. Foraging behavior differed among the observed species, with the wasp and bee preferring upper regions of the studied vine, and the flies, the middle and lower.

Drapalik (1969) captured small dipterans (all Chloropidae) on flowers of G. suberosus, but it remains unclear whether they are effective pollinators due to their size (1.5–3 mm) and lack of pollinaria on capture. Lipow and Wyatt (1998) also studied G. suberosus, but despite daily and nightly searches were unable to find pollinators.

Gonolobus suberosus appears to exhibit considerable variation in the numbers of flowers per individual plant, the number of flowers per inflorescence, and the number of inflorescences per individual plant (Lipow & Wyatt 1998). Only a small fraction of plants monitored by Lipow and Wyatt (1998)—less than 5%—were pollinated and per flower removal rate of pollen was only 0.31. This rate was less than previous reports in other asclepiads (Table 1).

Ollerton and Liede (1997) noted that subtribe Gonolobinae appears distinct in being predominantly dipteran pollinated, although this claim was based on only five Matelea species in the southeastern United States (Drapalik 1969). The claim remains mostly true today, although

only a single additional species of Fischeria and Gonolobus each has been studied since (Kunze 1998, 1999). Two additional studies examined species also studied by Drapalik (1969) and found additional dipteran floral visitors (Liede 1994; Krings 1999). Kunze (1999) found flowers of G. fraternus polyphilic and noted that they were not specialized for a single kind of pollinator. The ASCLEPOL database ([http://www.uni-bayreuth.de/departments/planta2/research\\_wgl/pollina/as\\_pol\\_d.html](http://www.uni-bayreuth.de/departments/planta2/research_wgl/pollina/as_pol_d.html)) currently also lists pollinators for G. argentinensis T. Mey. (1 sp. of Calliphoridae, Diptera), but the latter has most recently been recognized in Matelea.

#### INSECTS HOSTED

There are no published records of insects hosted by West Indian Gonolobus species known to the author. However, a few records of primarily dipterans and lepidopterans have been published for continental species in the genus. Castrejon-Ayala and Camino-Lavin (1991) reported Gonolobus sorodius, nom. nud., as host for papaya fruit fly (Toxotrypana curvicauda Gerstaecker)—the principal insect pest of commercial papaya (Carica papaya L.). Norrbom (unpubl.) suggested this plant may be Gonolobus barbatus Kunth. Baker et al. (1944) reported another asclep host plant of papaya fruit fly—a wild species known as talayote or talayotillo in northeastern Mexico (Santa Engracia and Cañon de Rosario). Castrejón-Ayala (1987) suggested the plant may be a species of Gonolobus and Landolt (1994) suggested perhaps G. erianthus DC. Gonolobus salvinii Hemsl.—commonly called champeron in Guatemala—may yet be another host for the papaya fruit fly (Norrbom & Muñiz, unpubl.).

Capinera (2005) reported “Gonolobus sp.” among hosts for the saltmarsh caterpillar (Estigmene acrea (Drury))—a species ranging from Canada to Central America. An unidentified

species of Gonolobus was reported as host for Erinnyis obscura obscura (Fabricius)—a sphingid found in Amazonas, Brazil (Silva Motta & Xavier-Filho 2005).

There are a number of reports of Gonolobus laevis Michx. serving as host plant for various lepidopterans, including Danaus gilippus Cramer and D. plexippus (Linnaeus), however G. laevis belongs to the Cynanchinae, not Gonolobinae, and should be recognized as Cynanchum laeve (Michx.) Pers. (Liede & Täuber 2002).

#### SEED DISPERSAL

The follicles of known West Indian Gonolobus species are smooth and uniformly 5-winged, dehiscing along a solitary suture between two wings to release the comose seeds. Seeds are very light (Table 2) and can travel on slight breezes. Unfortunately, mature follicles have been documented by collections for only three of the thirteen (23%) species of West Indian Gonolobus (Table 2). Immature follicles are known for G. stapelioides (see Additional specimens examined) and a photograph of follicles of G. rostratus (Vahl) Schultes appears to be archived at TRIN, but has not been seen by the author. The paucity of fruiting collections is echoed in West Indian Gonolobinae as a whole. Follicles have been collected for less than half of the estimated fifty species in the West Indies (Kings, unpubl.). The low rate of fruit collections may be due to naturally low levels of fruit set in the subtribe (Lipow & Wyatt 1998), as well as collector habit, flowers being necessary for most species level determinations. Lipow and Wyatt (1998) suggested that low fruit set in Gonolobinae may be attributable to pollen limitation. Less than 5% of flowers monitored were pollinated and only a single fruit matured from 352 flowers on 13 plants (Lipow & Wyatt 1998).

## CHROMOSOMES

There are no published reports of chromosome numbers in West Indian Gonolobus or Gonolobinae. Previously published reports for continental Gonolobinae, including continental Gonolobus, show the same basic chromosome number  $x = 11$  that predominates the subfamilies Asclepiadoideae, Periplocoideae, and Secamonoideae (Albers & Meve 2001). Only 6% of 672 species surveyed in the three subfamilies by Albers and Meve (2001) were polyploid and deviations (reductions or increases in chromosome numbers) were found only in the Asclepiadoideae. No deviations within the Gonolobinae from  $2n = 22$  were found by Albers and Meve (2001), although only five species in four genera were included from the subtribe in their survey.

## USES

No published accounts of human uses of West Indian Gonolobus species are known to the author. The Ecuadorian endemic and IUCN Vulnerable (VU) listed Gonolobus saraguranus Morillo has been reported to be used by the Saraguro native people as a medicinal plant (specific use unspecified), under the name sacha ango (Pitman 2003). Unspecified medicinal uses are also reported for Gonolobus yucatanensis (Woodson) W.D. Stevens, a taxon described in Trichostelma Baill. (Durán García et al. 1997). Standley and Williams (1969) noted that the tender, young fruits of Gonolobus species are commonly used as vegetables in Guatemala, and may be available in local markets under the name cuchamper, although this name has also been applied to the fruits of related genera. Specific uses are noted by Standley and Williams (1969)

for G. salvinii (tender follicles eaten raw when almost mature, and cooked and eaten at almost all stages of growth) and G. stenanthus (Standley) Woodson (young follicles boiled or otherwise cooked with sugar to make sweetmeats or dulces). Stevens (2005) noted that “most, if not all, species of Gonolobus have fruits that are eaten when young, either raw or cooked.” Numerous studies have examined potential medicinal properties of latex in Asclepiadinae (Asclepias L.: Liggieri et al. 2004; Calotropis R.Br.: Rasik et al. 1999; Kumar et al. 2001; Dubey & Jagganadham 2003; Shivkar & Kumar 2003; Ahmed et al. 2004; Alencar et al. 2004; Kumar & Shivkar 2004a & b; Shivkar & Kumar 2004; Al-Mezaine et al. 2005; Arya & Kumar 2004, 2005; Iqbal et al. 2005; Pahdy & Kumar 2005; Rajesh et al. 2005; Roy et al. 2005; Sehgal & Kumar 2005; Soares et al. 2005; Choedon et al. 2006; Kumar et al. 2006; Ramos et al. 2006a & b; Sehgal et al. 2006), Metastelmatinae (Funastrum E. Fourn.: Morcelle et al. 2004; Philibertia Kunth: Sequeiros et al. 2005), and Oxypetalinae (Araujia Brot.: Priolo et al. 2000; Gaig et al. 2005; Morrenia Lindl.: Vairo Cavalli et al. 2003), but no such studies are known to the author in Gonolobinae.

## CONSERVATION

Human disturbance disproportionately affects infrequent plant species more than common taxa, as further reductions of already low population sizes may not be sustainable (Lawton 1993; Casagrandi & Gatto 2000; Hendrix & Khyll 2000; Benítez-Malvido & Martínez-Ramos 2003). West Indian Gonolobus species, as many other species of Asclepiadoideae (Kunze & Liede 1991), appear to be quite infrequent, if not rare, and are in need of serious survey (particularly in Cuba, the Lesser Antilles, and Trinidad and Tobago) to establish their conservation status.

However, some provisional remarks are possible, based on study of collections and field observations associated with this study.

The habitat requirements of West Indian Gonolobus species are in need of further study, but preliminary evidence suggests that most species are largely limited to small gaps or openings in mid-elevation, moist or wet forests. They appear to be poor competitors along forest edges. The combined infrequency of occurrence of individuals, poor competitive ability along edges, likely low pollination and fruit set rates (see Pollination and Seed Dispersal above), and need for small gaps or openings in specific forest community types, suggests that Gonolobus species may be particularly vulnerable to loss of habitat. This is of particular concern considering the high rate of island endemism among the species. Nine of the twelve West Indian Gonolobus species are endemic to a single island (Fig. 3). Gonolobus dussii and G. stephanotrichus occur on two and three islands respectively. Gonolobus rostratus also appears to occur on mainland South America, although the conspecificity of South American and West Indian collections remains to be verified. Two-thirds of the species (N=8) are known from five or fewer collections or localities (Table 3). None of the remaining four species appears to be known from more than ten localities. Provisional estimates of conservation status according to the criteria outlined in Version 3.1 of the IUCN Red List Categories and Criteria (IUCN 2001) and Version 6.1 of NatureServe Conservation Status Ranks (NatureServe 2006) are provided in Table 3. Provisional estimates are based on historical collections, the number of known localities, whether taxa are known from protected areas, and inferred habitat or population changes. These estimates need to be followed by targeted survey to better establish the conservation status of the species.

## TAXONOMIC TREATMENT

GONOLOBUS Michaux, Fl. Bor.-Amer. 1: 119. 1803.—TYPE: Gonolobus suberosus (L.) R. Brown

Rhizomatous, perennial vines. Leaves opposite, blades simple, membranous or coriaceous, apices obtuse, acute, or acuminate, bases mostly cordate, but cuneate to rounded in some taxa; colleter present on the adaxial surface at the base of the midvein. Stipular colleters 2, one borne at the base of the petiole on each side. Inflorescences extra-axillary, racemiform. Floral aestivation imbricate, dextrorse. Sepals 5; colleters 1–2 per sinus. Corolla lobes 5, mostly uniformly-colored with various shades or green to reddish or maroon, sometimes multi-colored and basally maroon or dark purplish and apically green (e.g., G. suberosus), not ocellate, lobes overlapping at the base, glandular emergences present in the sinuses. Faucal annulus (Ca) present, sometimes interrupted and developed only in the staminal—or rarely interstaminal (e.g., G. stapelioides)—position. Gynostegial corona of fused staminal (Cs) and interstaminal parts (Ci); Cs not foliolate or free, not ligulate; Ci ligulate or not. Laminar dorsal anther appendages (Cd) present, reflexed, spreading, or erect. Styler head flat to slightly concave or convex, lacking a defined protuberance or elongate terminal appendage. Pollinaria with pollinia borne horizontally or essentially so. Follicles winged. Seeds essentially plane, distally entire or dentate, comose. Twelve species in the West Indies.

Perry (1938) chose Gonolobus macrophyllus Michx.—the first of three species listed by Michaux (loc. cit.)—as the lectotype for the genus Gonolobus. However, Michaux cited Vincetoxicum gonocarpos Walter as a synonym for his G. macrophyllus, rendering the latter

name illegitimate. Perry (1938) proposed the combination G. gonocarpos as the correct name for Michaux's G. macrophyllus. Recent study found the entity variously known as G. gonocarpos or G. macrophyllus conspecific with G. suberosus (Klings & Xiang 2004, 2005). The latter name has priority following Reveal and Barrie (1992) and is thus accepted here as type for the genus Gonolobus.

Some Robert Brown names have sometimes been incorrectly dated. In 1810, a preprint of his "On the Asclepiadeae, a Natural Order of Plants separated from the Apocinae of Jussieu" was made available. This same work later appeared in the first volume of the 1811 Memoirs of the Wernerian Natural History Society (Stearn 1960; Stafleu and Cowan 1976; Mabberley 1985). Although sometimes incorrectly cited from the first reading of the paper in 1809, communication at public meetings does not constitute effective publication (Forster 1991; Greuter et al. 2000). Names should also not be ascribed to the 1811 appearance of the Memoirs of the Wernerian Natural History Society but rather to the preprint released in 1810. Thus the combination Gonolobus suberosus (L.) R. Br. should be cited as above, rather than in Mem. Wern. Nat. Hist. Soc. 1:35 (1810). As Brown's 1810 combination in Asclepiadeae is validly published (by definite association of the final epithet with the genus name), it takes priority over the Schultes combination in Systema Vegetabilium 6:59 (1820).

#### KEY TO THE SPECIES OF GONOLOBUS IN THE ANTILLES

1. Leaf bases cuneate, rounded, or truncate, not cordate; corolla lobes with lateral margins strongly curled downward from base to apex; faucal annulus (corolline corona or Ca) interrupted, strongly developed into two mounds opposite each corolla lobe, appearing absent

opposite each corolla sinus, pubescent; laminar dorsal anther appendages erect (spreading when immature or spent), white, to 4.2 mm long, apices divergently and sharply bilobed.

7. G. stapelioides

1. Leaf bases cordate (uniformly cuneate only in G. stellatus, though upper leaves frequently also cuneate to rounded in G. jamaicensis); corolla lobes essentially plane, sometime reflexed, but margins not curled downward from base to apex; faucal annulus (corolline corona or Ca) uninterrupted or if interrupted then at most developed into a shallow ridge opposite each corolla lobe sinus; laminar dorsal anther appendages (Cd) descending or spreading, variously colored, < 2 mm long, apices rounded, truncate, slightly emarginate, or rounded-bilobed (divergently and sharply bilobed only in G. stellatus).

2. Faucal annulus of corolla (corolline corona or Ca) a conspicuously raised (0.4–0.9 mm tall), uninterrupted ring, pubescent along the entire rim or only opposite each corolla lobe sinus; gynostegial corona basally fused into an erect ring, obscured from view by the faucal annulus.

3. Gynostegial stipe dentate, a single tooth borne on the lower portion of the column, just above the upwardly rising segment of each Cs.

9. G. stephanotrichus

3. Gynostegial stipe edentate.

4. Adaxial corolla lobes green; rim of faucal annulus (corolline corona or Ca) not lobed, annulus to 0.5 mm tall; gynostegial corona appearing densely folded apically; gynostegial stipe not toothed.

11. G. waitukubuliensis

4. Adaxial corolla lobes purple-red to maroon; rim of faucal annulus (corolline corona or Ca) bilobed in the staminal position, annulus to 0.9 mm tall;

gynostegial corona upwardly folded only in the staminal position; gynostegial stipe toothed on the lower portion of the column, just above the upwardly rising segment of each Cs. 4. G. jamaicensis

2. Faucal annulus of corolla (corolline corona or Ca) reduced to an interrupted ridge, distinct only opposite each corolla lobe sinus, tufted pubescent to glabrate or, if uninterrupted, then very shallow, to 0.25 mm tall; gynostegial corona not basally fused into an erect ring that is obscured from view by the faucal annulus.

5. Interstaminal gynostegial corona double (i.e., a narrower upper ligulate corona lobe occurring on top of the broader lower corona).

6. Corolla robust, base of corolla tube subcampanulate, as broad as long or broader than long; sepals 6.1–6.7 mm x 1.6–1.8 mm; corolla lobes 10.2–17.3 mm x 2.7–4.8 mm; horizontal length of lower interstaminal gynostegial corona (Ci) from base of stipe to lobe apex 1.1–1.4 mm, narrow upper ligulate corona lobe of the Ci abruptly ending in a scooped out depression before reaching the stipe base, dorsally ridged. 3. G. iyanolensis

6. Corolla slender, base of corolla tube elongate-campanulate, distinctly longer than broad; sepals 4.3–6.7 mm x 1–1.2 mm; corolla lobes 9.7–11.4 mm x 2–3.5 mm; horizontal length of interstaminal gynostegial corona (Ci) from base of stipe to lobe apex = 0.7 mm, narrow upper ligulate corona lobe of the Ci ending essentially at the stipe base, dorsally plane or sometimes slightly raised into a shallow bump. 5. G. martinicensis

5. Interstaminal gynostegial corona single.

7. Gynostegial stipe with a single tooth below each anther.
8. Faucal annulus pubescent along the entire ring; teeth of gynostegial stipe borne on lower portion of the column, just above the upwardly rising segment of the Cs. 9. G. stephanotrichus
8. Faucal annulus pubescent only in the staminal position; teeth of gynostegial stipe borne on upper portion of the column, just below the anther. 12. G. youroumaynensis
7. Gynostegial stipe edentate.
9. Cs to 1 mm tall; interstaminal gynostegial corona (Ci) with two distinctly raised and rounded mounds; laminar dorsal anther appendages (Cd) truncate or rounded. 2. G. dussii
9. Cs < 0.3 mm tall; interstaminal gynostegial corona (Ci) smooth, lacking raised bumps; laminar dorsal anther appendages (Cd) emarginate.
10. Leaf bases uniformly cuneate; laminar dorsal anther appendages (Cd) slightly emarginate to divergently and sharply bilobed. 8. G. stellatus
10. Leaf bases cordate; laminar dorsal anther appendages truncate to rounded bilobed.
11. Laminar dorsal anther appendages (Cd) rounded bilobed. 1. G. absalonensis
11. Laminar dorsal anther appendages (Cd) truncate or rounded.
12. Sepals ovate; adaxial corolla lobes glabrous.

6. G. rostratus

12. Sepals linear-lanceolate; adaxial corolla lobes

pubescent.

10. G. tobagensis

#### REGIONAL KEYS TO THE SPECIES

##### GREATER ANTILLES

1. Leaf bases uniformly cuneate or rounded, not cordate; corolla lobes with margins strongly curled downward from base to apex; faucal annulus (corolline corona or Ca) interrupted, strongly developed into two mounds opposite each corolla lobe, absent opposite each corolla sinus, pubescent; laminar dorsal anther appendages erect (spreading when immature or spent), white, apices divergently and sharply bilobed, to 4.2 mm long; Jamaica. 7. G. stapelioides
1. Leaf bases cordate (uniformly cuneate only in G. stellatus, though upper leaves frequently also cuneate to rounded in G. jamaicensis); corolla lobes essentially plane, sometime reflexed, but margins not curled downward from base to apex; faucal annulus (corolline corona or Ca) uninterrupted or if interrupted then at most developed into a shallow ridge opposite each corolla lobe sinus; laminar dorsal anther appendages (Cd) descending or spreading, variously colored, apices rounded, truncate, slightly emarginate, or rounded-bilobed (divergently and sharply bilobed only in G. stellatus), < 2 mm long.
  2. Faucal annulus of corolla (corolline corona or Ca) a conspicuously raised (0.4–0.9 mm tall), uninterrupted ring, pubescent along the entire rim or only opposite each

corolla lobe sinus; gynostegial corona basally fused into an erect ring, obscured from view by the faucal annulus.

3. Adaxial corolla lobes purple-red to maroon; gynostegial stipe teeth appearing as notches, borne on the lower portion of the column, just above the upwardly rising segment of each Cs; Jamaica. 4. G. jamaicensis

3. Adaxial corolla lobes various shades of green; gynostegial stipe teeth not appearing as notches, instead truncate, borne on the lower portion of the column, just above the upwardly rising segment of each Cs; Cuba, Hispaniola, Puerto Rico. 9. G. stephanotrichus

2. Faucal annulus of corolla (corolline corona or Ca) reduced to an interrupted ridge, distinct only opposite each corolla lobe sinus, tufted pubescent to glabrate or, if uninterrupted, then very shallow, = 0.25 mm tall; gynostegial corona not basally fused into an erect ring that is obscured from view by the faucal annulus.

4. Leaf bases uniformly cuneate; gynostegial stipe edentate; laminar dorsal anther appendages (Cd) slightly emarginate to divergently and sharply bilobed; Jamaica. 8. G. stellatus

4. Leaf bases cordate; gynostegial stipe with a single tooth borne on lower portion of the column, just above the upwardly rising segment of each Cs; laminar dorsal anther appendages (Cd) truncate or rounded; Cuba, Hispaniola, Puerto Rico.

9. G. stephanotrichus

## LESSER ANTILLES

1. Faucal annulus of corolla (corolline corona or Ca) a conspicuously raised (to 0.5 mm tall), uninterrupted ring, pubescent along the entire rim or only opposite each corolla lobe sinus; gynostegial corona appearing densely folded apically, basally fused into a ring, obscured from view by the faucal annulus; gynostegial stipe 1–1.5 mm tall; Cd emarginate; Dominica.

### 11. G. waitukubuliensis

1. Faucal annulus of corolla (corolline corona or Ca) reduced to an interrupted ridge, distinct only opposite each corolla lobe sinus, tufted pubescent to glabrate or, if uninterrupted, then very shallow, mostly 0.08 mm tall, and glabrous, except to 0.16 mm tall and tufted pubescent opposite each corolla lobe sinus; gynostegial corona neither apically densely folded nor basally obscured by a faucal annulus; gynostegial stipe = 1 mm tall; Cd rounded or truncate (emarginate in G. absalonensis ).

2. Interstaminal gynostegial corona double (i.e., a narrower upper ligulate corona lobe occurring on top of the broader lower corona).

3. Corolla robust, base of corolla tube subcampanulate, as broad as long or broader than long; sepals 6.1–6.7 mm x 1.6–1.8 mm; corolla lobes 10.2–17.3 mm x 2.7–4.8 mm; horizontal length of lower interstaminal gynostegial corona (Ci) from base of stipe to lobe apex 1.1–1.4 mm, narrow upper ligulate corona lobe of the Ci abruptly ending in a scooped out depression before reaching the stipe base, dorsally ridged; St. Lucia.

### 3. G. iyanolensis

3. Corolla slender, base of corolla tube elongate-campanulate, distinctly longer than broad; sepals 4.3–6.7 mm x 1–1.2 mm; corolla lobes 9.7–11.4 mm x 2–3.5 mm;

horizontal length of interstaminal gynostegial corona (Ci) from base of stipe to lobe apex = 0.7 mm, narrow upper ligulate corona lobe of the Ci ending essentially at the stipe base, dorsally plane or sometimes slightly raised into a shallow bump; Martinique. 5. G. martinicensis

2. Interstaminal gynostegial corona single.

4. Gynostegial stipe with a single tooth ca. 0.2 mm long below each anther; St. Vincent. 12. G. youroumaynensis

4. Gynostegial stipe edentate.

5. Cs to 1 mm tall; interstaminal gynostegial corona (Ci) with two distinctly raised and rounded mounds; laminar dorsal anther appendages (Cd) truncate or rounded; Guadeloupe and Martinique. 2. G. dussii

5. Cs < 0.3 mm tall; interstaminal gynostegial corona (Ci) smooth, lacking raised bumps; laminar dorsal anther appendages (Cd) emarginate

6. Corolla lobes 4.8–6.7 mm long; laminar dorsal anther appendages (Cd) rounded bilobed; Martinique. 1. G. absalonensis

6. Corolla lobes > 15 mm long; laminar dorsal anther appendages (Cd) truncate or rounded.

7. Sepals ovate; adaxial corolla lobes glabrous; Trinidad.

6. G. rostratus

7. Sepals linear-lanceolate; adaxial corolla lobes pubescent; Tobago.

10. G. tobagensis

**1. *Gonolobus absalonensis*** Krings, Syst. Bot. 32: 181. 2007.—TYPE: MARTINIQUE. Absalon, Pres la cascade, Mai 1910 (fl), Herb. d'Alleizette s.n. [4801?] (holotype: L!). (Fig. 4)

Herbaceous perennial vines. Latex unknown, presumably white. Stems glabrate to very sparsely pubescent, both short, capitate-glandular, and longer, sharp, eglandular trichomes present, the latter retrorse internodally and antrorse-appressed along an indistinct, horizontal ridge between two opposite petioles and/or just above the node, to 0.5 mm long; nodes sparsely pubescent, gland field apparently absent. Leaf blades ovate to oblong-ovate, (3.4)6.6–8.6 cm × (1.3)3.4–4.5 cm, apices abruptly acuminate with the acumen narrowly obtuse, to 0.7 cm long, bases deeply or shallowly cordate, margins entire, adaxial surface sparsely strigose, abaxial surface more densely strigose with sharp, eglandular trichomes scattered along the major and minor veins, glandular emergences from the surface absent or very sparse, colleters 2, 0.5–0.9 mm long; petioles 3.6–5.7 cm long, glabrous or very sparsely pubescent on all sides, capitate trichomes to 0.1 mm long, sharp, eglandular trichomes ca. 0.3 mm long, antrorsely-appressed or -ascending; stipular colleters 2, ca. 0.3 mm long, one borne on each side of the petiole base. Inflorescences racemiform, peduncles 4.1–5.4 cm long, glabrate to very sparsely pubescent, capitate, as well as sharp, eglandular trichomes present, the latter antrorsely-appressed or -ascending, found primarily at the apex, ca. 0.3 mm long; pedicels 1.5–1.7 cm long, more pubescent at the apex than at the base, capitate-glandular trichomes ca. 0.05 mm long, longer, sharp, eglandular trichomes antrorsely-appressed or -ascending, ca. 0.13 mm long, bracts linear-lanceolate, ca. 0.9 mm × 0.21 mm long, caducous, adaxial surface glabrous, abaxial surface coarsely pubescent, trichomes sharp, eglandular, ca. 0.26 mm long, antrorse. Calyx lobes 5,

lanceolate, 1.95 mm x 1 mm, apices narrowly obtuse or acute, margins glabrous, abaxial surface pubescent mostly at the base, sharp, eglandular trichomes, antrorsely-ascending or -appressed, to 0.25 mm long; colleters 1 per sinus. Corolla lobes 5, lance-ovate, 4.8–6.7 mm x 2.5–2.8 mm, slightly lobed at the base, a glandular swelling frequently present in the sinus, adaxial glabrous, abaxial surface glabrous; faucal annulus (corolline corona or Ca) a shallow, uninterrupted ring, ca. 2.5 mm diam, ca. 0.08 mm tall, glabrous except where raised opposite each corolla lobe sinus, then to ca. 0.16 mm tall and short hispid; gynostegial corona of fused staminal (Cs) and interstaminal parts (Ci), single, 5-lobed, erect- or prostrate-undulating, 0.4–0.6 mm tall; anther guiderails without appendages; laminar dorsal anther appendages (Cd) 0.48–0.7 mm x 0.5–0.8 mm, emarginate; stylar head ca. 3.2 mm diam, stipe 0.3–0.5 mm long, not toothed. Pollinaria: corpuscula ca. 0.18 mm long, pollinia borne horizontally, ovate, ca. 0.9 mm x 0.3 mm. Follicles unknown.

Distribution and habitat. Gonolobus absalonensis is apparently endemic to Martinique (Fig. 1). Its habitat is poorly known, but likely primarily middle elevation rainforest based on the requirements of congenics in the Lesser Antilles. The type was apparently collected near a waterfall.

Etymology. The epithet is derived from the locality of the type collection—Absalon, Martinique.

Provisional conservation status. IUCN: Critically endangered (CR)—B1a,biii. NatureServe: GH NH.

Taxon concept mapping. < G. martinicensis sensu Duss (1897); < G. martinicensis sensu Schlechter (1899); < G. martinicensis sensu Howard (1988); < G. martinicensis sensu Fournet (2002).

Gonolobus absalonensis is the smallest-flowered Lesser Antillean Gonolobus species (corolla lobes reaching only to 6.7 mm) and one of three Gonolobus species apparently endemic to Martinique. It can be distinguished from other Gonolobus species on Martinique by the following key:

1. Corolla lobes to 6.7 mm long, both surfaces glabrous; interstaminal gynostegial corona (Ci) single, smooth, lacking raised bumps; laminar dorsal anther appendages (Cd) emarginate.

1. G. absalonensis

1. Corolla lobes > 9.5 mm long, either or both surfaces pubescent; interstaminal gynostegial corona (Ci) double or if single, then with defined raised bumps medially; laminar dorsal anther appendages (Cd) rounded or truncate.

2. Interstaminal gynostegial corona single.

2. G. dussii

2. Interstaminal gynostegial corona double (i.e., a narrower upper ligulate corona lobe occurring on top of the broader lower corona).

5. G. martinicensis

**2. Gonolobus dussii** Krings, Syst. Bot. 32: 183. 2007.—TYPE: GUADELOUPE. Chemin de la Soufriere, alt. 500 m, s.d. (fl), Quentin 732 (holotype: P!-fl; isotype: GH!-fl). (Fig. 5)

Herbaceous perennial vines. Latex unknown, presumably white. Stems glabrate to very sparsely pubescent, both short, capitate-glandular, and longer, sharp, eglandular trichomes

present, the latter retrorse internodally, and antrorse-appressed along an indistinct, horizontal ridge between two opposing petioles and/or just above the node, to 0.5 mm long; nodes pubescent or glabrous, gland field apparently absent. Leaf blades ovate to oblong-ovate, (3.3–)5.7–10.7 cm x (0.9–)2.5–6.1 cm, apices gradually acuminate with the acumen narrowly obtuse, to 2 cm long, bases deeply or shallowly cordate, margins entire, adaxial surface glabrate or sparsely strigose, abaxial surface glabrate or more densely strigose with sharp, eglandular trichomes scattered along the major and minor veins, glandular emergences from the surface absent or very sparse, colleters 2–3, 0.4–0.6 mm long; petioles (1.3–)2.1–5.5 cm long, glabrous or sparsely pubescent on all sides, capitate trichomes to 0.09 mm long, sharp, eglandular trichomes 0.3–0.4 mm long, mostly antrorsely appressed or ascending (some spreading and a very few retrorse); stipular colleters 2, ca. 0.3 mm long, one borne on each side of the petiole base. Inflorescences racemiform, peduncles 0.7–2.3 cm long, glabrate to very sparsely pubescent, capitate, as well as sharp, eglandular trichomes present, the latter antrorsely-appressed or -ascending, found primarily at the apex, ca. 0.3 mm long; pedicels 1.8–2.2 cm long, more pubescent at the apex than at the base, capitate-glandular trichomes ca. 0.08 mm long, longer sharp, eglandular trichomes antrorsely-appressed or -ascending, ca. 0.3 mm long, bracts linear-lanceolate, ca. 1.5 mm x 0.17 mm long, caducous, adaxial surface glabrous, abaxial surface coarsely pubescent, trichomes sharp, eglandular, ca. 0.2 mm long, antrorse. Calyx lobes 5, sublanceolate to elongate triangular (widest at or just above the base), 3.9–5.8 mm x 1–1.5 mm, apices obtuse to narrowly rounded, margins glabrous, abaxial surface coarsely pubescent at the base and variously toward the apex, trichomes antrorsely-appressed or -ascending, to 0.5 mm long; colleters 1 per sinus. Corolla lobes 5, narrowly lanceolate to elongate triangular, (10–)12–

17 mm x 3.2–3.7 mm, slightly overlapping at the base, a glandular swelling frequently present in the sinus, adaxial surface glabrous, abaxial surface with coarse, sharp, eglandular trichomes, antrorsely-appressed or -ascending, particularly at the base and variously toward the apex, ca. 0.36 mm long; faucal annulus (corolline corona or Ca) interrupted, a distinctly raised ridge opposite each corolla lobe sinus, short-hispid or glabrate; gynostegial corona of fused staminal (Cs) and interstaminal parts (Ci), single, erect-undulating, two distinctly raised and rounded mounds borne in the interstaminal position; anther guiderails without appendages, laminar dorsal anther appendages (Cd) ca. 0.8 mm wide, rounded or emarginate; stylar head 2.3–2.4 mm diam, stipe ca. 0.45 mm long, not toothed. Pollinaria: corpuscula 0.18–0.3 mm long, pollinia borne horizontally, ovate, ca. 0.5–1 mm x 0.25–0.35 mm. Follicles unknown.

Distribution and habitat. Gonolobus dussii occurs in Guadeloupe and Martinique (Fig. 1). Its habitat is not well known, but it appears to have been collected from riversides and at mid-elevations (480–500 m).

Etymology. The specific epithet honors Pere Duss, whose collections of the species are at once the oldest and broadest geographically.

Provisional conservation status. IUCN: Critically endangered (CR)—B1a,b,iii. NatureServe: Guadeloupe (GH NH); Martinique (GH NH).

Taxon concept mapping. < G. martinicensis sensu Duss (1897); < G. martinicensis sensu Schlechter (1899); < G. martinicensis sensu Howard (1988); < G. martinicensis sensu Fournet (2002).

ADDITIONAL SPECIMENS EXAMINED. **Guadeloupe.** Bord de la riviere Noire, 29 Jun 1895 (fl), Pere Duss 3775 (MO!-fragment, NY!); Porrite-Noire, 20 Oct 1895 (fl), Pere Duss 3714 (NY!-2 sheets). **Martinique.** Environs a St. Pierre, 1884 (fl), Pere Duss “1862, 4565” (NY!); Porrite (sp?)-Fine, pres de la riviere Calabre, April 1900 (fl), Pere Duss 4565 (NY!).

The numbering of Duss “1862, 4565” (NY) would seem to indicate mixed material, however the elements mounted on the sheet clearly belong to a single gathering from a single location. Although two segments of stem and associated leaves and flowers are present, they are naturally intertwined and not disparate. Intertwining of multiple stems is not infrequent among ramets of Gonolobus species, as well as other vines. Interestingly, Duss 4565 (NY) is comprised of two separately mounted elements, which makes one wonder whether the labels for the specimens at NY currently labelled Duss “1862, 4564” and Duss 4565 were mixed up. However, Duss “1862, 4565” (NY) also contains seeds of unknown provenance in its fragment pocket, which may be the material originally associated with 1862.

Gonolobus dussii can be distinguished from G. youroumaynensis of St. Vincent by the short pedicel trichomes, the edentate stipe, and the adaxially glabrous corolla lobes. The gynostegial coronas of the G. absalonensis, G. dussii, and G. youroumaynensis are most similar to each other among Lesser Antillean Gonolobus species, but G. dussii uniquely exhibits two distinctly raised and rounded mounds in the interstaminal position (Fig. 5). The mounds appear very close and near ridge-like in Martinique specimens, as well as Duss 3775 of Guadeloupe. Additional collections are needed to determine the extent of variation in the coronas and to evaluate whether additional taxa are represented.

**3. *Gonolobus iyanolensis*** Krings, Syst. Bot. 32: 185. 2007.—TYPE: ST. LUCIA. Gros Piton, 9 Aug 1999 [“9/8/76”] (fl), Roger Graveson 107 (holotype: GH!). (Fig. 6)

Herbaceous perennial vines. Latex white. Stems glabrous or glabrate, both short, capitate-glandular, and longer, sharp, eglandular trichomes present, the latter retrorse or spreading internodally, and antrorse-appressed along an indistinct, horizontal ridge between two opposing petioles, to 1.2 mm long; nodes pubescent or glabrous in age, gland field sometimes present. Leaf blades ovate to oblong-ovate, to 8 cm x 5.4 cm, apices obtuse or short-acuminate with the acumen obtuse, bases cordate, margins entire, adaxial surface glabrous, abaxial surface glabrous or with sharp, eglandular trichomes scattered along the major veins, glandular emergences from the surface present, colleters 2–4, 0.37–0.65 mm long; petioles to 6.2 cm long, glabrous or glabrate, capitate-glandular trichomes very sparse if present, sharp, eglandular trichomes near apex if present, to 0.9 mm long; stipular colleters 2, ca. 0.3 mm long, one borne on each side of the petiole base. Inflorescences racemiform, peduncles 2.1–2.8 cm long, glabrous or glabrate, sharp, eglandular hairs antrorsely-appressed or -ascending, most pronounced near apex, ca. 0.7 mm long; pedicels 2.8–3.1 cm long, glabrate, capitate-glandular trichomes scattered throughout or only near the apex, ca. 0.09 mm long, longer, sharp, eglandular hairs antrorsely-appressed or -ascending, occurring only near the apex, 0.3–0.9 mm long, bracts linear-lanceolate, ca. 2.8 mm x 0.5 mm long, caducous, adaxial surface glabrous, abaxial surface coarsely pubescent, trichomes sharp, eglandular, ca. 0.4 mm long, antrorse. Calyx lobes 5, lanceolate (widest distinctly above the base, ca. 1.5–2 mm above base), 6.1–6.6 mm x 1.6–1.8 mm, apices obtuse, margins glabrous,

abaxial surface glabrous or glabrate with the few trichomes present, coarse, antrorsely-ascending or -appressed, to 0.4 mm long; colleters 1 per sinus. Corolla lobes 5, lanceolate, 10.2–17.3 mm x 2.7–4.8 mm, slightly lobed at the base, a glandular swelling frequently present in the sinus, adaxial surface pubescent along the right half, trichomes flat, ribbon-like, 0.18–0.26 mm long, abaxial surface glabrous; faucal annulus (corolline corona or Ca) interrupted, a distinctly raised ridge, opposite each corolla lobe sinus, short hispid; gynostegial corona of fused staminal (Cs) and interstaminal parts (Ci), double, 5-lobed, prostrate, narrow upper ligulate corona lobe of the Ci appressed to the lower, abruptly ending in a scooped out depression before reaching the stipe base (horizontal length of lower interstaminal gynostegial corona (Ci) from base of stipe to lobe apex 1.1–1.4 mm), dorsally ridged; anther guiderails apparently without appendages, laminar dorsal anther appendages (Cd) 0.5–0.6 mm wide, rounded or truncate; stylar head ca. 2.5 mm diam, stipe ca. 0.23 mm long, not toothed. Pollinaria: corpuscula 0.16–0.18 mm long, pollinia borne horizontally, ovate, ca. 0.5–0.7 mm x 0.25–0.35 mm. Follicles ovoid, 10–11.6 cm x 3.3–4 cm, 5-winged, appearing glabrous, but with minute papillae or capitate trichomes evident at high magnification; seeds pyriform, compressed, not plano-convex, 8.8–10.5 mm x 4.2–5.9 mm, glabrous, margins dentate, coma to 3.7 cm long

Distribution and habitat. Gonolobus iyanolensis is apparently endemic to St. Lucia (Fig. 1). An established population occurs on Gros Piton. Roger Graveson (pers. comm.) noted having seen vines away from the Pitons, but that they have not established themselves well. Woodland boundaries and recent forest openings appear to be the preferred habitat.

Etymology. The epithet is derived from Iyanola (eye-a-NO-la), an Arawak name for St. Lucia (Winer, pers. comm.).

Provisional conservation status. IUCN: Endangered (EN)—B1a,biii. NatureServe: G1 N1.

Taxon concept mapping. < G. martinicensis sensu Schlechter (1899); < G. martinicensis sensu Howard (1988).

ADDITIONAL SPECIMENS EXAMINED. **St. Lucia.** Chassin, edge of clearing, alt. 600 ft, 7 Jan 1987 (fr), Slane 1056 (GH!); Soufriere, Gros Piton summit, facing Soufriere, semi-open, sunny, rocky spot, climbing on shrubs, elev. ca. 750 m, 13° 48.612' N 61° 04.527' W, herbaceous vine (3 m), green flowers, white latex, 5 Jul 2005 (fl), Johnny 57 with Samuel and Sealys (UPRRP!); Soufriere, Gros Piton summit, facing Soufriere, on shrubs in open, sunny spot, elev. ca. 800 m, 13° 48.689' N 61° 03.439' W, herbaceous vine (3 m), greenish petals, white latex, 13 Sep 2005 (fl), Graveson 1248 with Smith (UPRRP!); Gros Piton, seasonal deciduous woods, elev. ca. 1300 ft., 11 Mar 2006 (fl), Krings 1373 with Graveson and Smith (NCSC!).

Roger Graveson (pers. comm.) noted that the collection date is incorrect on the label of Graveson 107 (GH) and should instead be 9 Aug 1996. Gonolobus iyanolensis is immediately recognizable among Lesser Antillean Gonolobus species by its double interstaminal gynostegial corona (Ci). The only other species that shares this corona type in the area is G. martinicensis. (Fig. 8). In contrast to the robust-flowered G. iyanolensis, G. martinicensis exhibits distinctly more slender flowers with elongate-campanulate bases (ca. 2 mm long) that are longer than wide (as wide as long or wider than long in G. iyanolensis) and a narrower gynostegial corona (see key). The distinct dorsal ridge of the narrow upper ligulate corona lobe of the Ci in G.

iyanolensis has also not been seen in G. martinicensis, which is either plane in the homologous position or exhibits a slightly raised bump.

**4. *Gonolobus jamaicensis*** Rendle, J. Bot. 74: 345. 1936.—TYPE: JAMAICA. Harris 6368

(holotype: BM!). (Fig. 7)

Herbaceous perennial vines. Latex white. Stems pubescent, both short, capitate-glandular, and longer, sharp, eglandular trichomes present, the latter spreading or retrorse internodally, and antrorse-appressed along an indistinct, horizontal ridge between two opposing petioles and/or just above the node, to 1.8 mm long; nodes pubescent, gland field apparently absent. Leaf blades elliptic to ovate, (2–)3.9–9.7 cm x (1.3–)1.8–6.6 cm, apices acuminate, acumen narrowly obtuse, to 1.1 cm long, bases cuneate, rounded, truncate, or cordate (frequently all base types present on a single individual vine), margins entire, adaxial surface glabrate, abaxial surface sparsely pubescent to glabrate, sharp, eglandular trichomes relatively dense along the major and minor veins, glandular emergences from the surface absent or very sparse, colleters 2, ca. 0.45 mm long; petioles 0.9–3.5 cm long, pubescent on all sides, capitate trichomes to 0.13 mm long, sharp, eglandular trichomes ca. 1.25 mm long, mostly spreading or retrorse, less dense than the capitate trichomes; stipular colleters 2, ca. 0.29 mm long, one borne on each side of the petiole base. Inflorescences racemiform, peduncles to 4.3 cm long, pubescent, capitate, as well as sharp, eglandular trichomes present, the latter spreading, retrorse, or antrorsely-ascending or – appressed, ca. 0.5 mm long; pedicels 1.2–1.4 cm long, evenly pubescent throughout, capitate-glandular trichomes ca. 0.08 mm long, longer sharp, eglandular trichomes antrorsely-appressed

or -ascending, ca. 0.4 mm long, bracts linear-lanceolate, ca. 1.7 mm x 0.5 mm long, caducous, adaxial surface glabrous, abaxial surface coarsely pubescent, trichomes sharp, eglandular, ca. 0.3 mm long, antrorse. Calyx lobes 5, lanceolate, 4.3–7.45 mm x 1.6–2.2 mm, apices obtuse, margins glabrous or sparsely ciliolate, abaxial surface pubescent at the base and glabrous toward the apex, trichomes antrorsely-appressed, largest to 0.5 mm long; colleters 1 per sinus. Corolla lobes 5, lanceolate, 10–13 mm x 3.8–5 mm, slightly overlapping at the base, a glandular swelling frequently present in the sinus, adaxial surface pubescent along the right, abaxial surface glabrous; faucal annulus (corolline corona or Ca) a continuous ring, bilobed opposite each anther, ca. 0.93 mm tall, short-pubescent and papillate throughout; gynostegial corona of fused staminal (Cs) and interstaminal parts (Ci), single, erect-undulating, interstaminal secondary nectaries apparently absent or at least not formed into conspicuous bumps or mounds; anther guiderails without appendages, laminar dorsal anther appendages (Cd), ca. 2.3 x 1.7 mm, spreading, apices truncate; stylar head ca. 3.3 mm diam, stipe ca. 1 mm long, dentate, teeth appearing as notches, borne on the lower portion of the column, just above the upwardly rising segment of each Cs. Pollinaria: corpuscula ca. 0.18 mm long, pollinia borne horizontally, ovate, ca. 1.2 mm x 0.3 mm. Follicles unknown.

Distribution and habitat. Gonolobus jamaicensis is endemic to Jamaica. It is known only from montane rainforests.

Etymology. The specific epithet means “from Jamaica.”

Provisional conservation status. IUCN: Vulnerable (VU)—B1a,c. NatureServe: G3 N3.

Taxon concept mapping. = G. rostratus sensu Schlechter (1899); = G. jamaicensis sensu Adams (1972).

ADDITIONAL SPECIMENS EXAMINED. **Jamaica.** 1886 (fl), J. Hart 968 (MO! [2 single leaves and 2 flowers]; US!); John Crow Mountains, eastern Jamaica, in montane rainforest over limestone, thicket at ca. 1025 m, hurricane-damaged, SE of Millbank, climbing to 2 m, petals maroon with cream margins, latex white, 17 Mar 1992 (fl), D.L. Kelly, S. Iremonger and REA team 10207 (TCD!). PORTLAND PARISH: 0.5 mi N of Hardwar Gap, near the waterfall, ca. 3900 ft., montane rainforest, high-climbing woody vine with latex, flowers greenish outside, purple-red inside at base, 22 Jun 1952 (fl), G.R. Proctor 6828 (A!, IJ!); 0.5 mi N of Hardwar Gap, uphill from the trail above the “Waterfall,” ca. 3900 ft, montane rainforest, vines growing over trailside shrubs and in small forest openings, 3 Mar 2006 (st), A. Krings 1393 with D. Suiter and G.R. Proctor (IJ!, NCSC!).

Gonolobus jamaicensis was proposed by Rendle as a nomen novum for the Jamaican endemic taxon Schlechter (1899) treated as G. rostratus (Vahl) R.Br. Not only did Robert Brown never make the combination attributed to him (see *Memoirs of the Wernerian Natural History Society* 1: 35. 1810), but the true Gonolobus rostratus (Vahl) Schult. is only known from Trinidad (and perhaps South America). It is based on the type of Cynanchum rostratum Vahl. Because Rendle corrected a misapplication, his name—G. jamaicensis—is a new species name, not a nomen novum as he mistakenly stated. A nomen novum is an avowed substitute (replacement name) for a validly published but illegitimate name, the type of which would be the same as that of the name which it replaced.

5. **Gonolobus martinicensis** Decaisne in DC., Prodr. 8: 595. 1844.—TYPE: MARTINIQUE. Pleé  
s.n. (lectotype: P!, designated by Krings, in review) (Fig. 8)

Gonolobus scandens (Aublet) Urban, Repert. Spec. Nov. Regni Veg. 16: 151. 1919, nom.  
superfl.

Herbaceous perennial vines. Latex unknown, presumably white. Stems villous to glabrate, both short, capitate-glandular, and longer, sharp, eglandular trichomes present, the latter retrorse or spreading internodally, and antrorse-appressed along an indistinct, horizontal ridge between two opposing petioles, to 1.9 mm long; nodes pubescent or glabrous in age, gland fields sometimes present. Leaf blades ovate to oblong-ovate, to 6.4 cm x 4.9 cm, apices obtuse, gradually to abruptly acuminate with the acumen to 1.4 cm long, bases cordate, margins entire, adaxial surface sparsely strigillose, abaxial surface pubescent along the veins, trichomes strigillose (and longer, sharp, eglandular, scattered particularly along the midvein), glandular emergences from the surface present, colleters 2, 0.7 mm long; petioles to 4 cm long, villous, capitate-glandular trichomes sparse but throughout, sharp, eglandular trichomes ubiquitous, mostly antrorse-ascending and spreading, to 1 mm long; stipular colleters 2, ca. 0.24 mm long, one borne on each side of the petiole base. Inflorescences racemiform, peduncles 1.5–2.1 cm long, villous with sharp, eglandular hairs antrorsely- or retrorsely -appressed or -ascending/-descending and spreading, ca. 0.44 mm long, capitate trichomes throughout; pedicels to 1.9 cm long, less pubescent than peduncles, capitate-glandular trichomes throughout, ca. 0.09 mm long, longer, sharp, eglandular hairs antrorsely- appressed or -ascending, throughout, though most

dense at the apex, ca. 0.47 mm long, bracts linear-lanceolate, ca. 1.6 mm x 0.17 mm long, caducous, adaxial surface glabrous, abaxial surface coarsely pubescent, trichomes sharp, eglandular, ca. 0.2 mm long, antrorse. Calyx lobes 5, oblong lanceolate, 4.5–5 mm x 0.8 mm, apices obtuse or acute, margins sparsely ciliolate, abaxial surface glabrate with the few trichomes present, coarse, antrorsely-ascending or -appressed, to 0.3 mm long; colleters 1 per sinus. Corolla lobes 5, lanceolate, 9.7–11.4 mm x 2–3.5 mm, slightly lobed at the base, a glandular swelling frequently present in the sinus, adaxial surface pubescent along the right half, trichomes flat, ribbon-like, ca. 0.2 mm long, abaxial surface glabrate with a few, sparse, sharp, eglandular trichomes near the base, middle, and margin along the tip; faucal annulus (corolline corona or Ca) interrupted, a distinctly raised ridge, opposite each corolla lobe sinus, short hispid; gynostegial corona of fused staminal (Cs) and interstaminal parts (Ci), double, 5-lobed, prostrate, narrow upper ligulate corona lobe of the Ci appressed to the lower, ending essentially at the stipe base (horizontal length of interstaminal gynostegial corona (Ci) from base of stipe to lobe apex = 0.7 mm), dorsally plane or sometimes raised into a shallow bump; anther guiderails apparently without appendages, laminar dorsal anther appendages (Cd) 0.2 mm wide, rounded or truncate; stylar head 1.8–2.3 mm diam, stipe ca. 0.28 mm long, not toothed. Pollinaria: corpuscula 0.1–0.15 mm long, pollinia borne horizontally, ovate, 0.45–0.6 mm x 0.24–0.26 mm. Follicles unknown.

Distribution and habitat. Gonolobus martinicensis is apparently endemic to Martinique (Fig. 1). Its habitat is unknown, but likely primarily middle elevation rainforest based on the requirements of congeners in the Lesser Antilles.

Etymology. The specific epithet means “from Martinique.”

Provisional conservation status. IUCN: Critically endangered (CR)—B1a,biii. NatureServe: GH NH.

Taxon concept mapping. < G. martinicensis sensu Duss (1897); < G. martinicensis sensu Schlechter (1899); < G. martinicensis sensu Howard (1988); G. martinicensis sensu Fournet (2002).

ADDITIONAL SPECIMENS EXAMINED. **Martinique.** L.C. Rich. Herb. Guyanensi-Antillanum (P!-fl, 2 specimens [G. caribaeus Rich., nom. sched.]); Lieber s.n. (M!-fl).

Gonolobus martinicensis was originally described by Decaisne based on specimens from Martinique. Subsequent workers recognized the species as occurring also in Dominica, Guadeloupe, and St. Vincent (Urban 1919; Howard 1989; Fournet 2002). However, recent study revealed that G. martinicensis of prior authors actually includes six distinct entities, treated as species by Krings (Accepted2). Gonolobus martinicensis is immediately recognizable among Lesser Antillean Gonolobus species by its double (or ligulate) interstaminal gynostegial corona (Ci). The only other species that shares this corona type in the area is G. iyanolensis. (Fig. 6). In contrast to the robust-flowered G. iyanolensis, G. martinicensis exhibits distinctly more slender flowers with elongate-campanulate bases (ca. 2 mm long) that are longer than wide (as wide as long or wider than long in G. iyanolensis) and a narrower gynostegial corona (see key). The distinct dorsal ridge of the narrow upper ligulate corona lobe of the Ci in G. iyanolensis has also not been seen in G. martinicensis, which is either plane in the homologous position or exhibits a slightly raised bump.

**6. *Gonolobus rostratus*** (Vahl) Schultes in Roemer & Schultes, Syst. veg. 6: 61. 1820.

*Cynanchum rostratum* Vahl, Symb. Bot. 3: 45. 1794.—TYPE: TRINIDAD. (von Rohr?) Hb.

Liebmann (holotype: C [IDC microfiche photo: Vahl herbarium nr. 17: III, 5!]; isotype: BM!)

(Fig. 9)

*Gonolobus Broadwayae* Schlechter, Symb. antill. 7(3): 340-341. 1912.—TYPE: TRINIDAD.

Lopez 2419 (lectotype: Z!, designated by Krings, in review)

Herbaceous perennial vines. Latex unknown, presumably white. Stems pubescent, both short, capitate-glandular, and longer, sharp, eglandular trichomes present, the latter throughout, spreading, or retrorse internodally, and antrorse-appressed along an indistinct, horizontal ridge between two opposing petioles and/or just above the node, to 1.07 mm long; nodes pubescent, gland field apparently absent. Leaf blades ovate to oblong-ovate, 1.9–10.2 cm x 0.9–6.6 cm, apices gradually acuminate with the acumen narrowly obtuse, to 1.2 cm long, bases deeply cordate, margins entire, adaxial surface evenly strigillose, abaxial surface evenly strigillose, trichomes sharp, eglandular, to 1 mm long, glandular emergences from the surface apparently absent, colleters 2–3, 0.9–1 mm long; petioles 0.9–6.8 cm long, pubescent on all sides, capitate trichomes to 0.16 mm long, sharp, eglandular trichomes antrorsely-ascending or –appressed, ca. 0.7 mm long; stipular colleters 2, ca. 0.3 mm long, one borne on each side of the petiole base (rarely on the stem), ca. 0.3 mm long. Inflorescences racemiform, peduncles 0.4–2.2 cm long, capitate, as well as sharp, eglandular trichomes present, the latter mostly antrorsely-appressed or

-ascending, distributed throughout, ca. 0.4 mm long; pedicels 1.2–4 cm long, evenly pubescent from apex to base, capitate-glandular trichomes ca 0.1 mm long, longer, sharp, eglandular trichomes antrorsely-ascending, ca. 0.8 mm long, bracts linear-lanceolate, ca. 5.1–5.5 mm x 0.8–1.1 mm long, caducous, adaxial surface glabrous, abaxial surface coarsely pubescent, trichomes sharp, eglandular, 0.38–0.4 mm long, antrorse. Calyx lobes 5, ovate, 4.1–8.4 mm x 1.9–5.5 mm, apices obtuse to rounded, margins sparsely glabrous or ciliate, abaxial surface sparsely pubescent at the base and glabrous toward the apex, trichomes antrorsely appressed or -ascending, to 0.3 mm long; colleters 1 per sinus. Corolla lobes 5, linear-lanceolate or lanceolate, 12–22 mm x 4.3–6.7 mm, slightly lobed at the base, a glandular swelling frequently present in the sinus, adaxial surface glabrous, abaxial surface sparsely pubescent with coarse, sharp, eglandular, antrorsely-appressed or -ascending trichomes, trichomes ca. 0.25 mm long; faucal annulus (corolline corona or Ca) interrupted, a raised bump or indistinct ridge opposite each corolla lobe sinus, pubescent or glabrous; gynostegial corona of fused staminal (Cs) and interstaminal (Ci) parts, prostrate-undulating, single, secondary nectaries in interstaminal position absent or at least not formed into distinct bumps or mounds; anther guiderails without appendages, laminar dorsal anther appendages (Cd) 1.3–1.5 mm wide, truncate to rounded; stylar head ca. 5.4 mm diam, stipe = 0.8 mm long, edentate. Pollinaria: corpuscula ca. 0.23 mm long, pollinia borne horizontally, narrowly ovate, ca. 1.1 mm x 0.4 mm. Follicles apparently known only from a photo taken by P. and Y.S. Comeau, but this was not obtained on loan.

Distribution and habitat. In the West Indies, G. rostratus is known only from Trinidad. South American collections exist that have been referred to G. rostratus, however further study is

needed to determine the conspecificity of the entities. In Trinidad, G. rostratus is known from road banks.

Etymology. The specific epithet means “beaked.”

Provisional conservation status. IUCN: Trinidad: Critically endangered (CR)—B1a,biii.

NatureServe: G3G4? N1.

Taxon concept mapping. ? G. rostratus sensu Schlechter (1899); = G. broadwayae sensu Schlechter (1912); = G. broadwayi sensu Cheesman (1947).

ADDITIONAL SPECIMENS EXAMINED: Hab. in Ins. Carib., Anonymous s.n. (L!). **Trinidad**. Apr [18?]74 (st), O. Kuntze 881 (E); Morne Cocoa Road, bank, 9 Apr 1920 (fl), N.L. Britton and T.E. Hazen 1601 (GH!, K!); Gaura Old Rd., K5 spreading in bud, C5 strongly contorted, greenish yellow, lobes lanceolate, 20 x 7 mm, crown annular, connecting colum and cor. throat, dark chocolate brown, stig. flat, 19 May 1937 (fl), Cheesman 13168 (TRIN!); 1877-80 (fl), A. Fendler 637 (BM!, E!); Heights of Aripo Rd., close to small ravine or close to Rhapsey’s Estate, Mar 1987 (fl & fr [photo apparently at TRIN, but not sent on loan]), F. Moreau s.n. (TRIN!); March [18?]85 (fl), H. Prestoe s.n. (K!).

Cheesman (1947) mistakenly considered “Gonolobus rostratus R.Br. sens. Griseb Fl. 420” a synonym of “Matelea viridiflora (G.F.W. Meyer) Woods.” However, the latter clearly corresponds to Matelea denticulata (Vahl) Fontella & E.A. Schwarz based on Cheesman’s description (e.g., “cal[yx] lobes lanceolate,” “corolla [...] lobes ovate,” “anthers without dorsal appendages”) and not to Gonolobus rostratus sensu Grisebach (1864) (e.g., “calyx [...] segments

ovate,” “corolla [...] segments lanceolate-linear”). Grisebach’s (1864) taxon (also from Trinidad) is clearly referable to G. rostratus (Vahl) Schult. The two taxa are difficult to confuse by anyone familiar with them. The Schultes name has priority as Robert Brown never made the combination G. rostratus that has been attributed to him by some authors, such as Grisebach (1864) and Schlechter (1899).

**7. *Gonolobus stapelioides*** Desvaux ex Hamilton, Prodr. pl. Ind. occid. 32. 1825.—TYPE:

JAMAICA. Portland Parish, 0.5 mi N of Hardwar Gap, uphill from the trail above the “Waterfall,” ca. 3900 ft, montane rainforest, vines growing over trailside shrubs and in small forest openings, population J1, 3 Mar 2006 (fl), A. Krings 1395 with D. Suiter and G.R.

Proctor (neotype: P!; isoneotypes: BM!, IJ!, NCSC!, NY!, designated by Krings, in review).

(Fig. 10)

Fischeria cincta Grisebach, Fl. Brit. W. I. 421. 1862; Gonolobus cinctus (Grisebach) Bentham & Hooker f., Index Kewensis 2: 1054. 1895.—TYPE: JAMAICA. Higson s.n. (HT: K!)

Herbaceous perennial vines. Latex white. Stems pubescent, both short, capitate-glandular, and longer, sharp, eglandular trichomes present, the latter retrorse internodally, and antrorse-appressed along an indistinct, horizontal ridge between two opposing petioles and/or just above the node, to 1.3 mm long; nodes pubescent, gland field apparently absent. Leaf blades elliptic to ovate, 3–9 cm x 1.2–4.5 cm, apices acute or gradually acuminate with the acumen narrowly obtuse, to 0.75 cm long, bases cuneate, rounded, or truncate (frequently all base types present on

a single individual vine), margins entire, adaxial surface sparsely strigose, abaxial surface sparsely pubescent to glabrate, sharp, eglandular trichomes relatively dense along the major and minor veins, glandular emergences from the surface absent or very sparse, colleters 2(–3?), ca. 0.5 mm long; petioles 1–2.3 cm long, pubescent on all sides, capitate trichomes to 0.06 mm long, sharp, eglandular trichomes ca. 1.1 mm long, mostly spreading or somewhat retrorse, less dense than the capitate trichomes; stipular colleters 2, ca. 0.3 mm long, one borne on each side of the petiole base. Inflorescences racemiform, peduncles to 2.5 cm long, pubescent, capitate, as well as sharp, eglandular trichomes present, the latter spreading or retrorse, ca. 0.6 mm long; pedicels to 2.5 cm long, pubescent throughout, capitate-glandular trichomes ca. 0.05 mm long, longer sharp, eglandular trichomes spreading or antrorsely-appressed or -ascending, ca. 0.5 mm long, bracts linear-lanceolate, 2.8–3.7 mm x 0.45–0.5 mm long, caducous, adaxial surface glabrous, abaxial surface coarsely pubescent, trichomes sharp, eglandular, 0.36–0.4 mm long, antrorse. Calyx lobes 5, linear-lanceolate, 7–8.5 mm x 2–2.3 mm, apices acute to narrowly obtuse, margins glabrous or very sparsely ciliolate, abaxial surface weakly and finely pubescent at the base and glabrous toward the apex, trichomes antrorsely-appressed, to 0.9 mm long; colleters 1 per sinus. Corolla lobes 5, oblong-ovate, 12–15 mm x 4–6.5 mm, slightly overlapping at the base, a glandular swelling frequently present in the sinus, margins and apices strongly recurved, adaxial surface papillate-pubescent along the right, abaxial surface essentially glabrous; faucal annulus (corolline corona or Ca) interrupted, a pronounced twin-peaked thickening opposite each corolla lobe, apparently reduced opposite each corolla lobe sinus, short-hispid; gynostegial corona of fused staminal (Cs) and interstaminal parts (Ci), single, erect-undulating, interstaminal secondary nectaries apparently absent or at least not formed into conspicuous bumps or mounds;

anther guiderails without appendages, laminar dorsal anther appendages (Cd) white, ca. 4–4.2 x 1.8–2 mm, erect to spreading, apices bilobed; stylar head 3.6–4.8 mm diam, stipe ca. 1.6 mm long, not toothed, though with white ribs present at the base of each anther. Pollinaria: corpuscula ca. 0.2 mm long, pollinia borne horizontally, ovate, ca. 1.5 mm x 0.41 mm. Follicles fusiform, 5-winged, 1.7 x 7.2 cm. Seeds pyriform, compressed, not plano-convex, 4.6–5.7 x 2.5–3.5 mm, glabrous, margins dentate, coma to 2.4 cm long.

Distribution and habitat. Gonolobus stapelioides is endemic to Jamaica. It is known only from montane rainforests.

Etymology. The specific epithet means “stapelia-like.”

Provisional conservation status. IUCN: Least concern (LC). NatureServe: G4 N4.

Taxon concept mapping. = G. stapelioides sensu Schlechter (1899); = G. stapelioides sensu Adams (1972).

ADDITIONAL SPECIMENS EXAMINED. **Jamaica.** PORTLAND PARISH: Vinegar Hill, 21 Feb 1894 (fl), W. Harris 5561 (MO! [a single leaf and a single flower]); Vinegar Hill, 6.2.95 [1895] (fl), W. Harris 5561 (BM!); Hardwar Gap, ca. 4000 ft, subwoody twining vine, climbing on trees and shrubs, 25 Feb 1964 (fl), C.D. Adams 12705 (M!, MO!); Immediately N of the Grand Ridge of the Blue Mountains, between John Crow Peak and Morce’s Gap, 18 05’N 76 39’W, Series 1/13: 854602, ca. 1590 m, liane into the crown of a Palicourea alpina (Sw.) DC. (Rubiaceae) in a ridge flank, in montane rainforest, 15 May 1989 (fl), P.J. Bellingham 1156 (BM!); 0.5 mi N of Hardwar Gap, near “The Waterfall,” ca. 3800 ft, montane rainforest, high-climbing, slender vine with latex, flowers fragrant, green with white corona, 14 Jan 1980 (fl), G.R. Proctor 38534 (IJ!);

0.5 mi N of Hardwar Gap, uphill from the trail above the “Waterfall,” ca. 3900 ft, montane rainforest, vines growing over trailside shrubs and in small forest openings, population J2, 3 Mar 2006 (fl), A. Krings 1394 with D. Suiter and G.R. Proctor (IJ, NCSC); 0.5 mi N of Hardwar Gap, uphill from the trail above the “Waterfall,” ca. 3900 ft, montane rainforest, vines growing over trailside shrubs and in small forest openings, population J3, 3 Mar 2006 (fl), A. Krings 1396 with D. Suiter and G.R. Proctor (IJ, NCSC). ST. ANDREW PARISH: Grand Ridge of the Blue Mountains, E of the summit of John Crow Peak, 18 05'N 76 40'W, Series 1/13: 853603, ca. 1640 m, common trailing liane into low canopy in montane rainforest, 30 Apr 1990 (fl), P.J. Bellingham 1211 (BM!); Grand Ridge of the Blue Mountains, immediately E of John Crow Peak, 18 05' N 76 40' W, Series 1/13: 852603, ca. 1660 m, liane to 4 m high in a canopy gap created by Hurricane Gilbert (1988) in montane rainforest, corolla green, white at base, 11 Jun 1991 (fl-sheet 1; fr-sheet 2), P.J. Bellingham 1487 (BM-2 sheets!). ST. THOMAS PARISH: Monkey Hill, S spur of Mossmans Peak, ca. 5000 ft, montane rainforest, woody vine, flowers green with white corona, 16 Jun 1952 (fl), G.R. Proctor 6803 (BM!, IJ!).

Gonolobus stapelioides is immediately recognizable by the white Cd segments that are fully vertical at maturity (Fig. 10E, H).

**8. *Gonolobus stellatus*** Grisebach, Fl. Brit. W. I. 420. 1862.—TYPE: JAMAICA. Purdie s.n. (holotype: GOET!; isotypes: BM!, K!). (Fig. 11)

Herbaceous perennial vines. Latex white. Stems pubescent to glabrate in age, both short, capitate-glandular, and longer, sharp, eglandular trichomes present, the latter retrorse-appressed or -spreading internodally, and antrorse-appressed along an indistinct, horizontal ridge between two opposing petioles and/or just above the node, to 1.25 mm long; nodes pubescent to glabrate, gland field apparently absent. Leaf blades elliptic to oblong-elliptic, 2.2–11.5 cm x 0.8–4.2 cm, apices acute or gradually acuminate with the acumen narrowly obtuse, to 1.4 cm long, bases cuneate, margins entire, adaxial surface sparsely strigose, abaxial surface glabrate, trichomes sharp, eglandular, very sparsely scattered along the major and minor veins, glandular emergences from the surface apparently absent, colleters 2, 0.2–0.4 mm long; petioles 0.8–5.6 cm long, sparsely pubescent on all sides to glabrate, capitate-glandular trichomes, ca. 0.1 mm long, sharp, eglandular trichomes, ca. 0.6 mm long, antrorsely-appressed or -ascending; stipular colleters 2, ca. 0.25 mm long one borne on each side of the petiole base (rarely on the stem). Inflorescences racemiform, peduncles 0.7–3 cm long, sparsely pubescent to glabrate, capitate, as well as sharp, eglandular trichomes present, the latter antrorsely-appressed or -ascending, distributed throughout, ca. 0.8 mm long; pedicels 1.2–2.3 cm long, relatively evenly pubescent from apex to base, capitate-glandular trichomes ca 0.7 mm long, longer, sharp, eglandular trichomes antrorsely-ascending, ca. 0.26 mm long, bracts linear to linear-oblong, ca. 1.35 mm x 0.24 mm, caducous adaxial surface pubescence glabrous, abaxial surface coarsely pubescent, trichomes sharp, eglandular, ca. 0.22 mm long. Calyx lobes 5, lanceolate, 7–11 mm x 1.7–2.7 mm, apices obtuse, margins glabrous, abaxial surface very sparsely coarsely pubescent at the base, glabrous toward the apex, trichomes antrorsely appressed or -ascending, to 0.6 mm long; colleters 1–2 per sinus. Corolla lobes 5, linear-lanceolate, 15–18 mm x 4–5.3 mm, slightly lobed at the base, a

glandular swelling frequently present in the sinus, adaxial surface densely strigillose, not papillate-pubescent, on the right half, abaxial surface glabrous; faucal annulus (corolline corona or Ca) interrupted, a raised bump or ridge opposite each corolla lobe sinus, pubescent; gynostegial corona of fused staminal (Cs) and interstaminal (Ci) parts, prostrate-undulating, single, secondary nectaries in interstaminal position absent; anther guiderails without appendages, laminar dorsal anther appendages (Cd) 1.7–2.1 mm wide, slightly emarginate to divergently and sharply bilobed; stylar head ca. 4.3 mm diam, stipe ca. 1.7 mm long, edentate. Pollinaria: corpuscula ca. 0.25 mm long, pollinia borne horizontally, narrowly ovate, ca. 1.7 mm x 0.48 mm. Follicles (immature) fusiform, 5-winged, but with small murications between the wings, 7.1–7.3 cm x 1.6–1.7 cm. Seeds unknown.

Distribution and habitat. Endemic to Jamaica, G. stellatus is known only from montane rainforests.

Etymology. The specific epithet means “starry.”

Provisional conservation status. IUCN: Vulnerable (VU)—B1a,c. NatureServe: G3 N3.

Taxon concept mapping. = G. stellatus sensu Schlechter (1899); = G. stellatus sensu Adams (1972).

ADDITIONAL SPECIMENS EXAMINED. **Jamaica.** PORTLAND PARISH: Hog House Hill study area, ca. 4 mi S of Sherwood Forest, N edge of John Crow Mtns., ca. 1400 ft, climber 2 m high, 1976-78 (st), D.C. Kelly JCM 1490 (IJ!); Gorge of Stony River above junction of the Macungo River, 1300–1500 ft, moist primary rain-forest, herbaceous vine with white latex, fruit black, 25

Jul 1967 (fl & fr), G.R. Proctor 29378 (BM!, IJ!). ST. ANN PARISH: County of Middlesex, Mt.

Diablo, woods, 9 Mar 1936 (fl), F.W. Hunnewell 11032 (GH!).

**9. *Gonolobus stephanotrichus*** Grisebach, Cat. pl. Cub. 177. 1866.—TYPE: CUBA. Wright 2969, 1860–1864 (lectotype: GOET!, designated by Krings & Fantz 2006; syntypes: BREM!, MO, G!, GH!, HAC!, K!, NY!, P!, UC!, US!). (Fig. 12)

Herbaceous perennial vines. Latex white (rarely watery). Stems pubescent, both short, capitate-glandular, and longer, sharp, eglandular trichomes present, the latter throughout, spreading, or retrorse internodally, and antrorse-appressed along an indistinct, horizontal ridge between two opposing petioles and/or just above the node, to 1.08 mm long; nodes pubescent, gland field apparently absent. Leaf blades lanceolate, ovate, or oblong-ovate, 2–14.4 cm x 0.7–7.7 cm, apices gradually or abruptly acuminate with the acumen narrowly obtuse, to 2 cm long, bases deeply cordate, margins entire, adaxial surface sparsely but evenly strigillose to glabrate, abaxial surface sparsely but evenly strigillose, sharp, eglandular trichomes scattered along the major and minor veins, to ca. 0.58 mm long, glandular emergences from the surface apparently absent, colleters 3–4, ca. 0.4 mm long; petioles 0.9–7 cm long, evenly pubescent on all sides, some trichomes capitate, to 0.1 mm long, but mostly sharp, eglandular, antrorsely ascending or spreading, to 0.67 mm long; stipular colleters 2, ca. 0.39 mm long, one borne on each side of the petiole base (rarely on the stem). Inflorescences racemiform, peduncles 0.18–0.4 cm long, sparsely pubescent to glabrate, capitate trichomes apparently absent, sharp, eglandular trichomes sparse, antrorsely-appressed or -ascending, distributed throughout, ca. 0.4 mm long; pedicels

0.25–0.89 cm long, relatively evenly pubescent from apex to base, capitate-glandular trichomes very sparse, ca 0.07 mm long, longer, sharp, eglandular trichomes antrorsely-ascending, ca. 0.43 mm long, bracts linear-lanceolate, ca. 4.9 mm x 0.48 mm, caduous, adaxial surface glabrous, abaxial surface coarsely pubescent, trichomes sharp, eglandular, 0.22–0.47 mm long, antrorse. Calyx lobes 5, lanceolate, 2.7–6.7 mm x 1.6–2 mm, apices obtuse, margins glabrous, abaxial surface sparsely but coarsely pubescent, trichomes antrorsely appressed or -ascending, to 0.4 mm long; colleters 1 per sinus. Corolla lobes 5, elongate triangular or lanceolate, 8.7–14 mm x 2.4–3.7 mm, slightly lobed at the base, a glandular swelling frequently present in the sinus, adaxial surface glabrous, abaxial surface pubescent with coarse, sharp, eglandular, antrorsely-appressed or -ascending trichomes, ca. 0.7 mm long; faucal annulus (corolline corona or Ca) annular, pubescent; gynostegial corona of fused staminal (Cs) and interstaminal (Ci) parts, prostrate-undulating, single, secondary nectaries in interstaminal position absent or at least not developed into distinct bumps or mounds; anther guiderails without appendages, laminar dorsal anther appendages (Cd) ca. 0.6 mm wide, truncate; stylar head ca. 2.6 mm diam, stipe ca. 0.73 mm long, teeth not appearing as notches, instead truncate, borne individually on the lower portion of the column, just above the upwardly rising segment of each Cs. Pollinaria: corpuscula ca. 0.2 mm long, pollinia borne horizontally, narrowly ovate, ca. 0.84 mm x 0.3 mm. Follicles ovoid, 5-winged, 9.3–9.5 mm x 2.6–2.9 mm. Seeds pyriform, compressed, not plano-convex, 7–7.8 mm x 3.4–4.9 mm, glabrous, margins entire, not dentate, coma to 2.7 cm long.

Distribution and habitat. Gonolobus stephanotrichus occurs in Cuba, Hispaniola, and Puerto Rico (Fig. 1). It has primarily been collected in mid-elevation, moist to wet forests.

Etymology. The specific epithet means “hairy-crowned,” likely referring to the dense ring of hairs surrounding the gynostegial corona.

Provisional conservation status. IUCN: Least concern (LC). NatureServe: Cuba (G4 N4); Dominican Republic (G4 N4); Puerto Rico (G4 N4).

Taxon concept mapping. = G. stephanotrichus sensu Schlechter (1899); = G. stephanotrichus sensu Liogier (1957, 1994, 1995); = G. stephanotrichus sensu Acevedo-Rodríguez (2005).

ADDITIONAL SPECIMENS EXAMINED: **Cuba.** Cuba Orientali, 1856–1857 (fl, fr-imm), C. Wright 407 (GH!; blue label); Cuba Orientali, 1861 [1860 on white label, but with a one marked through the zero] (fl, fr-imm), C. Wright 164 (S!). SANTIAGO DE CUBA: Sierra Maestra, Parque Nacional Turquino, within 3 km of Campamento Joaquin on trail from the Alto de Naranjo, 3 June 2005, A. Krings, F. Areces, and J. Lazcano s.n. (HAJB, NCSC); Sierra Maestra, Parque Nacional Turquino, 2-3 km downhill from Campamento Joaquin in direction of the Alto de Naranjo, 2 June 2005, A. Krings, F. Areces, and J. Lazcano s.n. (NCSC).

**Dominican Republic.** DISTRITO NACIONAL: Santo Domingo, Cordillera Septentrional, prov. Espaillat, Mora, Colonia de Jamao, in forest, c. 800 m, rare, 21 May 1929 (fl), E.L. Ekman H12568 (K!). PUERTO PLATA: trepadora de 3 m de largo, flores verdes con centro parduzco, en cafetal, estribo Sur de Isabel de Torres, alt. 750 m, 16 Oct 1976 (fl), A. Liogier and P. Liogier 25627 (JBSD!). SAN CRISTÓBAL: Cordillera Central, Loma La Humeadora, Ladera Este, en el nacimiento del Arroyo Derrumdadero, en las margenes, con helechos arborescentes, Urera domingensis, Gyrotaenia sp., 18 28.5°N, 70 14.7° Oeste, elev. 900 m, 20 Apr 1994 (fr), F. Jiménez, M. Mejía, and A. Veloz 1304 (JBSD!).

**Puerto Rico.** ADJUNTAS: Bo. Guilarte, Guilarte Forest Reserve, along trail, wet mountain forest, elev. c 1100 m, vine, green, ovoidal, 5-ridged fr (10 cm) with milky latex, 21 Nov 1997 (fr), O. Romero and G. Nazario s.n. (UPRRP!). ARECIBO: Rio Abajo State Forest Reserve, 18 20' 06"N, 66 40' 47"W, elev. 340 m, moist forest on limestone substrate, valley with deep soil, twining vine, 1.5 m long, plant producing watery sap, 18 Jan 1996 (st), P. Acevedo-Rodríguez and F. Axelrod 7785 (US!); Rio Abajo State Forest, along Igartua trail, secondary forest along base of limestone hill, twining vine 5-6 m long, producing abundant milky sap, flower buds pendulous, opened flower plagiotropic, calyx green abaxially, burgundy tinged adaxially, corolla greenish abaxially, light burgundy adaxially, corona purple, stigmatic head burgundy, specimen preserved in 70% isopropyl alcohol before drying, 12 Jan 1999 (fl), P. Acevedo-Rodríguez 10596 (UPRRP!, US!); Rio Abajo State Forest, disturbed secondary moist forest at base of limestone hill, twining vine 3-4 m long, producing abundant milky sap, flowers horizontally oriented, calyx green, corolla green in flower bud, burgundy tinged adaxially, specimens preserved in 70% isopropyl alcohol before drying, 2 Feb 1999 (fl), P. Acevedo-Rodríguez 10814 (UPRRP!, US!); Rio Abajo State Forest, along Igartua trail, at edge of trail in rich cove with scattered limestone boulders, ca 3 m up trail from aging sign marking Coccoloba pubescens, juvenile, climbing to 4 m, crushed leaves not aromatic, 20 Apr 2006 (st), A. Krings 1390 (NCSC); Rio Abajo State Forest, rich cove at base of limestone hill, ca 30 ft uphill from small creek in valley, in vicinity of tall bamboo patch, juvenile, climbing to 2 m, 20 Apr 2006 (st), A. Krings 1391 (NCSC); Rio Abajo State Forest, edge of cove in valley, base of limestone hill, trail side, 20 Apr 2006 (st), A. Krings 1392 (NCSC). OROCOVIS: Toro Negro Forest Recreation area, twining vine 3.5 m long, producing abundant milky sap, fruits plagiotropically oriented, green,

specimen preserved in 70% isopropyl alcohol before drying, 11 Sep 2000 (fr), P. Acevedo-Rodríguez 11445 (UPRRP!, US!); Toro Negro State Forest, near uphill end of Sendero Piscina where it joins with Camino del Bolo, 21 Apr 2006 (st), A. Krings 1387 (NCSC); Toro Negro State Forest, Sendero Piscina, trailside, climbing to 1.5 m on melastome, 21 Apr 2006 (st), A. Krings 1388 (NCSC); Toro Negro State Forest, trail beside Quebrada Doña Juana on opposite side of river from Rt 143 entrance to camping area, 21 Apr 2006 (st), A. Krings 1389 (NCSC).

Gonolobus stephanotrichus was recently “re-discovered” from Cuba, from where it had been known only by the type collected sometime between 1860 and 1864 (Krings et al. 2005). Additional illustrations of G. stephanotrichus from Puerto Rico can be found in Acevedo-Rodríguez (2005). Readers should note however, that the gynostegium pictured in Fig. 36 D should be rotated so that the Cd are opposite the corolla lobe sinuses and not opposite the corolla lobes themselves as pictured.

**10. Gonolobus tobagensis** Urban, Repert. Spec. Nov. Regni Veg. 16: 37. 1919.—TYPE:

TOBAGO. The Widow, a climbing plant, 28 Apr 1913 (fl), W.E. Broadway 4467 (lectotype: BM!, designated by Krings, in review). (Fig. 13)

Herbaceous perennial vines. Latex unknown, presumably white. Stems pubescent, both short, capitate-glandular, and longer, sharp, eglandular trichomes present, the latter throughout, spreading, or retrorse internodally, and antrorse-appressed along an indistinct, horizontal ridge between two opposing petioles and/or just above the node, to 1.3 mm long; nodes pubescent,

gland field apparently absent. Leaf blades ovate to oblong-ovate, 3–10.8 cm x 1–5.7 cm, apices gradually or abruptly acuminate with the acumen narrowly obtuse, 0.9–1.9 cm long, bases deeply cordate, margins entire, adaxial surface evenly pubescent, abaxial surface evenly pubescent, trichomes sharp, eglandular, glandular emergences from the surface apparently absent, colleters 2, ca. 0.9 mm long; petioles 1–4.5 cm long, spreading pubescent on all sides, some trichomes capitate, to 0.2 mm long, but mostly sharp, eglandular, to 1.4 mm long; stipular colleters 2, ca. 0.3 mm long, one borne on each side of the petiole base (rarely on the stem). Inflorescences racemiform, peduncles 0.2–4.7 cm long, capitate, as well as sharp, eglandular trichomes present, the latter mostly spreading to somewhat retrorse, distributed throughout, ca. 1.5 mm long; pedicels ca. 3.6 cm long, relatively evenly pubescent from apex to base, capitate-glandular trichomes ca 0.16 mm long, longer, sharp, eglandular trichomes antrorsely-ascending, ca. 1.5 mm long, bracts linear to linear-oblong, 7.6–16 mm x 1.2–2.4 mm, persistent, adaxial surface glabrous, abaxial surface coarsely pubescent, trichomes sharp, eglandular, ca. 0.6 mm long, antrorse. Calyx lobes 5, linear-lanceolate, 8.5–13 mm x 1.7–2.6 mm, apices obtuse to rounded, margins sparsely ciliate or glabrous, abaxial surface densely and coarsely pubescent at the base and variously toward the apex, trichomes antrorsely appressed or -ascending, to 0.8 mm long; colleters 1 per sinus. Corolla lobes 5, narrowly lanceolate to elongate triangular, 13.8–18.4 mm x 4.2–5.3 mm, slightly lobed at the base, a glandular swelling frequently present in the sinus, adaxial surface papillate-pubescent on the right half, abaxial surface pubescent with coarse, sharp, eglandular, antrorsely-appressed or -ascending trichomes, particularly at the base and variously toward the apex, ca. 0.38 mm long; faucal annulus (corolline corona or Ca) interrupted, a raised bump or indistinct ridge opposite each corolla lobe sinus, pubescent; gynostegial corona

of fused staminal (Cs) and interstaminal (Ci) parts, prostrate-undulating, single, secondary nectaries in interstaminal position unknown (could not be determined from specimens); anther guiderails without appendages, laminar dorsal anther appendages (Cd) ca. 2.9 mm wide, truncate; stylar head ca. 4.3 mm diam, stipe ca. 1 mm long, edentate. Pollinaria: corpuscula ca. 0.3 mm long, pollinia borne horizontally, narrowly ovate, ca. 1.3 mm x 0.29 mm. Follicles unknown.

Distribution and habitat. Gonolobus tobagensis is endemic to Tobago and Trinidad (Fig. 1) and known from only four collections (including the type). Its habitat is unclear, but likely mid-elevation rainforests as for other West Indian congeners.

Etymology. The specific epithet means “from Tobago.”

Provisional conservation status. IUCN: Critically endangered (CR)—B1a,biii. NatureServe: GH NH.

Taxon concept mapping. = G. tobagensis sensu Cheesman (1947).

ADDITIONAL SPECIMENS EXAMINED. **Tobago.** Arima (sp?)-Blanchisseuse Rd. 8<sup>th</sup> m., 6 Nov 1938 (fl), Cheesman 13357 (TRIN!); Mount St. George-Castara Rd (sp?), in forest reserve of Main Ridge, climbing over trees, corolla green, gynostegium pale reddish-brown, 18 Oct 1937 (fl), N.Y. Sandwith 1840 (K!). **Trinidad.** Quare River forests, above the reservoir, 1 Apr 1928 (fls in fragment pocket only), W.E. Broadway 6876 (MO).

**11. *Gonolobus waitukubuliensis*** Krings, Syst. Bot. 32: 187. 2007.—TYPE: DOMINICA. In sylvis ad Laudat, Mai 1882 (fl), Eggers 728 (holotype: HBG! – 2 sheets; isotypes: FR!, G!, GH!, JE!, M!, P!, W!, Z!). (Fig. 14)

Herbaceous perennial vines. Latex white. Stems glabrous or glabrate, both short, capitate-glandular, and longer, sharp, eglandular trichomes present, the latter mostly retrorse or spreading internodally, and antrorse-appressed along an indistinct, horizontal ridge between two opposing petioles and/or just above the node, to 0.64 mm long; nodes pubescent or glabrous in age, gland field sometimes present. Leaf blades ovate to oblong-ovate, (2.1–)6.7–10.4 cm x (0.9–)3.2–5.7 cm, apices gradually or abruptly acuminate with the acumen acute, to 1.8 cm long, bases deeply or shallowly cordate (rarely rounded, but then other leaves present with cordate bases), margins entire, adaxial surface glabrate or sparsely strigose, abaxial surface glabrate or more densely strigose with sharp, eglandular trichomes scattered along the major and minor veins, glandular emergences from the surface present (less common in specimens from Martinique), colleters 2, (0.4–)0.7–0.9 mm long; petioles (0.9–)2.2–5.4 cm long, glabrate or sparsely pubescent primarily along the adaxial side and near the apex on the abaxial side, trichomes mostly capitate, to 0.09 mm long, with some short, sharp, eglandular trichomes mixed in, 0.2–0.4 mm long; stipular colleters 2, ca. 0.3 mm long, one borne on each side of the petiole base. Inflorescences racemiform, peduncles 4.1–5.2 cm long, glabrous or very sparsely pubescent with both capitate and sharp, eglandular hairs present, the latter antrorsely-appressed or –ascending, most pronounced near apex, ca. 0.3 mm long; pedicels 1.4–3.4 cm long, pubescence pronounced at apex and essentially absent elsewhere or sparsely to densely, relatively evenly pubescent from

apex to base, capitate-glandular trichomes ca. 0.08 mm long, longer, sharp, eglandular hairs antrorsely- appressed or -ascending, ca. 0.3 mm long, bracts linear-lanceolate, ca. 0.8 mm x 0.2 mm, caduous, adaxial surface glabrous, abaxial surface coarsely pubescent, trichomes sharp, eglandular, ca. 0.17 mm long, antrorse. Calyx lobes 5, sublanceolate to elongate triangular (widest at or just above the base), 2.2–5.3 mm x 0.8–1.4 mm, apices obtuse to narrowly rounded, margins glabrous, abaxial surface glabrous or pubescent primarily at the base and variously toward the apex, trichomes, if present, antrorsely-ascending or -appressed, to 0.27 mm long; colleters 1 per sinus. Corolla lobes 5, narrowly lanceolate to elongate triangular, 4.2–11.2 mm x 1.8–3.4(–3.7) mm, slightly lobed at the base, a glandular swelling frequently present in the sinus, adaxial surface glabrous, abaxial surface glabrous; faucal annulus (corolline corona or Ca) a distinctly raised ring, ca. 0.5 mm high, short-hispid along the entire rim or only opposite each corolla lobe sinus; gynostegial corona of fused staminal (Cs) and interstaminal (Ci) parts, single, fused at the base into an erect ring, 5-lobed, lobes appearing strongly folded; anther guiderails apparently without appendages, laminar dorsal anther appendages (Cd) 0.6–0.9 mm wide, emarginate or truncate; stylar head 2.8–3.14 mm diam, stipe 1–1.5 mm long, not toothed. Pollinaria: corpuscula 0.14–2 mm long, pollinia borne horizontally, ovate, ca. 0.6–0.85 mm x 0.3–0.38 mm. Follicles unknown.

Distribution and habitat. Gonolobus waitukubuliensis is apparently endemic to Dominica (Fig. 1). It has been found primarily in middle elevation rainforests (ca. 609–1067 m; 2000–3500 ft). On a recent expedition, it was not found in the high elevation Clusia dominated communities around Boeri Lake or Freshwater Lake and only rarely in a Clusia transitional community on Morne Diablotins. It was not found along the trail to Middleham Falls, Titou

Gorge, or Emerald Pool. The seasonal deciduous, lower elevation forests on Dominica's lee appear too dry. Like most West Indian Gonolobus taxa, G. waitukubuliensis appears to require small gaps in mature forests. It does not appear to be able to compete in large gaps or roadside edges in which other vines quickly become dominant. It is rather infrequent to rare, especially in mature forests with few gaps.

Etymology. The epithet is derived from Waitukubuli (why-too-KOO-boo-lee), a Carib name for Dominica.

Provisional conservation status. IUCN: Vulnerable (VU)—B1a,c. NatureServe: G3 N3.

Taxon concept mapping. < G. martinicensis sensu Schlechter (1899); < G. martinicensis sensu Howard (1988); < G. martinicensis sensu Nicolson (1991).

ADDITIONAL SPECIMENS EXAMINED. **Dominica.** Mar 1882 (fl), Eggers s.n. (US!); July 1882 (fl), Eggers 1100 (K!); May 1882 (fl), Eggers 1700 (MO!); Imray 263 (K!-fl); St. John/St. Peter, Hiking trail to Morne Diablotins, ca. 2000–2500 ft elev., forest rather open and marked by large diameter trees, 3 May 2006 (st), Krings 1375, 1376, 1377 (NCSC!); St. John/St. Peter, Syndicate hiking trail, trailside at edge of small gap in mature forest of large diam Sloanea spp., climbing to 1.5 m, 3 May 2006 (st), Krings 1378 (NCSC!); St. John/St. Peter, Hiking trail to Morne Diablotins, ca. 2000–2500 ft elev., in small gap, climbing on Miconia sp., to 2 m, about 10 seedlings observed in gap, rainforest of 60–80 ft tall trees, 4 May 2006 (st), Krings 1380 (NCSC!); St. John/St. Peter, Hiking trail to Morne Diablotins, ca. 2000–2500 ft elev., in small gap (same as Krings 1380), climbing to 20 ft, twining around 10 cm dbh liana, rainforest of 60–80 ft tall trees, 4 May 2006 (st), Krings 1381 (NCSC!); St. John/St. Peter, Hiking trail to Morne

Diablotins, small gap in small stature forest, below the Clusia dominated zone, but with an occasional Clusia present, 4 May 2006 (st), Krings 1382, 1383, 1384 (NCSC!); St. John/St. Peter, Hiking trail to Morne Diablotins, Clusia dominated, low stature forest, at opening in trail with westward vista of Portsmouth and Cabrits, 4 May 2006 (st), Krings 1385 (NCSC!); St. John/St. Peter, Hiking trail to Morne Diablotins, right side of trail (when facing uphill), just below Clusia dominated zone, canopy ca. 20 ft tall, vine climbing into canopy, 4 May 2006 (st), Krings 1386 (NCSC!); St. Joseph, En Haut Jean, alt. 2750 ft., 24 Jun 1965 (fl), G.L. Webster 13505 (BM!, US!).

Gonolobus waitukubuliensis is immediately recognizable among Lesser Antillean Gonolobus species by the combination of a distinctly raised, completely circular faucal annulus (ca. 0.5 mm tall), an erect gynostegial corona that appears quite folded apically, and a relatively tall gynostegial stipe (1–1.5 mm). It shares with G. absalonensis, G. iyanolensis, and sometimes G. martinicensis, the absence of hairs from the abaxial corolla lobe surface. The trichomes of the pedicel are fine and not as long (ca. 0.3 mm) as in G. iyanolensis (0.3–0.9 mm).

**12. Gonolobus youroumaynensis** Krings, Syst. Bot. 32: 191. 2007.—TYPE: ST. VINCENT.

Orange Hill Estate, roadbank in banana and pigeon pea plantations, uphill from fork in road to the C.W.S.A. water intake site, Kiss-me, 14 Mar 2006 (fl), Krings 1374 with Springer (holotype: NCSC!; isotypes: GH!, K!, NY!, US!, P!). (Fig. 15)

Herbaceous perennial vines. Latex white. Stems glabrate to pubescent, both short, capitate-glandular, and longer, sharp, eglandular trichomes present, the latter throughout, spreading, or retrorse internodally, and antrorse-appressed along an indistinct, horizontal ridge between two opposing petioles and/or just above the node, to 1.2 mm long; nodes pubescent, gland field apparently absent. Leaf blades ovate to oblong-ovate, (3.0–)5.4–9.6 cm x (1.2–)2.4–6.3 cm, apices gradually or abruptly acuminate with the acumen narrowly obtuse, to 1.5 cm long, bases deeply or shallowly cordate, margins entire, adaxial surface glabrate or sparsely strigose, abaxial surface glabrate or more densely strigose with sharp, eglandular trichomes scattered along the major and minor veins, glandular emergences from the surface present, colleters 2–4, 0.35–1 mm long; petioles (1.2–)2.7–5.3 cm long, spreading pubescent on all sides, some trichomes capitate, to 0.09 mm long, but mostly sharp, eglandular, 1–1.2 mm long; stipular colleters 2, ca. 0.26 mm long, one borne on each side of the petiole base. Inflorescences racemiform, peduncles 0.7–3.1 cm long, capitate, as well as sharp, eglandular trichomes present, the latter mostly spreading, but also some antrorsely-appressed or -ascending, distributed throughout, 0.7–0.9 mm long; pedicels 1.3–1.8 cm long, relatively evenly pubescent from apex to base, capitate-glandular trichomes ca. 0.08 mm long, longer, sharp, eglandular trichomes mostly spreading, but some antrorsely-appressed or -ascending, ca. 0.9 mm long, bracts linear-lanceolate, 1.1–1.7 mm x 0.2–0.25 mm, caduous, adaxial surface glabrous, abaxial surface coarsely pubescent, trichomes sharp, eglandular, ca. 0.53 mm long, antrorse. Calyx lobes 5, sublanceolate to elongate triangular (widest at or just above the base), 3.8–5.8 mm x 1–1.3 mm, apices obtuse to narrowly rounded, margins ciliate or glabrate, abaxial surface densely and coarsely pubescent at the base and variously toward the apex, trichomes spreading and antrorsely appressed or -ascending, to 0.8

mm long; colleters 1 per sinus. Corolla lobes 5, narrowly lanceolate to elongate triangular, (7.5–)8.7–10.1 mm x 1.9–3.1 mm, slightly lobed at the base, a glandular swelling frequently present in the sinus, adaxial surface pubescent on the right half, trichomes capitate, ca. 0.1 mm long, abaxial surface pubescent with coarse, sharp, eglandular, antrorsely-appressed or -ascending trichomes, particularly at the base and variously toward the apex, 0.36–0.5 mm long; faucal annulus (corolline corona or Ca) interrupted, a raised bump or indistinct ridge opposite each corolla lobe sinus, pubescent or glabrous; gynostegial corona of fused staminal (Cs) and interstaminal (Ci) parts, prostrate-undulating, single, a small bump borne near the base in the interstaminal position; anther guiderails without appendages, laminar dorsal anther appendages (Cd) ca. 0.5 mm wide, rounded or truncate; stylar head 2.8–3.95 mm diam, stipe 0.48–0.7 mm long, bearing a single tooth ca. 0.2 mm long below each anther. Pollinaria: corpuscula 0.2–0.23 mm long, pollinia borne horizontally, ovate, 0.6–0.9 mm x 0.32–0.45 mm. Follicles unknown.

Distribution and habitat. Gonolobus youroumaynensis is apparently endemic to St. Vincent (Fig. 3). It occurs on the windward side of the island at the foot of La Soufriere in the Orange Hill Estate area. Vines were found growing along the road to the water intake amidst banana and pigeon pea plantations. Vines were not found along the trail to the crater of La Soufriere.

However, only a half day was spent searching this trail and they could have been overlooked.

Etymology. The epithet is derived from Youroumayn (YOO-roo-MAYN), a Kalina name for St. Vincent (Divonne 1998; Winer, pers. comm.).

Provisional conservation status. IUCN: Critically Endangered (CR)—B1a,biii. NatureServe: G1 N1.

Taxon concept mapping. < G. martinicensis sensu Schlechter (1899); < G. martinicensis sensu Howard (1988).

ADDITIONAL SPECIMENS EXAMINED. **St. Vincent.** Mar 1890 (fl), H.H. and G.W. Smith 382 (BM!, E!, GH!, K!, NY!); Orange Hill Estate, 10 Feb 1980 (fl), R.A. Howard 19584 (BM!, GH!, NY!, US!).

Gonolobus youroumaynensis is immediately recognizable among Lesser Antillean Gonolobus species by the combination of a single, prostrate-undulating gynostegial corona exhibiting a small bump towards the base of the Ci, a toothed stipe, and long, spreading trichomes (to 0.9 mm) found on stems, peduncles, and pedicels.

#### DOUBTFUL AND EXCLUDED NAMES

The following list includes names that are excluded from Gonolobus s.s. based on their morphology (e.g., lack of laminar dorsal anther appendages), as well as those of uncertain status.

Two new combinations are made below: Matelea dictyopetala and M. pubescens.

Gonolobus bakeri Schltr., Symb. antill. 7(3): 341. 1912.—TYPE: CUBA. Cult. in Santiago de las Vegas, Majo 1907, C.F. Baker n. 7286 (holotype: location unknown).

Gonolobus bakeri is apparently only known from the type collection, which has not been located despite query of nearly one hundred institutions known to house West Indian collections.

It may have been destroyed in WW II. The position of G. bakeri appears uncertain. Schlechter does not describe dorsal anther appendages in the protologue. Combined with his note that the species is “mit G. variifolius Schltr. [now Matelea variifolia (Schltr.) Woodson] am nächsten verwandt,” there is reason to believe that G. bakeri may better belong in Matelea. Matelea variifolia clearly lacks laminar dorsal anther appendages and also exhibits suborbicular corolla lobes. It is known only from Puerto Rico (Schlechter 1899; Acevedo-Rodríguez 2003, 2005). As the single specimen representing G. bakeri was cultivated in Cuba, it may be that the species is merely a pubescent form of M. variifolia. Among West Indian Gonolobus s.s. (if not the entire genus), G. bakeri would be the only species with suborbicular corolla lobes.

Gonolobus bayatensis Urb., Symb. antill. 9(3): 420. 1925.—TYPE: CUBA. Arth. Engström in herb. Ekman n. 3056 (lectotype, designated by Krings, in review: S!; isolectotype: NY!) = Matelea bayatensis (Urb.) Woodson, Ann. Missouri Bot. Gard. 28: 226. 1941.

Gonolobus bicolor (Britton & P. Wilson) Urb., Symb. antill. 9(3): 421. 1925.—TYPE: CUBA. Léon 10787 (holotype: NY!) = Matelea bicolor (Britton & P. Wilson) Woodson, Ann. Missouri Bot. Gard. 28: 236. 1941.

Gonolobus denticulatus (Vahl) W.D. Stevens, Phytologia 64: 334. 1988.—TYPE: von Rohr120 (holotype: C [IDC microfiche photo: Vahl herbarium nr. 17: III, 1!]) = Matelea denticulata (Vahl) Fontella & E.A. Schwarz, Bol. Mus. Bot. Munic. 46: 4. 1981.

Gonolobus dictyopetalus Urb. & Ekman, Arkiv för Botanik utgivet av K. Svenska

Vetenskapsakademien 20A(5): 41. 1926.—TYPE: HAITI. Ekman H 1625 (lectotype, designated by Krings, in review: S!; isolectotype: IJ! – fragment [single leaf]) = Matelea dictyopetala (Urb. & Ekman) Krings, comb. nov.

Gonolobus domingensis Alain, Moscosoa 3: 46. 1978.—TYPE: DOMINICAN REPUBLIC. Alain & Perfa Liogier 23780 (lectotype, designated by Krings 2005d: JBSD!) = Matelea domingensis (Alain) Krings, Sida 21: 2081. 2005.

Gonolobus floccosus Bertol., Opusc. Sci. 4: 225. 1823.—TYPE: GUADELOUPE (holotype: BOLO!) = Matelea maritima (Jacq.) Woodson, Ann. Missouri Bot. Gard. 28: 222. 1941.

Gonolobus grenadensis Schltr., Symb. antill. 7(3): 339. 1912.—TYPE: GRENADA. St. Mark Parish, Wooded hillsides near Victoria, elev. 100–300 ft., 24 Nov 1957, G.R. Proctor 17225 (neotype, designated by Krings, in review: IJ!) = Matelea denticulata (Vahl) Fontella & E.A. Schwarz, Bol. Mus. Bot. Munic. 46: 4. 1981.

Based on Schlechter's (1912) description, Gonolobus grenadensis Schltr. is a synonym of Matelea denticulata (Vahl) Fontella & E.A. Schwarz. Schlechter (1912) considered it a close relative to G. ciliatus Schltr. (also a synonym of M. denticulata), from which he distinguished it only by larger leaves and flowers. Howard (1989b) also treated G. grenadensis as a synonym of M. denticulata, although confusing it with G. martinicensis in key and description (though not in illustration).

Gonolobus grisebachianus Schltr., Symb. antill. 1(2): 287. 1899.—TYPE: CUBA. Wright s.n.

(holotype: location unknown) = Matelea grisebachiana (Schltr.) Alain, Mem. Soc. Cub. Hist. Nat. “Felipe Poey” 22: 120. 1955.

Matelea grisebachiana is apparently known only from the type collection, which has not been located despite query of nearly one hundred institutions known to house West Indian collections. It may have been destroyed in WW II. Thus, the species can be placed solely based on the protologue and past treatments. Although Krings et al. (2005) maintained the taxon in Gonolobus, the combination in Matelea may be more correct based on the glabrous, reticulate corolla lobes and very narrow, linear-lanceolate leaves (0.5-0.7 cm wide)—a leaf form quite atypical for Gonolobus. The description of the corolla lobes as being 9 cm long, is likely a print-setting error to be corrected to 9 mm. Grisebach (1866) did not mention laminar dorsal anther appendages in his protologue for G. tigrinus var. angustifolia and, upon reconsideration, it is unclear to me whether Schlechter (1899) was referring to them or not [italics mine]: “Diese Art ist trotz ihrer habituellen Aehnlichkeit mit G. tigrinus Griseb. von diesem vollständig verschieden. Die Blätter sind schmaler, die Blüten grösser, die äussere Corona ganz verschieden und die Schuppen der inneren Corona viel deutlicher vom Antherenrücken abgehoben, ausserdem, von oben gesehen, in der Mitte nicht ausgerandet, sondern eher verdickt.” I am hesitant to presume the taxon extinct, as another Cuban Gonolobinae species—G. stephanotrichus—was recently rediscovered in the country after having been known from the island only from the type, collected between 1860 and 1864 (Krings et al. 2005).

Gonolobus haitiensis P.T. Li, J. South China Agric. Univ. 14(1): 58. 1993.—TYPE: HAITI. E.L.

Ekman 4693 (holotype: S!; isotypes: B!, US!). = Matelea crispiflora (Urb.) Jiménez, Rhodora 62: 238. 1960, syn. nov.

Gonolobus haitiensis P.T. Li is a nomen novum for Gonolobus stipitatus Alain (Phytologia 64: 345. 1988). It is here reduced to synonymy beneath Matelea crispiflora, as its type (Ekman H 4693) clearly belongs with Poicillopsis crispiflora Urb. However, see also note for Gonolobus membranaceus Schltr.

Gonolobus maritimus (Jacq.) R.Br., Mem. Wern. Nat. Hist. Soc. 1: 24. 1810.—TYPE: Herbar. Du

Jacquín, 2 Insulae Caribaea. De Ponthieu (lectotype, designated by Krings & Saville, in review: BM!) = Matelea maritima (Jacq.) Woodson, Ann. Missouri Bot. Gard. 28: 222. 1941.

Gonolobus membranaceus Schltr., Symb. antill. 1(2): 285. 1899.—TYPE: HAITI. Poiteau s.n.

(holotype: location unknown) = Matelea crispiflora (Urb.) Jiménez, Rhodora 62: 238. 1960.

The location of the type remains unknown. Ekman H4693 (IJ!) is labelled Gonolobus membranaceus. The specimen consists of mostly stem and 3–4 leaf fragments held in a fragment pocket. It appears to match Poicillopsis crispiflora Urb. Gonolobus membranaceus is likely very closely related to Matelea haitiensis as, based on the protologues, the two appear to differ only in the shape and apices of the leaf blades and calyx lobes. Additional collections and discovery of the type may prove them synonymous.

Gonolobus nipensis Urb., Symb. antill. 9(3): 421. 1925.—TYPE: CUBA. Ekman 9710 (lectotype, designated by Krings, in review: S!; isolectotype: NY!). = Matelea nipensis (Urb.) Woodson, Ann. Missouri Bot. Gard. 28: 226. 1941.

Gonolobus ottonis C. Koch & Bouche, Ind. Sem. Hort. Berol. 13. 1855.—TYPE: unknown.

Sometimes cited as Gonolobus ottonis Walp. (Ann. Bot. Syst. 5: 502. 1859.). However, Walpers (1859) clearly cited G. ottonis C. Koch & Bouche and should not be considered author of a homonym if the Koch and Bouche name is indeed legitimate. Walpers (1859) also cited: ‘Ex insula Cuba reportavit Otto.’ However, no copy of the Koch and Bouche’s protologue of G. ottonis could be obtained. Schlechter (1899) thought that the specimen collected by Otto (apparently formerly at B) was from Caracas, Venezuela, not from Cuba. The location of the type is unknown.

Gonolobus oxyanthus Turcz., Bull. Soc. Imp. Naturalistes Moscou 25(2): 318. 1852.—TYPE:

VENEZUELA. 1845–1852, Funk 2 (G, n. v.; P, n. v.) fide TROPICOS.

Fide Fontella and Schwarz (1981), a synonym of Gonolobus rostratus (Vahl) R. Br. ex Schult. (Systema Vegetabilium 6: 61. 1820). TROPICOS (23 Aug 2006) cited Funk 2 (Venezuela) as the type, but a copy of the protologue could not be located. Specimens were not found on either of two visits to P.

Gonolobus pauciflorus Spreng., Syst. veg. 1: 846. 1824.—TYPE: HISPANIOLA. ‘St. Domingue,’

Bertero s.n. (holotype: G-DC [IDC microfiche Candolle Prodromus Herbarium, fiche #

1543!]; isotype: P!). = Matelea pauciflora (Spreng.) Woodson, Ann. Missouri Bot. Gard. 28: 226. 1941.

Gonolobus pubescens Griseb., Fl. Brit. W. I. 420. 1862.—TYPE: JAMAICA. Macfadyen s.n.  
(holotype: GOET!; isotype: K!) = Matelea pubescens (Griseb.) Krings, comb. nov.

Gonolobus rhamnifolius Griseb., Fl. Brit. W. I. 420. 1862.—TYPE: JAMAICA, R.C. Alexander s.n.  
(holotype: GOET!) = Matelea rhamnifolia (Griseb.) Krings, Sida 21: 1515. 2005.

Gonolobus sintensisii Schltr., Symb. antill. 1(2): 288. 1899.—TYPE: PUERTO RICO. Sierra de Luquillo, Jimenes mts., Sintensis 1354 (lectotype, designated by Krings, in review: HBG!; isolectotypes: BM!, G!, GH!, K!, US!). = Matelea sintensisii (Schltr.) Woodson, Ann. Missouri Bot. Gard. 28: 226. 1941.

Gonolobus stipitatus Alain, Phytologia 64(5): 345. 1988, nom. illeg.; non Gonolobus stipitatus Morillo, 1987.—TYPE: HAITI. Massif du Nord, St. Louis du Nord, Morne Baron, 20 Aug 1925, Ekman H 4693 (holotype: S!; isotypes: B!, US!) = Matelea crispiflora (Urb.) Jiménez, Rhodora 62: 238. 1960.

See discussion under Gonolobus haitiensis.

Gonolobus tigrinus Griseb., Mem. Amer. Acad. Arts 8: 520. 1863.—TYPE: CUBA. Holguín, 19 Mar, Wright 1667 (holotype: GOET, n. v.; syntypes: MO [image online!], G!, GH!, K!). = Matelea tigrina (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28: 226. 1941.

Gonolobus tigrinus Griseb. var. angustifolius Griseb., Cat. pl. Cub. 177. 1866.—TYPE: CUBA. Wright s.n. (holotype: location unknown) = Matelea grisebachiana (Schltr.) Alain, Mem. Soc. Cub. Hist. Nat. “Felipe Poey” 22: 120. 1955.  
See G. grisebachianus

Gonolobus variifolius Schltr., Symb. antill. 1(2): 286. 1899.—TYPE: PUERTO RICO. P. Sintenis 1653 (lectotype, designated by Krings, in review: NY!; isolectotypes: G!, GH!, MO!, P!, US!) = Matelea variifolia (Schltr.) Woodson, Ann. Missouri Bot. Gard. 28: 226. 1941.

Gonolobus virescens Desv. ex Ham., Prodr. pl. Ind. occid. 32. 1825.—TYPE: “JAMAICA.”  
Desvaux s.n. (holotype: P!).

Rendle (1936) considered G. virescens Desv. a species inceria. Schlechter (1899) noted that there was likely a label mix-up between G. stapelioides and G. virescens, and that the latter was likely collected from Tobago and not Jamaica. The morphology of the flowers of Desvaux s.n. (P!) places it in Marsdenieae Benth., rather than Gonolobinae.

Gonolobus viridiflorus (G.F.W. Meyer) Schult. in Roem. & Schult., Syst. veg. 6: 61. 1820.; nom. illeg., non G. viridiflorus Nutt. (1818).—TYPE: Meyer (holotype: location unknown) = Matelea denticulata (Vahl) Fontella & E.A. Schwarz, Bol. Mus. Bot. Munic. 46: 4. 1981.

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## NUMERICAL LIST OF SPECIES

1. *G. absalonensis*
2. *G. dussii*
3. *G. iyanolensis*
4. *G. jamaicensis*
5. *G. martinicensis*
6. *G. rostratus*
7. *G. stapelioides*
8. *G. stellatus*
9. *G. stephanotrichus*
10. *G. tobagensis*
11. *G. waitukubuliensis*
12. *G. youroumaynensis*

## INDEX TO NUMBERED COLLECTIONS EXAMINED

The numbers in parentheses refer to the corresponding names in the text and in the Numerical List of Species presented above.

Acevedo-Rodríguez 7785 (9); 10596 (9); 10814 (9); 11445 (9).	Herb. Liebmann s.n.(6). Higson s.n. (7).
Adams 12705 (7).	Howard 19584 (12).
Bellingham 1156 (7); 1211 (7); 1487 (7).	Hunnewell 11032 (8).
Britton 1601 (6).	Imray 263 (11).
Broadway 4467 (10).	Jiménez 1304 (9).
Cheesman 13168 (6); 13357 (10).	Johnny 57 (3).
Duss "1862, 4565" (2); 3714 (2); 3775 (2); 4565 (2).	Kelly 1490 (8); 10207 (4). Krings s.n. (9); 1373 (3); 1374 (12); 1375 (11); 1376 (11); 1377 (11); 1378 (11); 1380 (11); 1381 (11); 1382 (11); 1383 (11); 1384 (11); 1385 (11); 1386 (11); 1387 (9); 1388 (9); 1389 (9); 1390 (9); 1391 (9); 1392 (9); 1393 (4); 1394 (7); 1395(7); 1396 (7).
Eggers s.n. (11); 728 (11); 1100 (11); 1700 (11).	
Ekman H12568 (9).	
Fendler 637 (6).	
Graveson 107 (3); 1248 (3).	
Harris 5561 (7); 6368 (4).	
Hart 968 (4).	L.C. Rich. Herb. Guyanensi-Antillanum (5).
Herb. d'Alleizette s.n. [4801?] (1).	Lieber s.n. (5).
Herb. Ludg. Bat. s.n. (6).	Liogier 25627(9).

López 2419 (6).

Moreau s.n. (6).

Pleé s.n. (5).

Prestoe s.n. (6).

Proctor 6803 (7); 6828 (4); 29378 (8);

38534 (7).

Purdie s.n. (8).

Quentin 732 (2).

Romero (9).

Sandwith 1840 (10).

Slane 1056 (3).

Smith 382 (12).

(von Rohr?) Herb. Liebmann (6).

Webster 13505 (11).

Wright 164 (9); 407 (9); 2969 (9).

## LIST OF SCIENTIFIC NAMES

Accepted names are in Roman type. Synonyms are underlined.

Apidae	Cynanchinae
Apis mellifera Linnaeus	Cynanchum L.
Apocinae	laeve (Michx.) Pers.
Apocynaceae	<u>rostratum</u> Vahl
Araujia Brot.	Danaus gilippus Cramer
Asclepiadeae	plexippus (Linnaeus)
Asclepiadoideae	Dioscorea L.
Asclepias L.	Diptera
curassavica L.	Erinnyis obscura obscura (Fabricius)
exaltata L.	Estigmene acrea (Drury)
quadrifolia Jacq.	Fimbristemma Turcz.
solanoana Woodson	Fischeria DC.
syriaca L.	<u>cincta</u> Griseb.
tuberosa L.	Funastrum E. Fourn.
Calliphoridae	clausum (Jacq.) Schltr.
Calotropis R.Br.	pannosum (Decne.) Schltr.
Carica papaya L.	Gonolobinae
Chloropidae	Gonolobus Michx.

absalonensis Krings  
 albomarginatus (Pittier) Woodson  
argentinensis T. Mey.  
bakeri Schltr.  
 barbatus Kunth.  
bayatensis Urb.  
bicolor (Britton & P. Wilson) Urb.  
broadwayae Schltr.  
caribaeus Rich., nom. sched.  
 chloranthus Schldl.  
ciliatus Schltr.  
cinctus (Griseb.) Benth. & Hook. f.  
denticulatus (Vahl) W.D. Stevens  
dictyopetalus Urb. & Ekman  
domingensis Alain  
 dussii Krings  
 erianthus DC.  
floccosus Bertol.  
 fraternus Schldl.  
gonocarpos (Walter) L.M. Perry  
grenadensis Schltr.  
grisebachianus Schltr.  
haitiensis P.T. Li  
 incerianus W.D. Stevens & Montiel  
 iyanolensis Krings  
 jamaicensis Rendle  
laevis Michx.  
 lasiostemma (Hemsl.) Woodson  
macrophyllus Michx.  
maritimus (Jacq.) R.Br.  
 martinicensis Decne.  
membranaceus Schltr.  
nipensis Urb.  
ottonis C. Koch & Bouche  
ottonis Walp.  
oxyanthus Turcz.  
pauciflorus Spreng.  
pubescens Griseb.  
rhamnifolius Griseb.  
 rostratus (Vahl) Schultes  
rostratus sensu Schlechter, non (Vahl)  
 R.Br.  
 salvinii Hemsl.  
 saraguranus Morillo

<u>scandens</u> (Aubl.) Urb.	Ipomoea L.
<u>sintenisii</u> Schltr.	Jacaima Rendle
<u>sorodius</u> , nom. nud.	Lepidoptera
stapelioides Desv. ex Ham.	Macroscepis Kunth
stellatus Griseb.	Marsdenieae Benth.
stenanthus (Standley) Woodson	Matelea Aubl.
stephanotrichus Griseb.	acuminata (Griseb.) Woodson
<u>stipitatus</u> Alain, non Morillo	argentinensis (T. Mey.) Pontir.
<u>stipitatus</u> Morillo	bayatensis (Urb.) Woodson
suberosus (L.) R.Br.	bicolor (Britton & P. Wilson)
<u>tigrinus</u> Griseb.	Woodson
<u>tigrinus</u> Griseb. var. <u>angustifolius</u>	correllii Spellman
Griseb.	corynephora Krings
tobagensis Urb.	costata (Urb.) Morillo
<u>variifolius</u> Schltr.	crispiflora (Urb.) Jiménez
<u>virescens</u> Desv. ex Ham.	denticulata (Vahl) Fontella & E.A.
<u>viridiflorus</u> (G.F.W. Meyer) Schult.	Schwarz
waitukubuliensis Krings	dictyantha Woodson
youroumaynensis Krings	dictyopetala (Urb. & Ekman) Krings
yucatanensis (Woodson) W.D.	domingensis (Alain) Krings
Stevens	grisebachiana (Schltr.) Alain
<u>Ibatia</u> Decne.	lanata (Zucc.) Woodson

linearipetala Alain	torulosa Krings
maritima (Jacq.) Woodson	variifolia (Schltr.) Woodson
nipensis (Urb.) Woodson	viridiflora (G.F.W. Meyer) Woodson
oblongata (Griseb.) Woodson	Metalepis Griseb.
ovatifolia (Griseb.) Woodson	Metastelmatinae
pauciflora (Spreng.) Woodson	Morrenia Lindl.
pentactina Krings	Oxypetalinae
phainops Krings	Periplocoideae
pubescens (Griseb.) Krings	Philibertia Kunth
pubiflora (Decne.) Woodson	<u>Poicilla</u> Griseb.
pusilliflora L.O. Williams	<u>Poicillopsis</u> Schltr.
reticulata (Engelm. ex A. Gray)	<u>crispiflora</u> Urb.
Woodson	<u>Ptycanthera</u> Decne.
rhamnifolia (Griseb.) Krings	Secamonoideae
rhynchocephala Krings	Tachinidae
rubra (H. Karst.) Spellman & Morillo	Toxotrypana curvicauda Gerstaecker
sintenisii (Schltr.) Woodson	<u>Trichostelma</u> Baill.
tamnifolia (Griseb.) Woodson	Vespidae
tigrina (Griseb.) Woodson	<u>Vincetoxicum gonocarpos</u> Walter

TABLE 1. Per flower rates of pollen removal and pollinium deposition within Asclepiadoideae.

<i>Species</i>	<i>Per flower rate of pollen removal</i>	<i>Per flower rate of pollinium deposition</i>	<i>Source</i>
<i>Gonolobus suberosus</i> (L.) R.Br.	0.31	0.043	Lipow & Wyatt (1998)
<i>Asclepias exaltata</i> L.	0.23–1.38	0.39–0.66	Queller (1985); Wyatt & Shannon* (1986); Broyles & Wyatt (1990, 1995)
<i>Matelea reticulata</i> (Engelm. ex A. Gray) Woodson	0.54–0.94	--	Liede (1994); Krings (1999)
<i>Asclepias curassavica</i> L.	0.62–1.7	0.13	Wyatt* (1980); Willson & Melampy (1983); Wolfe (1987)
<i>Asclepias syriaca</i> L.	0.62–1.7	--	Willson & Rathcke (1974)
<i>Asclepias quadrifolia</i> Jacq.	0.81–2.41	--	Chaplin & Walker (1982)
<i>Asclepias tuberosa</i> L.	1.64	0.71	Wyatt (1978)
<i>Funastrum pannosum</i> (Decne.) Schltr.	2.43–2.48	0.57–1.52	Kunze & Liede (1991)
<i>Funastrum clausum</i> (Jacq.) Schltr.	2.64	2.16	Kunze & Liede (1991)

TABLE 1 (continued).

<i>Species</i>	<i>Per flower rate of pollen removal</i>	<i>Per flower rate of pollinium deposition</i>	<i>Source</i>
<i>Asclepias solanoana</i> Woodson	2.91–4.3	1.23–1.81	Lynch (1977)

TABLE 2. Seed weight and size in West Indian *Gonolobus* species for which mature fruits have been seen by the author. Arranged from lightest to heaviest seed. Seeds obtained from a single follicle for each species.

<i>Species</i>	<i>Average seed weight</i> [N=number of seeds sampled]	<i>Length</i> <sup>1</sup>	<i>Width</i> <sup>1</sup>
<b><i>G. stephanotrichus</i></b> (Acevedo-Rodríguez 11445, UPRRP)	0.0035 g [N=10]	(7.1) 7.4 (7.8) [N=10; s.d.=0.2066]	(3.4) 4.23 (4.7) [N=10; s.d.=0.4083]
<b><i>G. stapelioides</i></b> (Bellingham 1487, BM)	0.0044 g [N=81]	(4.6) 5.0 (5.6) [N=10; s.d.=0.2914]	(2.5) 2.93 (3.5) [N=10; s.d.=0.2627]
<b><i>G. iyanolensis</i></b> (Graveson s.n., NCSC)	0.0116 g [N=26]	(8.8) 9.92 (10.5) [N=10; s.d.=0.4848]	(4.9) 5.38 (5.9) [N=10; s.d.=0.3084]

<sup>1</sup>Format for length and width measurements = (Min) Avg (Max) [number of seeds sampled; standard deviation]

TABLE 3. Number of collections and localities, distribution, and provisional conservation status of West Indian *Gonolobus* species. Arranged by number of localities represented, then number of collections. NatureServe conservation ranks follow IUCN ranks. IUCN conservation ranks are global, except for *G. rostratus* for which only a national status is provided, given the unresolved taxonomic questions regarding mainland populations. Critically endangered taxa are unknown from protected areas.

<u>Species</u>	<u>No. of localities</u>	<u>No. of collections</u>	<u>Distribution</u>	<u>Provisional conservation status</u>
<u><i>G. absalonensis</i></u>	1	1	Martinique	Critically endangered (CR); GH NH
<u><i>G. martinicensis</i></u>	1–3	3	Martinique	Critically endangered (CR); GH NH
<u><i>G. youroumaynensis</i></u>	1–2	3	St. Vincent	Critically endangered (CR); G1 N1
<u><i>G. tobagensis</i></u>	4	4	Trinidad and Tobago	Critically endangered (CR); GH NH (both islands)
<u><i>G. dussii</i></u>	5	5	Guadeloupe and Martinique	Critically endangered (CR); GH NH (both islands)

TABLE 3 (continued). <u>Species</u>	<u>No. of localities</u>	<u>No. of collections</u>	<u>Distribution</u>	<u>Provisional conservation status</u>
<u>G. rostratus</u>	5–9	9	Trinidad (and S. America?)	Critically endangered (CR); G3G4? N1 in Trinidad
<u>G. iyanolensis</u>	2	5	St. Lucia	Endangered (EN); G1 N1
<u>G. stellatus</u>	4	4	Jamaica	Vulnerable (VU); G3 N3
<u>G. jamaicensis</u>	4	5	Jamaica	Vulnerable (VU); G3 N3
<u>G. waitukubuliensis</u>	4–8	17	Dominica	Vulnerable (VU); G3 N3
<u>G. stapelioides</u>	5–7	13	Jamaica	Least concern (LC); G4 N4
<u>G. stephanotrichus</u>	7–10	19	Greater Antilles	Least concern (LC); G4 N4 (all islands of occurrence)

**GH:** Possibly Extinct (species)—Missing; known from only historical occurrences but still some hope of rediscovery. **G1:** Critically Imperiled—At very high risk of extinction due to extreme rarity (often 5 or fewer populations), very steep declines, or other factors. **G3:** Vulnerable—At moderate risk of extinction due to a restricted range, relatively few populations (often 80 or fewer), recent and widespread declines, or other factors. **G4:** Apparently Secure—Uncommon but not rare; some cause for long-term concern due to declines or other factors. **NH:** Possibly Extirpated (Historical)—Species or community occurred historically in the nation or state/province, and there is some possibility that it may be rediscovered. Its presence may not have been verified in the past 20-40 years. **N1:** Critically Imperiled—Critically imperiled in the nation or state/province because of extreme rarity (often 5 or fewer occurrences) or because of

some factor(s) such as very steep declines making it especially vulnerable to extirpation from the state/province. **N3: Vulnerable**—Vulnerable in the nation or state/province due to a restricted range, relatively few populations (often 80 or fewer), recent and widespread declines, or other factors making it vulnerable to extirpation. **N4: Apparently Secure**—Uncommon but not rare; some cause for long-term concern due to declines or other factors.

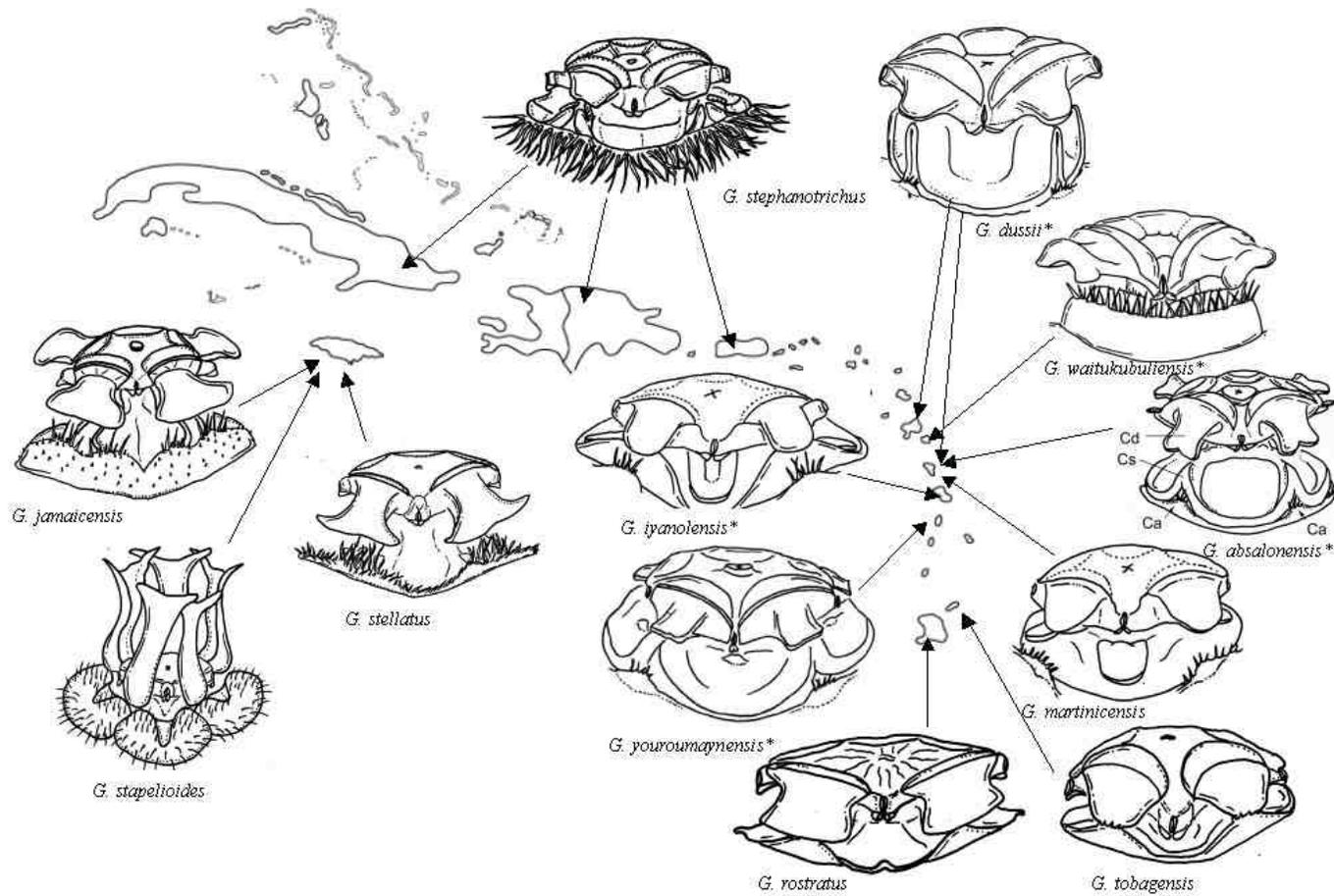


FIG. 1. Distribution of and gynostegial variation in *Gonolobus* in the West Indies. Asterisks indicate recently described species (Krings 2007). *Gonolobus* remains unknown from the Bahamas and the Leeward Antillean islands of Aruba, Bonaire, and Curaçao.

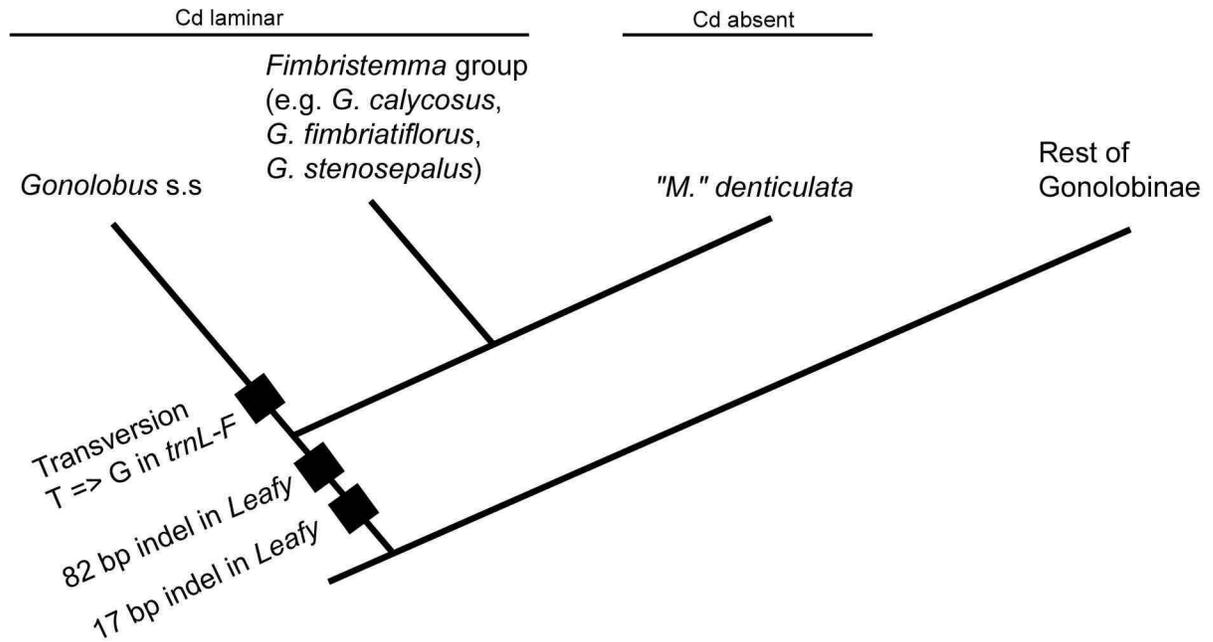


FIG. 2. Model of evolution of *Gonolobus* s.l. based on current evidence, with molecular synapomorphies mapped on branches (from Krings et al, in review). Cd = dorsal anther appendages. G. = Gonolobus; M. = Matelea.

FIG. 3. Morphological characteristics and variation in *Gonolobus*. A. Twining growth form (*G. dussii*). B. Trichome variation from multicellular, sharp, eglandular (left three) to glandular capitate to papillate (rightmost) (*G. youroumaynensis*, except papillae from corolla of *G. rostratus*). C. Variation in leaf shape (cordate: *G. jamaicensis*; cuneate: *G. stellatus*). D. Laminar colleters (*G. youroumaynensis*). E. Stipular colleters (*G. youroumaynensis*). F. Inflorescence (*G. tobagensis*). G. Dextrorse flower bud (*G. tobagensis*). H. Five-parted calyx (*G. stephanotrichus*). I. Calycine colleter (*G. stephanotrichus*). J. Variation in corollas (left: *G. stephanotrichus*; right: *G. stapelioides*). Ki–iii. Variation in faucal annuli, as well as gynostegial coronas (i: *G. stapelioides*; ii: *G. dussii*; iii: *G. jamaicensis*). L. Ligulate staminal segment of gynostegial corona (*G. martinicensis*). M. Variation in laminar dorsal anther appendages (left: *G. rostratus*; right: *G. stellatus*; see also Ki–ii, L). N. Pollinarium (*G. stephanotrichus*). O. Winged follicle (*G. stephanotrichus*). P. Seeds distally dentate (*G. iyanolensis*) and entire (*G. stephanotrichus*).

Ca = faucal annulus of corolla; Cau = caudicle; Ci = interstaminal gynostegial corona segment; Cd = laminar dorsal anther appendage; Co = corpusculum; Cr = crest; Cs = staminal gynostegial corona segment; Po = pollinium.

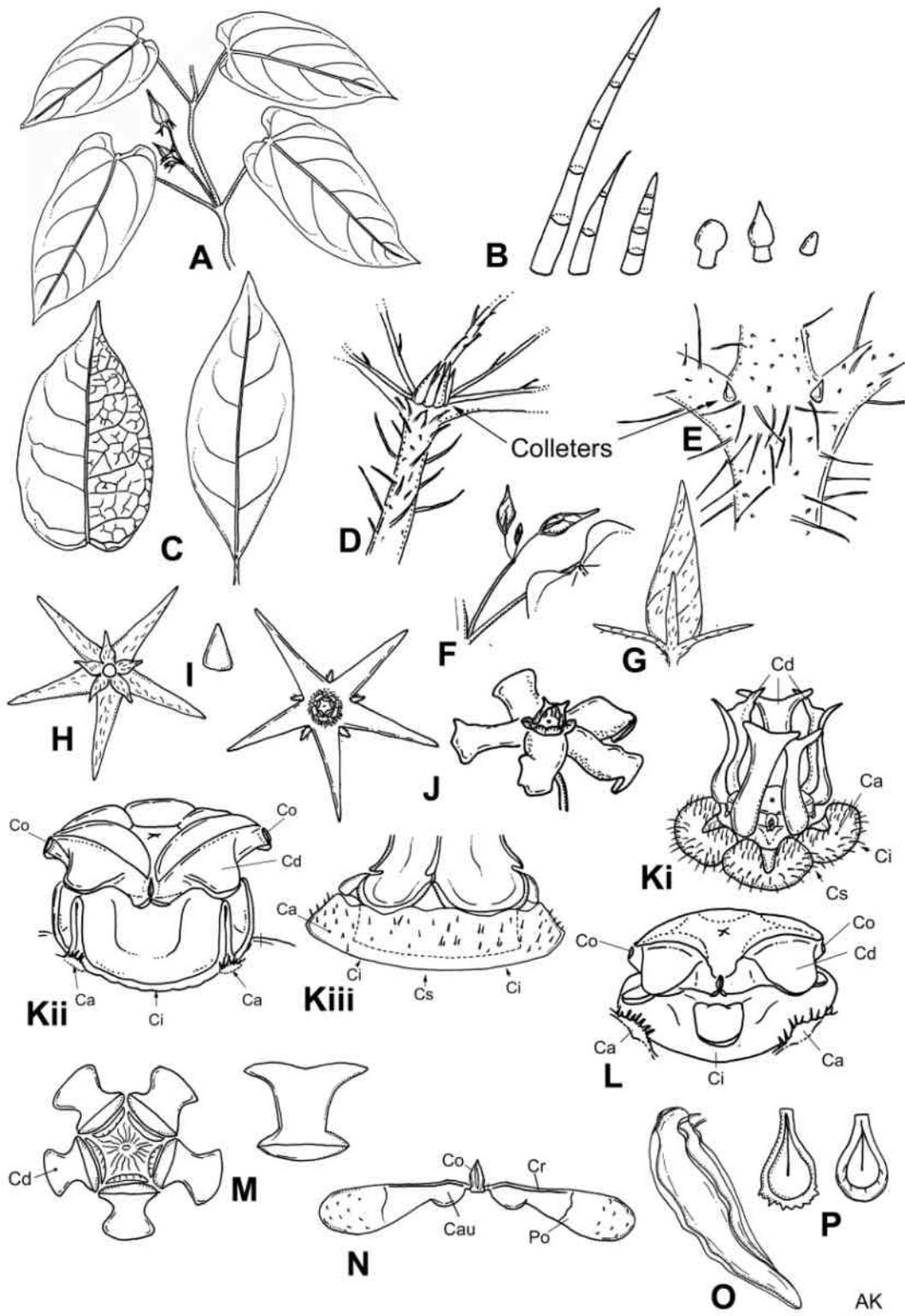


FIG. 4. *Gonolobus absalonensis*. A. Leaves and inflorescence. B. Open flower. C. Faucal annulus of the corolla (Ca), gynostegial corona, and stylar head. D. Gynostegial corona of fused staminal (Cs) and interstaminal (Ci) segments (stylar head removed). E. Laminar dorsal anther appendage (Cd). F. Pollinarium. Based on Herb. d'Alleizette *s.n.* [4801?] (L).  
Ca = faucal annulus of corolla; Ci = interstaminal gynostegial corona segment; Cd = laminar dorsal anther appendage; Co = Corpusculum; Cs = staminal gynostegial corona segment.

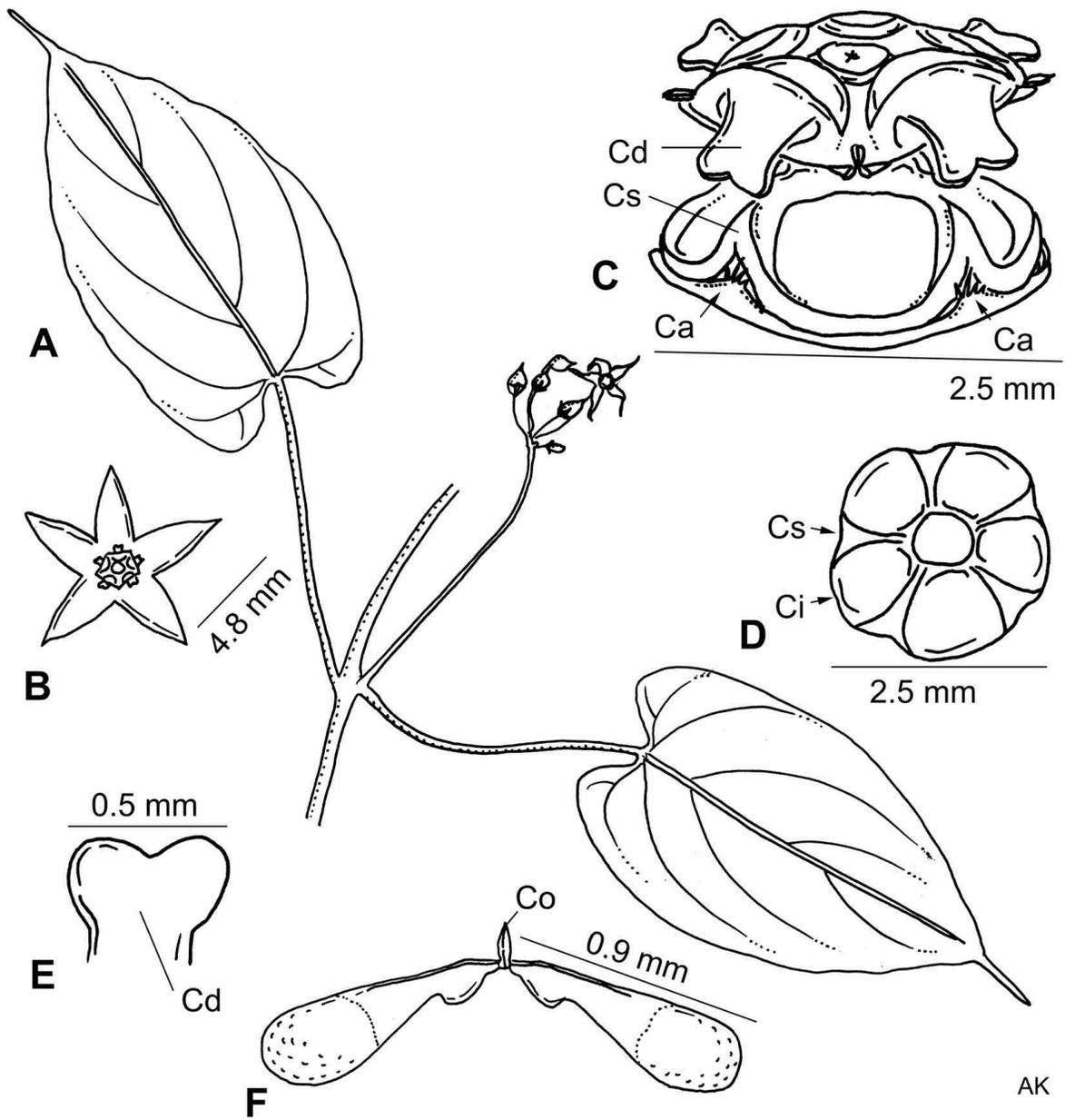
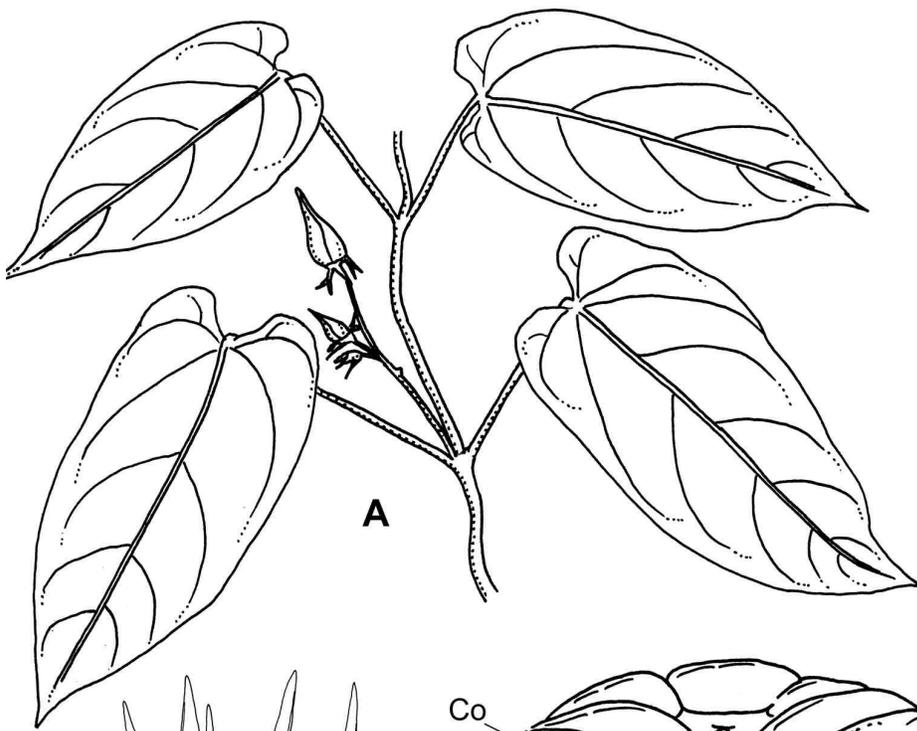
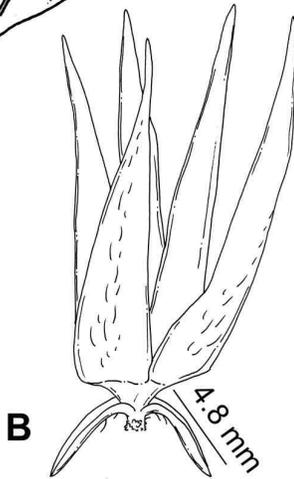


FIG. 5. *Gonolobus dussii*. A. Leaves and inflorescence. B. Flower showing coarse abaxial pubescence of the corolla lobes. C. Faucal annulus of the corolla (Ca), gynostegial corona, and stylar head. D. Gynostegial corona of fused staminal (Cs) and interstaminal (Ci) segments (stylar head removed). E. Laminar dorsal anther appendage (Cd). F. Pollinarium. A–B based on *Duss 3775* (NY). C and E–F based on *Duss 4565* (NY). D based on *Quentin 732* (P). Ca = faucal annulus of corolla; Ci = interstaminal gynostegial corona segment; Cd = laminar dorsal anther appendage; Co = corpusculum; Cs = staminal gynostegial corona segment.

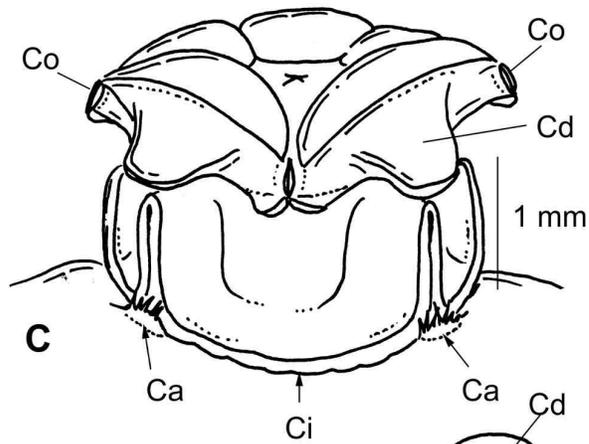


**A**



**B**

4.8 mm



**C**

Co

Co

Cd

1 mm

Ca

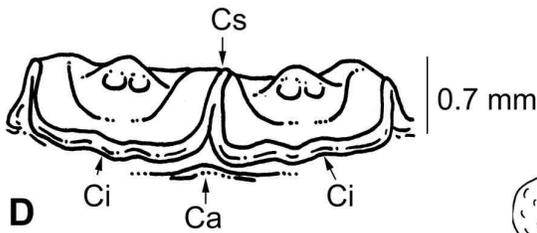
Ci

Ca

Cd

**E**

0.8 mm



**D**

Cs

0.7 mm

Ci

Ca

Ci

**F**

Co

1 mm

AK

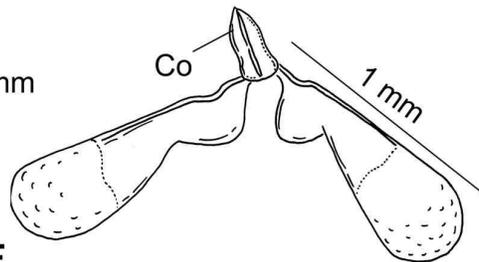


FIG. 6. *Gonolobus iyanolensis*. A. Leaves and inflorescence. B. Open flower. C. Flower showing adaxial pubescence of the corolla lobes. D. Faucal annulus of the corolla (Ca), gynostegial corona, and stylar head. E. Gynostegial corona of fused staminal (Cs) and interstaminal (Ci) segments (stylar head removed), showing dorsal ridge of upper ligulate corona lobe of the Ci. F. Top view of gynostegial corona (stylar head removed). G. Cross-section of corolla tube showing position of corollar and gynostegial corona elements. H. Pollinarium. I. Follicle. J. Seed. A–B based on *Johnny 57 et al.* (UPRRP). C and E based on *Graveson 107* (GH). D and F–H based on *Krings 1373 et al.* (NCSC). I–J based on *Graveson s.n.* (NCSC). Ca = faucal annulus of corolla; Ci = interstaminal gynostegial corona segment; Cd = laminar dorsal anther appendage; Co = corpusculum; Cs = staminal gynostegial corona segment.

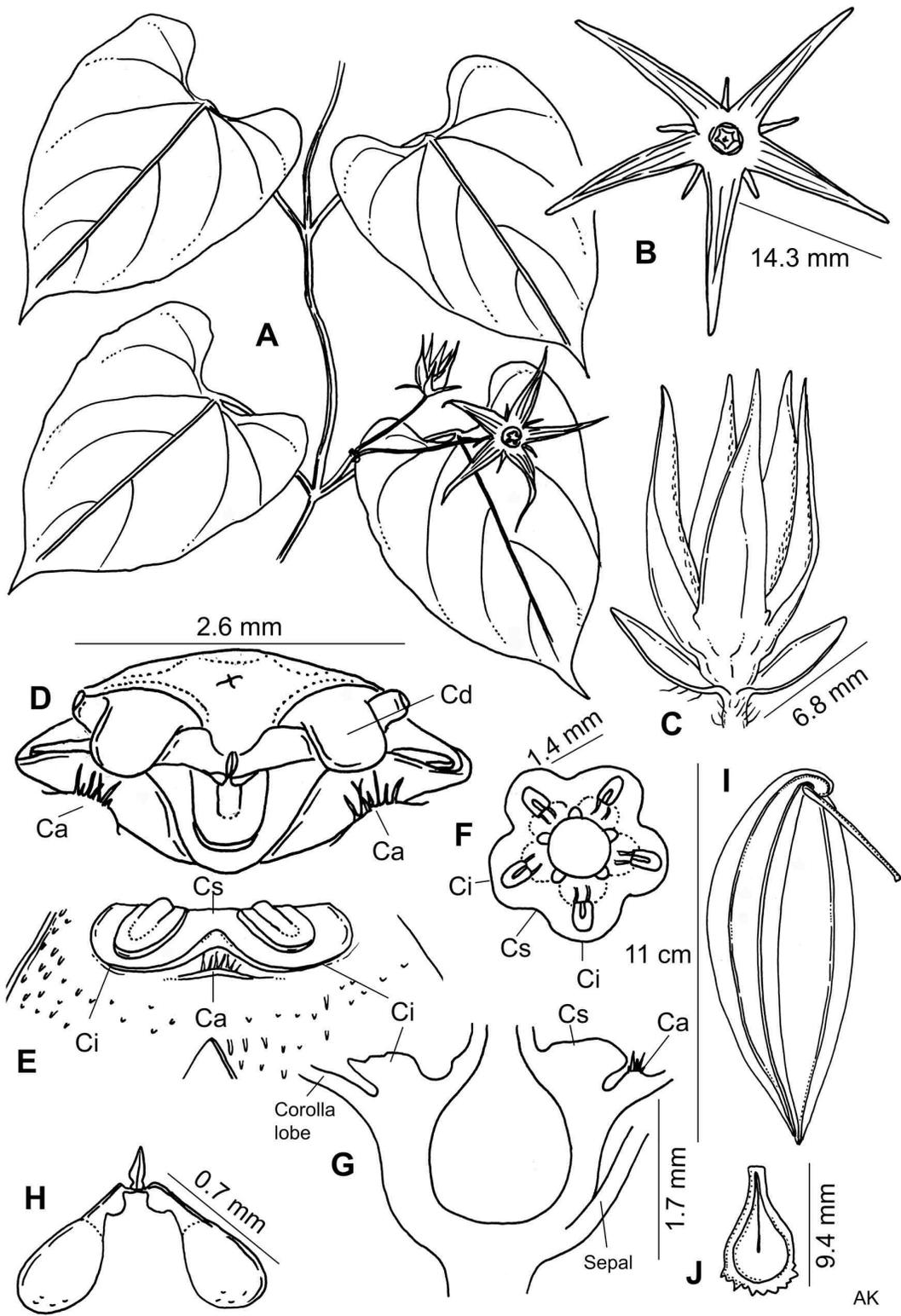
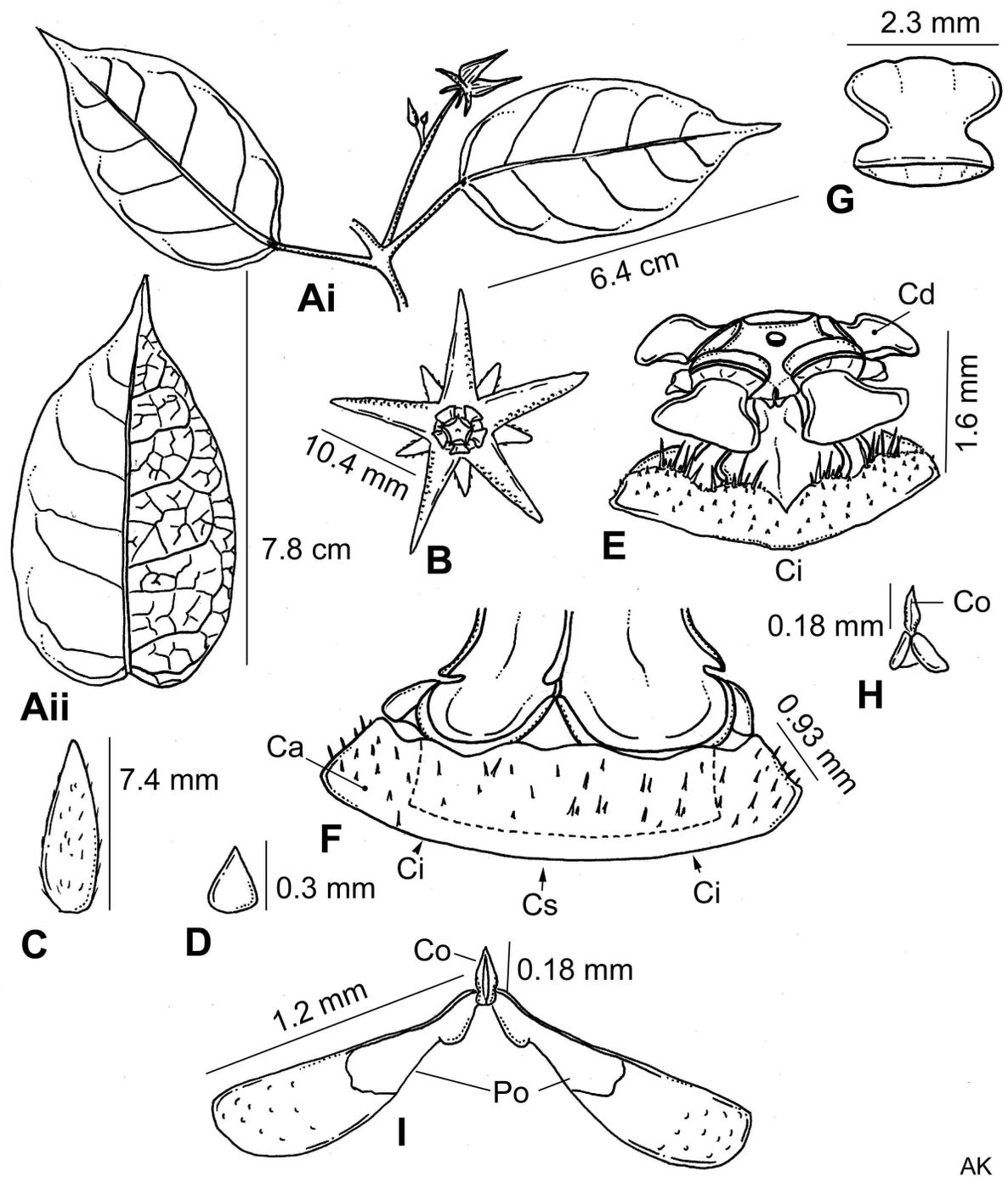
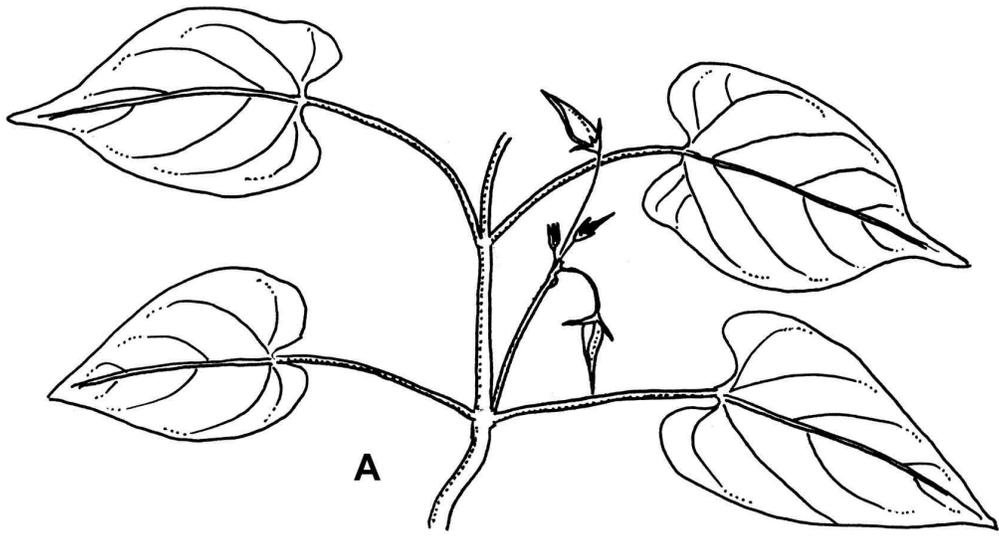


FIG. 7. *Gonolobus jamaicensis*. Ai–ii. Leaves and inflorescence. B. Open flower. C. Sepal. D. Calycine colleter. E. Faucal annulus of the corolla, gynostegial corona, and stylar head. F. Detail of faucal annulus and base of gystegial stipe. G. Laminar dorsal anther appendage. H. Corpusculum and subtending anther wings. I. Pollinarium. Ai–I based on *Kelly et al. 10207* (TCD). Aii based on *Proctor 6828* (GH). Ca = faucal annulus of corolla; Ci = interstaminal gynostegial corona segment; Cd = laminar dorsal anther appendage; Co = corpusculum; Cs = staminal gynostegial corona segment; Po = pollinium.

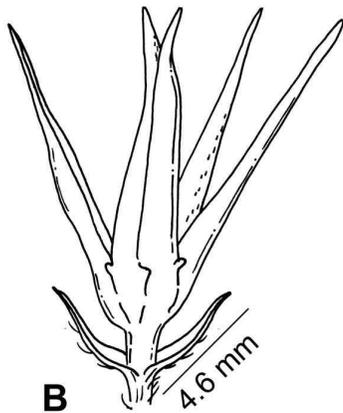


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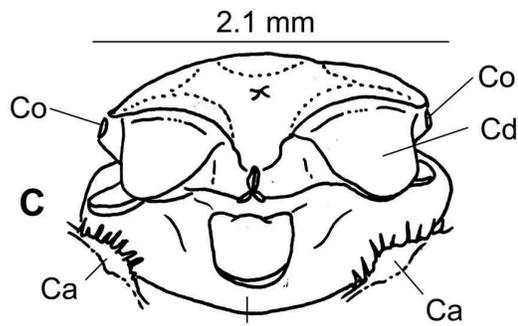
FIG. 8. *Gonolobus martinicensis*. A. Leaves and inflorescence. B. Flower showing narrow corolla tube. C. Faucal annulus (Ca), gynostegial corona, and stylar head. D. Top view of gynostegial corona (stylar head removed). E. Gynostegial corona of fused staminal (Cs) and interstaminal (Ci) segments (stylar head removed), showing upper ligulate corona lobe of the Ci. F. Laminar dorsal anther appendage (Cd). G. Pollinarium. A based on Herb. Mart. Suppl. Nr. 63 (MO). B and E–F based on *Lieber s.n.* (M). C–D and G based on L.C. Rich. Herb. Guyanensi-Antillanum (P). Ca = faucal annulus of corolla; Ci = interstaminal gynostegial corona segment; Cd = laminar dorsal anther appendage; Co = corpusculum; Cs = staminal gynostegial corona segment.



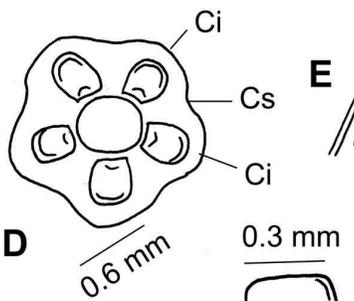
**A**



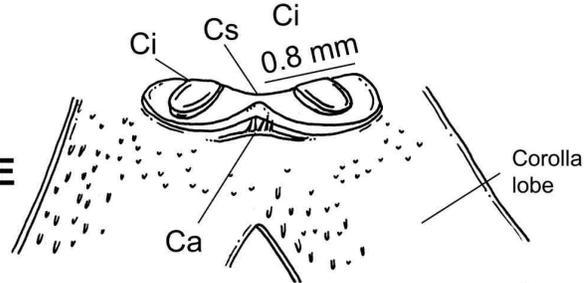
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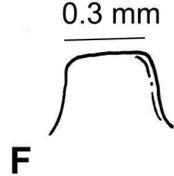
**C**



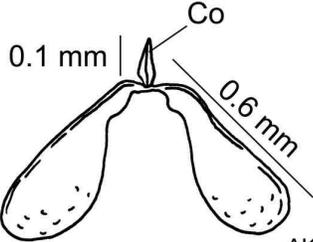
**D**



**E**



**F**



**G**

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FIG. 9. *Gonolobus rostratus*. A. Leaves and inflorescence. Bi. Open flower (adaxial view). Bii. Open flower (abaxial view). C. Calycine colleter. D. Faucal annulus of the corolla, gynostegial corona, and stylar head. E. Detail of faucal annulus. F. Gynostegial corona of fused staminal (Cs) and interstaminal (Ci) segments (stylar head removed). G. Side view of gynostegial corona. H. Stylar head and laminar dorsal anther appendages (viewed from above). I. Laminar dorsal anther appendage. J. Corpusculum and subtending anther wings. K. Pollinarium. A, C–K based on *Britton & Hazen 1601* (GH). Bi–ii based on *Fendler 637* (E). Ca = faucal annulus of corolla; Ci = interstaminal gynostegial corona segment; Cd = laminar dorsal anther appendage; Co = corpusculum; Cs = staminal gynostegial corona segment; Po = pollinium.

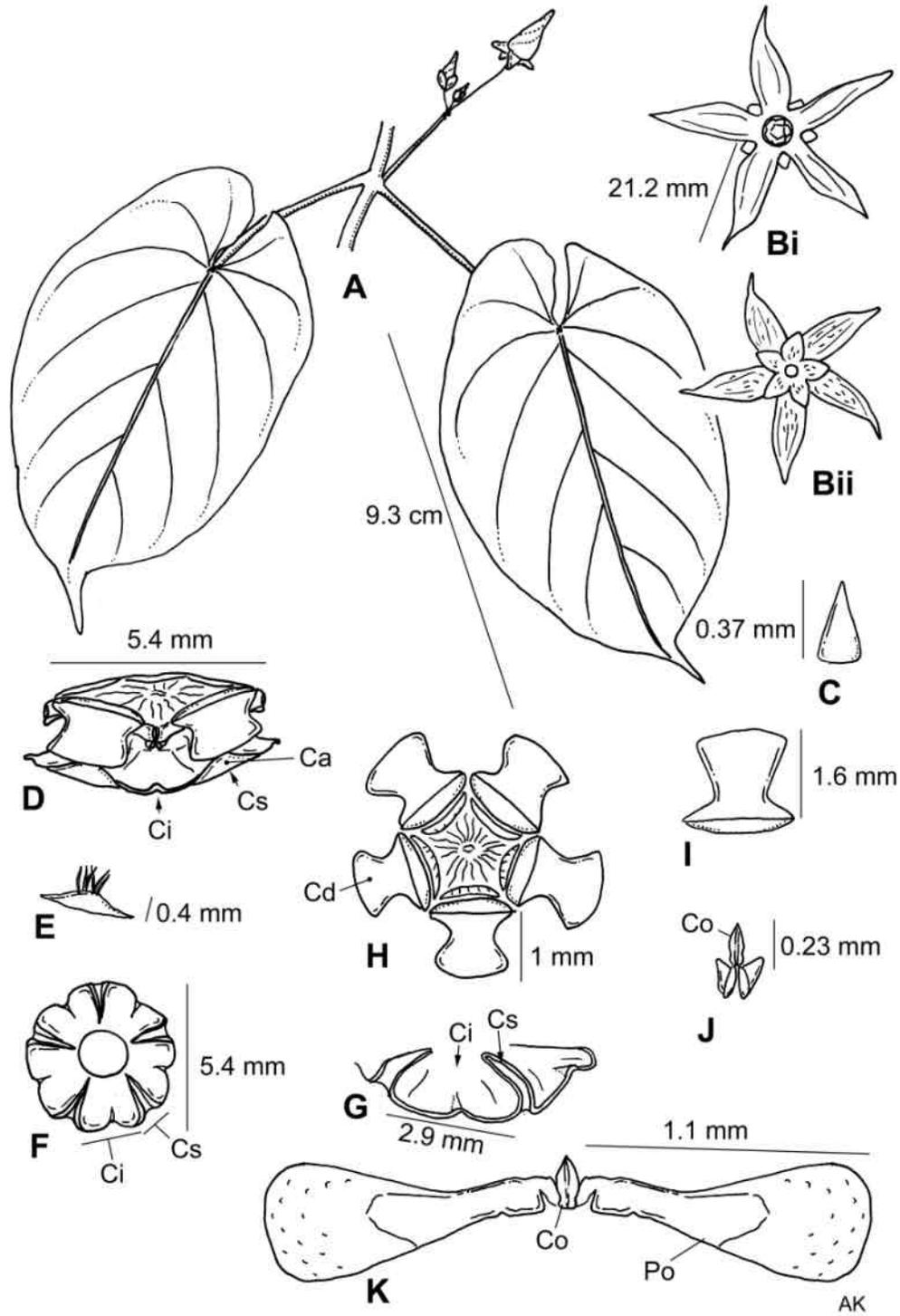


FIG. 10. *Gonolobus stapelioides*. A. Leaves and inflorescence. Bi. Open flower (adaxial view). Bii. Open flower (abaxial view). C. Sepal. D. Calycine colleter. E. Faucal annulus of the corolla, gynostegial corona, and stylar head. F. Cross-section of flower. G. Detail of gynostegial corona of fused staminal (Cs) and interstaminal (Ci) segments and stipe (stylar head removed). H. Stylar head and laminar dorsal anther appendages (viewed from above). I. Pollinarium. J. Follicle. K. Seed. J–K based on *Bellingham 1487* (BM), rest based on *Krings 1394* (NCSC). Aw = anther wings; Ca = faucal annulus of corolla; Ci = interstaminal gynostegial corona segment; Cd = laminar dorsal anther appendage; Co = corpusculum; Cs = staminal gynostegial corona segment; Po = pollinium; Sh = stylar head.

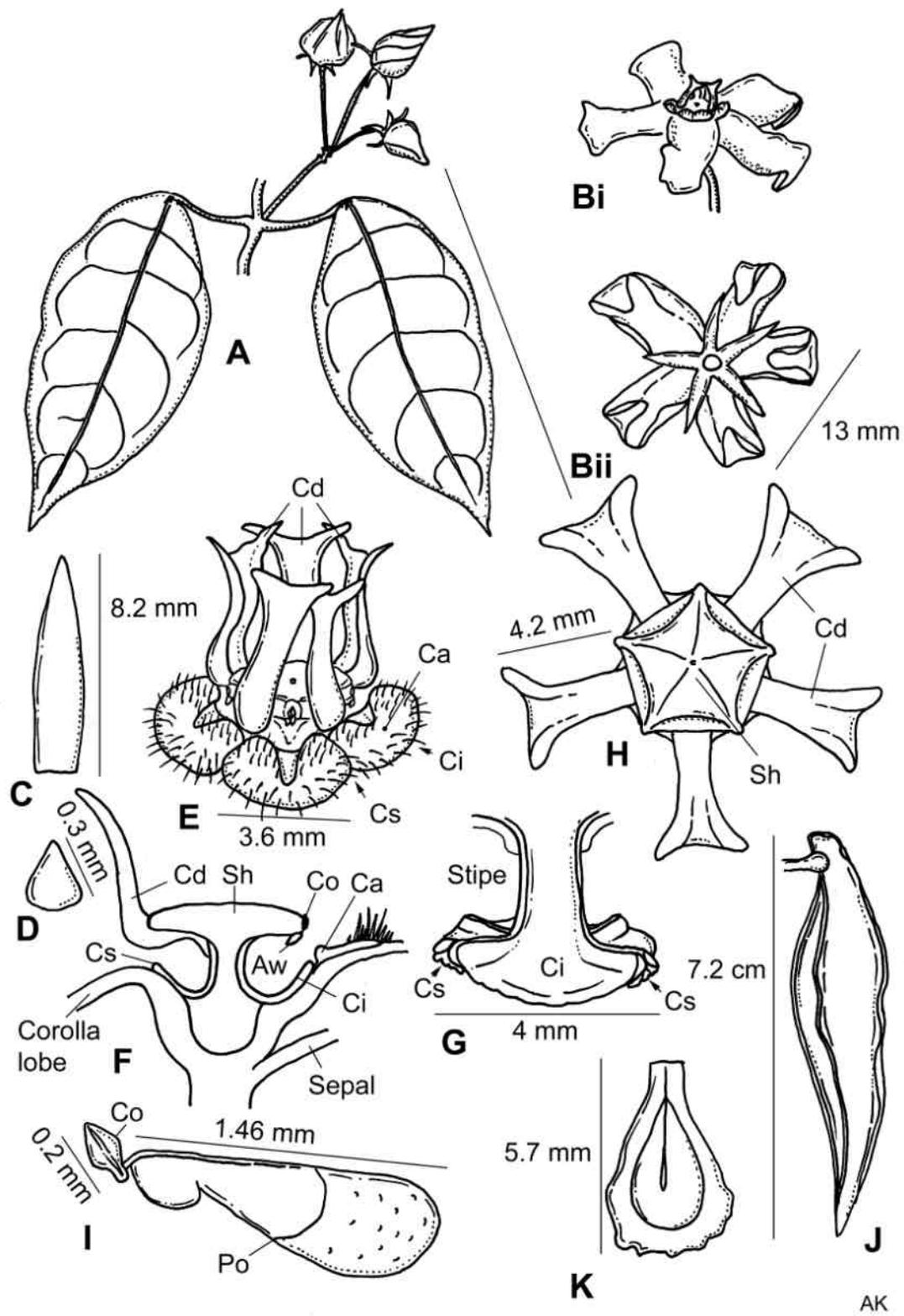
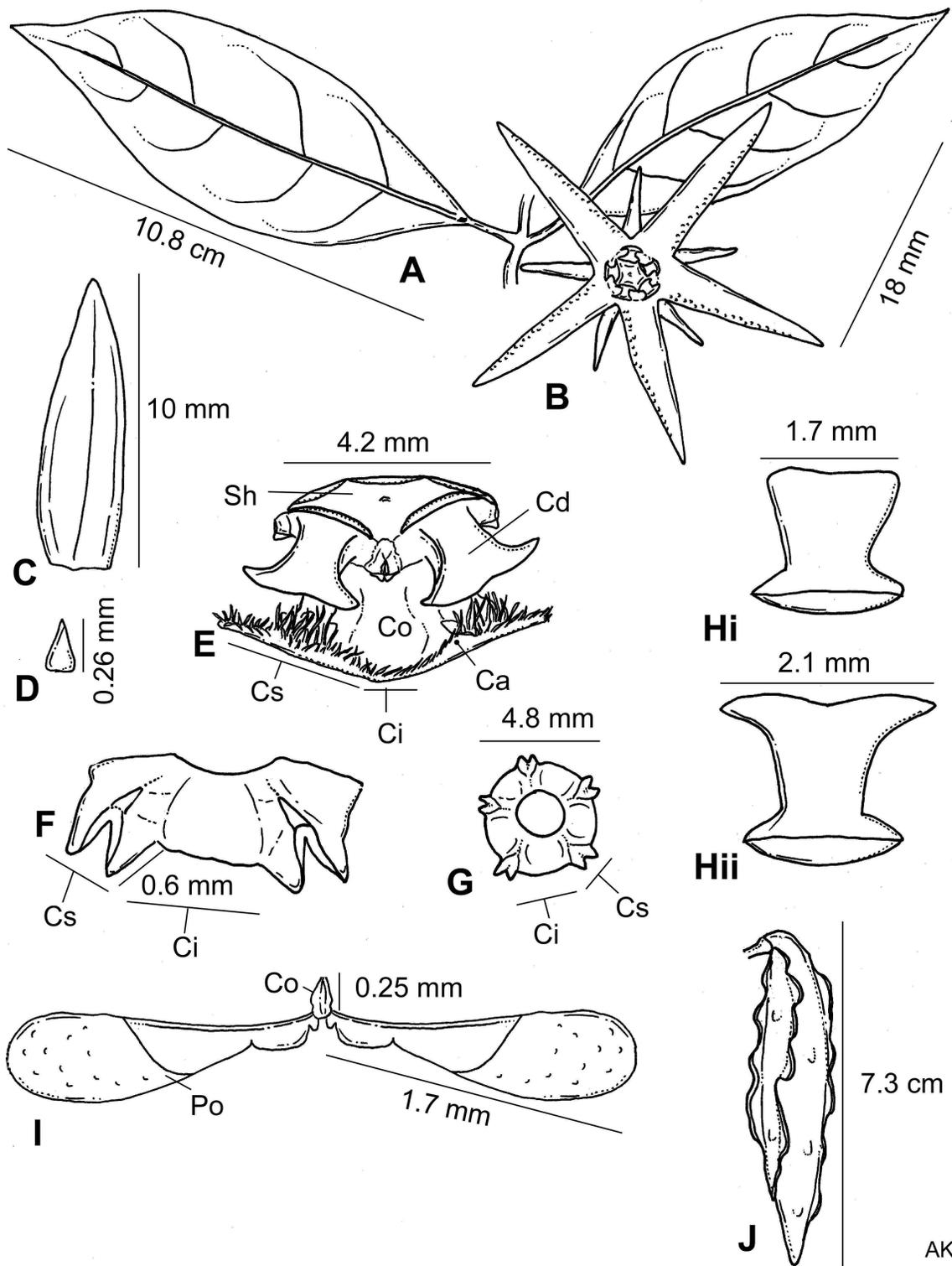


FIG. 11. *Gonolobus stellatus*. A. Leaves. B. Open flower. C. Sepal. D. Calycine colleter. E. Faucal annulus of the corolla, gynostegial corona, and stylar head. F. Detail of gynostegial corona of fused staminal (Cs) and interstaminal (Ci) segments (side view). G. Detail of gynostegial corona (top view). Hi–ii. Variation in laminar dorsal anther appendages. I. Pollinarium. J. Follicle. A, C–D, and J based on *Proctor 29378* (BM). B and Hi–ii based on *Purdie s.n.* (K). E–G and I based on *Hunnewell 11032* (GH). Aw = anther wings; Ca = faucal annulus of corolla; Ci = interstaminal gynostegial corona segment; Cd = laminar dorsal anther appendage; Co = corpusculum; Cs = staminal gynostegial corona segment; Po = pollinium; Sh = stylar head.



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FIG. 12. *Gonolobus stephanotrichus*. A. Leaves and inflorescence. Bi. Open flower (adaxial view). Bii. Open flower (abaxial view). C. Sepal. D. Calycine colleter. E. Faucal annulus of the corolla, gynostegial corona, and stylar head. F. Detail of gynostegial corona of fused staminal (Cs) and interstaminal (Ci) segments (top view). G. Detail of gynostegial stipe and basal appendages. H. Pollinarium. I. Follicle. J. Seed. A–D based on *Wright 2969* (NY). E–H based on *Acevedo-Rodríguez 10596* (US). I–J based on *Acevedo-Rodríguez 11445* (US). Aw = anther wings; Ca = faucal annulus of corolla; Ci = interstaminal gynostegial corona segment; Cd = laminar dorsal anther appendage; Co = corpusculum; Cs = staminal gynostegial corona segment; Po = pollinium; Sh = stylar head.

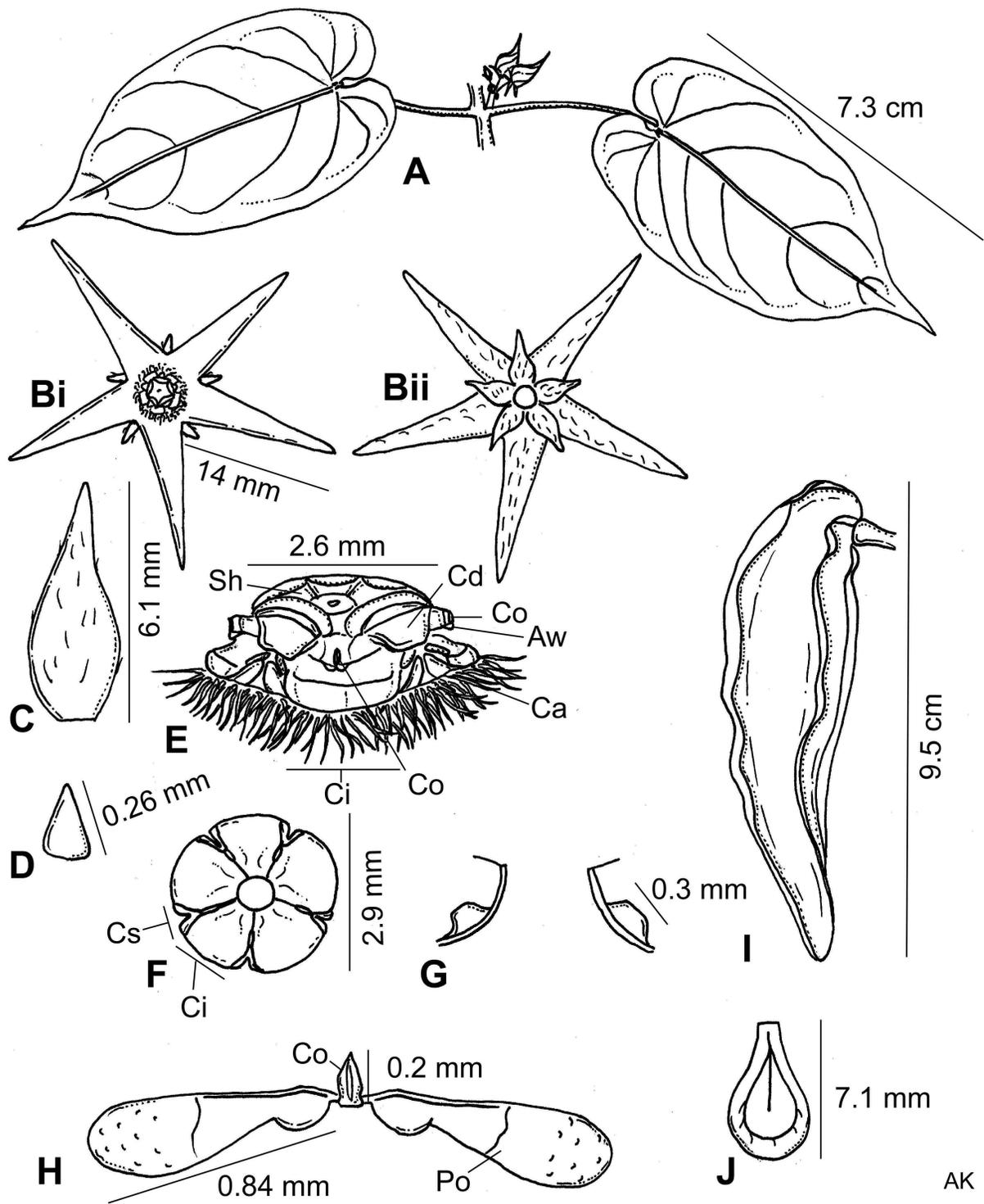
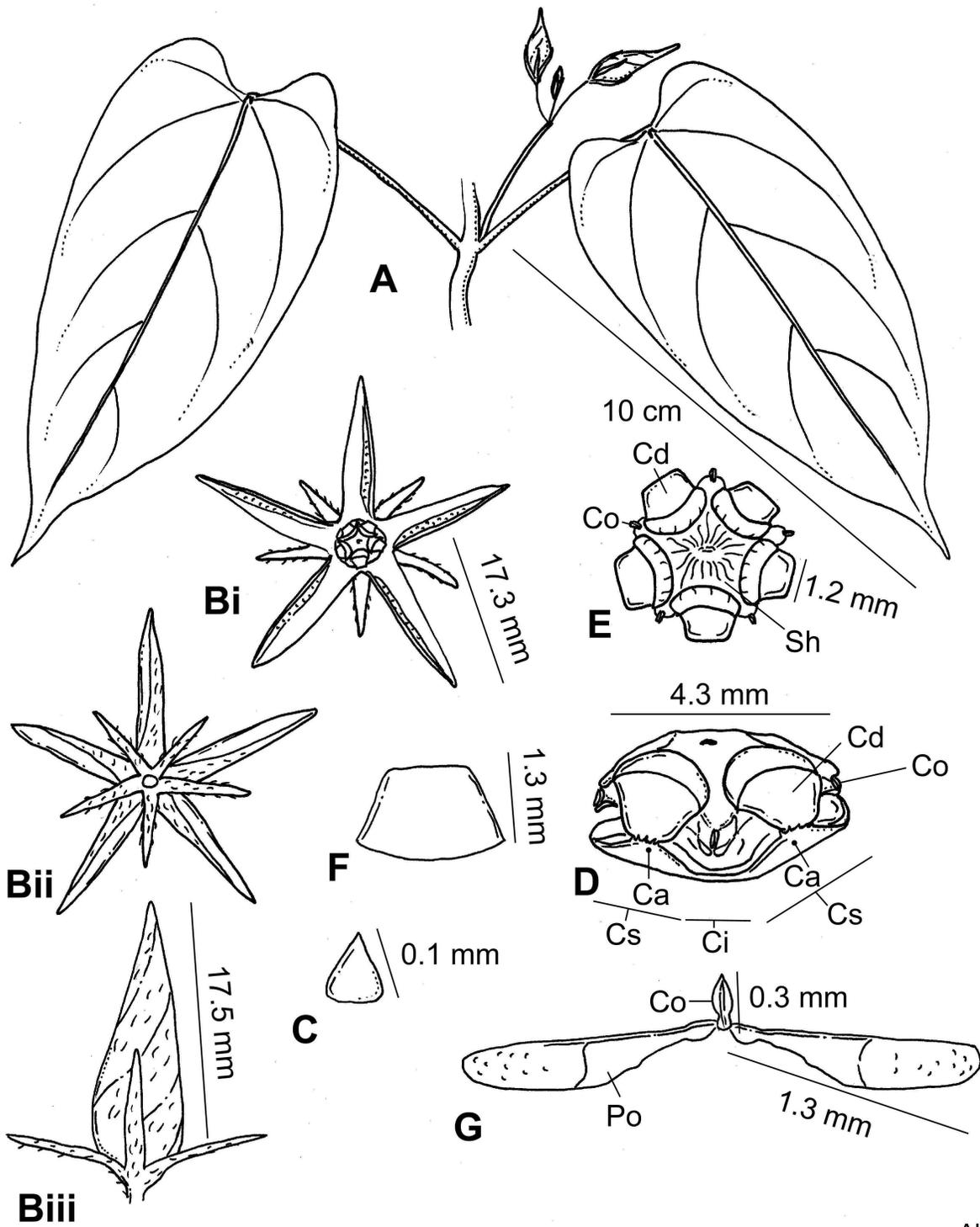


FIG. 13. *Gonolobus tobagensis*. A. Leaves and inflorescence. Bi. Open flower (adaxial view). Bii. Open flower (abaxial view). Biii. Flower bud. C. Calycine colleter. D. Faucal annulus of the corolla, gynostegial corona, and stylar head. E. Stylar head and laminar dorsal anther appendages (top view). F. Detail of laminar dorsal anther appendage. G. Pollinarium. Based on *Sandwith 1840* (K). Aw = anther wings; Ca = faucal annulus of corolla; Ci = interstaminal gynostegial corona segment; Cd = laminar dorsal anther appendage; Co = corpusculum; Cs = staminal gynostegial corona segment; Po = pollinium; Sh = stylar head.



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FIG. 14. *Gonolobus waitukubuliensis*. A. Leaves and inflorescence. B. Flower. C. Raised and completely circular faucal annulus of the corolla (Ca) and stylar head (gynostegial corona obscured behind the Ca). D. Gynostegial corona of fused staminal (Cs) and interstaminal (Ci) segments (stylar head removed). E. Top view of gynostegial corona (stylar head removed). F. Cross-section of corolla tube showing position of corollar and gynostegial corona elements. G. Laminar dorsal anther appendage (Cd). H. Pollinarium. A and C based on *Eggers 728* (M). B and D–H based on *Webster 13505* (US). Ca = faucal annulus of corolla; Ci = interstaminal gynostegial corona segment; Cd = laminar dorsal anther appendage; co = Corpusculum; Cs = staminal gynostegial corona segment.

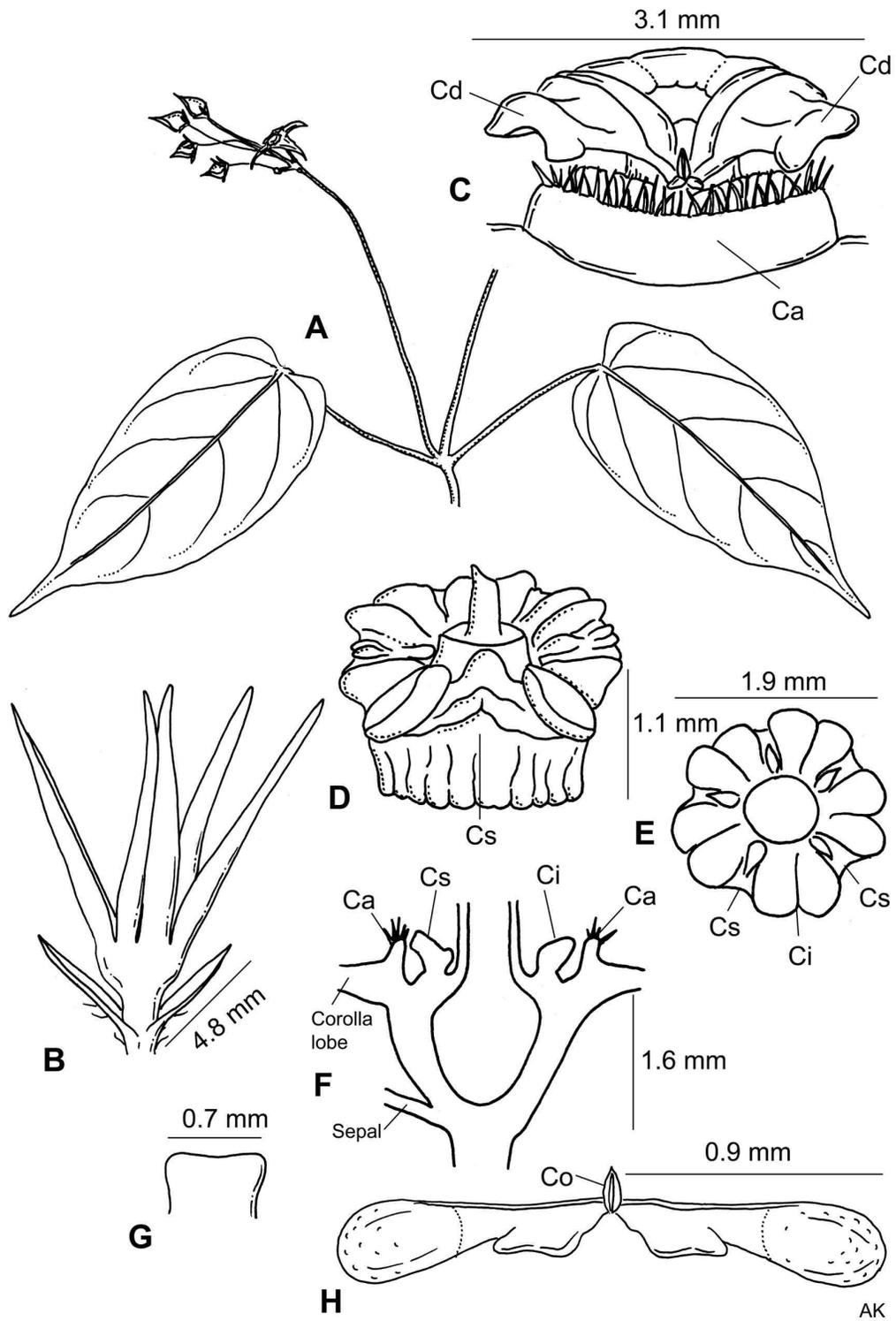
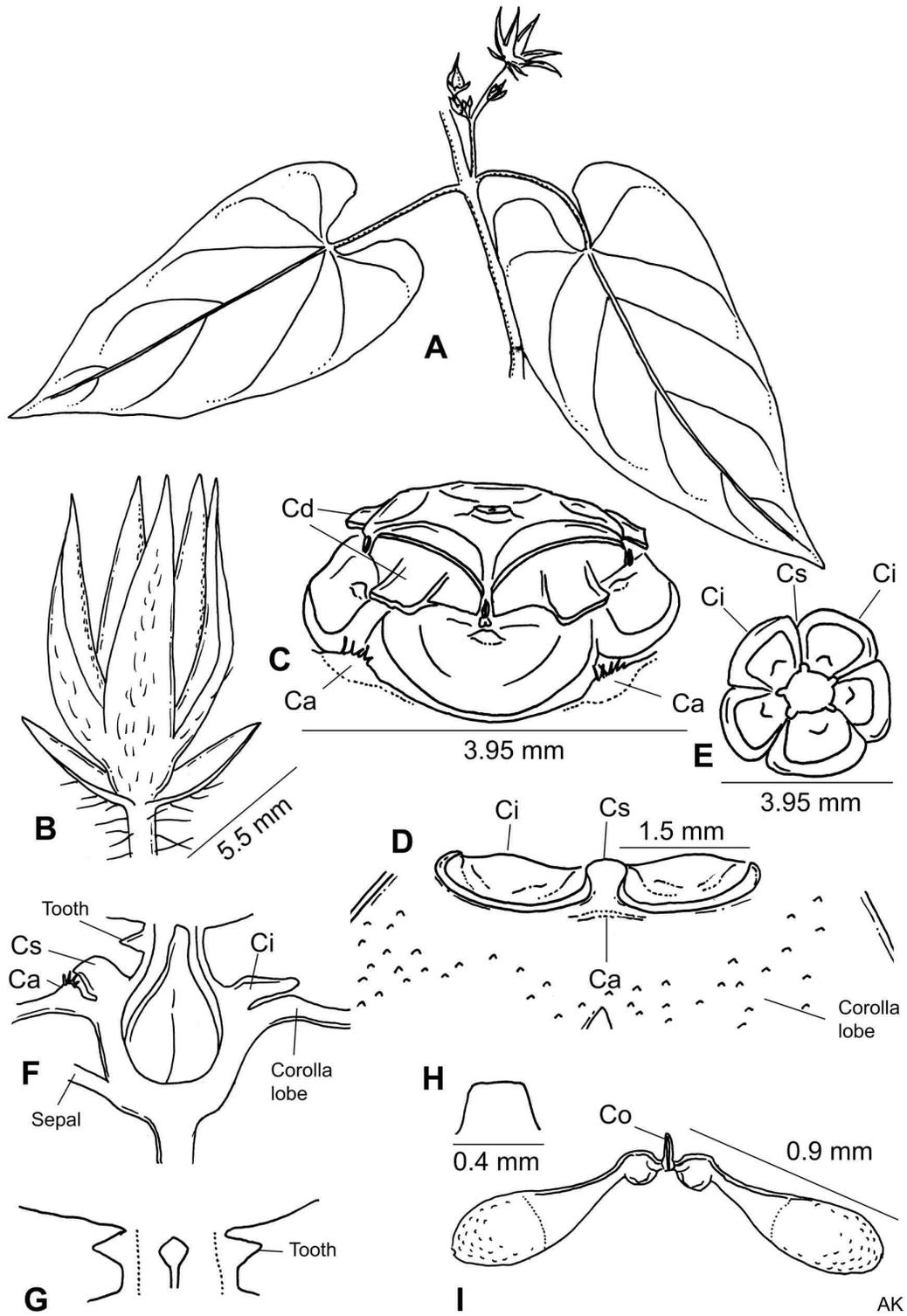


FIG. 15. *Gonolobus youroumaynensis*. A. Leaves and inflorescence. B. Flower showing coarse abaxial corolla lobe pubescence. C. Faucal annulus of the corolla (Ca), gynostegial corona, and stylar head. D. Gynostegial corona of fused staminal (Cs) and interstaminal segments (Ci) (stylar head removed). E. Top view of gynostegial corona (stylar head removed). F. Cross-section of corolla tube showing position of corollar and gynostegial corona elements. G. Detail of teeth of the gynostegial stipe. H. Laminar dorsal anther appendage (Cd). I. Pollinarium. A–B and D based on *Howard 19584* (GH, NY, US). C and E–I based on *Krings 1374 with Springer* (NCSC). Ca = faucal annulus of corolla; Ci = interstaminal gynostegial corona segment; Cd = laminar dorsal anther appendage; Co = corpusculum; Cs = staminal gynostegial corona segment.



## **Additional studies in West Indian Gonolobinae**

## Chapter VII

### New and rediscovered milkweeds from Cuba: *Calotropis gigantea* and *Gonolobus stephanotrichus* (Apocynaceae: Asclepiadoideae)

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Reproduced from: Krings, A., F. Areces Berazaín, and J.C. Lazcano Lara. 2005.

*Willdenowia* 35: 315-318.

## Abstract

Krings, A., Areces Berazaín, F. & Lazcano Lara, J.C.: New and rediscovered milkweeds from Cuba: *Calotropis gigantea* and *Gonolobus stephanotrichus* (Apocynaceae – Asclepiadoideae).

*Calotropis gigantea* (L.) R.Br. is reported new to Cuba and *Gonolobus stephanotrichus* Griseb. is reported rediscovered after previously being known only from type collections taken between 1860-64. Specimens are cited and keys to Cuban species of both genera are provided.

## Introduction

A recent expedition in search of milkweeds (Apocynaceae – Asclepiadoideae) for the development of a treatment of subtribe Gonolobinae for the Flora de la Republica de Cuba, resulted in the discovery of *Calotropis gigantea* (L.) R.Br. – a new record for the island – and the rediscovery of *Gonolobus stephanotrichus* Griseb.

## *Calotropis gigantea* (Asclepiadinae)

Previously only a single species of *Calotropis* R.Br. was reported for Cuba – *Calotropis procera* (Ait.) R.Br. (Schlechter 1899; Liogier 1957; Rahman & Wilcock 1991). While *Calotropis gigantea* apparently has a native range spanning the Indian subcontinent, southern China, Southeast Asia, and Indonesia, it is now introduced into New Guinea and the Hawaiian islands (Rahman & Wilcock 1991). Rahman & Wilcock (1991) did not report it for the West Indies. The TROPICOS database (<http://www.tropicos.org>) currently lists two collections from the Caribbean region: Trinidad (*Broadway s.n.*, MO – fide annotation by W.D. Stevens 1987, specimen not seen) and Tobago (*Worthington 18023*, MO – fide annotation W.D. Stevens 2000, specimen not seen). Howard (1989) noted the presence of *C. gigantea* in cultivation in Barbados based on a report by Maycock (1830). The records from Cuba are apparently the first report of *C. gigantea* for the Greater

Antilles. Based on a collection previously assigned to *C. procera*, *C. gigantea* appears to have been in Cuba for at least thirty years:

Cuba: Prov. Villa Clara, Mun. Santa Clara, Presa Agabama, 30 Mar 1974, *H.F.C. 24991* (Col. *A. Areces*) (HAJB); Prov. Santiago de Cuba, Bayate (seco), in open pasture, 27 May 2005, *A. Krings, F. Areces, and J. Lazcano s.n.* (NCSC); Prov. Santiago de Cuba, Mun. Mella, zona de Bayate, El Ocho, potreros en el camino a Arroyo Martín, 27 May 2005, *H.F.C. 83524* (Cols. *F. Areces, J. Lazcano, and A. Krings*) (HAJB).

### **Key to *Calotropis* in Cuba**

1. Corolla lobes 10-15 mm long; staminal corona segments (Cs sensu Kunze 1990) 5-12.3 mm long, shorter than the gynostegial head .....*Calotropis gigantea* (Fig. 1A)  
– Corolla lobes 6-8 mm long; staminal corona segments (Cs) to 4 mm long, equalling to taller than the gynostegial head .....*Calotropis procera* (Fig. 1B)

### ***Gonolobus stephanotrichus* (Gonolobinae)**

*Gonolobus stephanotrichus* is known only from Puerto Rico, Hispaniola, and Cuba (Schlechter 1899; Urban 1910; Liogier 1957; Adams 1972; Howard 1989; Liogier 1994, 1995; Acevedo-Rodríguez 2003, 2005). However, although numerous collections exist from the former islands, *G. stephanotrichus* was known in Cuba only from the syntypes taken by Charles Wright between 1860 and 1864 (*Wright 2969*, BREM!, G!, GH!, GOET!, HAC!, K!, MO, NY!, P!, UC!, US!). However, during a June 2005 ascent of Pico Joaquin in Parque Nacional Turquino (Oriente, Sierra Maestra), the species was found growing along the ridgeline between about 1000-1300 m. At least fifty vines were counted within 3 km of the Campamento Joaquin at the base of Pico Joaquin. Most vines were sterile, but some were starting to bear flower buds and a few bore immature flowers sufficiently developed to allow positive determination of the species. Specimens seen:

Cuba: Prov. Santiago de Cuba, Sierra Maestra, Parque Nacional Turquino, within 3 km of Campamento Joaquin on trail from the Alto de Naranjo, 3 June 2005, A. Krings, F. Areces, and J. Lazcano s.n. (HAJB, NCSC); Prov. Santiago de Cuba, Sierra Maestra, Parque Nacional Turquino, 2-3 km downhill from Campamento Joaquin in direction of the Alto de Naranjo, 2 June 2005, A. Krings, F. Areces, and J. Lazcano s.n. (NCSC).

### Provisional key to *Gonolobus* in Cuba

- 1. Leaves linear-lanceolate, 0.5-0.7 cm wide .....*Gonolobus grisebachianus*
- Leaves ovate to elliptic,  $\geq 2$  cm wide..... 2.
- 2. Corolla lobes suborbicular ..... *Gonolobus bakeri*
- Corolla lobes linear-lanceolate ..... *Gonolobus stephanotrichus*

It is important to note that *G. grisebachianus* Schltr. (holotype: *Wright s.n.*) and *G. bakeri* Schltr. (holotype: *Baker 7286*) are apparently only known from their type collections, which have not been located despite query of nearly one hundred institutions known to house West Indian collections. They may have been destroyed in WW II. Thus, the two species are included here provisionally and based solely on their protologues and past treatments. Despite the recent combination *Matelea grisebachiana* (Schltr.) Alain, *G. grisebachianus* should clearly be assigned to *Gonolobus* based on the description provided by Schlechter (1899) and following Woodson's (1941) circumscription of *Gonolobus* Michx. to include only species with laminar dorsal anther appendages. Although Grisebach (1866) did not mention laminar dorsal anther appendages in his protologue for *G. tigrinus* Griseb. var. *angustifolia* Griseb. (a synonym of *G. grisebachianus*), Schlechter (1899) clearly noted the presence of well-developed anther appendages in his description [italics ours]: "Diese Art ist trotz ihrer habituellen Aehnlichkeit mit *G. tigrinus* Griseb. von diesem vollständig verschieden. Die Blätter sind schmaler, die Blüten grösser, die äussere Corona ganz verschieden und die *Schuppen der inneren Corona viel deutlicher vom Antherenrücken abgehoben*, ausserdem, von oben gesehen, in der Mitte nicht ausgerandet, sondern eher verdickt." The position of *G. bakeri* appears more uncertain. Schlechter does

not describe dorsal anther appendages in the protologue. Combined with his note that the species is “mit *G. variifolius* Schltr. [now *Matelea variifolia* (Schltr.) Woodson] am nächsten verwandt,” there is reason to believe that *G. bakeri* may better belong in *Matelea*. *Matelea variifolia* clearly lacks laminar dorsal anther appendages and also exhibits suborbicular corolla lobes. It is known only from Puerto Rico (Schlechter 1899; Acevedo-Rodríguez 2003, 2005). As the single specimen representing *G. bakeri* was cultivated in Cuba, it may be that the species is merely a pubescent form of *M. variifolia*.

### *Acknowledgments*

We are grateful to the following institutions for facilitating access and collecting permits: Centro de Inspección y Control Ambiental (CICA), Delegaciones del Ministerio de Ciencia, Tecnología y Medio Ambiente (CITMA) de Santiago de Cuba y Granma, Regiones Militares de Santiago de Cuba y Granma, and Delegación del Ministerio del Interior de Santiago de Cuba. In addition, we are grateful for guidance in the field by Anel Matos Viñals and Mino Leyeba. Krings also thanks the curators and staff of the following herbaria for access to their collections or loans of specimens: B, BH, BM, BOLO, BREM, BSC, C, CGE, DUKE, E, F, FI, FR, FTG, G, GH, GOET, H, HAC, HAJB, HBG, IJ, JE, K, M, MICH, MIN, MO, NY, O, OXF, P, PH, RSA, S, U, UC, US, USF, WU, Z. I also thank the curators and staff of the following herbaria for searching their collections for West Indian Gonolobinae material, although finding no representation: BG, BKL, BR, BUF, COLO, CR, FLAS, IA, ISC, LD, MSU, NEU, NSW, UPS, TUR.

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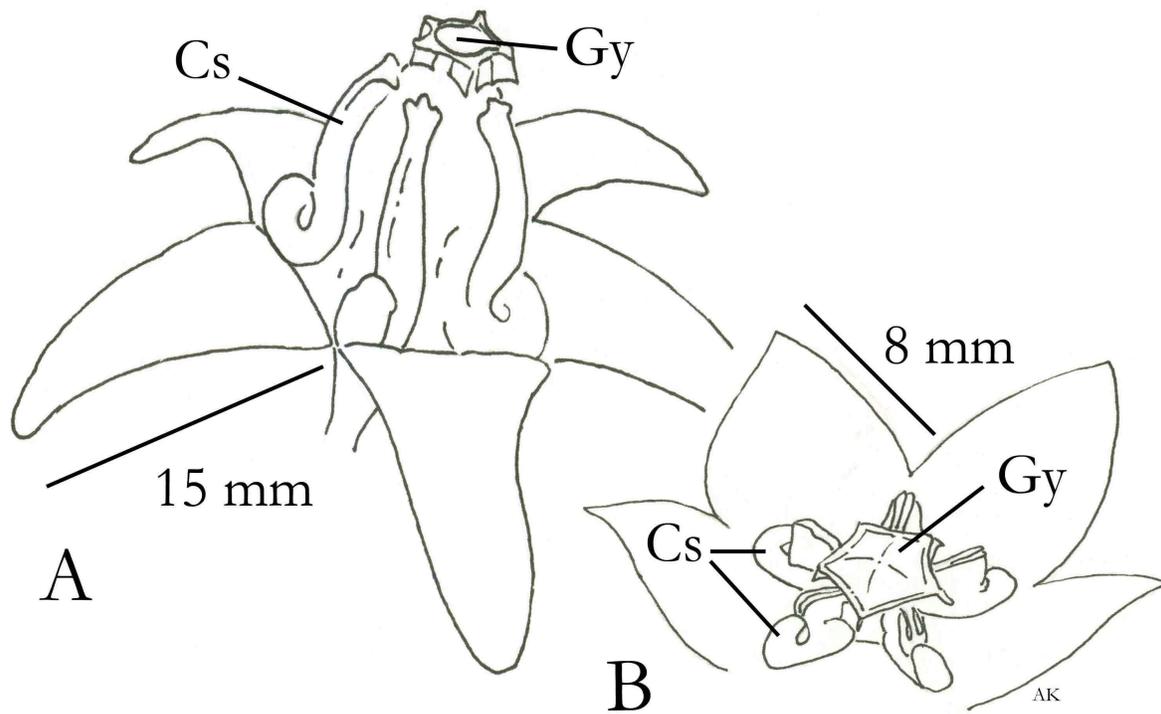


FIG. 1. Flowers of the two Cuban *Calotropis* species: A, *C. gigantea* (based on *Krings & al. s.n.*, NCSC); B, *C. procera* (based on *Krings & al. s.n.*, NCSC). Cs = staminal corona segment (sensu Kunze 1990); Gy = gynostegial head.

## Chapter VIII

**A new combination in *Matelea* (Apocynaceae: Asclepiadoideae)  
for an endemic Jamaican vine**

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Reproduced from: Krings, A. 2005. *Sida* 21: 1515–1517.

## ABSTRACT

Critical study of West Indian specimens of subtribe Gonolobinae (Apocynaceae – Asclepiadoideae) has resulted in the need for a new combination for an endemic Jamaican vine:

***Matelea rhamnifolia*** (Griseb.) Krings, comb. nov.

*Gonolobus rhamnifolius* Griseb., Fl. Brit. W.I. 420. 1862.

Protologue: 'Jamaica!, *Al.*, S. Anns, near Moneague'

Type: JAMAICA. *R. C. Alexander s.n.* (holotype: GOET!)

The critical character defining placement in *Gonolobus* Michx.—dorsal anther appendages (Woodson 1941; Rosatti 1989; Stevens 2001)—is lacking, although mistakenly attributed to the species by Adams (1972). Other characters that have been used to refer taxa to *Gonolobus* include winged follicles and the absence of glandular hairs (see Woodson 1941). Follicles are unknown for *Matelea rhamnifolia*, although suspected to be winged, not muricate, based on its affinities to *M. correllii* Spellman. The follicle character is moot, however, as few fruit collections were apparently available to Woodson (1941) and more recent analysis has shown the character not to be useful in generic delimitation (Krings, unpubl.). Glandular hairs, although thought characteristic of *Matelea* Aubl. by Woodson (1941), are also without circumscriptional value in the *Gonolobus-Matelea* question, being present in both the type of *Gonolobus* Michx. (i.e., *G. suberosus* (L.) R. Br.) and numerous species lacking dorsal anther appendages (Rosatti 1989), including *M. rhamnifolia*.

The Jamaican endemic *Matelea rhamnifolia* appears most closely related to the Cuban endemic *M. nipensis* (Urb.) Woodson (at least among West Indian taxa); both likely belonging to a complex also including the Cuban endemics *M. bayatensis* (Urb.) Woodson and *M. tigrina* (Griseb.) Woodson and the Bahaman endemic *M. correllii*. *Matelea rhamnifolia* and *M. nipensis* share oblong leaves that are basally truncate or rounded, reduced peduncles, short corolla lobes, and gynostegial coronas of similar morphology.

Both species exhibit a low, somewhat undulating outer corona which subtends an inner corona and the associated staminal tube (Fig. 1A, B). The same morphology is present in *M. correllii* and was well-illustrated in the protologue of this latter species (Fig. 1C). The corolla lobes of both *M. rhamnifolia* and *M. nipensis* are also reticulate (at least when dry) and bear a white spot at each of the apices—both characters shared by the larger-flowered members of the complex mentioned above and the continental *M. pusilliflora* L.O. Williams. *Matelea rhamnifolia* is distinguished from *M. nipensis* by its larger leaves, a longer and more well-developed floral tube (ca. 1.3 mm vs.  $\leq 0.5$  mm), and a shorter filament tube (0.5 mm vs. 0.7 mm).

### **Representative specimens examined**

*Matelea nipensis* (Urb.) Woodson: CUBA. *Ekman 9710* (isotype: NY, S); *Berazain & Alvarez 24357* (HAJB); *Clemente 4342* (NY); *Webster 3813* (GH).

*Matelea rhamnifolia* (Griseb.) Krings: JAMAICA. *Alexander s.n.* (holotype: GOET); *Proctor 11825* (GH, IJ).

### **ACKNOWLEDGMENTS**

I thank the curators and staff of the following herbaria for access to their collections or loans of specimens: BH, BM, BOLO, BREM, BRIT, C, CGE, DUKE, E, F, FI, FLAS, FR, FTG, G, GA, GH, GOET, H, HAC, HAJB, HBG, IJ, JE, K, KY, LL, M, MICH, MIN, MISS, MO, NCU, NO, NY, O, OK, OXF, P, PH, RSA, S, TENN, TEX, U, UC, UNA, US, USCH, USF, WILLI, WU, Z. I also thank the curators and staff of the following herbaria for searching their collections for West Indian Gonolobinae material, although finding no representation: BG, BKL, BR, BUF, COLO, CR, FLAS, IA, ISC, LD, MSU, NEU, NSW, UPS, TUR.

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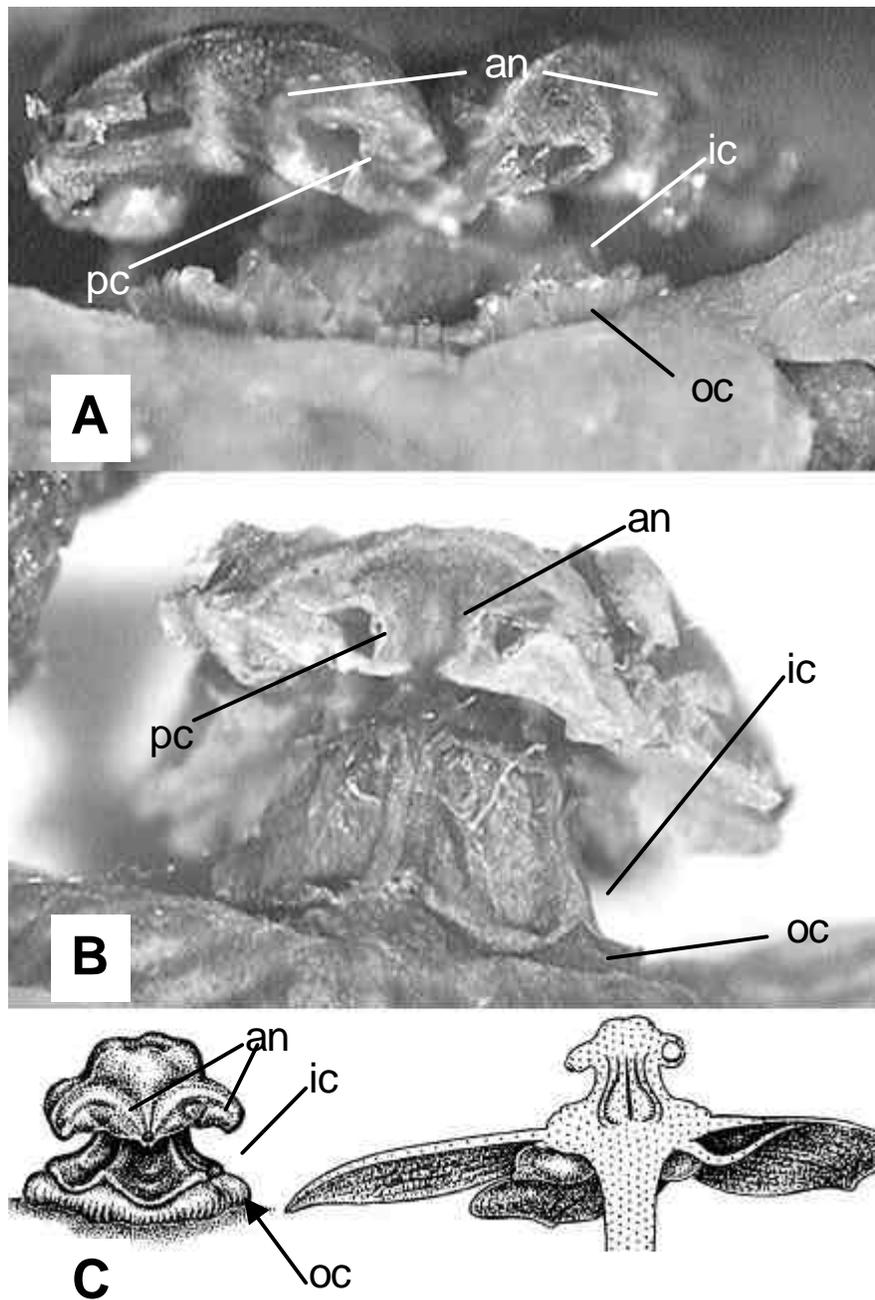


FIG. 1. Corona and gynostegium morphology of: (A) the Jamaican endemic *Matelea rhamnifolia* (from Proctor 11825, GH) and the related (B) Cuban endemic *M. nipensis* (from Webster 3813, GH) and (C) Bahaman endemic *M. correllii* (from Spellman 1978). Note absence of dorsal anther appendages in all three species. an=anther; ic=inner corona; oc=outer corona; pc=pollinium cavity.

## Chapter IX

**A new species of *Matelea* (Apocynaceae: Asclepiadoideae)  
from Hispaniola**

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Reproduced from: Krings, A. 2005. *Sida* 21: 1519–1523.

## ABSTRACT

A new species of *Matelea* is described from Hispaniola, resulting from study of subtribe Gonolobinae (Apocynaceae – Asclepiadoideae) in the West Indies.

## RESUMEN

Se describe una especie nueva de *Matelea* de Española como resultado del estudio del subtribo Gonolobinae (Apocynaceae – Asclepiadoideae) en las Indias Occidentales.

In the course of on-going systematic study of subtribe Gonolobinae (Apocynaceae – Asclepiadoideae) in the West Indies, a new species of *Matelea* Aubl. was discovered from Hispaniola:

*Matelea pentactina* Krings, sp. nov. (Fig. 1, A-B, E)

Type: Haiti. Les Roseaux, Massif de la Hotte western group, rocky ledge, c. 1300 m, 16 Sept 1928, *Ekman H 10685* (holotype: S!).

*Species nova distinguibili a Matelea tamnifolia (Griseb.) Woodson folio basi rotundata, non cordata vel auriculata, a Matelea constanzana Jiménez corolla viridis vel flava, lobis utrinque reticulato-venosis, superne puberulis, et a Matelea ovatifolia (Griseb.) Woodson corolla trichomata 0.11 mm longa, corona segmentis erectis ovatis, (1.5) 1.7-1.9 mm, via antheram 0.5-0.6 mm.*

Twining vine; stems herbaceous when young, becoming woody with age, the bark cream-colored, somewhat corky; stems pubescent in lines, the trichomes white, multi-cellular, retrorsely curved or sometimes straight, to 0.2 mm long; leaves opposite, simple, the blades ovate to elliptic, (6.5) 12.7-21 mm x (2.6) 6.8-13.6 mm, both surfaces glabrous or glabrate, the apices obtuse to narrowly rounded, apiculate, the apiculum to 1.2 mm long, the bases rounded the margins entire, glabrous or ciliolate, the cilia ca. 0.08 mm long, colleters 2, yellow to orange, borne adaxially on the midvein at the base of the blade, to 0.2 mm long, petioles 2.9-9.4 mm long, grooved adaxially, glabrous except for the groove, trichomes mostly antrorse, to 0.18 mm long; inflorescence axillary, umbelliform, the peduncles severely reduced to obsolete, pedicels 5-12 mm long, puberulous with trichomes to 0.12 mm long or glabrate; sepals 5, ovate to lanceolate, ca. 1 mm long, the apices rounded to obtuse, both surfaces glabrous, the margins glabrous or very sparsely ciliolate; corolla rotate, pale green or yellow with dark green reticulations, 5-lobed, the lobes ovate, to 4.2 mm long, the adaxial surface pubescent near the base of the lobes, the trichomes whitish to 0.11 mm long, the abaxial surface glabrous; faucal annulus [Ca] pubescent; corona of fused staminal and interstaminal parts [C(is)], glabrous, the staminal segments [Cs] erect, foliate, ovate (1.5) 1.7-1.9 mm long, the apices obtuse, deeply notched, higher than the apex of the gynostegium; gynostegium stipitate, the stipe ca. 0.2 mm long; dorsal anther appendages [Cd] lacking; anther guide rails outwardly pronounced, 0.5-0.6 mm long; pollinaria descending; follicles unknown.

The epithet *pentactina* refers to the five, elongate, outwardly projecting anther guide rails, reminiscent of rays.

ADDITIONAL SPECIMENS EXAMINED: Massif de la Selle, gr. Crete-a-Piquants, Port-au-Prince, between Carrefour-Martin and Bois d'Orme, c. 800 m, limestone, 17 Dec 1926, *Ekman H 7402 (S!)*.

*Matelea pentactina* is most closely related to *Matelea ovatifolia* (Griseb.) Woodson (Fig. 1, C-E) and both its holotype and paratype have previously been referred to the latter (see Liogier 1981). Vegetatively the two species are exceedingly similar and may not be conclusively distinguished. However, a number of floral character states distinctly separate them (see Table 1 and key below). *Matelea ovatifolia* appears endemic to Cuba and *M. pentactina* to Hispaniola, although the single specimen seen from the Dominican Republic (*Fuertes 991*, GH) is sterile and thus cannot be conclusively referred to either based on morphology. A handwritten note with the holotype of *M. pentactina*, presumably by Ekman, indicates it was “seen occasionally throughout southern Haiti (at least), although seldom with flrs!” A similar note on the paratype reads: “Rare, although I think I have seen it sterile before and taken it for some *Metastelma* [sic].” *Matelea pentactina* also appears closely related to the Hispaniolan *Matelea constanzana* Jiménez (nom. nov. for *Poicillopsis tuerckheimii* Schltr. as the epithet is not available in *Matelea*). This latter species was apparently known only from the type (Sto. Domingo prope Constanza, *Tuerckheim 3466*, Jul 1910; see also Liogier 1981) and appears to no longer be extant. The protologue indicated that *M. constanzana* also bears obtuse staminal corona segments, but exhibits glabrous white flowers. The striking reticulations evident in the pubescent, green or yellow-flowered *M. pentactina* were not described for *M. constanzana*.

According to the subgeneric classification erected by Woodson (1941), *Matelea pentactina* and *M. ovatifolia*, as well as *M. tamnifolia* (Griseb.) Woodson (endemic to Cuba; Fig. 1, F), belong to the entirely Antillean subgenus *Poicilla*. Woodson (1941) did not include the entity now known as *M. constanzana* in his treatment, but its affinities would seem to place it in his subg. *Poicilla* as well. Although many of Woodson's (1941) subgenera are likely ill-conceived (Stevens 1988), subgenus *Poicilla* is maintained here in the absence of a rigorous test of Woodson's (1941) concept. A key to the subgenus is provided below. Ongoing systematic study of West Indian Gonolobinae aims to improve generic and subgeneric circumscriptions.

Key to *Matelea* subgenus *Poicilla*

1. Leaf blades lanceolate, the bases cordate to auriculate.....*Matelea tamnifolia*
- 1.' Leaf blades ovate, the bases rounded to truncate (very rarely shallowly cordate) ..... 2.
2. Vine exhibiting the combination of corolla lobes white, glabrous on both surfaces, not reticulate, and staminal corona segments rhombic, obtuse.....*Matelea constanzana*
- 2.' Vine not exhibiting the above combination of characters (i.e., if corolla lobes white, then corona segments obovate to suborbicular, the apices rounded to emarginate OR if corona segments obtuse, then corollas green to yellow, reticulate) ..... 3.
3. Adaxial corolla pubescence 0.13-0.2 mm long; erect staminal corona segments 0.99-1.28 mm long, obovate to suborbicular, the apices rounded to emarginate; anther guide rails to 0.26 mm long.....*Matelea ovatifolia*

3.' Adaxial corolla pubescence to 0.11 mm long; erect staminal corona segments (1.5) 1.7-1.9 mm long, ovate, the apices obtuse; anther guide rails 0.5-0.6 mm long .....*Matelea pentactina*

#### ACKNOWLEDGEMENTS

I thank the curators and staff of the following herbaria for access to their collections or loans of specimens: BH, BM, BOLO, BREM, C, CGE, DUKE, E, F, FI, FR, FTG, G, GH, GOET, H, HAC, HAJB, HBG, IJ, JE, K, M, MICH, MIN, MO, NY, O, OXF, P, PH, RSA, S, U, UC, US, USF, WU, Z. I also thank the curators and staff of the following herbaria for searching their collections for West Indian Gonolobinae material, although finding no representation: BG, BKL, BR, BUF, COLO, CR, FLAS, IA, ISC, LD, MSU, NEU, NSW, UPS, TUR. The thoughtful review of a previous version of the manuscript by Mary E. Endress, Alain Liogier, and Paul Fantz is gratefully acknowledged.

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TABLE 1. Floral morphological characters distinguishing *Matelea pentactina* from the related *M. ovatifolia* (Apocynaceae – Asclepiadoideae).

CHARACTER	<i>Matelea pentactina</i>	<i>Matelea ovatifolia</i>
Adaxial corolla surface trichomes	To 0.11 mm long	0.13 -- 0.20 mm long
Erect staminal corona segments [C(s)]	(1.5) 1.7 -- 1.9 mm long, ovate, the apices obtuse	0.99 --1.28 mm long, obovate to suborbicular, the apices rounded to emarginate
Anther guide rails	0.5 -- 0.6 mm long	To 0.26 mm long

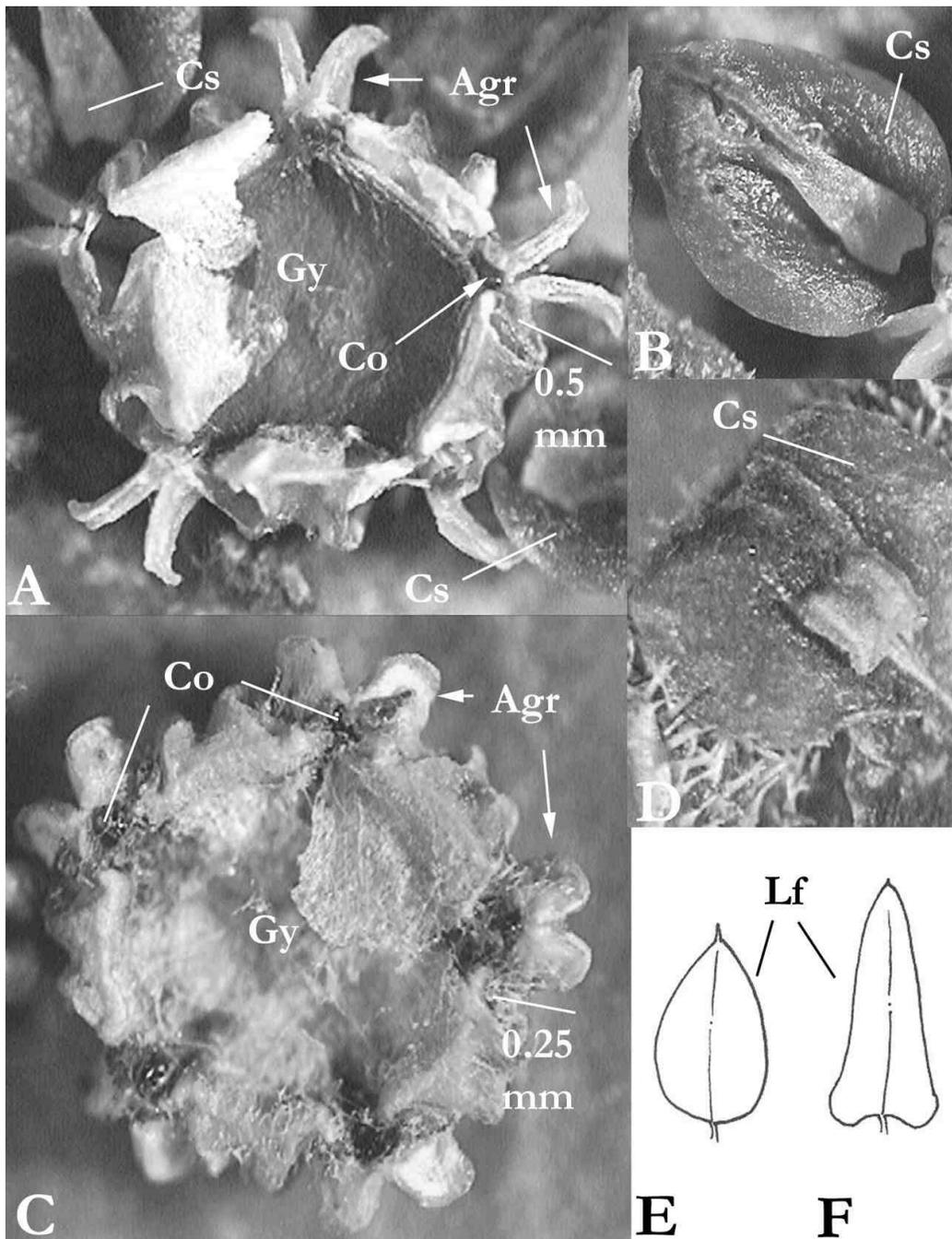


FIG. 1. *Matelea* subgenus *Poicilla*: A-B & E, *Matelea pentactina* Krings (Ekman H 10685, S); C-E, *Matelea ovatifolia* (Griseb.) Woodson (Wright 2965, GH); F, *Matelea tamnifolia* (Griseb.) Woodson (Wright s.n., GH). Agr = Anther guide rail; Co = Corpusculum; Cs = erect staminal corona segment; Gy = Gynostegium; Lf = leaf.

## Chapter X

Notes on the *Matelea bayatensis-correllii-tigrina* complex

(Apocynaceae: Asclepiadoideae: Gonolobinae)

in the Greater Antilles and Bahamas

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## ABSTRACT

As a component of a larger study of the West Indian *Matelea* subgenus *Ptycanthera*, this study sought to critically examine patterns of morphological variation within the embedded *M. bayatensis-correllii-tigrina* complex. Resolution of species-level circumscriptions are necessary before larger issues of subgeneric and generic circumscription can be adequately addressed. Morphological characters were analyzed using parsimony analysis, neighbor-joining, and ANOVA. Results show that *Matelea bayatensis*, *M. correllii*, and *M. tigrina* are very closely related morphologically. The three species appear to differ only in pubescence and relatively minor floral character states, some of which overlap. At present, none of the observed variation appears important enough to warrant the continued recognition of three distinct species.

The Metastelmatinae-Oxypetalinae-Gonolobinae clade sensu Rapini et al. (2003) is the most morphologically diverse of the New World Asclepiadeae and most members have never been monographed. The circumscription of two Gonolobinae genera—*Gonolobus* Michx. and *Matelea* Aubl.—has been particularly complicated by the swelling of the latter by Woodson (1941). Unable to come to terms with the large variation in corona morphology, Woodson (1941) submerged numerous genera within *Matelea*, increasing its size from four to over 100 species. Estimates of species numbers of *Gonolobus* vary from 100 to 150 (Rosatti 1989; Mabberly 1997; Stevens 2001). The degree of variation is largely the result of differences regarding generic limits, as well as still poorly known tropical taxa. Woodson (1941) considered the entirely Antillean subgenus *Ptycanthera* to be “largely the deciding factor” for his inclusive treatment of *Matelea*, noting that “were it not for the Antillean species, one might compose a fairly respectable key to several genera upon the continent.” As a component of a larger study of *M.* subg. *Ptycanthera*, that ultimately seeks to bear on issues of generic circumscription, this study sought to critically examine patterns of morphological variation within the embedded *M. bayatensis-correllii-tigrina* complex. Resolution of species-level circumscriptions are necessary before larger issues of subgeneric and generic circumscription can be adequately addressed.

## METHODS

Based on study of available specimens (Table 1), a matrix of morphological character states (Tables 2 & 3) was developed for seven species and subjected to parsimony analysis using PAUP\* (Swofford 2003). Besides *Matelea bayatensis* (Urb.) Woodson, *M. correllii* Spellman, and *M. tigrina* (Griseb.) Woodson (all members of subg. *Ptycanthera* sensu Woodson 1941), the matrix also included three additional West Indian taxa, representing other members of subg. *Ptycanthera*, as well as subg. *Poicilla* sensu Woodson (1941). Closely allied to *Matelea* (Rapini et al. 2003), the type for the genus *Gonolobus* Michx. (i.e., *Gonolobus suberosus* (L.) R.Br.) was chosen as the outgroup (see also Krings & Xiang 2004). The morphological data matrix (Table 2) was comprised of sixteen qualitative characters. Multistate characters were treated as polymorphisms. Bootstrap support values were determined using the branch-and-bound algorithm with 10,000 replicates. To examine phenetic similarity, the morphological character matrix was also subjected to Neighbor-joining (NJ) analysis using PAUP\* (Swofford 2003). Continuous data represented by pedicel and corolla lobe length, both characters historically used by authors to delimit taxa in the complex (see Grisebach 1863; Urban 1925), were critically analyzed using ANOVA. In all, thirteen herbarium sheets of *Matelea bayatensis*, *M. correllii*, and *M. tigrina* were examined, although only four individual collections exhibited flowers (Table 1). These specimens essentially represent the sum total of available herbarium specimens of the group, as material was requested from eighty-three institutions known or likely to house material of subtribe Gonolobinae in the West Indies. Only the holotype of *M. correllii* (MO), the lectotype of *M. tigrina* (GOET fide Howard 1988), and a syntype of *M. tigrina* (MO), were not studied as they could not be obtained on loan.

## RESULTS

*Parsimony.* An exhaustive search using PAUP\* (Swofford 2003) evaluated 945 trees and yielded two of shortest length (Length=29; CI=0.862; RI=0.692; Fig. 1). Nine of the sixteen morphological characters (56%) were parsimony informative. The two trees are identical except for resolution of the *Matelea bayatensis-correllii-tigrina* clade. The clade

itself appears well-supported by bootstrap values, as is the *Matelea ovatifolia-oblongata* clade. The two Cuban taxa, *Matelea bayatensis* and *M. tigrina* emerged nearer one another than either to *M. correllii* in one of the trees, although with very weak bootstrap support.

*NJ and ANOVA.* The neighbor-joining (NJ) analysis showed the Cuban taxa – *M. bayatensis* and *M. tigrina* – to be more similar to each other than either is to the Bahaman taxon *M. correllii* (Fig. 2). The NJ tree is identical to the second of the shortest trees identified by parsimony analysis (Fig. 1, B). *Matelea tigrina* bears sepals that are densely pubescent with both glandular and eglandular hairs and corolla lobes that are pubescent (though not densely so) on the abaxial surface. In contrast, *Matelea correllii* bears glabrous calyces and corollas. *Matelea bayatensis* is intermediate. Its sepals are scattered (not densely) pubescent, with glandular and eglandular hairs, and the abaxial corolla lobes are glabrous. Sepals are lanceolate in *Matelea bayatensis* and *M. tigrina*, and ovate in *M. correllii*. All three taxa in the complex show strong reticulations of their corolla lobes, white dots at the corolla lobe apices, and similar corona and gynostegial morphology. Although pedicel length and corolla lobe length have been used to delimit taxa in the complex (see Grisebach 1863; Urban 1925), an analysis of variance showed no statistically significant difference in mean pedicel or corolla lobe length at the 95% confidence level between the three species (pedicel length:  $F = 1.98 < F_{\text{crit}} = 3.49$ ; corolla lobe length:  $F = 3.65 < F_{\text{crit}} = 3.86$ ). A graphical representation of these data shows evident overlap (Fig. 3).

## DISCUSSION

The oldest name in the *Matelea bayatensis-correllii-tigrina* complex was provided by Grisebach (1863) for a Cuban taxon then referred to the genus *Gonolobus*: *G. tigrinus* Griseb. Urban (1925) later added *G. bayatensis* Urb. to the complex, distinguishing it from *G. tigrinus* by shorter pedicels, lanceolate sepals (vs. elliptic-oblong) which are scarcely pilose abaxially (vs. pilose), and longer corolla lobes, these ovate to ovate-rotund (vs. orbicular). A study of the types of both taxa quickly shows these characters to be problematic (*M. tigrina*: Wright 1667, G!, GH!; *M. bayatensis*: Arth. Engström in herb. Ekman 3056, NY!, S!). Urban's interpretation of sepal and corolla lobe shapes is

subjective and these features appear to intergrade. Perhaps his pedicel measurements were not made on extant material, as pedicels on the remaining types are 2.71-3.96 mm long and thus well within the range of *G. tigrinus* (i.e., 2.6-3.69 mm). Furthermore, corollas of *G. tigrinus* were described in Grisebach's protologue as 5-6 mm long, just a millimeter shorter than *G. bayatensis*. When dried both taxa have similar corolla lobe lengths (to 4.18 mm in *G. bayatensis*; to 4.4 mm in *G. tigrinus*) - although differential shrinkage has been shown in other *Matelea* species (see Drapalik 1969). The sepal vestiture trait remains true. However, this seems insufficient basis for recognizing two separate species.

Without publishing a critical study of the complex, Woodson (1941) later provided new combinations for both taxa in *Matelea*, applying his concept that *Gonolobus* should be characterized primarily by dorsal anther appendages and smooth, winged follicles. Dorsal anther appendages appear to be lacking in both *M. tigrina* and *M. bayatensis*. Follicles of the two were unknown to Woodson (1941), as they are today, as both species are known only from the type specimens, none of which bear fruit. However, the interpretation of the presence of dorsal anther appendages can be difficult from herbarium specimens. At least six species transferred from *Gonolobus* to *Matelea* by Woodson (1941) were considered by Schlechter (1899) and Urban (1925) to bear dorsal anther appendages to some degree. The controversial taxa fall into two *Matelea* subgenera sensu Woodson (1941) – *Pachystelma* and the Antillean *Ptycanthera* – and include *M. bayatensis* and *M. tigrina*. The utility of the follicle character (primarily winged in *Gonolobus* vs. primarily muricate in *Matelea*) is also problematic. With greater collections since Woodson (1941), it has become clear that several taxa apparently lacking dorsal anther appendages bear winged instead of muricate follicles. These taxa include the more recently described *Matelea correllii* Spellman (1978) from the Bahamas, which bears extreme resemblance in habit, foliar, and floral characters to *M. bayatensis* and *M. tigrina*.

*Matelea bayatensis*, *M. correllii*, and *M. tigrina* are clearly closely related morphologically (Figs. 1-3). The three taxa appear to differ only in pubescence and relatively minor floral character states, some of which overlap (Fig. 3). This minor variation may be due to the

very limited number of collections and might be completely indistinct if more collections were available. Flower sizes (including pedicel lengths) can likely be influenced by growing conditions, as can pubescence. At present, none of the observed variation appears important enough to warrant the continued recognition of three distinct species. At the least, based on current evidence (albeit limited), the two Cuban species - *Matelea bayatensis* and *Matelea tigrina* - can be considered synonymous. Considering geographic distribution, that the Cuban taxa appear more closely related to each other than each is to the Bahaman taxon, and that *Gonolobus tigrinus* is the oldest basionym, it also seems appropriate to treat the Bahaman taxon as a subspecies within *Matelea tigrina*. The question of whether the species should be referred to *Gonolobus* cannot yet be answered based on the material at hand. On-going work toward a robust phylogeny based on molecular data aims to address this question. Until then, new combinations are avoided to limit unnecessary names.

#### TAXONOMIC TREATMENT

***Matelea tigrina*** (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28: 226. 1941.

*Gonolobus tigrinus* Griseb., Mem. Amer. Acad. Arts ser. 2, 8: 520. 1863.

TYPE: Cuba, *Wright 1667*, 1860 (lectotype: GOET (fide Howard 1988); syntypes: MO [image online!], G!, GH!).

*Gonolobus bayatensis* Urb., Symb. Antill. 9(3): 420-421. 1925. [synon. nov.]

*Matelea bayatensis* (Urb.) Woodson, Ann. Missouri Bot. Gard. 28: 226. 1941.

TYPE: Cuba, *Arth. Engström* in herb. Ekman n. 3056 (syntypes: NY!, S!).

*Matelea correllii* Spellman, Ann. Missouri Bot. Gard. 65(4): 1255-1257. 1978. [synon. nov.]

TYPE: Bahamas, Long Island, *D.S. Correll 49112* (holotype: MO; isotypes: F!, FTG!, GH!, NY!, US!)

DISTRIBUTION: The putative subspecific entity comprised by *M. tigrina* and *M. bayatensis* is apparently restricted to Cuba. The putative subspecific entity comprised by *M. correllii* is apparently endemic to the Bahamas.

NOTES: Spellman's (1978) note of a resemblance between *M. correllii* and *M. grisebachiana* (Schltr.) Alain is puzzling as the latter was described with leaves only to 0.7 cm wide (initially described as *Gonolobus tigrinus* var. *angustifolius* Griseb.) and oblong corolla lobes. Leaves of *M. correllii* average 1.5–2.5 cm diam. Schlechter (1899) also noted differences between *M. tigrina* and *M. grisebachiana* in the outer corona and in the presence of conspicuous dorsal anther appendages ('Cd' sensu Kunze 1995) in the latter. Unfortunately, the type of *M. grisebachiana* (Cuba, Wright s.n.) has not yet been located and may have been destroyed. Additional specimens of *M. grisebachiana* have also not been located and could thus not be analyzed.

#### ACKNOWLEDGEMENTS

I thank the curators and staff of the following herbaria for access to their collections or loans of specimens: BH, BM, BOLO, BREM, C, CGE, DUKE, E, F, FI, FR, FTG, G, GH, GOET, H, HAC, HAJB, HBG, IJ, JE, K, M, MICH, MIN, MO, NY, O, OXF, P, PH, RSA, S, U, UC, US, USF, WU, Z. I also thank the curators and staff of the following herbaria for searching their collections for West Indian Gonolobinae material, although finding no representation: BG, BKL, BR, BUF, COLO, CR, FLAS, IA, ISC, LD, MSU, NEU, NSW, UPS, TUR. The assistance of the North Carolina State University Libraries Inter-Library Loan Service is also gratefully acknowledged, as are the manuscript reviews by Bruce Hansen and Justin Williams.

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TABLE 1. Specimens examined and chosen for analysis.

<i>Subgenus of</i>	<i>Species</i>	<i>Locality</i>	<i>Source</i>
Matelea <i>sensu</i> Woodson (1941)			
--	<i>Gonolobus suberosus</i> (L.) R.Br.	Southeastern U.S.A.	Krings & Xiang (2004)
Poicilla	<i>Matelea ovatifolia</i> (Griseb.) Woodson	Cuba, Oriente	Wright 2965 (ST: G, GH, BREM, UC)
Ptycanthera	<i>Matelea bayatensis</i> (Urb.) Woodson	Cuba, Oriente	Engström 3056 (ST: NY, S)
Ptycanthera	<i>Matelea correllii</i> Spellman	Bahamas, Long Island	Spellman (1978), Correll 49112 (IT: F, FTG, GH, NY, US), Correll 48157 (topotype: FTG, MO, NY); Correll 44937 (FTG)
Ptycanthera	<i>Matelea oblongata</i> (Griseb.) Woodson	Cuba, Occidente	Britton & Wilson 14867 (NY), Britton et al. 7379 (NY), Ekman 17625 (S), Leon 17423 (NY), Shafer 13508 (NY)
Ptycanthera	<i>Matelea pauciflora</i> (Spreng.) Woodson	Hispaniola	Ekman H14296 (S), Garcia & Pimentel 2531 (MO)
Ptycanthera	<i>Matelea tigrina</i> (Griseb.) Woodson	Cuba, Oriente	Wright 1667 (ST: G, GH)

TABLE 2. Characters and states scored for the parsimony and neighbor-joining analyses.

<i>Character</i>	<i>State</i>
1. Adaxial leaf blade vestiture	0 = glabrous/labrate; 1 = pubescent
2. Abaxial leaf blade vestiture	0 = glabrous/labrate; 1 = pubescent
3. Leaf blade apex	0 = acuminate; 1 = acute or obtuse; 2 = rounded or emarginate
4. Leaf blade bases	0 = cordate; 1 = rounded/truncate; 2 = cuneate
5. Adaxial sepal vestiture	0 = glabrous; 1 = pubescent
6. Abaxial sepal vestiture	0 = glabrous; 1 = pubescent
7. Corolla coloration	0 = uniformly colored; 1 = reticulate; 2 = center differently colored
8. Corolla adornment	0 = absent; 1 = each lobe bearing a white spot apically
9. Corolla lobe shape	0 = broadly ovate to suborbicular; 1 = oblong, triangular-deltate, or lanceolate
10. Adaxial corolla lobe vestiture	0 = glabrous; 1 = pubescent
11. Abaxial corolla lobe vestiture	0 = glabrous; 1 = pubescent
12. Cs (staminal corona, see Kunze 1995)	0 = absent or shallow; 1 = well-developed, and/or foliate
13. Styler head shape	0 = flat or depressed; 1 = conical
14. Styler head appendage	0 = absent; 1 = present
15. Cd (dorsal anther appendages, see Kunze 1995)	0 = absent; 1 = present
16. Orientation of pollinium cavity in the gynostegial head	0 = +/- horizontal; 1 = descending

TABLE 3. Morphological character matrix used in the parsimony and neighbor-joining analyses of the *Matelea bayatensis-corrrellii-tigrina* complex.

<i>Taxon</i>	<i>Character states</i>
<i>Gonolobus suberosus</i>	{01}10001{02}01{01}110010
<i>Matelea bayatensis</i>	001{01}011100001000
<i>Matelea corrrellii</i>	0011001100001000
<i>Matelea oblongata</i>	00{01}{12}000010021001
<i>Matelea ovatifolia</i>	001{01}000001020001
<i>Matelea pauciflora</i>	{01}1{12}1010010001100
<i>Matelea tigrina</i>	001{01}011100101000

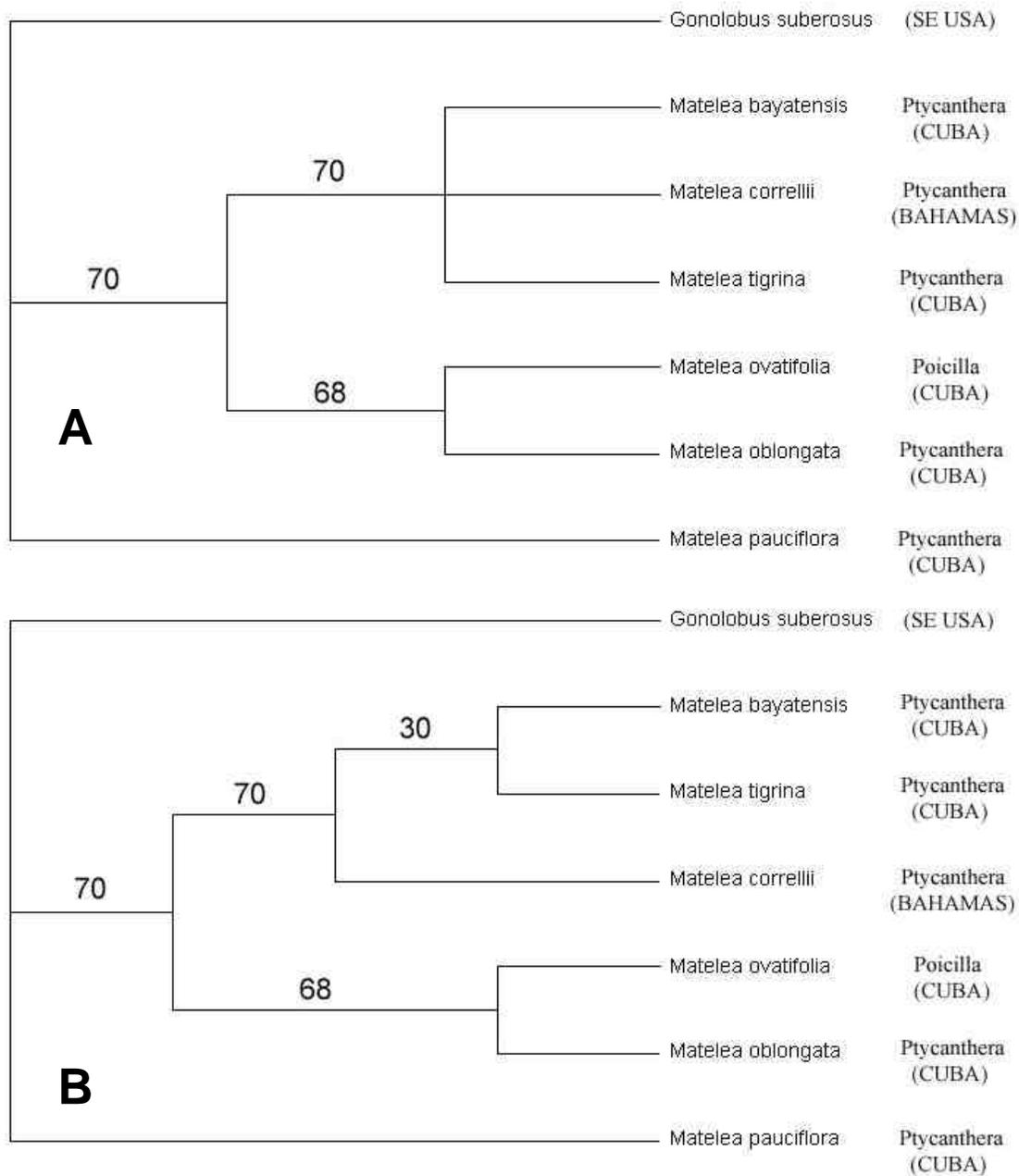


FIG. 1. The two shortest trees (A-B) resulting from a parsimony analysis of morphological characters (exhaustive search) in study of the Antillean *Matelea bayatensis-corrrellii-tigrina* complex (each tree: length = 29; CI = 0.862; RI = 0.692). Bootstrap support values appear above branches. Marginal annotations indicate subgenus of *Matelea* sensu Woodson (1941) (if applicable), followed by geographic distribution of the species.

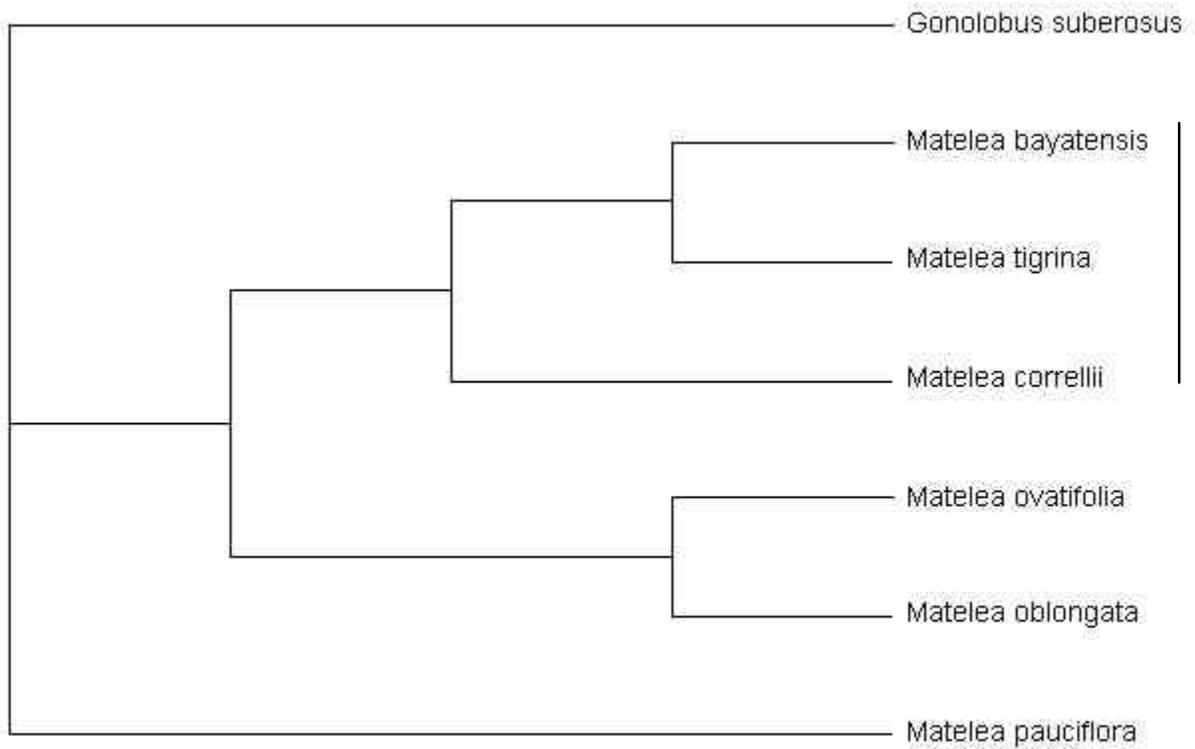


FIG. 2. Neighbor-joining tree showing phenetic similarity in the Antillean *Mateleia bayatensis-correllii-tigrina* complex based on sixteen morphological character states.

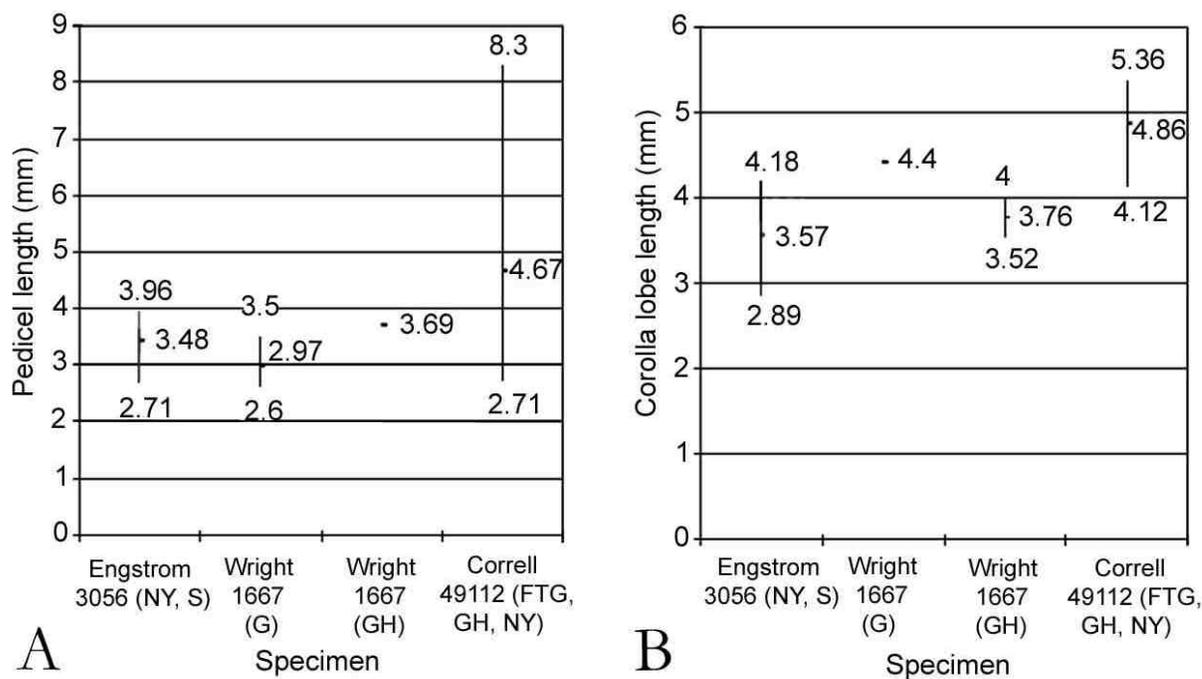


FIG. 3. Continuous floral characters historically used to delimit *Matelea bayatensis*, *M. correllii*, and *M. tigrina*: A, pedicel length; B, corolla lobe length. Measurements indicate maximum, mean, and minimum from top to bottom (in mm), unless only a single measurement was available. Engström 3056 = *M. bayatensis*; Wright 1667 = *M. tigrina*; Correll 49112 = *M. correllii*. The two Wright specimens likely represent two different individuals collected at different times and localities (see Howard 1988).

## Chapter XI

### Lectotypification and a new combination in *Matelea* (Apocynaceae: Asclepiadoideae) for an endemic Hispaniolan vine

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Reproduced from: Krings, A. 2005. *Sida* 21: 2081–2085.

## ABSTRACT

A new combination in *Matelea* is proposed: *Matelea domingensis*.

## RESUMEN

Se propone una nueva combinación en *Matelea*: *Matelea domingensis*.

Critical study of West Indian specimens of subtribe Gonolobinae (Apocynaceae – Asclepiadoideae) has resulted in the need for a new combination for an endemic Hispaniolan vine:

***Matelea domingensis*** (Alain) Krings, comb. nov.

Basionym: *Gonolobus domingensis* Alain, *Moscosa* 3: 46. 1978.

Type: Republica Dominicana, trepadora de 50-60 cm de largo; flores verde amarillentas; sobre rocas, al pie de un farallón, estribo sur del Isabel de Torres, Puerto Plata, alt. 750 m, 16-17 Aug 1975, Alain & Perfa Liogier 23780 (lectotype: JBSD!, here designated)

The critical character defining placement in *Gonolobus* Michx.—laminar dorsal anther appendages (Woodson 1941; Rosatti 1989; Stevens 2001)—is lacking, although mistakenly attributed to the species by Alain Henri Liogier (loc. cit., 1994). When pressed, the apically bilobed, staminal coronal segments (Cs sensu Liede & Kunze 1993, Kunze 1995) of the single prominent open flower of the type specimen were flattened in such a manner to perhaps superficially appear as dorsal anther appendages (Cd sensu Kunze 1995) (Fig. 1, A). However, close scrutiny, as well as study of an additional flower on the type (pressed sideways), reveals that the ‘appendages’ are in fact erect staminal coronal segments (Fig. 1, B; Fig. 2). Other characters that have been used to refer taxa to *Gonolobus* include winged follicles and the absence of glandular hairs (see Woodson 1941). Follicles are unknown for *Matelea domingensis*, but this character appears to be moot. Few fruit collections were apparently available to Woodson (1941) and more recent analysis has shown the character

not to be useful in generic delimitation (Krings, unpubl.). Glandular hairs, although thought characteristic of *Matelea* Aubl. by Woodson (1941), are also without circumscriptional value in the *Gonolobus-Matelea* question, being present in both the type of *Gonolobus* Michx. (i.e., *G. suberosus* (L.) R. Br.) and numerous species lacking dorsal anther appendages (Rosatti 1989). From study of *Gonolobus* species in the West Indies and the southeastern United States (including the type; see Krings & Xiang 2004), it appears that characters useful for the recognition of *Gonolobus* s.s. include the combined presence of dorsal anther appendages and cordate leaf bases, although at least *G. pubescens* Griseb., *G. stellatus* Griseb., and *G. stapelioides* Desv. ex Ham. have rounded to cuneate leaf bases. A cushion-like gynostegial corona of fused staminal and interstaminal segments that is more or less prostrate, rather than erect, is also nearly ubiquitous among West Indian and southeastern United States *Gonolobus* taxa, including *G. suberosus*, *G. martinicensis* Decne., *G. stellatus*, and *G. stephanotrichus* Griseb. It appears absent in *G. jamaicensis* Rendle, although additional material is needed for further study. A reticulate corolla, as found in *M. domingensis*, does not occur in West Indian or Southeast United States taxa bearing dorsal anther appendages (these referable to *Gonolobus*). Reticulate corollas however, are common in several West Indian taxa that bear winged follicles but lack dorsal anther appendages (see Krings, in press, a, b). On-going research aims to resolve the relationships among these taxa using molecular data. Recent progress has shown monophyly for the Gonolobinae (Liede-Schumann et al. 2005), however, with the inclusion of only five *Matelea* and *Gonolobus* taxa, intra-subtribal relationships were not a focus of the study and were not resolved. The emergence of '*Matelea gonocarpa*' (type for *Gonolobus*) within a clade of other *Gonolobus* taxa supports prior treatment of the taxon in *Gonolobus* (see Rosatti 1989; Krings & Xiang 2004). Until a better resolution is achieved and rather than maintaining two internally very polymorphic genera, taxa lacking laminar, dorsal anther appendages, including *M. domingensis*, appear best treated in *Matelea*.

Some discrepancies exist between the protologue and the type specimen for *Matelea domingensis*. Two syntypes were cited in the protologue: "Alain & Perfa Liogier 13780 (SDM, NY)"; "A. & P. Liogier & N. Melo 23348 (SDM)." As cited, "SDM" is not an

official *Index Herbariorum* acronym, rather an abbreviation for the herbarium of the Jardín Botánico Nacional Dr. Rafael M. Moscoso in Santo Domingo, Dominican Republic or JBSD. However, on the sheet at JBSD, the collection number is typed as 23780. The rest of the label information on the sheet is consistent with the protologue. A handwritten determination on the label reads: “*Gonolobus domingensis* Alain, sp. nov.” The collection number “13780” is also cited by Liogier (1994), although the collector recently indicated that it should be 23780 as on the specimen label (Liogier, pers. comm.). Specimens were requested as well from NY, however, *G. domingensis* does not appear to be part of their collections. The additional syntype “A. & P. Liogier & N. Melo 23348 (SDM)” was not included in a loan from JBSD and it remains unclear whether it is extant. Considering that no other specimens could be found, Alain & Perfa Liogier 23780 (JBSD) is here designated lectotype for *Gonolobus domingensis* Alain.

#### ACKNOWLEDGMENTS

I thank the curators and staff of the following herbaria for access to their collections or loans of specimens: BH, BM, BOLO, BREM, BRIT, C, CGE, DUKE, E, F, FI, FLAS, FR, FTG, G, GA, GH, GOET, H, HAC, HAJB, HBG, IJ, JBSD, JE, K, KY, LL, M, MICH, MIN, MISS, MO, NCU, NO, NY, O, OK, OXF, P, PH, RSA, S, TENN, TEX, U, UC, UNA, US, USCH, USF, WILLI, WU, Z. I also thank the curators and staff of the following herbaria for searching their collections for West Indian Gonolobinae material, although finding no representation: BG, BKL, BR, BUF, COLO, CR, FLAS, IA, ISC, LD, MSU, NEU, NSW, UPS, TUR. The thoughtful review of a previous version of the manuscript by Alain Liogier and Mary Endress is gratefully acknowledged.

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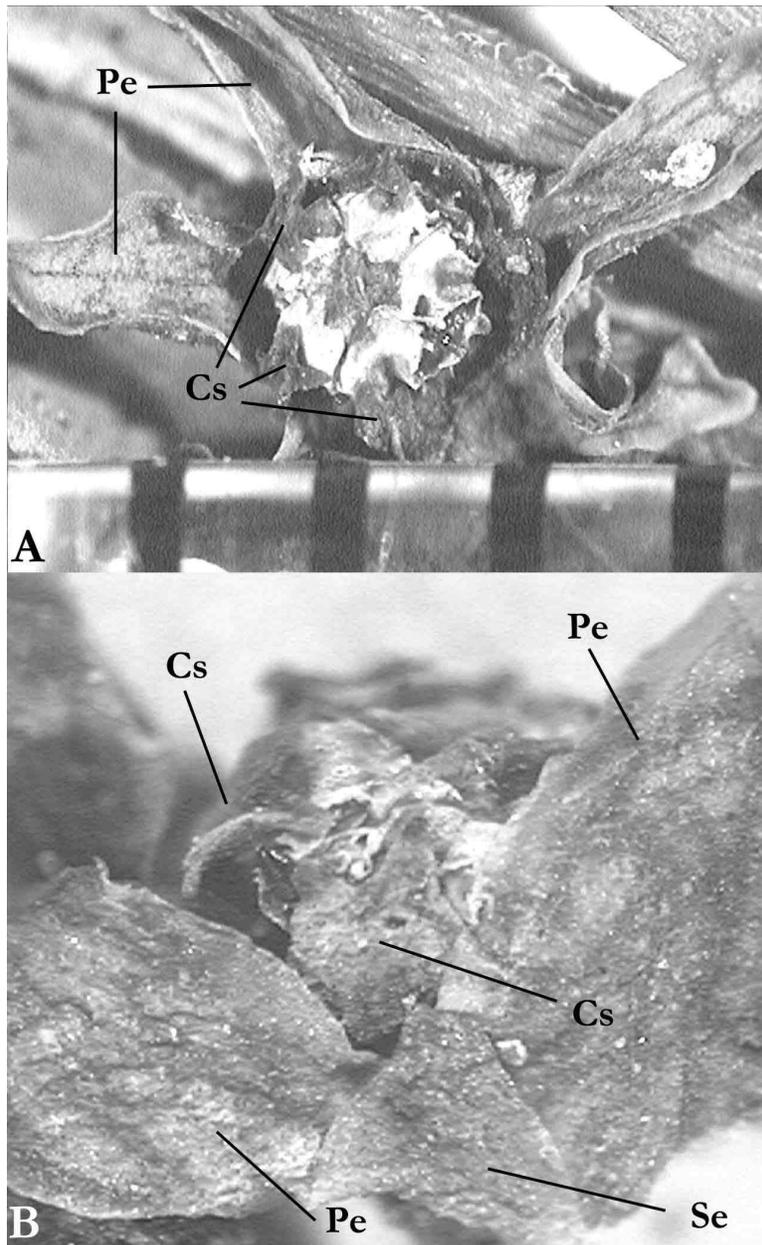


FIG. 1. Flowers of the lectotype of *Matelea domingensis* (Alain) Krings (Alain & Perfa Liogier 23780, JBSD): A, Openly pressed flower, showing reticulate petals and staminal corona segments arching over the gynostegium; B, sideways pressed flower, showing an apically bilobed, erect staminal coronal segment (center). Cs = staminal coronal segment; Pe = petal; Se = sepal. Scale in millimeters.

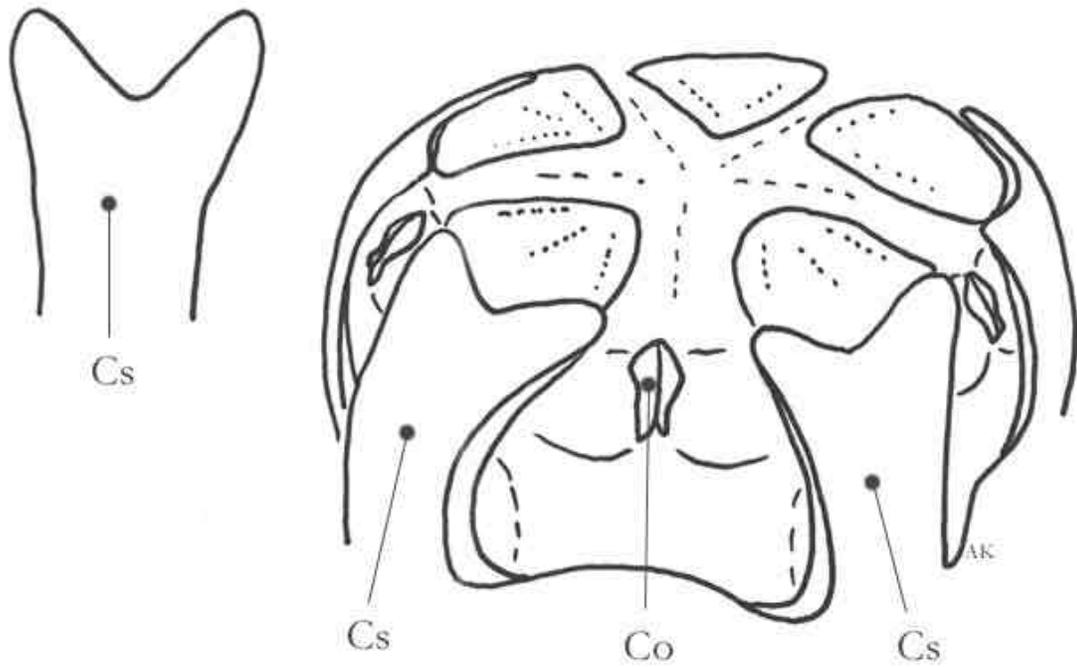


FIG. 2. Corona of *Matelea domingensis* (Alain) Krings (based on Alain & Perfa Liogier 23780, JBSD). Co = corpusculum; Cs = staminal coronal segment.

## Chapter XII

### Notes on types in Apocynaceae – Asclepiadoideae in Cuban herbaria and four lectotypifications in West Indian Gonolobinae

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Krings did all the work reported in this paper, but Dr. Paul Fantz provided scientific guidance and advice.

## ABSTRACT

Four asclepiadaceous types not listed in a previous type catalogue of the collections of the Instituto de Ecología y Sistemática, Habana, Cuba (HAC) are provided, along with a discussion of typification problems associated with the associated Charles Wright collections. Lectotypifications are provided for *Gonolobus stephanotrichus* Griseb., *Orthosia acuminata* Griseb., *Orthosia oblongata* Griseb., and *Poicilla ovatifolia* Griseb.

A revision in progress by Krings of subtribe Gonolobinae (Apocynaceae – Asclepiadoideae) in the West Indies has led to the discovery of four additional types at the Instituto de Ecología y Sistemática, Habana, Cuba (HAC). These specimens were not listed in a previous catalogue of types at HAC (Cardenas & Herrera 1991). Types in subtribe Gonolobinae were not found at the Jardín Botánico Nacional, Habana (HAJB; for a complete list see Gutiérrez et al. 1997). The expanded list of asclep types at HAC is presented in Table 1.

The asclepiadaceous original material at HAC belongs to two groups: (1) species with unproblematic typification due to designations by the original author(s) and (2) species requiring lectotypification due to complications in collecting practice and lack of holotype designations.

Typification is unproblematic for *Marsdenia micrantha* Alain, *Matelea alainii* Woodson, and *Marsdenia bicolor* Britton & P. Wilson, as these species were described relatively recently and as each original author designated holotypes. Thus, corresponding material at HAC (Table 1), was identified easily as either holotype, isotype, or paratype based on the respective protologues. An isotype of *Marsdenia bicolor* was reported previously by Cardenas & Herrera (1991), but not seen as part of this study. A paratype (*Léon 10788*) at HAC was not listed by Cardenas & Herrera (1991).

Grisebach (1866) described a number of taxa based on material collected by Charles Wright in the Antilles. These included the following four species for which original material was found at HAC and for which lectotypification is necessary: *Gonolobus stephanotrichus* Griseb., *Orthosia acuminata* Griseb., *Orthosia oblongata* Griseb., and *Poicilla ovatifolia* Griseb. (Table 1).

Grisebach studied Wright material distributed to him by Asa Gray (GH). However, these specimens were not necessarily true duplicates of a single gathering. Indeed, there have been instances of mixed material joined by a single number, as Gray appears to have provided the same number to specimens Wright may have collected from different locations on different dates (Howard 1986, 1988). Thus, Howard (1986) stated [brackets ours]:

“The determination of the type collection, therefore, depends on examining the sheet Grisebach saw and named, which is preserved in Göttingen [GOET, Universität Göttingen]. This should match one of the fragments preserved by Gray. The GOET specimens however, rarely have field tickets, so the date and location of the type collection can only be determined, if at all, from the GH sheet.”

Howard (1988) noted that Grisebach likely did not see the Wright collections sent to the Sauvalle herbarium in Habana (currently deposited in HAC), as Asa Gray distributed this material from GH. In contrast to Howard (1988), however, it should be noted that the fact that Grisebach may not have seen the Wright specimens in the Sauvalle herbarium, has no bearing on their status as original material and availability for lectotypification in the future. If judged only by this fact, according to Div. 2, Ch.2, Sect. 2, Art. 9 of the International Code of Botanical Nomenclature or ICBN (Greuter et al. 2000), they would nonetheless be considered part of the original material and, as duplicates of one cited collection, would be syntypes as articulated by Fantz (1993).

*Gonolobus stephanotrichus*. Two specimens of *Wright 2969* reside at GOET!. No field tickets accompany the GOET specimens. Both sheets include flowers and one also includes a fruit. Fruits are not described in Grisebach's protologue. Duplicates of this number are found at BREM!, G!, GH!, HAC!, K!, NY!, P!, UC!, US!, and reported for MO, although this specimen could not be obtained on loan. The collection labels of the sheets at GOET are blue and bear the dates 1856-7 crossed out. No additional dates are given. The collection labels for duplicate numbers housed everywhere else, but HAC, are white and bear the dates 1860-64 (including the MO specimen, an image of which could be seen from the Missouri Botanical Garden website: <http://www.mobot.org>). The collection label for the HAC specimen is white and bears the date 1865. This specimen is sterile and quite poor due to insect damage. Field tickets remaining with the sheet at GH seem to indicate that the three mounted fragments (all in flower) were collected at different times (Jan., Mar., Apr.). However, it is impossible to tell which fragment is associated with which field ticket and furthermore, none can be correlated with the GOET sheets, as these lack field tickets altogether. All material under the number 2969 (incl. the duplicate at HAC) does appear to belong to the same species. Thus, in light of the available facts, the *Wright 2969* sheet at GOET that bears flowers, but lacks fruit, is herein designated lectotype for *Gonolobus stephanotrichus* Griseb. This action agrees with a 1984 annotation by R.A. Howard whose lectotypification (1988) appeared in a microfiche appendix, not in print, and thus is not effectively published and has no standing in nomenclature. Rankin & Greuter (2000) reported a similar case in Antillean *Aristolochia*. The remaining extant sheets distributed under *Wright 2969* retain their status as syntypes. An additional fruiting specimen of *Gonolobus stephanotrichus* is housed at S, bearing a Wright label of 1861 and the preliminary number 164. Although a determination on the label is provided in Grisebach's hand, we do not consider the specimen original material as fruits were not mentioned in the protologue.

*Orthosia*. The only known type material for *O. acuminata* (*Wright 2966*) is deposited at BM, G, GH, HAC (2 sheets), and K. These specimens bear white labels with the dates 1860-64. The mounted field ticket on the GH sheet reads: "Asclepias – Fl. (except the

white stigma) green. Farallones San Andre Oct 27.” As *Wright 2966* (GH!) contains fifteen inflorescences and is in very good condition; it is here designated as the lectotype for *Orthosia acuminata* Griseb. *Wright 2966* (G!) contains four inflorescences and is in superior condition to the HAC material. *Wright 2966* (BM!, G!, HAC!, K!) should be considered isolectotypes.

Original material of *O. oblongata* was located at BM!, G!, GH!, HAC!, K!, and S!, and reported for MO, although the specimen could not be obtained on loan. These specimens all bear white labels with the dates 1860-64 (including the MO specimen, an image of which could be seen from the Missouri Botanical Garden website). The mounted field ticket of *Wright 2967* (GH) reads: “Asclepias – Fl. green – a white speck at the tips of the segments. Stigma white. Loma de Ranjel June 17.” Field tickets do not accompany the other specimens. *Wright 2967* (GH) is herein designated lectotype for *Orthosia oblongata* Griseb., considering the duplicates at G, HAC, K, MO (provided that the specimen does not constitute another species), and S isolectotypes. *Wright 2967* (GH) is in good condition, with numerous inflorescences.

Lectotypification decisions for both *Orthosia* names were based on the interpretation that sheets of both *Wright 2966* & *2967* are original material, as they were respectively cited in the according protologues. There is no evidence that they were collected from different localities, although this cannot be ruled out altogether, given the notorious problems with Wright collections. However, in our opinion, when there is no specific evidence to the contrary, if collection number and identification match, the protocol ought to hold that the specimens be considered duplicates of a single gathering. We recognize that “isolectotype” is not an ICBN type designation, but assign it herein should lectotypes become lost or destroyed or additional syntypes are located that we have not examined.

*Poicilla ovatifolia*. Syntype material (*Wright 2965*) was located at BM!, BREM!, G!, GH!, GOET!, HAC!, K, NY!, P!, S!, and UC! No field tickets accompany the GOET specimen or any syntype, except the GH specimen. Accompanying field tickets of the GH specimen

suggest that the sheet is comprised of at least two collections made at different times (Mar., June), although three fragments are mounted. The two fragments mounted on the right contain inflorescences; the fragment mounted on the left contains infructescences. Both field tickets refer to flowers with neither one mentioning fruits. Fruits are not described in Grisebach's protologue and are not present on any other syntype beside the GH specimen. Except for the GOET specimen, collection labels of all other known specimens are white and bear the dates 1860-64. The GOET specimen bears a tan label with a printed date of 1860, although the zero appears to have been crossed out. It is heavily written on in Grisebach's hand and is herein designated lectotype for *Poicilla ovatifolia* Griseb. The studied (and matching) duplicately-numbered material in other herbaria remain syntypes.

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TABLE 1. List of Apocynaceae – Asclepiadoideae types at the Instituto de Ecología y Sistemática, Habana, Cuba (HAC). Previously unlisted types (Cardenas & Herrera 1991) are marked by an asterisk.

**(1) Species with unproblematic typification:**

\**Marsdenia bicolor* Britton & P. Wilson, Bulletin of the Torrey Botanical Club 50: 47. 1923.

TYPE: CUBA. *Léon 10787* (Isotype: not seen); *Léon 10788* (Paratype!)

*Marsdenia micrantha* Alain, Revista de la Sociedad Cubana de Botánica 13: 59. 1956.

TYPE: CUBA. *Alain, Acuña & López 5678* (Holotype, Isotype, not seen)

*Matelea alainii* Woodson, Contribuciones Ocasionales del Museo de Historia Natural del Colegio "De La Salle" 15: 23-24. 1956.

TYPE: CUBA. *Alain & Morton 5029* (Isotype!)

**(2) Species lectotypified herein (see text):**

*Gonolobus stephanotrichus* Griseb., Catalogus plantarum cubensium 177. 1866.

TYPE: CUBA. *Wright 2969* (Syntype!)

\**Orthosia acuminata* Griseb., Catalogus plantarum cubensium 175. 1866.

TYPE: CUBA. *Wright 2966* (Isolectotype!)

\**Orthosia oblongata* Griseb., Catalogus plantarum cubensium 176. 1866.

TYPE: CUBA. *Wright 2967* (Isolectotype!)

\**Poicilla ovatifolia* Griseb., Catalogus plantarum cubensium 177. 1866.

TYPE: CUBA. *Wright 2965* (Syntype!)

## Chapter XIII

### Four novelties and a lectotypification in *Matelea* (Apocynaceae: Asclepiadoideae) from Hispaniola

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Reproduced from Krings, A. 2006. *Sida* 22: 941–953.

#### ABSTRACT

On-going study of subtribe Gonolobinae (Apocynaceae: Asclepiadoideae) in the West Indies resulted in the discovery of four new species from Hispaniola: *Matelea corynephora*, *M. phainops*, *M. rhynchocephala*, and *M. torulosa*. *Matelea pauciflora* is lectotypified.

#### RESUMEN

Se describen cuatro especies nuevas de *Matelea* de la Española como resultado del estudio de la subtribu Gonolobinae (Apocynaceae: Asclepiadoideae) en las Indias Occidentales: *Matelea corynephora*, *M. phainops*, *M. rhynchocephala* y *M. torulosa*. Se lectotipifica *Matelea pauciflora*.

*Gonolobus pauciflorus* Spreng. (Apocynaceae: Asclepiadoideae) was described in 1824 based on a Bertero specimen from Hispaniola (P!). Schlechter (1899) recognized the species, noting that at the time, it still remained known only from the Bertero collection. Erik Ekman subsequently contributed numerous new collections that were referred to *G. pauciflorus* by Ignatz Urban of B (fide annotations) and later accepted as well by Alain H. Liogier (fide annotations), author of the most recent treatment of Asclepiadoideae for Hispaniola (Liogier 1994). Woodson (1941) transferred *G. pauciflorus* to *Matelea* Aubl. as one of 105 new combinations that resulted in a very broadly circumscribed genus that is, in large part, still currently followed (see Stevens 2005). According to Woodson's (1941) generic concept, *Matelea* is distinguished from *Gonolobus* Michx. in part by the absence of laminar dorsal anther appendages (Cd sensu Kunze 1995) in the former. A seemingly

related species—*Matelea linearipetala* Alain—was described in 1988 from a single 1926 Haitian specimen (*Ekman H7136*, S!) not seen by Urban. However, in the course of ongoing systematic study of subtribe Gonolobinae in the West Indies, it has become clear that *M. pauciflora* (Spreng.) Woodson sensu Urban and Liogier contains four additional undescribed species. The four new species are described and illustrated below. For clarity, amplified descriptions, as well as illustrations, are also provided for *M. linearipetala* and *M. pauciflora*. The six species are nearly indistinguishable in the absence of flowers—each bearing small, opposite, ovate-oblong leaves—but differ dramatically in various floral characteristics. A key follows. Corona terminology primarily follows Liede and Kunze (1993) and Kunze (1995), although it is recognized that additional work is needed to clarify family-wide homology (see Endress & Bruyns 2000; Livshultz 2003).

1. Calyx colleters 2 per sinus; long eglandular sharp trichomes (ca. 0.2 mm) of the pedicels retrorse; corolla lobes ocellate (i.e., each bearing a single white spot on the adaxial surface near the apex); gynostegial corona (C(is)) columnar at the base and appearing as a ca. 0.6 mm tall stipe; stylar head lacking a terminal appendage .....*M. phainops*
1. Calyx colleters 0–1 per sinus; long eglandular sharp trichomes of the pedicels predominantly, if not exclusively, antrorse or spreading; corolla lobes ocellate or not; gynostegial corona (C(is)) not basally columnar nor appearing as a stipe; stylar head with or without a terminal appendage..... 2.

2. Gynostegial corona (C(is)) with a broad, hardening, lobe-like, translucent yellow-golden secretion in the interstaminal position (i.e., between the raised portions of the corona segments that rise to meet the lower portion of the anther in the staminal position); interstaminal gynostegial corona (Ci) unlobed; anther wings horizontally divergent; stylar head exhibiting a terminal appendage or not..... 3.
2. Gynostegial corona (C(is)) lacking a hardening, lobe-like, translucent yellow-golden secretion in the interstaminal position; interstaminal gynostegial corona (Ci) lobed (or if not, then the stylar head with a knob-shaped terminal appendage); anther wings horizontally convergent at least at the apex or parallel; stylar head exhibiting a terminal appendage ..... 4.
3. Gynostegial corona (C(is)) ca. 0.6–0.7 mm tall, staminal gynostegial corona (Cs) unlobed apically (i.e., descending smoothly in an arc from the apical ridge to the base); anther wings slightly longer than the corpusculum; terminal appendage of stylar head absent, sometime a short protuberance present, to 0.2 mm tall.....*M. linearipetala*
3. Gynostegial corona (C(is)) > 1 mm tall, staminal gynostegial corona (Cs) slightly vertically lobed apically (i.e., each ridge slightly rising vertically immediately before descending to the base); anther wings slightly shorter than the corpusculum; terminal appendage of stylar head conic (volcano-shaped; broader at the base than at the apex), 0.9–1.2 mm tall .....*M. pauciflora*
4. Calyx colleters absent; corolla lobe bases each with two round, distinct, lateral thickenings, basal lobe surfaces concave (“scooped-out”); interstaminal gynostegial corona

- (Ci) unlobed, staminal gynostegial corona (Cs) apically ungrooved, unlobed laterally, scallop-shaped in broad outline, margins entire or somewhat undulating; anther wings parallel; terminal appendage of stylar head capitate (e.g., reminiscent of a round door knob), to 1.1 mm tall .....*M. torulosa*
4. Calyx colleters 1 per sinus; corolla lobe bases lacking round lateral thickenings, lobes plane; interstaminal gynostegial corona (Ci) shallowly to broadly lobed, staminal gynostegial corona (Cs) apically grooved or laterally lobed, not scallop-shaped; anther wings convergent at least apically; terminal appendage of stylar head clavate or narrowly elongate-conic (obelisk-shaped), > 1.8 mm tall ..... 5.
5. Interstaminal gynostegial corona (Ci) a large lobe, staminal gynostegial corona (Cs) grooved apically, lacking two broad, lateral lobes; terminal appendage of stylar head clavate .....*M. corynephora*
5. Interstaminal gynostegial corona (Ci) a shallow lobe, staminal gynostegial corona (Cs) apically not grooved, broadly lobed laterally to appear 3-lobed; terminal appendage of stylar head narrowly elongate-conic (obelisk-shaped).....*M. rhynchocephala*

***Matelea corynephora*** Krings, sp. nov. (Fig. 1)

Type: HAITI. Ile la Tortue, la Vallée, top of Morne Barranca, c. 300 m, 21 Mar 1928 (fl),

*E.L. Ekman H9740* (holotype: S!).

*Species nova* Matelea Aubl. differt a *Matelea antillanarum* corona magnilobata  
*interstaminer, non lobata staminer, gynostegio corynephor.*

Slender, woody vine. Latex unknown. Stems ca. 1.8 mm diam., pubescent, glandular-capitate trichomes throughout, ca. 0.09 mm long, eglandular sharp trichomes mostly in 2 lines, one on each side of the stem, retrorse, ca. 0.4 mm long. Leaves opposite, simple, blades oblong to linear-oblong, (7.2)12–25 x (3.6)5.2–8.6 mm, apex obtuse, apiculate, base broadly cuneate to rounded, margins entire, adaxial surface dark green, glossy on drying, glabrous or minutely pubescent along midvein with short glandular-capitate trichomes, abaxial surface pubescent along midvein and sometime secondary veins, trichomes mostly glandular-capitate, eglandular sharp trichomes few and scattered, colleters 2; petioles 3.8–7 x ca. 0.6 mm, glandular-capitate trichomes dense, ca. 0.1 mm long, eglandular sharp trichomes dense, antrorse, ca. 0.2 mm long, both trichome types found throughout, but the longer sharp trichomes tending to be slightly denser along the adaxial petiolar ridge; stipular colleters 2, one on each side of petiole base, ca. 0.3 mm long. Inflorescence racemiform, peduncles 0.6–1.7 x ca. 1 mm, glandular capitate trichomes absent, eglandular sharp trichomes 0.2–0.3 mm long, antrorse; pedicels 3–5 x ca. 0.6 mm, glandular-capitate trichomes dense, ca. 0.04 mm long, longer eglandular sharp trichomes dense, ca. 0.2 mm long, antrorse. Calyx 5-lobed, lobes oblong-ovate, ca. 0.9 x 0.6 mm, apices obtuse, margins entire, adaxial surface glabrous, abaxial surface very sparsely pubescent with eglandular trichomes scattered near center and along the margins; colleters 1 per sinus. Corolla subrotate, bases campanulate, tube ca. 0.9–1.2 x 1.2–1.3 mm, 5-lobed, lobes imbricate in bud (not or only slightly dextrorse), green (fide collectoris), lanceolate-linear,

4.5–5.5 x 1.6–1.8 mm, apex obtuse, at least some ocellate (i.e., each lobe bearing a white eye adaxially at its apex), adaxial surface glabrous, abaxial surface glabrous or very sparsely pubescent with trichomes eglandular. Faucal annulus (corolline corona or Ca) indistinct. Gynostegial corona of fused staminal (Cs) and interstaminal parts (Ci), ca. 0.7 mm tall, not appearing as a stipe, Cs rising to meet the bottom of the anther, rising segment lacking two broad, lateral lobes, but grooved apically, Ci broadly lobed; laminar dorsal anther appendages (Cd) absent. Pollinarium: corpuscula dark reddish-brown, ca. 0.15 mm long; pollinia borne horizontally or with the cavity slanting upwards at an angle, ovate, ca. 0.37 x 0.27 mm. Styler head with a terminal appendage, appendage clavate, 1.9–2.2 mm long, 1.4–1.5 mm wide at the apex, generally broader at the apex than at the base, papillate throughout, a tuft of eglandular sharp trichomes present in the center of the apex, trichomes ca. 0.3 mm long. Follicles unknown. Apparently endemic to Haiti [known only from the type].

The specific epithet refers to the conspicuous, clavate, terminal styler head appendage.

*Matelea corynephora* appears closely related to *M. rhynchocephala* (Fig. 5) and *M. torulosa* (Fig. 6)—both latter species also exhibiting a styler head with a terminal appendage. All three can be easily distinguished by the shape of the gynostegial corona, as well as that of the appendage (see key above and Figs. 1, 5–6). All three lack the broad, translucent yellow-golden, hardening secretions in the interstaminal position as seen in *M. linearipetala* (Fig. 2) and *M. pauciflora* (Fig. 3).

*Matelea linearipetala* Alain, Phytologia 64: 346. 1988. (Fig. 2)

Type: HAITI. On olig. limestone, c. 200 m, Massif des Matheux, Thomazeau, Morne à Cabrits, a vine, fr. "luteis," Oct. 24, 1926 (fl & fr), *E.L. Ekman H7136* (holotype: S!)  
[n.v. Urban]

Slender, woody vine. Latex unknown. Stems ca. 0.9 mm diam., pubescent in two lines, less densely so with age, glandular-capitate trichomes, ca. 0.08 mm long, eglandular sharp trichomes to 0.45 mm long, retrorse. Leaves opposite, simple, blades oblong, oblong-ovate, or ovate, 17–45 x 9–21 mm, apices obtuse to rounded, apiculate, bases rounded to truncate, margins entire, adaxial surface dull glabrous, except minutely pubescent along the midvein, glandular-capitate trichomes ca. 0.08 mm long, eglandular sharp trichomes absent, abaxial surface glabrous, except minutely pubescent along the veins, glandular-capitate trichomes ca. 0.08 mm long, eglandular sharp trichomes very sparse if present, ca. 0.2 mm long, colleters 2; petioles 4.4–17 x ca. 0.4 mm, densely pubescent throughout, glandular-capitate trichomes ca. 0.07 mm long, eglandular sharp trichomes very sparse, ca. 0.3 mm long, antrorse to antrorse-appressed; stipular colleters 2, one on each side of petiole base, ca. 0.3 mm long. Inflorescence racemiform, peduncles 0.6–2 x ca. 0.7 mm, essentially glabrous; pedicels 2.5–5 x ca. 0.7 mm, densely pubescent throughout, glandular-capitate trichomes ca. 0.08 mm long, eglandular sharp trichomes absent or more or less uniform throughout, though sparsely so, ca. 0.18 mm long, predominantly antrorse or spreading. Calyx 5-lobed, lobes lanceolate to ovate-oblong, 1.7–2 x 0.8–1.2 mm, apices obtuse, pubescent, glandular-capitate trichomes ca. 0.08 mm long; colleters 1 per sinus. Corolla

subrotate, bases subcampanulate, tube ca. 0.8 x 1 mm, 5-lobed, lobes imbricate in bud (not or only slightly dextrorse), green (fide collectoris), apparently not ocellate, linear lanceolate, 4.8–6.5 x 1.6–2 mm, apices obtuse, margins entire, adaxial surface glabrous, reticulate at least on drying, abaxial surface glabrous, except tube pubescent, glandular-capitate trichomes ca. 0.08 mm long. Faucal annulus (corolline corona or Ca) indistinct. Gynostegial corona of fused staminal (Cs) and interstaminal parts (Ci), Cs rising to meet the lower portion of the anther, rising segment a narrow ridge, triangular when viewed directly from the front, neither laterally nor vertically lobed, ca. 0.67 mm tall, Ci unlobed, exhibiting a broad, hardening, lobe-like, translucent yellow-golden, secretion; anther wings with divergent apices, only nearly touching at the base immediately subtending the corpusculum, vertical length immediately subtending corpusculum ca. 0.09 mm long, horizontal length ca. 0.15 mm long; laminar dorsal anther appendages (Cd) absent. Pollinaria: corpuscula dark reddish-brown, ca. 0.15 mm long; pollinia borne horizontally, ovate, ca. 0.34 x 0.2 mm. Styler head lacking a pronounced terminal appendage, sometimes exhibiting a slightly raised, circular or angular protuberance, ca. 0.2 mm tall. Follicle (immature?) 3.7 x 1.4 cm, 5-winged, wings interrupted and appearing as dentate lobes, surface appearing glabrous, but minutely papillate throughout. Seeds unknown. Apparently endemic to Haiti.

ADDITIONAL SPECIMENS SEEN: HAITI. Massif des Cabos, Les Gonaïves, Petite-Gouyne, dry limestone region, hillsides, in thickets, vine, fl. green, c. 150 m, 26 Sep 1927 (fl), *E.L. Ekman H9067* (C!, GH!, S!) [Referred to *G. pauciflorus* by Urban and *M. pauciflora* by Liogier fide annotations. A handwritten note in pencil by Ekman on the S sheet indicates

Ekman's suspicion of its novelty, although without recognizing salient characters: "Seems to come close to *G. pauciflorus*, but the umbellae are mostly one-flowered and the peduncle very short."]; Ile la Gonave, Pte-à-Raquettes, hillsides, fl. green, 3 Aug 1927 (fl), *E.L. Ekman H8809* (US!, S!) [Referred to *G. pauciflorus* by Urban and *M. pauciflora* by Liogier fide annotations. Ekman's handwritten note in pencil on the S sheet adds to the locality information: "I have not analyzed the flowers but the veg. characters seem to agree fairly well with this [*G. pauciflorus*]. Better plant. Coll. before!" However, "*pauciflorus*" was crossed out in pencil and a question mark placed above the epithet, suggesting perhaps a later second-guess by Ekman.].

***Matelea pauciflora*** (Spreng.) Woodson, Ann. Missouri Bot. Gard. 28: 226. 1941. (Fig. 3)

Basionym: *Gonolobus pauciflorus* Spreng., Systema Vegetabilium, editio decima sexta 1: 846. 1824.

Type: HISPANIOLA. 'St. Dominique,' *Bertero s.n.* (lectotype: P!, here designated).

Slender, woody vine. Latex unknown. Stems ca. 1.7 mm diam., pubescent throughout or in two lines, glandular-capitate trichomes ca. 0.07 mm long, eglandular sharp trichomes ca. 0.3 mm long, retrorse. Leaves opposite, simple, blades oblong or ovate, 8.5–56.5 x 5.3–27.8 mm, apices obtuse, bases rounded to truncate, margins entire, adaxial surface dull, glabrous except minutely pubescent along midvein, glandular-capitate trichomes ca. 0.05 mm long, eglandular sharp trichomes sparsely scattered, ca. 0.18 mm long, abaxial surface glabrous except pubescent along the veins, glandular-capitate trichomes ca. 0.08 mm long,

eglandular sharp trichomes sparsely scattered, ca. 0.4 mm long, colleters 2; petioles 3.6–22.2 x ca. 0.4 mm, densely pubescent throughout, glandular-capitate trichomes ca. 0.1 mm long, eglandular sharp trichomes scattered throughout, ca. 0.23 mm long, predominantly antrorse or spreading; stipular colleters 2, one on each side of petiole base, ca. 0.2 mm long. Inflorescence racemiform, peduncles to 5 x ca. 0.4 mm, glabrous or pubescent, glandular-capitate trichomes ca. 0.08 mm long, eglandular sharp trichomes sparse, ca. 0.36 mm long, antrorse or spreading; pedicels to 9 x ca. 0.4 mm, densely pubescent, glandular-capitate trichomes ca. 0.05 mm long, eglandular sharp trichomes ca. 0.3 mm long, predominantly antrorse or spreading. Calyx 5-lobed, lobes lanceolate to lance-ovate, 1.3–2.5 x 0.4–1 mm, apices obtuse, bases pubescent, glandular-capitate trichomes ca. 0.05 mm long, margins with eglandular sharp trichomes ca. 0.1 mm long, otherwise glabrous; colleters 1 per sinus. Corolla subrotate, bases subcampanulate, tube ca. 0.9 x 1.2 mm, 5-lobed, lobes imbricate in bud (not dextrorse), green (fide collectoris), apparently not ocellate, linear-lanceolate, 4.7–7.5 x 2–2.8 mm, apices obtuse, margins entire, adaxial surface glabrous, abaxial surface glabrous, except tube pubescent, glandular-capitate trichomes ca. 0.05 mm long. Faucal annulus (corolline corona or Ca) indistinct. Gynostegial corona of fused staminal (Cs) and interstaminal (Ci) parts, Cs rising to meet the lower portion of the anther, rising segment swollen at the base, slightly vertically lobed along the apical ridge, ca. 1.25 mm tall, Ci unlobed, exhibiting a broad, hardening, lobe-like, translucent yellow-golden, secretion; anther wings with divergent apices, only nearly touching at the base immediately subtending the corpusculum, vertical length immediately subtending corpusculum ca. 0.08 mm long, horizontal length ca. 0.18 mm; laminar dorsal anther appendages (Cd) lacking. Pollinarium: corpuscula dark reddish-brown, 0.18–0.2 mm long; pollinia borne horizontally

or at a slightly upwards angle, oblong, ca. 0.42 x 0.24 mm. Styler head with a terminal appendage, appendage volcano-shaped, ca. 0.9–1.2 mm tall. Follicle unknown. Haiti and Dominican Republic.

Although bearing a conic terminal appendage of the styler head, *M. pauciflora* (Fig. 3) appears more closely related to *M. linearipetala* (Fig. 2) than the other three terminally-appendaged species—*M. corynephora* (Fig. 1), *M. rhynchocephala* (Fig. 5), and *M. torulosa* (Fig. 6)—based on the shape of the gynostegial corona, the presence of broad, hardening, lobe-like, translucent yellow-golden, secretion in the interstaminal position, and the shape of the anther wings. *Matelea linearipetala* lacks a terminal appendage of the styler head and can be additionally distinguished from *M. pauciflora* by the height and shape of the gynostegial corona (Fig. 2).

ADDITIONAL SPECIMENS SEEN: HAITI. Départ. d'Artibonite, in a little valley not far from Mirabalais, shrubby Laubwald, 26 Oct 1924 (fl), *E.L. Ekman H2266* (GH!, IJ!, NY!, US!) [The sheet at US additionally includes the text: “on roadside, rare, 150 m.” Annotations referring the specimens here appear by Urban, Woodson, and Liogier. Ekman slips in pencil are lacking.]; Massif du Nord, Hinche, Morne Juan-Gomez, oligocene limestone, in thickets, c. 700 m, 23 May 1926 (fl), *E.L. Ekman H6171* (K!, S!) [In referring the collection only to *Poicillopsis*, Ekman's handwritten note in pencil on the S sheet indicates his unfamiliarity with the taxon. This specimen is the second earliest of his collections in the *M. pauciflora* “complex.” He is correct in noting “same as n. 2266.”]. DOMINICAN REPUBLIC. Prov. Azua, Cordillera Central, 5 km al S del Pueblo de Padre Las Casas, en una

lomita situada en el lado E de la carretera hacia Las Yayas, bosque seco con *Ziziphus*, *Agave* y *Bursera*, 18° 41'N, 70° 55'W, elev. 680-700 m, 2 Oct 1987 (fl), *R. Garcia y J. Pimentel 2531* (MO!) [Referred only to *Matelea* prior to this study]; Bani, vine flowers greenish, in thickets, 24 Sep 1966 (fl), *Bro. B.A. Lavastre 2290* (NY!) [Referred here by Liogier fide annotation].

***Matelea phainops*** Krings, sp. nov. (Fig. 4)

Type: DOMINICAN REPUBLIC. Vine, up to 1.5 m high, flowers yellowish green, in thickets, about 2 mi W of Oviedo, alt. about sea level, on limestone, 3 Nov 1989 (fl), *A.H. Liogier 16617* (holotype: GH!; isotypes: NY!, USF!).

*Species nova* *Matelea* *Aubl. differt a* *Matelea antillanarum forma coronae et gynostegi* (v. *Fig. 4*).

Slender, woody vine. Latex unknown. Stems ca. 2.12 mm diam., pubescent, glandular-capitate trichomes throughout, ca. 0.12 mm long, eglandular sharp trichomes mostly in 2 lines, one on each side of the stem, retrorse, ca. 0.36 mm long. Leaves opposite, simple, blades oblong or ovate, (8)12–31 x (4)6–14 mm, apices obtuse, apiculate, bases broadly cuneate to rounded or subtruncate, margins entire, adaxial surface dull to somewhat glossy on drying, glandular-capitate trichomes throughout, but most dense along the veins, ca. 0.13 mm long, eglandular sharp trichomes scattered on midvein or absent, to 0.4 mm long, abaxial surface glabrous, except for short glandular-capitate trichomes along the vines, ca.

0.05 mm long, colleters 2–3; petioles to 10 x ca. 0.6 mm, glandular-capitate trichomes dense, ca. 0.1 mm long, eglandular sharp trichomes occasional or scattered, antrorse, ca. 0.22 mm long; stipular colleters 2, one on each side of petiole base, ca. 0.23 mm long. Inflorescence racemiform, peduncles to ca. 2.5 x 0.6 mm, glandular-capitate trichomes dense throughout, ca. 0.08 mm long, eglandular sharp trichomes scattered, spreading or antrorse, 0.17–0.2 mm long; pedicels 4–7 x ca. 0.36 mm, short trichomes both capitate and sharp, dense, ca. 0.09 mm long, longer eglandular sharp trichomes, if present, scattered and retrorse, ca. 0.2 mm long. Calyx 5-lobed, lobes ovate, 0.85–1.3 x 0.6–0.9 mm, apices obtuse, margins entire, glabrous, adaxial surface glabrous, abaxial surface minutely glandular pubescent; colleters 2 per sinus. Corolla subrotate, bases subcampanulate, tube ca. 0.4 x 0.5 mm, 5-lobed, lobes imbricate in bud (not or only slightly dextrorse), oblong-linear, 2.5–2.7 x 1.2–1.4 mm (width at base), apex obtuse, yellowish green (fide Liogier), each lobe bearing a white eye at its apex, adaxial surface glabrous, abaxial surface glabrous, except tube pubescent, glandular trichomes ca. 0.09 mm. Faucal annulus (corolline corona or Ca) indistinct. Gynostegial corona of fused staminal (Cs) and interstaminal parts (Ci), basally fused and appearing as a stipe, ca. 0.6 mm tall, upper Cs undulating, rising to meet the bottom of the anther in the staminal position, Ci unlobed; laminar dorsal anther appendages (Cd) absent. Pollinarium: corpuscula dark reddish-brown, ca. 0.13 mm long; pollinia borne horizontally, ovate, ca. 0.4 x 0.2 mm. Styler head lacking a terminal appendage. Follicles unknown. Apparently endemic to the Dominican Republic [known only from the type].

This vine is named in honor of my wife, the ‘Bright eyes’ in my life. The epithet also reflects the ocellate corolla lobes exhibited by this species.

*Matelea phainops* appears related to the Cuban *Matelea oblongata*, *M. acuminata*, and *M. nipensis* (Urb.) Woodson and, perhaps, Jamaican *Jacaima costata* (Urb.) Rendle. It is one of several mostly West Indian taxa exhibiting ocellate corolla lobes. Continental representatives likely include *M. pusilliflora* W.O. Williams, *M. ocellatus* W.D. Stevens, and the recently described *M. emmartinezii* W.D. Stevens. In addition to the aforementioned, small flowered species, larger flowered taxa likely belonging to the complex in the West Indies include *M. bayatensis* (Urb.) Woodson, *M. correllii* Spellman, and *M. tigrina* (Griseb.) Woodson. The latter may not be specifically distinct (see Krings 2005). The morphology of the gynostegial corona is variable in the group—from indistinct to well-developed—and additional research is necessary to clarify specific relationships.

***Matelea rhynchocephala*** Krings, sp. nov. (Fig. 5)

Type: DOMINICAN REPUBLIC. Prov. Santiago, Valle del Cibao, Santiago, Hato del Yaque, in thickets, fl. green, fruiting, 15 Feb 1930 (fl & fr), *E.L. Ekman HI4296* (holotype: S!)  
[n.v. Urban; referred to *M. pauciflora* by Liogier fide annotation]

*Species nova* *Matelea* *Aubl. differt a* *Matelea antillanarum corona parvilobata interstaminer, lobata staminer, gynostegio rhynchophoro* .

Slender, woody vine. Latex unknown. Stems ca. 1.2 mm diam., densely pubescent throughout, though 2 lines somewhat evident on older stems, glandular-capitate trichomes ca. 0.06 mm long, eglandular sharp trichomes ca. 0.4 mm long, retrorse or spreading. Leaves opposite, simple, blades oblong or ovate, 19–48 x 7–20 mm, apices obtuse, apiculate, bases rounded to truncate, margins entire, adaxial surface dull on drying, not glossy, glabrous or pubescent along the midvein, glandular-capitate trichomes ca. 0.1 mm long, eglandular sharp trichomes absent or essentially so, abaxial surface glabrous, pubescent along the veins, glandular-capitate trichomes ca. 0.1 mm long, eglandular sharp trichomes to 0.2 mm long, colleters 2; petioles to 14 x ca. 0.45 mm, densely pubescent, glandular-capitate trichomes ca. 0.07 mm long, eglandular sharp trichomes ca. 0.3 mm long, throughout, antrorse; stipular colleters 2, one on each side of petiole base, ca. 0.2 mm long. Inflorescence racemiform, peduncles ca. 0.8 x 0.5 mm, pubescence as that of stems; pedicels 1.7–1.8 x ca. 0.44 mm, densely pubescent, glandular-capitate trichomes ca. 0.09 mm long, eglandular sharp trichomes ca. 0.2 mm long, antrorse or spreading. Calyx 5-lobed, lobes lanceolate, 1.5–1.6 x 0.5–0.6 mm, glandular-capitate trichomes mostly at the base, ca. 0.07 mm long, glandular sharp trichomes mostly near the middle, ca. 0.2 mm long; colleters 1 per sinus. Corolla subrotate, bases subcampanulate, tube ca. 1 x 1 mm, 5-lobed, lobes imbricate in bud (not or only slightly dextrorse), green (fide collectoris), linear-lanceolate, 4.9–5.9 x 1.1–1.4 mm, apex obtuse, margins white, adaxial surface glabrous, abaxial surface glabrous in age, except tube densely pubescent, glandular-capitate trichomes ca. 0.07 mm long. Faucal annulus (corolline corona or Ca) indistinct. Gynostegial corona of fused staminal (Cs) and interstaminal (Ci) parts, Cs rising to meet the lower portion of the anther, rising segment with a single, broad lobe on either side, ca.

0.8–0.9 mm tall, Ci shallowly lobed; anther wings triangular in frontal view, nearly touching; laminar dorsal anther appendages (Cd) absent. Pollinarium: corpuscula dark reddish-brown, ca. 0.3 mm long, pollinia borne horizontally or with the cavity slanting upwards at an angle, ovate, ca. 0.4 x 0.25 mm. Stylar head with a terminal appendage, appendage narrowly elongate-conical (obelisk-shaped), 2.8–3.3 x 0.6–0.8 mm, papillate, apex obtuse, with a tuft of eglandular trichomes or glabrous. Follicles ovate, 5.3–1.9 cm, 5-winged, wings interrupted and appearing as dentate lobes, glabrous. Seeds ovate, ca. 4.9 x 3.4 mm, glabrous, margins smooth, neither warty, nor dentate. Apparently endemic to the Dominican Republic.

The specific epithet refers to the obelisk-shaped or snout-like terminal appendage of the stylar head.

*Matelea rhynchocephala* (Fig. 5) appears most closely related to *M. corynephora* (Fig. 1) of Haiti. Notable differences between the two are the shape of the terminal appendage of the stylar head (obelisk-shaped in *M. rhynchocephala* vs. clavate in *M. corynephora*) and the shape of the gynostegial corona (Figs. 1 & 5).

ADDITIONAL SPECIMENS SEEN: DOMINICAN REPUBLIC. El Rubio, 22 Nov 1940 (fl), *M. Canela s.n.* (NY!) [Referred to *M. pauciflora* by Liogier fide annotation].

*Matelea torulosa* Krings, sp. nov. (Fig. 6)

Type: DOMINICAN REPUBLIC. Distr. Nacional, Los 3 Ojos de Agua, near Santo Domingo, 31 Oct 1959 (fl), *E. Marcano [J.J. Jiménez]* 4096 (holotype: US!) [referred to *M. pauciflora* by Liogier fide annotation].

*Species nova* *Matelea Aubl. differt a Matelea antillanarum corona non lobata interstaminer, non lobata staminer, gynostegio toruloso.*

Slender, woody vine. Latex unknown. Stems ca. 1.2 mm diam., densely pubescent in two lines, glandular-capitate trichomes ca. 0.05 mm long, eglandular sharp trichomes ca. 0.4 mm long, retrorse. Leaves opposite, simple, blades oblong or ovate, 9–28 x 3–8.8 mm, apices obtuse, apiculate, bases rounded or broadly cuneate, margins entire, adaxial surface dull, glabrous except pubescent along the midvein, glandular-capitate trichomes ca. 0.07 mm long, eglandular sharp trichomes sparse, to 0.18 mm long, abaxial surface pubescent primarily along the veins, glandular-capitate trichomes ca. 0.1 mm long, eglandular sharp trichomes to 0.4 mm long, colleters 2–3; petioles 2–6 x ca. 0.4 mm, densely pubescent throughout, glandular-capitate trichomes ca. 0.05 mm long, eglandular sharp trichomes ca. 0.33 mm long, antrorse to antrorse-appressed, not spreading or rarely so; stipular colleters 2, one on each side of petiole base, ca. 0.22 mm long. Inflorescence racemiform, peduncles to 4.9 x ca. 0.7 mm, densely pubescent throughout, glandular-capitate trichomes ca. 0.07 mm long, eglandular sharp trichomes ca. 0.2 mm long, predominantly antrorse, some retrorse, sparser than glandular-capitate trichomes; pedicels 4.5–6.1 x 0.4 mm, densely pubescent, glandular-capitate trichomes ca. 0.07 mm long, eglandular sharp trichomes ca. 0.18 mm long, predominantly antrorse or antrorse appressed. Calyx 5-lobed, lobes

lanceolate or lance-ovate, ca. 1.8 x 0.8 mm, apices obtuse, margins entire, scattered pubescent, glandular-capitate trichomes to 0.07 mm long, eglandular sharp trichomes to 0.2 mm long; colleters lacking. Corolla subrotate, bases subcampanulate, tube 0.9 x 1 mm, 5-lobed, lobes imbricate in bud (not dextrorse), linear-lanceolate, 4.5–5 x 1.3–1.6 mm, apices obtuse, margins entire, marginally thickened at the base on each side, scooped-out and forming a distinct pit near the base, otherwise plane, adaxial surface papillate, abaxial surface glabrous or with a few, eglandular sharp trichomes ca. 0.2 mm long. Faucal annulus (corolline corona or Ca) indistinct. Gynostegial corona of fused staminal (Cs) and interstaminal (Ci) parts, Cs rising to meet the lower portion of the anther, rising segment scallop-shaped in outline, ca. 0.5 mm tall, not lobed on either side, yet exhibiting a smaller segment immediately in front, margins somewhat undulating to entire, Ci unlobed; anther wings parallel, nearly touching, well-developed toward the center of the stylar head, ca. 0.4–0.5 mm long, the vertical segment immediately subtending the corpusculum ca. 0.2 mm long, slightly longer than the corpusculum or as long; laminar dorsal anther appendages (Cd) absent. Pollinarium: corpuscula dark reddish-brown, ca. 1.8–1.9 mm long; pollinia borne horizontally, ovate, ca. 0.37 x 0.25 mm. Stylar head with a terminal appendage, appendage capitate (“door knob-shaped”), ca. 1–1.1 mm tall, apex ca. 1 mm broad. Follicles unknown. Apparently endemic to the Dominican Republic [known only from the type].

The epithet refers to the capitate, door knob-like terminal appendage of the stylar head.

The appendage is among the shortest of the four species bearing them in Hispaniola. Only *Matelea corynephora* (Fig. 1) exhibits an appendage similarly broader at the apex than at

the base, but the appendage is much longer than in *M. torulosa* and clavate. The two species also differ in a number of additional floral characteristics, such as the morphology of the gynostegial corona. The other appendaged species—*M. pauciflora* (Fig. 3) and *M. rhynchocephala* (Fig. 5)—exhibit terminal appendages that are narrower at the apex than at the base.

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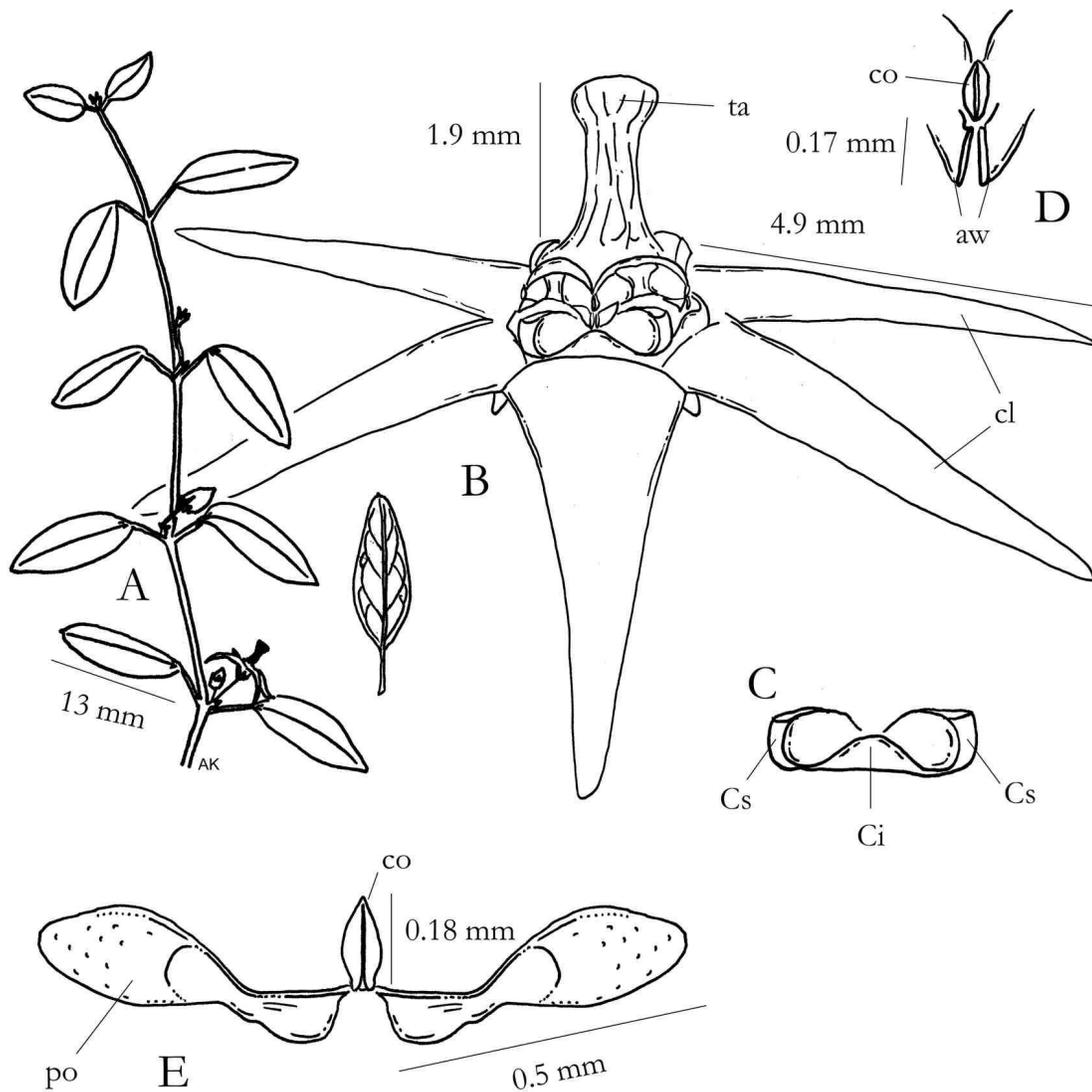


FIG. 1. *Matelea corynephora* Krings: A, habit and detail of leaf; B, flower with clavate terminal appendage of stylar head; C, gynostegial corona—note the laterally unlobed Cs, and the rounded lobe of the Ci; D, corpusculum and anther wings; E, pollinarium, caudicle shape approximate. Based on *Ekman H9740* (S). aw = anther wings; Ci = interstaminal gynostegial corona; cl = corolla lobes; co = corpusculum; Cs = staminal gynostegial corona; po = pollinium; ta = terminal appendage of stylar head.

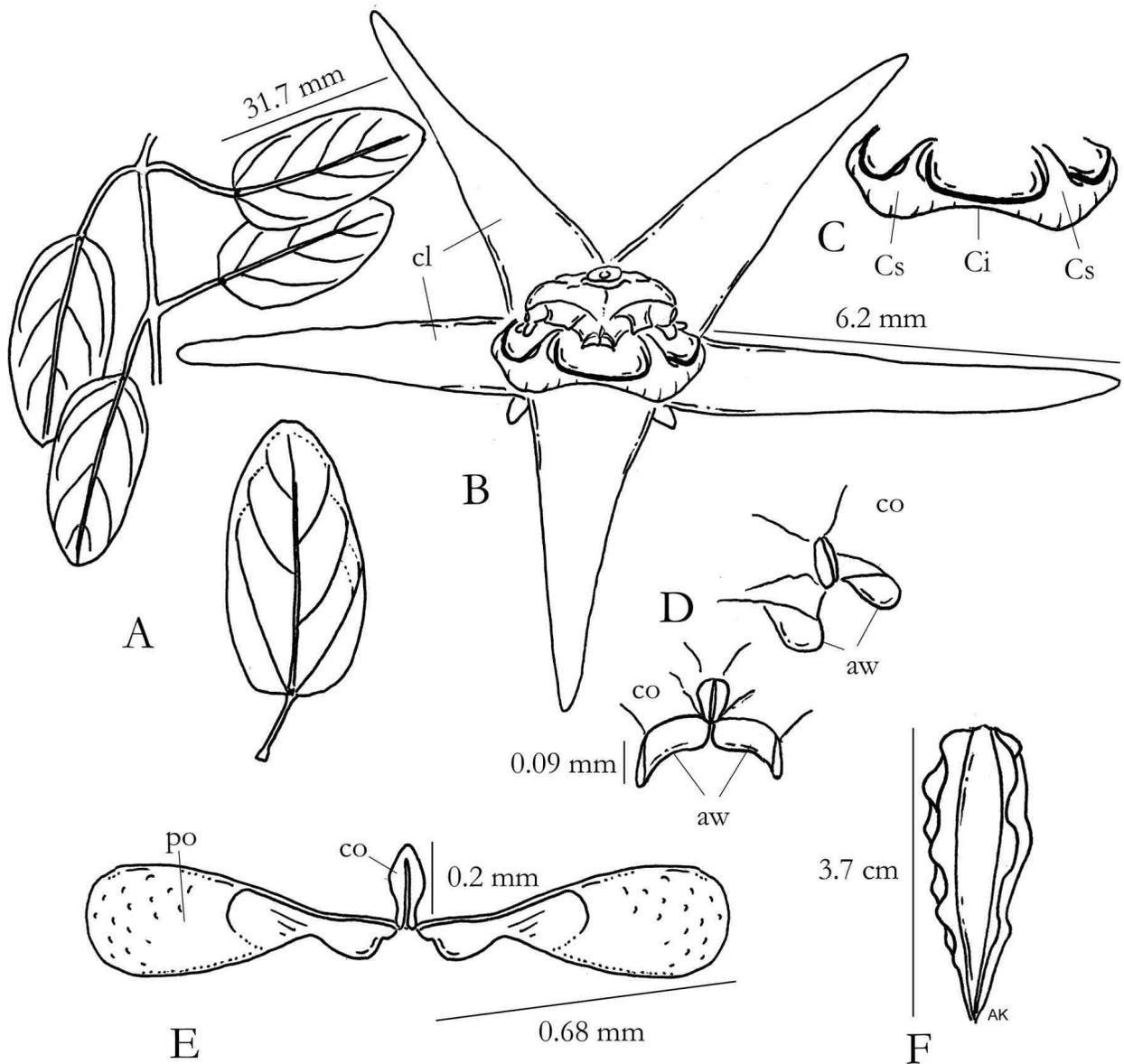


FIG. 2. *Matelea linearipetala* Alain: A, habit and leaf detail; B, flower; C, gynostegial corona; D, corpuscula and anther wings; E, pollinarium, caudicle shape approximate; F, follicle. Based on Ekman H7136 & H9067 (S). aw = anther wings; Ci = interstaminal gynostegial corona; cl = corolla lobes; co = corpusculum; Cs = staminal gynostegial corona; po = pollinium.

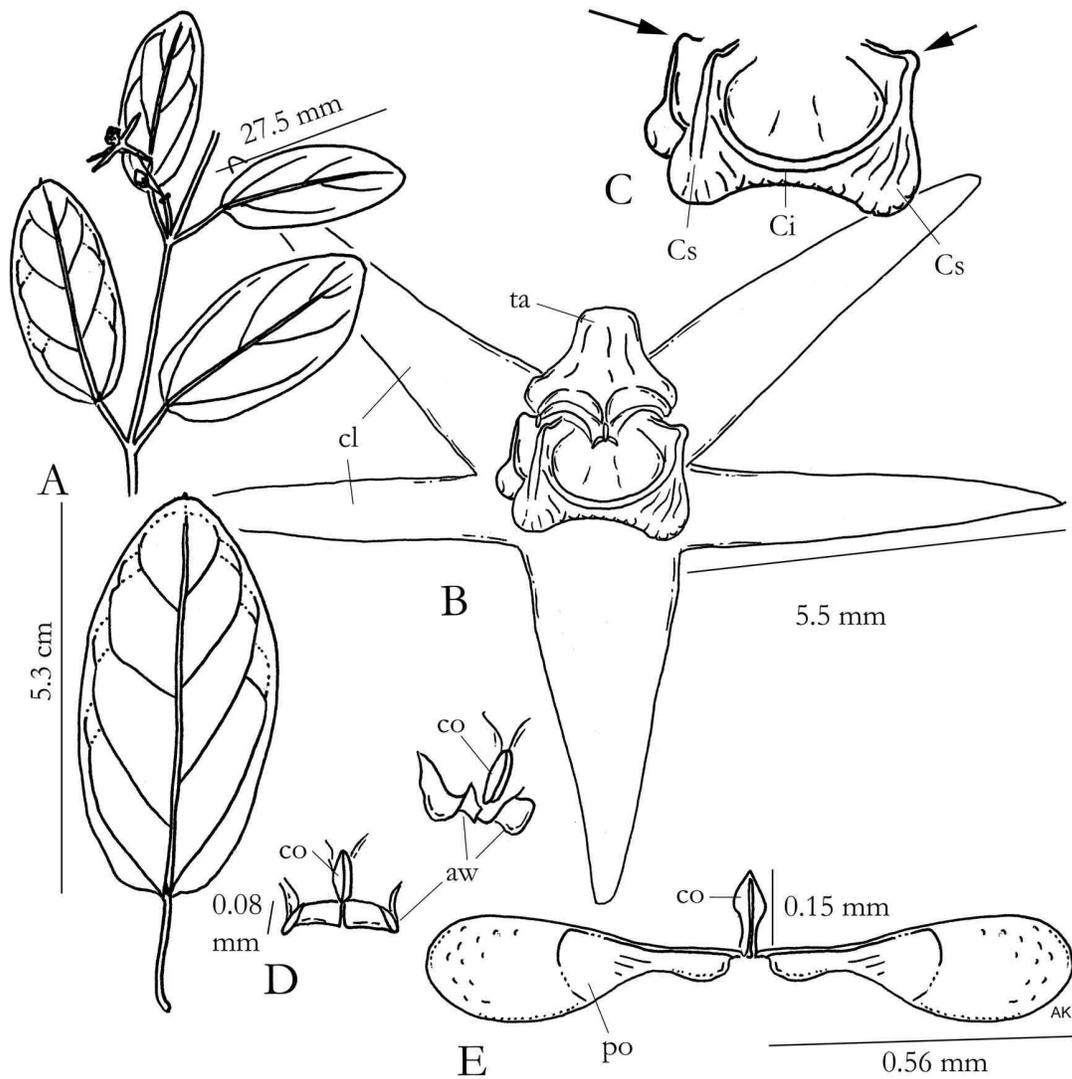


FIG. 3. *Matelea pauciflora* (Spreng.) Woodson: A, habit and leaf detail; B, flower with conic terminal appendage of stylar head; C, gynostegial corona—note slight vertical lobe of each Cs ridge (arrowed); D, corpuscula and anther wings; E, pollinarium, caudicle shape approximate. Based on *Ekman H6171* (K). aw = anther wings; Ci = interstaminal gynostegial corona; cl = corolla lobes; co = corpusculum; Cs = staminal gynostegial corona; po = pollinium; ta = terminal appendage of stylar head.

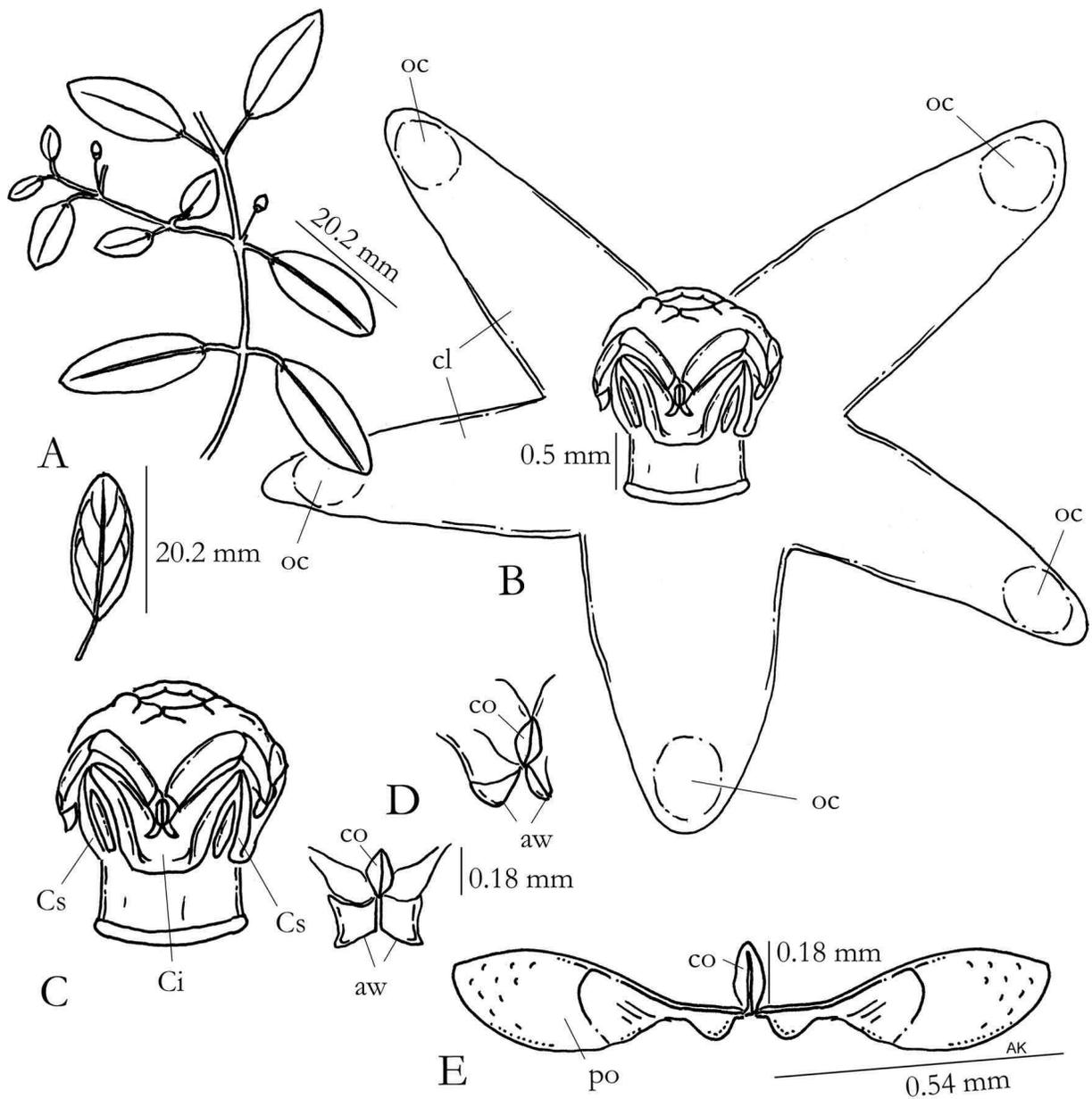


FIG. 4. *Matelea phainops* Krings: A, habit and leaf detail; B, flower—note ocellate corolla lobes; C, gynostegium with stipe-like base; D, corpuscula and anther wings; E, pollinarium, caudicle shape approximate. Based on *Liogier 16617* (GH). aw = anther wings; Ci = interstaminal gynostegial corona; cl = corolla lobes; co = corpusculum; Cs = staminal gynostegial corona; oc = ocellae; po = pollinium.

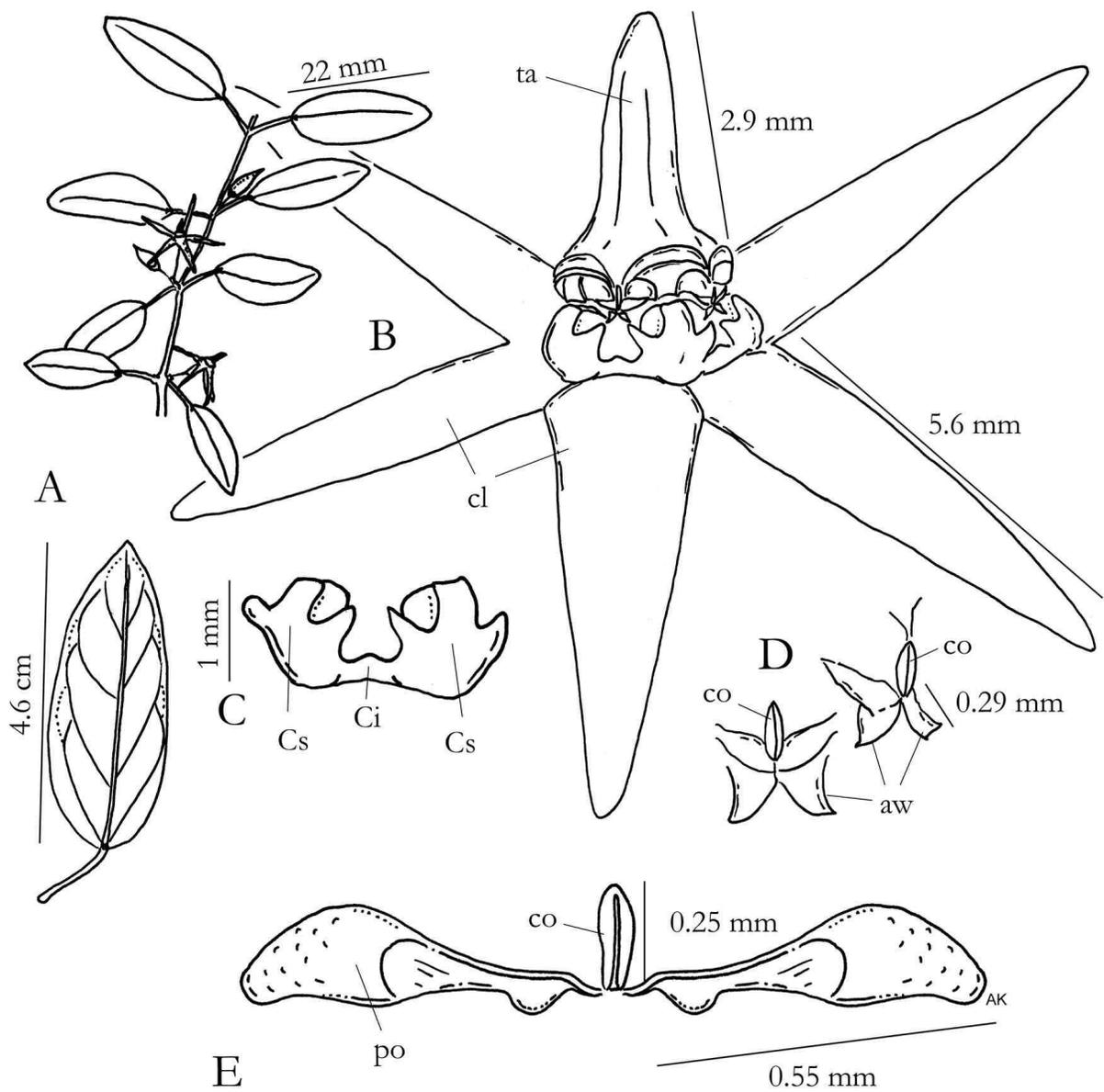


FIG. 5. *Matelea rhynchocephala* Krings: A, habit and leaf detail; B, flower; C, gynostegial corona—note trilobed Cs and shallow lobe of Ci; D, corpuscula and anther wings; E, pollinarium, caudicle shape approximate. Based on *Ekman H14296 (S)*. aw = anther wings; Ci = interstaminal gynostegial corona; cl = corolla lobes; co = corpusculum; Cs = staminal gynostegial corona; po = pollinium; ta = terminal appendage of stylar head.

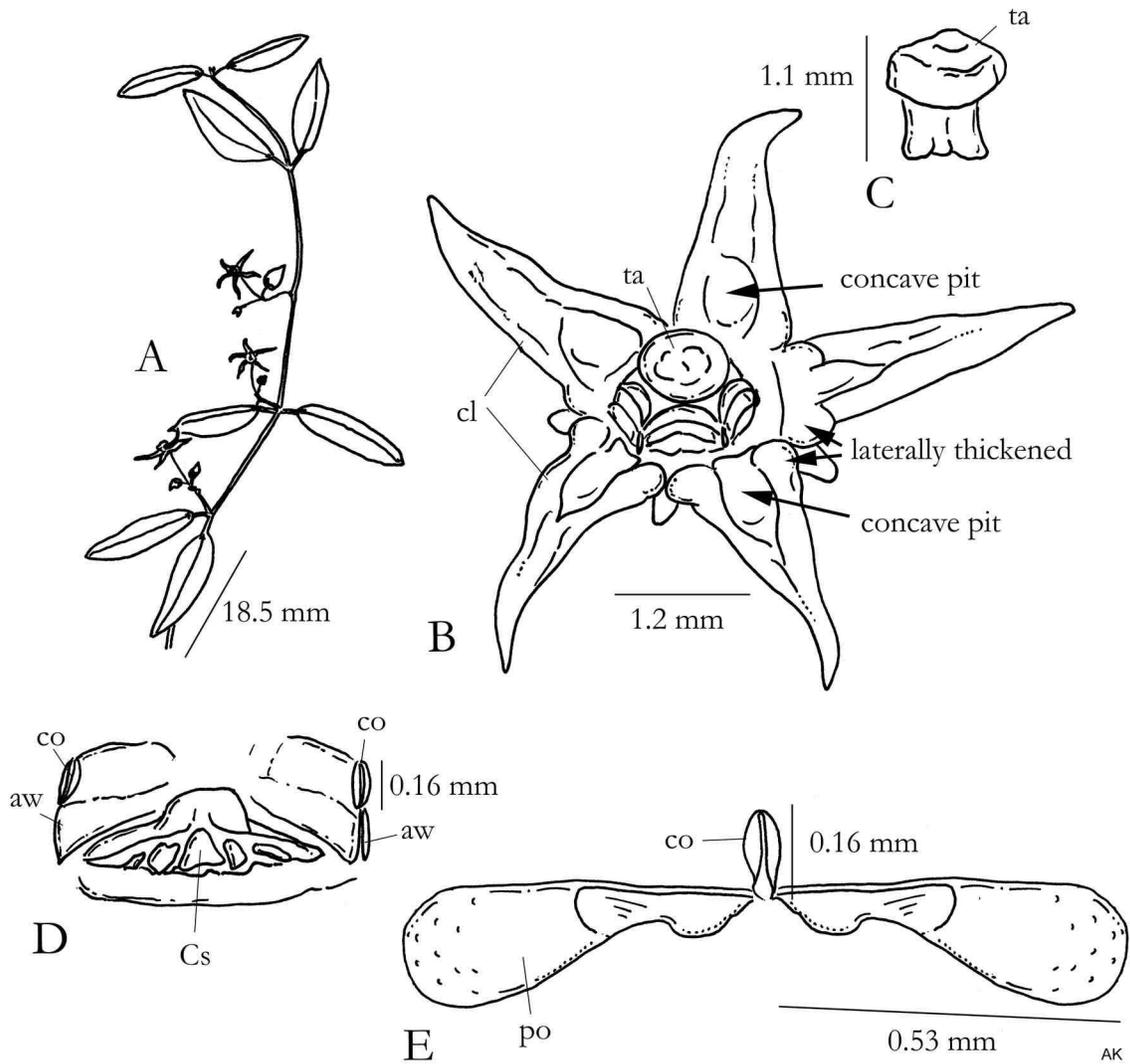


FIG. 6. *Matelea torulosa* Krings: A, habit; B, flower—note corolla lobes marginally thickened at the base, concave (“scooped-out”) and forming a distinct pit (arrowed); C, stylar head appendage; D, gynostegial corona—note long, parallel anther wings; E, pollinarium, caudicle shape approximate. Based on *Marcano [Jiménez] 4096* (US). aw = anther wings; Ci = interstaminal gynostegial corona; cl = corolla lobes; co = corpusculum; Cs = staminal gynostegial corona; po = pollinium; ta = terminal appendage of stylar head.

## Chapter XIV

### Typification of West Indian Gonolobinae (Apocynaceae: Asclepiadoideae)

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Types and their location of deposit are provided for taxa of subtribe Gonolobinae (Apocynaceae – Asclepiadoideae) in the West Indies. The following fourteen taxa are lectotypified: *Gonolobus bayatensis* Urb., *G. broadwayae* Schltr., *G. ciliatus* Schltr., *G. dictyopetalus* Urb. & Ekman, *G. ekmanii* Urb., *G. nipensis* Urb., *G. sintenisii* Schltr., *G. tigrinus* Griseb., *G. tobagensis* Urb., *G. variifolius* Schltr., *Ibatia mollis* Griseb., *Poicilla costata* Urb., *Poicilla tamnifolia* Griseb., and *Poicillopsis crispiflora* Urb. *Gonolobus grenadensis* Schltr. and *G. stapelioides* Desv. ex Ham. are neotypified. A new name and a new combination in *Matelea* Aubl. are respectively proposed for *Jacaima parvifolia* Proctor and *J. costata* (Urb.) Rendle var. *goodfriendii* Proctor.

KEYWORDS: Typification, Gonolobinae, Grisebach, Schlechter, Urban, Antilles, Caribbean

## INTRODUCTION

Subtribe Gonolobinae (Apocynaceae: Asclepiadoideae) comprises about fifty species in the West Indies (here considered to include the Greater and Lesser Antilles, the Bahamas, Trinidad and Tobago, Aruba and the Netherland Antilles, and the Cayman Islands).

Evidence from the chloroplast (Rapini & al., 2003; Liede-Schumann & al., 2005; Rapini & al., 2006; Krings et al., accepted) and nuclear genomes (Krings et al., accepted) supports the monophyly of Gonolobinae. Generic circumscriptions remain poorly defined and it is likely that the broad concept of *Matelea* Aubl. sensu Woodson (1941) is not monophyletic. Genera referred to the subtribe with representation in the region include *Fischeria* DC.,

*Gonolobus* Michx., *Matelea* (incl. *Ibatia* Decne., *Jacaima* Rendle, *Poicilla* Griseb., *Poicillopsis* Schltr., *Ptycanthera* Decne.), *Macroscepis* Kunth, and *Metalepis* Griseb. (Fontella & Schwarz, 1981a; Kunze, 1995; Liede, 1997; Morillo, 1997; Rapini & al., 2003; Liede-Schumann & al., 2005; Rapini & al., 2006). Subtribal position has been most controversial for *Metalepis*, which some workers have also placed within in a broad concept of *Cynanchum* L. (Woodson, 1941; Spellman, 1975; Sundell, 1981). Recent evidence places it basal to a well-supported Metastelmatinae-Oxypetalinae-Gonolobinae clade (Liede & Kunze, 2002; Liede-Schumann & al., 2005). The last regional treatment of Gonolobinae is now over 100 years old (Schlechter, 1899) and a number of new species have been described by various workers, including Britton, Krings, Liogier, Proctor, Spellman, Urban, and Woodson (see Krings, 2005b, 2006, 2007, as well as the present study). Recent effort as part of a larger systematic study of Gonolobinae and treatment for the *Flora de la República de Cuba* (Krings, 2005a–d, 2006, 2007; Krings & al., 2005; Krings & Fantz, 2006; Krings & Saville, accepted), has revealed that a number of lectotypifications and neotypifications are necessary. Publishing and compiling these designations separately allows for greater discussion of some issues than is possible in a flora format. Fourteen lectotypes and two neotypes are designated here. A new name and a new combination in *Matelea* are proposed for *Jacaima parvifolia* Proctor and *J. costata* (Urb.) Rendle var. *goodfriendii* Proctor. The treatment includes all names in Gonolobinae used in the region, except for names in *Fischeria* (1 sp.) which have been treated previously by Murphy (1986).

## MATERIALS & METHODS

Names in West Indian Gonolobinae were compiled from searches of the TROPICOS database (<http://www.tropicos.org>) for species with West Indian types, as well as from review of pertinent literature (i.e., Grisebach, 1862, 1866; Duss, 1897; Schlechter, 1899; Millspaugh, 1902; Boldingh, 1909, 1914; Woodson, 1941; Moscoso, 1943; Cheesman, 1947; Alain, 1957; Gooding & al., 1965; D'Arcy, 1967; Adams, 1972; Little & al., 1976; Correll & Correll, 1982; Proctor, 1984; Howard, 1989b; Nicolson, 1991; Liogier, 1994, 1995; Fournet, 2002; Acevedo-Rodríguez, 2005). Protologues were compiled from works held at the North Carolina State University Libraries or obtained through inter-library loans. Subsequently, queries were made to ninety institutions known to house West Indian collections—of which sixty-five responded with either loans, digital images, or negative search results (see Acknowledgments). Visits were also undertaken to BM, BSC, DUKE, HAC, HAJB, IJ, K, UCWI, UPRRP, US, and P.

Nearly half of the species names in West Indian Gonolobinae can be attributed to three German workers: August Heinrich Rudolf Grisebach (1814–1879), Friedrich Richard Rudolf Schlechter (1872–1925), and Ignatz Urban (1848–1931). The former worked from the University of Göttingen (GOET) and the latter two from the Botanical Garden and Museum Berlin-Dahlem (B).

The general philosophy followed herein, is that for taxa described by Grisebach, applicable specimens judged original material at GOET are considered holotypes—although, in a strict sense, Grisebach did not designate them as such, although his use of them is evident by his

notes and annotations. However, typification of Grisebach names based on collections by Charles Wright (1811–1885) can be problematic, as collections cited under a single collection number frequently represent gatherings from different localities and different times (Howard, 1986, 1989a). The philosophy adopted herein is that Grisebach names based on Wright collections should be lectotypified when (1) it can be shown that specimens distributed under a single number represent gatherings from different localities at different times, and/or (2) no specimen of a Wright number remains extant at GOET. When it cannot be shown that gatherings came from different localities and different times, duplicates of a Wright number designated lectotype are considered isolectotypes (see Krings & Fantz 2006). When it can be shown that gatherings came from different localities and different times, duplicates of a designated lectotype are treated as syntypes.

Urban described West Indian taxa largely based on specimens received by him from Erik Ekman (Cuba and Hispaniola), William Harris (Jamaica), and Walter Elias Broadway (Trinidad, Tobago, and Grenada). For these taxa, holotypes are presumed to have remained at B until their destruction in a fire in World War II. Thus, lectotypes are chosen for Urban names from duplicates of numbers cited in his protologues.

## RESULTS

**Overview.**---Names of novelties in West Indian Gonolobinae can be attributed to seventeen workers (Table 1). The majority of taxa were described during four phases of intensive interest in the region that occurred at ca. 20–30 yr intervals over the past 140 yrs. The first phase was dominated by Grisebach and based on the collections of Wulfschlagel (Antigua),

Charles Wright (Cuba), Imray (Dominica), and Alexander, Higson, Macfadyen, and Purdie (all Jamaica). Important works resulting from activity during this phase include the *Flora of the British West Indian Islands* (Grisebach, 1862) and the *Catalogus Plantarum Cubensium* (Grisebach, 1866). The second phase was dominated by the activity of Schlechter—based primarily on collections by Broadway (Grenada; Trinidad & Tobago), Eggers (Tobago), Poiteau (Haiti), Sintenis (Puerto Rico), and Wright (Cuba)—and Urban—based primarily on the collections of Broadway (Tobago), Buch (Haiti), Ekman (Cuba & Hispaniola), and Harris (Jamaica). The most important relevant work resulting from this period of activity is Urban’s multi-volume *Symbolae Antillanae* (1898–1928). The third phase was dominated by Liogier (a.k.a. Hermano Alain), who published more West Indian Gonolobinae novelties based on his own collections than any other worker before or since. Additional species described by Liogier are based on collections by Ekman (Hispaniola) and Howard (Dominican Republic). Important works resulting from his efforts or contributions include floras of Cuba, Hispaniola, and Puerto Rico (Alain, 1957; Liogier 1994, 1995). The fourth phase of interest is the result of current efforts undertaken by the present author (Krings, 2005b, 2006, 2007). New discoveries during this phase are based on collections by Eggers (Dominica), Ekman (Hispaniola), Graveson (St. Lucia), Krings & Springer (St. Vincent), Liogier (Dominican Republic), Marcano & Jiménez (Dominican Republic), and Quentin (Guadeloupe). No new names in West Indian Gonolobinae resulted from R. A. Howard’s efforts toward his *Flora of the Lesser Antilles* (Howard, 1989b).

**List.**---Names are listed index style and include legitimate, illegitimate, and misapplied names. They are arranged strictly alphabetically by basionym or combination. The most recent combination for a respective name follows the basionym. Specimens seen and verified by the author are indicated by an exclamation point (!) following the herbarium of deposit. The very few specimens not seen are indicated by 'n. v.' (*non vidi*). 'Loc. not cited' signifies that the herbarium of deposit was not indicated in the protologue.

Herbarium abbreviations follow *Index Herbariorum* (Holmgren & Holmgren, 1998–present). Book abbreviations follow TL-2 (Stafleu & Cowan, 1976–1988) and journal abbreviations B-P-H (Lawrence & al., 1968) and B-P-H/S (Bridson & Smith, 1991). Author abbreviations follow Brummitt & Powell (1992).

*Asclepias maritima* Jacq., Enum. Syst. Pl. 17. 1760. = *Matelea maritima* (Jacq.) Woodson, Ann. Missouri Bot. Gard. 28: 222. 1941.

**Protologue:** Neither specimens, nor locality cited.

**Type(s):** Herbar. Du Jacquin, 2 Insulae Caribaea. De Ponthieu (lectotype: BM!, designated by Krings & Saville, accepted)

**Notes:** Only a single sheet of *Asclepias maritima* Jacq. was located that could qualify as belonging to the original material. Eight fragments, all *Asclepias maritima*, are mounted on a single sheet held at BM and barcoded (BM000834432). A handwritten note on the top left of the back of the sheet reads “Herbar. Du Jacquin.” followed by “2 Insulae Caribaea. De Ponthieu.” Based on the note, the fragments appear to represent two elements, but they cannot be delineated. A dehisced follicle is mounted along with leaves in relatively good condition and a few flowers in poor condition. Fruits and flowers are not mentioned by

Jacquín in the protologue, and these elements may represent the collection later combined with the vegetative fragment used for the protologue. Considering that this sheet appears to represent the only remaining collection of *Asclepias maritima* from the herbarium of Jacquín, was designated lectotype by Krings & Saville (accepted).

*Cynanchum denticulatum* Vahl, *Eclog. Amer.* 2: 23. 1798. = *Matelea denticulata* (Vahl) Fontella & E.A. Schwarz, *Bol. Mus. Bot. Munic.* 46: 4. 1981.

**Protologue:** “Habitat in Guiana. von Rohr,” loc. not cited.

**Type(s):** *von Rohr* 120 (holotype: C [IDC microfiche photo: Vahl herbarium nr. 17: III, 1!])

**Notes:** Most recent authors have accepted this entity under the name *Matelea denticulata* (Vahl) Fontella & E.A. Schwarz, however, in a recent phylogenetic analysis based on chloroplast and nuclear data, the taxon emerged in a clade of *Gonolobus* s.l. (Krings et al., accepted).

*Cynanchum hirsutum* Vahl, *Eclog. Amer.* 2: 24. 1798. = *Matelea hirsuta* (Vahl) Woodson E. E. Cheesman, *Fl. Trinidad* 2: 170. 1947.

**Protologue:** “Habitat in insula Trinitatis. von Rohr,” loc. not cited.

**Type(s):** Trinidad, *von Rohr* 92 (holotype: C [IDC microfiche photo: Vahl herbarium nr. 17: III, 3!; isotype: BM!])

**Notes:** An annotation on *von Rohr* 92 indicates that it was studied by Ignatz Urban.

*Cynanchum maritimum* (Jacq.) Jacq., *Select. Stirp. Amer. Hist.* 83, t. 56. 1763. = *Matelea maritima* (Jacq.) Woodson, *Ann. Missouri Bot. Gard.* 28: 222. 1941.

**Notes:** Some authors have mistakenly attributed the combination in *Cynanchum* to Linnaeus' *Syst. Nat.* (1767). However Linnaeus (1767) clearly referenced Jacquin (1763). In *Syst. Nat.* (1767), he writes: "C. caule volubili, fol. cordatis hirsutis subtus tomentosus, pedunc. Aggregatis. Mant. 54." The *Mantissa plantarum* (Mant.) was published originally as an appendix to volume 2 of his *Syst. Nat.* (1767). In the *Mantissa*, Linnaeus (1767) provides further detail, referring to 'Jacq. *amer.* 86, t. 56,' and describing corollas of *C. maritimum* as 'atropurpurea.' Although *C. maritimum* is described on pages 83 and 84 in Jacquin's *Select. Stirp. Amer. Hist.* (1763), rather than on page 86 as cited by Linnaeus (1767), the illustration reference (plate 56) is correct and is not inconsistent with plants known most recently as *Matelea maritima* in the West Indies. Thus, it is clear that Linnaeus accepted Jacquin's combination and was not himself proposing a new one. Continued citation of *Cynanchum maritimum* L. is incorrect.

See *Asclepias maritima* Jacq.

*Cynanchum maritimum* (Jacq.) L., *Syst. Nat.* 2: 192. 1767, err. cit. [= *C. maritimum* (Jacq.) Jacq., see above]

**Notes:** Linnaeus (1767) never made this combination mistakenly attributed to him by subsequent workers.

*Cynanchum rostratum* Vahl, *Symb. Bot.* 3: 45. 1794. = *Gonolobus rostratus* (Vahl) Schult. in Roemer & Schultes, *Syst. Veg.* 6: 61. 1820.

**Protologue:** "In insula Trinitatis legit Dn. v. Rohr," loc. not cited.

**Type(s):** Trinidad, (von Rohr?) Hb. Liebmann (holotype: C [IDC microfiche photo: Vahl herbarium nr. 17: III, 5!]; isotype: BM!)

**Notes:** Although Stafleu & Cowan (1986) noted that “Vahl’s *Symbolae Botanicae* are based on the Forsskål material at C,” *Cynanchum rostratum* is not listed in the index accompanying the IDC microfiche of the Forsskål herbarium. However, there is a specimen in the Vahl herbarium corresponding to *Cynanchum rostratum*. The specimen label identifies it as having been part of the Hb. Liebmann at some point, however the hand, identifying the collection as *Cynanchum rostratum*, belongs to Vahl. Von Rohr is not indicated on the label.

Cheesman (1947) mistakenly considered “*Gonolobus rostratus* R.Br. sens. Griseb Fl. 420” a synonym of “*Matelea viridiflora* (G.F.W. Meyer) Woods.” However, the latter clearly corresponds to *Matelea denticulata* (Vahl) Fontella & E.A. Schwarz based on Cheesman’s description (e.g., “cal[yx] lobes lanceolate,” “corolla [...] lobes ovate,” “anthers without dorsal appendages”) and not to *Gonolobus rostratus* sensu Grisebach (1864) (e.g., “calyx [...] segments ovate,” “corolla [...] segments lanceolate-linear”). Grisebach’s (1864) taxon (also from Trinidad) is clearly referable to *G. rostratus* (Vahl) Schult. The two taxa are difficult to confuse by anyone familiar with them. The combination in *Gonolobus* is to be attributed to Schultes as Robert Brown never made the combination erroneously attributed to him by some authors such as Grisebach (1864) and Schlechter (1899).

*Cynanchum viridiflorum* G. Mey., Prim. Fl. Esseq. 141. 1818, nom illegit., non Sims, 1817.

**Protologue:** “in fruticetis plantationis Hamburg,” loc. not cited.

**Type(s):** The type could not be located.

**Notes:** A synonym of *Cynanchum denticulatum* Vahl fide Howard (1989b).

*Fischeria cincta* Griseb., Fl. Brit. W. I. 421. 1862. = *Gonolobus cinctus* (Griseb.) Benth. & Hook. f., Index Kewensis 2: 1054. 1895.

**Protologue:** “Jamaica!, *Higson*,” loc. not cited.

**Type(s):** Jamaica, *Higson s.n.* (holotype: K!)

**Notes:** Syn. of *Gonolobus stapelioides* Desv. ex Ham. fide Adams (1972).

*Gonolobus absalonensis* Krings, Syst. Bot. 32: 181. 2007.

**Protologue:** “Martinique. Absalon, Pres la cascade, Mai 1910 (fl), Herb. d’Alleizette *s.n.* [4801?] (holotype: L!).”

**Type(s):** Martinique. Absalon, Pres la cascade, Mai 1910 (fl), Herb. d’Alleizette *s.n.* [4801?] (holotype: L!).

*Gonolobus bakeri* Schltr. in Urban, Symb. Antill. 7(3): 341. 1912.

**Protologue:** “Hab. in Cuba cult. in Santiago de las Vegas: *C.F. Baker n. 7286*, flor. m. Majo 1907,” loc. not cited.

**Type(s):** Location of type is unknown. No additional matching material was located from which a lectotype or neotype could be designated.

*Gonolobus bayatensis* Urb., Symb. Antill. 9(3): 420. 1925. = *Matelea bayatensis* (Urb.) Woodson, Ann. Missouri Bot. Gard. 28: 226. 1941.

**Protologue:** “Prov. Oriente prope Bayate, m. Oct. flor.: Arth. Engström in herb. Ekman n. 3056,” loc. not cited.

**Type(s):** Cuba, *Engström 3056* (lectotype: S!, here designated; isolectotype: NY!).

**Notes:** Two sheets of *Engström 3056* are extant – one at S and one at NY. The sheet at S is superior in condition to the NY sheet, exhibiting much more floral and vegetative material and is therefore designated lectotype. See Krings (2005c) for additional notes on this species.

*Gonolobus bicolor* (Britton & P. Wilson) Urb., Symb. Antill. 9(3): 421. 1925. = *Matelea bicolor* (Britton & P. Wilson) Woodson, Ann. Missouri Bot. Gard. 28: 236. 1941.

See *Marsdenia bicolor* Britton & P. Wilson.

*Gonolobus broadwayae* Schltr. in Urban, Symb. Antill. 7(3): 340. 1912.

**Protologue:** “in Trinidad, ad St. Clair Experiment Station inter Bambusas volubilis: *W.E. Broadway n. 2743*,” loc. not cited; ‘ad Santa Cruz: *López* (Herb. Broadway n. 2419),’ loc. not cited.

**Type(s):** Trinidad, *López 2419* (lectotype: Z!, here designated)

**Notes:** Of the two syntypes cited in the protologue, only *López 2419* (Z) appears to be extant.

*Gonolobus ciliatus* Schltr. in Urban, Symb. Antill. 1(2): 282. 1899.

**Protologue:** “Tobago, in silvis prope Frenchfield, alt. 400 ped., Oct.: *Eggers 5561*,” loc. not cited; ‘Trinidad, prope La Ventilla: *Crüger s.n.*,’ loc. not cited; ‘Venezuela,’ loc. not cited.

**Type(s):** Tobago, *Eggers 5561* (lectotype: P!, here designated; isolectotype: UCWI!)

**Notes:** Unidentified as a type, *Eggers 5561* had been filed at P with *Matelea denticulata* (Vahl) Fontella & E.A. Schwarz (of which it is a synonym). The *Crüger* specimen could not be located.

*Gonolobus cinctus* (Griseb.) Benth. & Hook. f., Index Kewensis 2: 1054. 1895.

See *Fischeria cincta* Griseb.

*Gonolobus denticulatus* (Vahl) W.D. Stevens, Phytologia 64: 334. 1988.

See *Cynanchum denticulatum* Vahl

*Gonolobus dictyopetalus* Urb. & Ekman, Ark. Bot. 20A(5): 41. 1926. = *Matelea*

*dictyopetala* (Urb. & Ekman) Krings, Syst. Bot. Monogr., in rev.

**Protologue:** Haiti, “Massif de la Selle in Morne Cabaio ad Jardin Bois [...] n. H. 1625,” loc. not cited.

**Type(s):** Haiti. *Ekman H 1625* (lectotype: S!, here designated; isolectotype: IJ! – fragment [single leaf])

**Notes:** Two sheets of *Ekman H 1625* appear to be extant – at IJ and S. Whereas the sheet at IJ consists of a stem fragment with a single leaf (plus several more leaf fragments and a flower bud in the fragment pocket), the sheet at S (determined in Urban’s hand) consists of

numerous leaves and flowers and is in good condition. Ekman specimens were sent to Urban at B for critical study (Howard, 1952; Nordenstam & al., 1994). Nordenstam & al. (1994) noted that Urban was to identify and publish on the work of Ekman and return the principal (full) set of vascular and non-vascular plants to Stockholm (S). Nordenstam & al. (1994) also noted that it is obvious that Urban returned the original specimens to Stockholm as many Ekman sheets are annotated as types in Urban's handwriting. Urban could keep one duplicate of the material upon which any of his and Ekman's publications were based (Nordenstam & al., 1994). Urban published a number of names in West Indian Gonolobinae based on Ekman material and it can be assumed that holotypes were kept at B. However, all of Gonolobinae types at B were destroyed in World War II, necessitating lectotypification.

*Gonolobus domingensis* Alain, *Moscoso* 1(3): 46. 1978. = *Matelea domingensis* (Alain) Krings, *Sida* 21: 2081. 2005.

**Protologue:** “Loma Isabel de Torres, Puerto Plata [...] *Alain & Perfa Liogier 13780* (SDM, NY); en bosque, id. *A. & P. Liogier & N. Melo 23348* (SDM).”

**Type(s):** Dominican Republic, *Alain & Perfa Liogier 23780* (lectotype: JBSD!, designated by Krings 2005d)

**Notes:** See Krings (2005d) for a detailed discussion of lectotypification of this taxon.

*Gonolobus dussii* Krings, *Syst. Bot.* 32: 183. 2007.

**Protologue:** “Guadeloupe. Chemin de la Soufriere, alt. 500 m, *Quentin 732* (holotype: P!-fl; isotype: GH!-fl).”

**Type(s):** Guadeloupe. Chemin de la Soufriere, alt. 500 m, *Quentin 732* (holotype: P!-fl; isotype: GH!-fl)

*Gonolobus ekmanii* Urb., Symb. Antill. 9(3): 422. 1925. = *Matelea ekmanii* (Urb.)

Woodson, Ann. Missouri Bot. Gard. 28: 226. 1941.

**Protologue:** “Prov. Oriente in Sierra Maestra inter Rio Yara et Rio Palmamocha cr. 1300 m. alt., m. Jul. flor., n. 14453,” loc. not cited.

**Type(s):** Cuba, *Ekman 14453* (lectotype: S!, here designated; isolectotype: NY!).

**Notes:** Two sheets of *Ekman 14453* are held at S. One sheet holds a nicely, openly pressed flower in its fragment pocket. Considering that the condition of both sheets is otherwise comparable, the sheet with the openly pressed flower in the fragment pocket is here designated lectotype. As accession numbers are the same on both sheets, the lectotype can be identified by the label header: “Mus. Botan. Stockholm. Plantae Indiae Occidentalis N:o 14453” [sic].

*Gonolobus floccosus* Bertol., Opusc. Sci. 4: 225. 1823.

**Protologue:** “[...] ex Guadalupa, et Portorico,” Anonymous (loc. not cited)

**Type(s):** Guadeloupe, *Anonymous s.n.* (holotype: BOLO!)

**Notes:** Syn. of *Matelea maritima* (Jacq.) Woodson

*Gonolobus grenadensis* Schltr. in Urban, Symb. Antill. 7(3): 339. 1912.

**Protologue:** “in Grenada ad Annandale, *W.E. Broadway n. 3477*,” loc. not cited .

**Type(s):** Grenada, St. Mark Parish, Wooded hillsides near Victoria, elev. 100–300 ft., 24 Nov 1957, *G.R. Proctor 17225* (neotype: IJ!, here designated).

**Notes:** Based on Schlechter's (1912) description, *Gonolobus grenadensis* Schltr. is a synonym of *Matelea denticulata* (Vahl) Fontella & E.A. Schwarz. Schlechter (1912) considered it a close relative to *G. ciliatus* Schltr. (also a synonym of *M. denticulata*), from which he distinguished it only by larger leaves and flowers. Howard (1989b) also treated *G. grenadensis* as a synonym of *M. denticulata*, although confusing it with *G. martinicensis* in key and description (though not in illustration). Unfortunately no original material of *G. grenadensis* could be located. *Proctor 17225* (IJ) appears to be the only extant specimen of this taxon from Grenada. It is here designated neotype.

*Gonolobus grisebachianus* Schltr. in Urban, Symb. Antill. 1(2): 287. 1899. = *Matelea grisebachiana* (Schltr.) Alain, Mem. Soc. Cub. Hist. Nat. "Felipe Poey" 22: 120. 1955.

**Protologue:** "Cuba, loco speciali haud indicato: *Wright s.n.*," loc. not cited.

**Type(s):** Location of type is unknown. No additional matching material was located.

*Gonolobus haitiensis* P.T. Li, J. South China Agric. Univ. 14(1): 58. 1993.

**Type(s):** Haiti, *E.L. Ekman 4693* (holotype: S!; isotypes: B!, US!).

**Notes:** A nomen nov. for *Gonolobus stipitatus* Alain, Phytologia 64: 345. 1988, non Morillo, 1987.

*Gonolobus iyanolensis* Krings, Syst. Bot. 32: 185. 2007.

**Protologue:** “St. Lucia. Gros Piton, 9 Aug 1996 [“9/8/76”] (fl), *Roger Graveson 107* (holotype: GH!).”

**Type(s):** St. Lucia. Gros Piton, 9 Aug 1996 [“9/8/76”] (fl), *Roger Graveson 107* (holotype: GH!).

**Notes:** Roger Graveson noted that the collection date is incorrect on the label of the type and should be 9 Aug 1996 instead (Graveson, pers. comm.).

*Gonolobus jamaicensis* Rendle, J. Bot. 74: 345. 1936.

**Type(s):** *Harris 6368* (holotype: BM!).

**Notes:** *Gonolobus jamaicensis* was proposed by Rendle as a nomen novum for the Jamaican endemic taxon Schlechter (1899) attributed to *G. rostratus* (Vahl) R.Br. Robert Brown never made the combination attributed to his *Memoirs of the Wernerian Natural History Society* 1: 35. 1810. The true *Gonolobus rostratus* (Vahl) Schult. is known only from Trinidad and is based on the type of *Cynanchum rostratum* Vahl. Because Rendle corrected a misapplication, his name—*G. jamaicensis*—is a new species name, not a nomen novum as he incorrectly stated. A nomen novum is an avowed substitute (replacement name) for a validly published but illegitimate name, the type of which would be the same as that of the name which it replaced.

*Gonolobus maritimus* (Jacq.) R. Br., *Mem. Wern. Nat. Hist. Soc.* 1: 24. 1810. = *Matelea maritima* (Jacq.) Woodson, *Ann. Missouri Bot. Gard.* 28: 222. 1941.

See *Asclepias maritima* Jacq.

*Gonolobus maritimus* (Jacq.) R. Br. ex Schult. in Roemer & Schultes, Syst. Veg. 6: 59. 1820, err. cit. [=*G. maritimus* (Jacq.) R. Br.]

**Notes:** Brown (1810) validly and effectively published the combination *Gonolobus maritimus* (Jacq.) R. Br. The sometimes mistakenly cited combination *Gonolobus maritimus* (Jacq.) R. Br. ex Schult., Syst. Veg. 6: 59. 1820, is an error in citation as Schultes clearly accepted Brown's combination, correctly additionally citing Jacquin. See *Asclepias maritima* Jacq.

*Gonolobus martinicensis* Decne. in De Candolle, Prodr. 8: 595. 1844.

**Protologue:** "in Martinicae sylvis umbrosis, (cl. *Pleé.*) *Tourimibi* Caribeorum *Plum. et Surian* 821 (v.s.h. Mus. par.)."

**Type(s):** Martinique, *Pleé s.n.* (lectotype: P! [2 sheets], designated by Krings 2007)

**Notes:** Two syntypes were cited in the protologue, but only *Pleé s.n.* (P) could be re-located. *Plum. et Surian* 821 could not be found.

*Gonolobus membranaceus* Schltr. in Urban, Symb. Antill. 1(2): 285. 1899.

**Protologue:** "Haiti, loco speciali haud indicato: *Poiteau s.n.*," loc. not cited.

**Type(s):** The location of the type remains unknown. No additional matching material was found.

**Notes:** *Ekman H4693* (IJ!) is labelled *Gonolobus membranaceus*. The specimen consists of mostly stem and 3–4 leaf fragments held in a fragment pocket. It appears to match *Poicillopsis crispiflora* Urb. *Gonolobus membranaceus* is likely very closely related to *Matelea haitiensis* as, based on the protologues, the two appear to differ only in the shape

and apices of the leaf blades and calyx lobes. Additional collections and discovery of the type may prove them synonymous.

*Gonolobus nipensis* Urb., Symb. Antill. 9(3): 421. 1925. = *Matelea nipensis* (Urb.)

Woodson, Ann. Missouri Bot. Gard. 28: 226. 1941.

**Protologue:** “Prov. Oriente in Sierra de Nipe ad pedem Loma Mensura in savannis pinetorum umbrosis cr. 725 m. alt., m. Jul. flor.: n. 9710,” loc. not cited.

**Type(s):** Cuba, *Ekman 9710* (lectotype: S!, here designated; isolectotype: NY!).

**Notes:** *Ekman 9710* (S) is a superior specimen relative to *Ekman 9710* (NY) in that it bears many more leaves, inflorescences, and flowers. It is here designated lectotype for *Gonolobus nipensis*.

*Gonolobus pauciflorus* Spreng., Syst. Veg. 1: 846. 1824. = *Matelea pauciflora* (Spreng.)

Woodson, Ann. Missouri Bot. Gard. 28: 226. 1941.

**Protologue:** “Hispaniola, *Bertero*,” loc. not cited.

**Type:** Hispaniola, ‘St. Domingue,’ *Bertero s.n.* (lectotype: P!, designated by Krings 2006; isolectotype: G-DC [IDC microfiche Candolle Prodromus Herbarium, fiche # 1543!]).

**Notes:** Bertero collections were among specimens in the fragmented Sprengel collection acquired by B in 1890, but no Bertero specimen corresponding to *G. pauciflorus* was found extant at that institution. As neither extant duplicate of *Bertero s.n.* at either G-DC or P corresponding to *G. pauciflorus* bears the hand of Sprengel and as no other Bertero material corresponding to the taxon has been located at the other institutions queried (see Acknowledgments), it is assumed that the holotype was destroyed. Consequently, having

been able to examine the specimen at P, but only the microfiche of the specimen at G-DC, Krings (2006) designated the sheet at P lectotype for *G. pauciflorus*.

*Gonolobus pubescens* Griseb., Fl. Brit. W. I. 420. 1862. = *Matelea pubescens* (Griseb.)

Krings, Syst. Bot. Monogr., in rev.

**Protologue:** “Jamaica, *Macf.*,” loc. not cited.

**Type(s):** Jamaica, *Macfadyen s.n.* (holotype: GOET!; isotype: K!)

**Notes:** The GOET specimen consists of an unmounted section of stem with five nodes, but only three developed leaves. A fourth developed leaf and a fragment of a fifth are loose in the pocket. A smaller fragment pocket contains floral parts. *Macfadyen s.n.* (K) is a superior specimen relative to *Macfadyen s.n.* (GOET) in bearing many more leaves, as well as an openly pressed flower kept in the fragment pocket. Both the K and GOET specimens are annotated in Grisebach’s hand.

*Gonolobus rhamnifolius* Griseb., Fl. Brit. W. I. 420. 1862. = *Matelea rhamnifolia* (Griseb.)

Krings, Sida 21: 1515. 2005.

**Protologue:** “Jamaica!, *Al.*, S. Anns, near Moneague,” loc. not cited.

**Type(s):** Jamaica, *R.C. Alexander s.n.* (holotype: GOET!)

**Notes:** See Krings (2005a) for a discussion of the morphology of this taxon. The type locality was visited on an expedition to Jamaica by the present author and Dale Suiter in March 2006. However, the area was unfortunately flooded (houses under 10–15 feet of water) and inaccessible. The species was not observed on any of the access roads up to the flooded valley. Dr. George Proctor noted collecting a specimen in a narrow patch of woods

between a road and a pasture. The area appears to be in similar condition currently, with many pastures separated from rural roads by narrow patches of woods.

*Gonolobus rostratus* (Vahl) Schult. in Roemer & Schultes, Syst. Veg. 6: 61. 1820.

**Notes:** Schultes (1820) cited Vahl's protologue of *Cynanchum rostratum* (see above) and attributed the combination in *Gonolobus* to Robert Brown. However, as Brown never made the combination in *Gonolobus* that has been attributed to him, Schultes should be considered the author of the valid combination.

See *Cynanchum rostratum* Vahl

“*Gonolobus rostratus*” auct. non (Vahl) Schult.: Schlechter, Symb. Antill. 1: 284. 1899.

**Notes:** Schlechter (1899) mistakenly attributed a Jamaican entity to the name *Gonolobus rostratus* (Vahl) R.Br., for which Rendle later proposed the name *G. jamaicensis* (see above). Robert Brown never made this combination attributed to him (see Memoirs of the Wernerian Natural History Society 1: 35. 1810).

See also *Cynanchum rostratum* Vahl

*Gonolobus scandens* (Aubl.) Urb., Repert. Spec. Nov. Regni Veg. 16: 151. 1919; nom. illeg.

**Notes:** Based on an invalid polynomial, see Nicolson (1991). The basionym is *Periploca scandens* Aubl., Histoire des plantes de la Guiane Françoise 2 (Tabl. Nom. Lat.): 23. 1775. 260.

*Gonolobus scandens* Urb., Repert. Spec. Nov. Regni Veg. 16: 151. 1919; nom. illeg.

**Notes:** A superfluous name and synonym of *Gonolobus martinicensis* Decne. (Prodromus Systematis Naturalis Regni Vegetabilis 8: 595. 1844.).

*Gonolobus sintenisii* Schltr. in Urban, Symb. Antill. 1(2): 288. 1899. = *Matelea sintenisii* (Schltr.) Woodson, Ann. Missouri Bot. Gard. 28: 226. 1941.

**Protologue:** “Portorico, Sierra de Luquillo, in regione superiore montis Jimenes in silvis, Jul. 1885: *Sintenis n. 1354*; in silva primaeva montis Andubo prope Adjuntas, Jun. 1886: *Sintenis n. 4643*,” loc. not cited.

**Type(s):** Puerto Rico, Sierra de Luquillo, Jimenes mts., *Sintenis 1354* (lectotype: HBG!, here designated; isoelectotypes: BM!, G!, GH!, K!, US!).

**Notes:** Among the syntypes, *Sintenis 1354* (HBG) is chosen as lectotype as the specimen bears flowers in relatively superior condition to the duplicates under this number. The two specimens respectively at G and GH are sterile. The K specimen bears a single flower in bud. Specimens of *Sintenis 4643* could not be located.

*Gonolobus stapelioides* Desv. ex Ham., Prodr. Pl. Ind. Occid. 32. 1825.

**Protologue:** “Habitat in fruticetis circa Alfred Hall, prope Scarborough, Tobago, cum *Echite quinquangulare* etc. ubi florentem inveni mense Octobris (V. et S. v.),” loc. not cited.

**Type(s):** Jamaica, Portland Parish, 0.5 mi N of Hardwar Gap, uphill from the trail above the “Waterfall,” ca. 3900 ft, montane rainforest, vines growing over trailside shrubs and in

small forest openings, population J1, 3 Mar 2006 (fl), A. Krings 1395 with D. Suiter and G.R. Proctor (neotype: P!; isoneotypes: BM!, IJ!, NCSC!, NY!, designated here)

**Notes:** An appropriately labeled red type folder is present at P, but was found empty during visits in 2004 and 2006. In the absence of the specimen the species is neotypified here.

Schlechter (1899) noted that there was likely a label mix-up between the Jamaican entity *G. stapelioides* and the Tobagoan *G. virescens* Ham. It would indeed be unlikely for *G. stapelioides* to be limited in distribution to Jamaica and Tobago. The taxon is not represented by any other specimens from Tobago. Similarly, *G. virescens* is not known from Jamaica by another specimen.

*Gonolobus stellatus* Griseb., Fl. Brit. W. I. 420. 1862.

**Protologue:** “Jamaica!, *Pd.*, Manchester, rare, near Knockpatrick,” loc. not cited.

**Type(s):** Jamaica, *Purdie s.n.* (holotype: GOET!; isotypes: BM!, K!)

**Notes:** *Purdie s.n.* (K) is the best specimen of the three extant sheets. It bears numerous leaves, inflorescences, and an openly pressed flower. The specimen also bears an annotation in Grisebach’s hand. The specimen at BM is also in good condition, bearing a nicely preserved flower. However, this specimen does not bear annotations in Grisebach’s hand. The specimen at GOET consists entirely of fragments (two leaves and immature flowers in bud; no stem).

*Gonolobus stephanotrichus* Griseb., Cat. Pl. Cub. 177. 1866.

**Protologue:** “Cuba or. (*Wr.* 2969 [...],” loc. not cited.

**Type(s):** Cuba, *Wright 2969*, 1860–1864 (lectotype: GOET!, designated by Krings & Fantz (2006); syntypes: BM!, BREM!, G!, GH!, HAC!, K!, MO, NY!, P!, UC!, US![not sent on loan to NCSC]).

**Notes:** The Wright collection of *G. stephanotrichus* at S bears the number 164 and does not appear to be part of the type collection. See Krings & Fantz (2006) for a detailed discussion of the lectotypification of *G. stephanotrichus*.

*Gonolobus stipitatus* Alain, *Phytologia* 64(5): 345. 1988, nom. illeg.; non *Gonolobus stipitatus* Morillo, 1987. = *Gonolobus haitiensis* P.T.Li, *J. South China Agric. Univ.* 14(1): 58. 1993.

**Protologue:** “Haiti: On hard limestone, Massif du Nord, St. Louis du Nord, on top of Morne Baron, July 20, 1925, *Ekman 4693* (holotypus, S).”

**Type(s):** Haiti, Massif du Nord, St. Louis du Nord, Morne Baron, 20 Aug 1925, *Ekman H 4693* (holotype: S!; isotypes: B!, US!)

“*Gonolobus suberosus*” auct. non (L.) R.Br.: Spreng., *Syst. Veg.* 1: 846. 1824.

**Notes:** Cited as *Gonolobus suberosus* Spreng. by Schlechter (1899) and Woodson (1941), although Sprengel (1824) clearly cited Robert Brown as author of the combination in *Gonolobus* based on the basionym *Cynanchum suberosum* L. Although the typification of *C. suberosum* L. is complex (Drapalik, 1969; Reveal & Barrie, 1992), the basionym has most recently been recognized to apply to the single *Gonolobus* species in the southeastern United States (see Krings & Xiang 2004, 2005). Schlechter (1899) and Woodson (1941)

considered Sprengel's *G. suberosus* to be a synonym of what is now known as *Matelea maritima* (Jacq.) Woodson. Sprengel's description is not inconsistent with their decision:

*Gonolobus tigrinus* Griseb., Mem. Amer. Acad. Arts 8: 520. 1863. = *Matelea tigrina* (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28: 226. 1941.

**Protologue:** “[Wright] (1667),” loc. not cited.

**Type(s):** Cuba, Holguín, 19 Mar, *Wright 1667* (lectotype: GOET, n. v., fide Howard 1989a, designated here; syntypes: MO [image online!], G!, GH!, K!).

**Notes:** Specimens distributed under *Wright 1667* were collected by Wright from at least two different localities at two different times (GH: “in coffee fields, Josephina, Nov 1”; GOET: “Holguin, 19 Mar”). Krings (2005c) mistakenly stated that Howard lectotypified *G. tigrinus* based on *Wright 1667* at GOET. However, Howard's “lectotypification” (1989a) appeared in a microfiche appendix, not in print, and thus is not effectively published and has no standing in nomenclature. Rankin & Greuter (2000) reported a similar case in Antillean *Aristolochia*.

*Gonolobus tigrinus* Griseb. var. *angustifolius* Griseb., Cat. Pl. Cub. 177. 1866.

**Protologue:** “Wr. [Wright],” loc. not cited.

**Type(s):** The location of the type remains unknown. No additional matching material was found.

**Notes:** This taxon was recognized at the specific rank by Schlechter (1899) as *G. grisebachianus* Schltr.

*Gonolobus tobagensis* Urb., Repert. Spec. Nov. Regni Veg. 16: 37. 1919.

**Protologue:** “in Tobago in districtu The Widow nominato, m. April. flor, *W.E. Broadway* no. 4467 [loc. not cited].”

**Type(s):** Tobago, the Widow, 28 Apr 1913, *W.E. Broadway 4467* (lectotype: BM!, designated here).

**Notes:** Among the great bulk of collections received by Urban from Erik Ekman (Cuba and Hispaniola) and William Harris (Jamaica), are specimens sent to him by W.E. Broadway from Trinidad, Tobago, and Grenada. Holotypes are presumed to have remained at B until their destruction in a fire in World War II. There is no indication on *Broadway 4467* (BM) that it was seen by Urban, but as the only apparently extant sheet of the number cited by Urban in the protologue, it is here designated lectotype of *G. tobagensis*.

*Gonolobus variifolius* Schltr. in Urban, Symb. Antill. 1(2): 286. 1899. = *Matelea variifolia* (Schltr.) Woodson, Ann. Missouri Bot. Gard. 28: 226. 1941.

**Protologue:** “Portorico, Sierra de Luquillo, in regione media montis Jimenes in fruticetis, Jun. 1885: *Sintenis n. 1653*,’ loc. not cited; ‘montis Cienega prope Adjuntas, Jun. 1886: *Sintenis n. 4687*,” loc. not cited.

**Type(s):** Puerto Rico, *P. Sintenis 1653* (lectotype: NY!, here designated; isolectotypes: G!, GH!, MO!, P!, US!); *P. Sintenis 4687* (syntype: K!).

**Notes:** *Sintenis 1653* (NY) is here designated as lectotype for *Gonolobus variifolius* Schltr. as, unlike the other specimens, it bears a diversity of leaves, a number of inflorescences, and flowers.

*Gonolobus viridiflorus* Schult. in Roemer & Schultes, Syst. Veg. 6: 61. 1820.; nom. illeg., non *G. viridiflorus* Nutt. (1818).

**Protologue:** “*Meyer*,” loc. not cited.

**Type(s):** unknown.

**Notes:** Schultes (1820) clearly cited Meyer’s basionym, *Cynanchum viridiflorum*.

However, *C. viridiflorum* G. Mey. is illegitimate, being a later homonym of *C. viridiflorum* Sims (1817). The basionym epithet is not available in *Gonolobus* due to the earlier *G. viridiflorus* Nutt. (1818). Most recent authors have accepted this entity under the name *Matelea denticulata* (Vahl) Fontella & E.A. Schwarz (Boletim do Museu Botânico Municipal 46: 4. 1981.).

*Gonolobus waitukubuliensis* Krings, Syst. Bot. 32: 187. 2007.

**Protologue:** “Dominica. In sylvis ad Laudat, Mai 1882 (fl), *Eggers* 728 (holotype: HBG! [2 sheets]; isotypes: FR!, G!, GH!, JE!, M!, W!, Z!)”

**Type(s):** Dominica. In sylvis ad Laudat, Mai 1882 (fl), *Eggers* 728 (holotype: HBG! [2 sheets]; isotypes: FR!, G!, GH!, JE!, M!, W!, Z!)

*Gonolobus youroumaynensis* Krings, Syst. Bot. 32: 191. 2007.

**Protologue:** “Orange Hill Estate, roadbank in banana and pigeon pea plantations, uphill from fork in road to the C.W.S.A. water intake site, Kiss-me, 14 Mar 2006 (fl), *Krings* 1374 with *Springer* (holotype: NCSC!; isotypes: GH!, K!, NY!, US!, P!).”

**Type(s):** St. Vincent. Orange Hill Estate, roadbank in banana and pigeon pea plantations, uphill from fork in road to the C.W.S.A. water intake site, Kiss-me, 14 Mar 2006 (fl), *Krings 1374 with Springer* (holotype: NCSC!; isotypes: GH!, K!, NY!, US!, P!).

*Ibatia maritima* (Jacq.) Decne. in De Candolle, Prodr. 8: 599. 1844. = *Matelea maritima* (Jacq.) Woodson, Ann. Missouri Bot. Gard. 28: 222. 1941.

See *Asclepias maritima* Jacq.

*Ibatia mollis* Griseb., Cat. Pl. Cub. 177. 1866. = *Matelea mollis* (Griseb.) Woods., Ann. Missouri Bot. Gard. 28: 223. 1941.

**Protologue:** “Cuba occ. - pr. La Concordia (*Wr.* 2978),” loc. not cited.

**Type(s):** Cuba, *Wright 2978* (lectotype: GH!, here designated; syntypes: K!, MO! [image online])

**Notes:** See discussion under *Gonolobus tigrinus* regarding problems of typification of Grisebach names based on Wright collections. Unfortunately, there is no extant Wright material of number 2978 at GOET. However, a specimen does exist at GH, which can be designated lectotype following Howard (1989a). Two elements are mounted on the specimen – one with flowers and one with fruits. As fruits were not mentioned in the protologue, the flowering element of *Wright 2978* (GH) is here designated as lectotype for *Ibatia mollis* Griseb. Other combinations include: *Ptycanthera mollis* (Griseb.) Schltr., Symb. Antill. 1(2): 280. 1899.

*Ibatia muricata* Griseb., Fl. Brit. W. I. 421. 1862.

**Protologue:** “Antigua!, *Wullschl.*, Dominica!, *Imr.*; [Guadeloupe! ; Venezuela!],” loc. not cited.

**Type(s):** Cedar Hall, Antigua, 1849, *Wullschlagel* (lectotype: M! [2 sheets], designated by Krings & Saville, accepted)

**Notes:** Although not identified as a type, the material at M was the only *Wullschlagel* specimen from Antigua found in the course of a study by Krings & Saville (accepted) and was designated lectotype of *Ibatia muricata*. Grisebach’s name is a synonym of *Matelea maritima* (Jacq.) Woodson, Ann. Missouri Bot. Gard. 28: 222. 1941.

*Jacaima costata* (Urb.) Rendle, J. Bot. 74: 340. 1936. = *Matelea costata* (Urb.) Morillo, Anales Jard. Bot. Madrid 43: 239. 1987 [“1986”].

See *Poicilla costata* Urb.

*Jacaima costata* (Urb.) Rendle var. *goodfriendii* Proctor, J. Arnold Arbor. 63: 290. 1982. = *Matelea costata* (Urb.) Morillo var. *goodfriendii* (Proctor) Krings, comb. nov.

**Protologue:** “St. Ann: Cedar Valley distr., ca. 1.5 mi NE of Cave Valley Square, ca. 2000 ft, *Goodfriend s.n.* (IJ 65657), May 17, 1977 (flowers) (holotype), *Goodfriend s.n.* (IJ 66697), July 1977 (fruit).”

**Type(s):** Jamaica, St. Ann: Cedar Valley distr., ca. 1.5 mi NE of Cave Valley Square, wooded limestone hills, ca. 2000 ft, 17 May 1977, *Goodfriend s.n.* (holotype: IJ!); July 1977, *Goodfriend s.n.* (paratype: IJ!)

*Jacaima parvifolia* Proctor, J. Arnold Arbor. 63: 291. 1982. = *Matelea proctori* Krings, nom. nov.

**Protologue:** “Clarendon: Broom Hall hills, 1.2 mi SW of Cave Valley Square, 1800–2000 ft, *Proctor 37887*, July 9, 1978 (holotype).”

**Type(s):** Jamaica. Clarendon: Broom Hall hills, 1.2 mi SW of Cave Valley Square, 1800–2000 ft, 9 July 1978, *Proctor 37887* (holotype: GH!; isotype: IJ!).

**Notes:** A new name is required as a new combination in *Matelea* is blocked by *M. parvifolia* (Torr.) Woodson. As *Proctor 37887* (IJ) is labelled isotype, it is assumed that the GH duplicate was intended to serve as the holotype. Dr. Proctor accompanied the current author, Dale Suiter, and Davian Campbell, on an expedition to the type locality in March of 2006. At the time the type was described the area was called Broom Hall and the valley was mostly in pineapple cultivation (Proctor, pers. comm.). On a change of ownership, the area is now mostly in coffee and under the name Baron Hall. Although the hills maintain forest cover, much is disturbed and has either been converted to coffee or is in the process of conversion. Specimens of *J. parvifolia* were not located. There are forests not owned by Baron Hall which are part of the endemic Peckham complex and may retain populations of *J. parvifolia*, but further research is needed.

*Lachnostoma maritimum* (Jacq.) G. Nicholson, Ill. Dict. Gard. 2: 226. 1884. = *Matelea maritima* (Jacq.) Woodson, Ann. Missouri Bot. Gard. 28: 222. 1941.

See *Asclepias maritima* Jacq.

*Lachnostoma mollis* (Griseb.) M. Gómez, Anales Hist. Nat. 23: 276. 1894. = *Matelea mollis* (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28: 223. 1941.

See *Ibatia mollis* Griseb.

*Macroscepis hirsuta* (Vahl) Schltr. in Urban, Symb. Antill. 1: 265. 1899. = *Matelea hirsuta* (Vahl) Woodson in E.E. Cheesman, Fl. Trinidad 2: 170. 1947.

See *Cynanchum hirsutum* Vahl

“*Macroscepis obovata*” auct. non Kunth: Griseb., Fl. Brit. W. I. 421. 1861.

**Notes:** The most recent combination to which Grisebach misapplied the name *Macroscepis obovata* is *Matelea hirsuta* (Vahl) Woodson in E. E. Cheesman, Fl. Trinidad 2: 170. 1947.

See *Cynanchum hirsutum* Vahl

*Marsdenia bicolor* Britton & P. Wilson, Bulletin of the Torrey Botanical Club 50: 47. 1923.  
= *Matelea bicolor* (Britton & P. Wilson) Woodson, Ann. Missouri Bot. Gard. 28: 236.  
1941.

**Protologue:** “Sierra Maestra, Oriente (*Léon 10787*, type; *10788*),” loc. not cited.

**Type(s):** Cuba, *Léon 10787* (holotype: NY!; isotype: HAC, n. v.); Cuba, *Léon 10788* (paratypes: NY!, US!)

**Notes:** Although TROPICOS currently indicates the holotype to be at GH (as of 12 April 2006), the specimen is not listed in the GH online catalogue nor was it sent on loan or found in a targeted search by collection manager Emily Wood. In addition, there is a discrepancy in the label data, particularly the altitude of collection, for the paratype *Léon*

10788, suggesting that the sheets at NY and US are not duplicates of the same collection. The NY sheet indicates only “Maestra ridge, 1300 m,” whereas the US sheet indicates “Woods: Sierra Maestra. Region of Pico Turquino. Alt. near 2000 m.” Collector, collector number, and date are the same on both sheets.

*Matelea acuminata* (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28: 225. 1941.

See *Orthosia acuminata* Griseb.

*Matelea alainii* Woodson, Contr. Ocas. Mus. Hist. Nat. Colegio “De La Salle” 15: 23. 1956.

**Protologue:** “Cuba: Oriente: on coastal limestone rocks, Km. 90 between Imías and Cajobabo, Vía Azul, Jan. 12, 1956,” *Brother Alain & C.V. Morton 5029* (HT: MO); “on coastal limestone rocks. Km 50 of Via Azul, Jan 10, 1956,” *Brother Alain & C.V. Morton 4959* (PT: MO).

**Type(s):** Cuba, *Brother Alain & Morton 5029* (holotype: MO; isotypes: GH!, HAC!, US!); *Alain & Morton 4959* (paratypes: GH!, MO!, IJ!).

*Matelea annulata* Woodson ex Alain, Brittonia 20: 149. 1968.

**Protologue:** “Hispaniola: Dominican Republic: Montiada Nueva, Barahona Prov., 21–25 Aug 1946, R. & E. Howard 8512 (Type: NY; Isotype: GH); Howard 8590 (GH).”

**Type(s):** Dominican Republic, Montiada Nueva, Barahona Prov., 21–25 Aug 1946, R.A. & E.S. Howard 8512 (holotype: NY! [2 sheets]; isotypes: GH!, MO!)

**Notes:** Alain H. Liogier described *Matelea annulata* based on suggestions from Robert E. Woodson, Jr. and legitimized the latter's *nomen in schedula*. Three sheets were cited in the protologue: *R. & E. Howard 8512* (HT: NY!; IT: GH!) and *Howard 8590* (PT: GH!). The former two contain matching material. However, the latter collection (the paratype), which incidentally was also collected by both Howards, contains material that clearly does not belong to the holotype and isotype. Although also glabrous, leaves of *R. & E. Howard 8590* exhibit: (1) more numerous secondary veins, and (2) secondary veins nearly straight (vs. ascending in *R. & E. Howard 8512*). The seeds associated with *R. & E. Howard 8590* are also: (1) significantly longer (11–11.6 mm vs. 5 mm in *R. & E. Howard 8512*), (2) of a thin papery texture (vs. hardened in *R. & E. Howard 8512*), and (3) lack the distally swollen margin seen in *Howard 8512* (and other West Indian *Matelea* species). Although published as a paratype, *R. & E. Howard 8590* (GH) must be excluded from *Matelea annulata*. It remains unclear to what taxon it should be referred instead. Typification of *M. annulata* should be as indicated above. As a final note, in contrast to the indication by Liogier (1968), the flowers of *Matelea annulata* are not solitary. They appear to be borne sequentially on inflorescences subtended by a very reduced peduncle.

*Matelea bayatensis* (Urb.) Woodson, Ann. Missouri Bot. Gard. 28: 226. 1941.

See *Gonolobus bayatensis* Urb.

*Matelea bicolor* (Britton & P. Wilson) Woodson, Ann. Missouri Bot. Gard. 28: 236. 1941.

See *Marsdenia bicolor* Britton & P. Wilson.

*Matelea borinquensis* Alain, Phytologia 61: 360. 1986.

**Protologue:** “Puerto Rico: Cerro Pelucho, San Lorenzo, alt. 400–500 m, March 8, 1984,

*Alain & Perfa Liogier, Luis F. Martorell 35111* (holotypus: UPR).”

**Type(s):** Puerto Rico, *Liogier & al. 35111* (holotype: UPR, n. v.).

**Notes:** Syn. of *Matelea variifolia* (Schltr.) Woodson fide Acevedo-Rodríguez (2005).

*Matelea constanzana* Jiménez, Rhodora 62: 238. 1960.

**Protologue:** “in Sto. Domingo prope Constanza, inter frutices volubilis 1400 m. alt., *H. von Tuerckheim n. 3466*, flor. Jul. 1910,” loc. not cited.

**Type(s):** The location of the type remains unknown. No additional matching material was found.

**Notes:** Nomen nov. for *Poicillopsis tuerckheimii* Schltr., Symb. Antill. 7(3): 339. 1912.

Jiménez proposed the new name as Schlechter’s epithet was unavailable in *Matelea*.

*Matelea correllii* Spellman, Ann. Missouri Bot. Gard. 65(4): 1255. 1979 [“1978”].

**Protologue:** “Bahama Islands. Long Island: ... low places along Queen's Highway about 4 miles north of Clarence Town center, 18 Nov. 1977, *D.S. Correll 49112* (MO, holotype; F, FTG, GH, NY, US, isotypes).”

**Type(s):** Bahamas, Long Island, *D.S. Correll 49112* (holotype: MO; isotypes: F!, FTG!, GH!, NY!, US!)

*Matelea corynephora* Krings, Sida 22: 942. 2006.

**Protologue:** “Haiti. Ile la Tortue, la Vallée, top of Morne Barranca, c. 300 m, 21 Mar 1928 (fl), *E.L. Ekman H9740* (holotype: S!).”

**Type(s):** Haiti. Ile la Tortue, la Vallée, top of Morne Barranca, c. 300 m, 21 Mar 1928 (fl), *E.L. Ekman H9740* (holotype: S!).

*Matelea costata* (Urb.) Morillo, *Anales Jard. Bot. Madrid* 43: 239. 1987 [“1986”].

See *Poicilla costata* Urb.

*Matelea crispiflora* (Urb.) Jiménez, *Rhodora* 62: 238. 1960.

See *Poicillopsis crispiflora* Urb.

*Matelea ekmanii* (Urb.) Woodson, *Ann. Missouri Bot. Gard.* 28: 226. 1941.

See *Gonolobus ekmanii* Urb.

*Matelea denticulata* (Vahl) Fontella & E.A. Schwarz, *Bol. Mus. Bot. Munic.* 46: 4. 1981.

See *Cynanchum denticulatum* Vahl

*Matelea dictyopetala* (Urb. & Ekman) Krings, in review.

See *Gonolobus dictyopetalus* Urb. & Ekman

*Matelea domingensis* (Alain) Krings, *Sida* 21: 2081. 2005.

See *Gonolobus domingensis* Alain

*Matelea grisebachiana* (Schltr.) Alain, Mem. Soc. Cub. Hist. Nat. "Felipe Poey" 22: 120. 1955.

See *Gonolobus grisebachianus* Schltr.

*Matelea hastata* Alain, Brittonia 20: 150. 1968.

**Protologue:** "Haiti: Massif des Matheux, Croix des Bouquets, Morne a Cabrits, 18 Jul 1924, *Ekman H. 973* (Type: US; Isotype: NY)."

**Type(s):** Haiti, *Ekman H 973* (holotype: US!; isotypes: K!, NY!)

*Matelea hirsuta* (Vahl) Woodson in E.E. Cheesman, Fl. Trinidad 2: 170. 1947.

See *Cynanchum hirsutum* Vahl

*Matelea linearipetala* Alain, Phytologia 64: 346. 1988.

**Protologue:** "Haiti: On oligostene limestone, 200 m alt., Massif des Matheux, Thomazeau, Morne à Cabrits, Oct. 24, 1926, *E.L. Ekman 7136* (Holotypus: S)."

**Type(s):** Haiti, *Ekman H 7136* (holotype: S!)

*Matelea maritima* (Jacq.) Woodson, Ann. Missouri Bot. Gard. 28: 222. 1941.

See *Asclepias maritima* Jacq.

*Matelea mollis* (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28: 223. 1941.

See *Ibatia mollis* Griseb.

*Matelea monticola* Alain, Sida 20: 1645. 2003.

**Protologue:** “Ciénaga de la Culata, Constanza, alt 1600–1700 m, 15–16 Oct 1968, Alain Liogier 13029 (holotype: NY; isotype, US); in woods, Cabezada de la Ciénaga de la Culata, Constanza, alt 1650 m, 16 Oct 1968, Alain Liogier 13069 (NY, US).”

**Type(s):** Dominican Republic, *Liogier 13029* (holotype: NY!).

**Notes:** A nom. nov. for *Matelea sylvicola* Alain, Phytologia 22: 168. 1971, nom illeg., non L.O. Williams 1968. Neither isotype nor paratype are housed at US, despite so cited in the protologue. The paratype is also neither listed in the NY type catalogue, nor included in a loan from NY. Its location remains unknown.

*Matelea nipensis* (Urb.) Woodson, Ann. Missouri Bot. Gard. 28: 226. 1941.

See *Gonolobus nipensis* Urb.

*Matelea oblongata* (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28: 226. 1941.

See *Orthosia oblongata* Griseb.

*Matelea ovatifolia* (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28: 225. 1941.

See *Poicilla ovatifolia* Griseb.

*Matelea pauciflora* (Spreng.) Woodson, Ann. Missouri Bot. Gard. 28: 226. 1941.

See *Gonolobus pauciflorus* Spreng.

*Matelea pentactina* Krings, Sida 21: 1519. 2005.

**Protologue:** “Haiti. Les Roseaux, Massif de la Hotte western group, rocky ledge, c. 1300 m, 16 Sept 1928, *Ekman H 10685* (holotype: S!); Massif de la Selle, gr. Crete-a-Piquants, Port-au-Prince, between Carrefour-Martin and Bois d’Orme, c. 800 m, limestone, 17 Dec 1926, *Ekman H 7402* (paratype: S!).”

**Type(s):** Haiti. Les Roseaux, Massif de la Hotte western group, rocky ledge, c. 1300 m, 16 Sept 1928, *Ekman H 10685* (holotype: S!; isotypes: B!, US!, EHH n. v.); Massif de la Selle, gr. Crete-a-Piquants, Port-au-Prince, between Carrefour-Martin and Bois d’Orme, c. 800 m, limestone, 17 Dec 1926, *Ekman H 7402* (paratype: S!, EHH n. v.).

*Matelea phainops* Krings, *Sida* 22: 948. 2006.

**Protologue:** “Dominican Republic. Vine, up to 1.5 m high, flowers yellowish green, in thickets, about 2 mi W of Oviedo, alt. about sea level, on limestone, 3 Nov 1989 (fl), *A.H. Liogier 16617* (holotype: GH!; isotypes: NY!, USF!).”

**Type(s):** Dominican Republic. Vine, up to 1.5 m high, flowers yellowish green, in thickets, about 2 mi W of Oviedo, alt. about sea level, on limestone, 3 Nov 1989 (fl), *A.H. Liogier 16617* (holotype: GH!; isotypes: NY!, USF!).

*Matelea proctori* Krings, comb. nov.

See *Jacaima parvifolia* Proctor

*Matelea pubescens* (Griseb.) Krings, in review

See *Gonolobus pubescens* Griseb.

*Matelea rhamnifolia* (Griseb.) Krings, Sida 21: 1515. 2005.

See *Gonolobus rhamnifolius* Griseb.

*Matelea rhynchocephala* Krings, Sida 22: 949. 2006.

**Protologue:** “Dominican Republic. Prov. Santiago, Valle del Cibao, Santiago, Hato del Yaque, in thickets, fl. green, fruiting, 15 Feb 1930 (fl & fr), *E.L. Ekman HI4296* (holotype: S!).”

**Type(s):** Dominican Republic. Prov. Santiago, Valle del Cibao, Santiago, Hato del Yaque, in thickets, fl. green, fruiting, 15 Feb 1930 (fl & fr), *E.L. Ekman HI4296* (holotype: S!)

*Matelea rubra* (H. Karst.) Spellman & Morillo, Phytologia 34: 152. 1976.

See *Omphalophthalma rubra* H. Karst.

*Matelea rubra* (H. Karst.) Aa & Stoffers, Proc. Kon. Ned. Akad. Wetensch., C 84(3): 309. 1981.

**Notes:** *Matelea rubra* (H. Karst.) Aa & Soffers is nomenclaturally superfluous as the combination by Spellman & Morillo (loc. cit.) has priority.

See *Matelea rubra* (H. Karst.) Spellman & Morillo

*Matelea sintenisii* (Schltr.) Woodson, Ann. Missouri Bot. Gard. 28: 226. 1941.

See *Gonolobus sintenisii* Schltr.

*Matelea sylvicola* Alain, Phytologia 22: 168. 1971, nom. illeg., non L.O. Williams 1968.

See *Matelea monticola* Alain

*Matelea tamnifolia* (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28: 225. 1941.

See *Poicilla tamnifolia* Griseb.

*Matelea tigrina* (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28: 226. 1941.

See *Gonolobus tigrinus* Griseb.

*Matelea torulosa* Krings, Sida 22: 951. 2006.

**Protologue:** “Dominican Republic. Distr. Nacional, Los 3 Ojos de Agua, near Santo Domingo, 31 Oct 1959 (fl), *E. Marcano [J.J. Jiménez]* 4096 (holotype: US!).”

**Type(s):** Dominican Republic. Distr. Nacional, Los 3 Ojos de Agua, near Santo Domingo, 31 Oct 1959 (fl), *E. Marcano [J.J. Jiménez]* 4096 (holotype: US!)

*Matelea variifolia* (Schltr.) Woodson, Ann. Missouri Bot. Gard. 28: 226. 1941.

See *Gonolobus variifolius* Schltr.

*Matelea viridiflora* (G. Mey.) Woodson, Ann. Missouri Bot. Gard. 28: 325. 1941.

See *Cynanchum denticulatum* Vahl (syn. fide Howard, 1989b)

*Matelea viridivenia* Alain, Phytologia 22: 169. 1971.

**Protologue:** “Cabo Rojo, Pedernales, 4 Nov 1969, Alain Liogier 16637 (holotype, NY; isotypes, US, GH, P, IJ); about 5 miles E of Cabo Rojo, 8 Feb 1969, Alain Liogier 13620

fruiting specimen (NY); in thickets, km 92 from Bani to Azua, alt 80 m, 3 Nov 1969, Alain Liogier 16598 (NY, US, GH, P); on limestone, los Guanitos, 7 mi E of Cabo Rojo, Pedernales, 13 Nov 1969, Alain Liogier 16961b (NY, US, GH, P, IJ).”

**Type(s):** Cabo Rojo, Pedernales, 4 Nov 1969, *Alain Liogier 16637* (holotype: NY!); about 5 miles E of Cabo Rojo, 8 Feb 1969, *Alain Liogier 13620* fruiting specimen (paratype: NY!); in thickets, km 92 from Bani to Azua, alt 80 m, 3 Nov 1969, *Alain Liogier 16598* (paratype: NY!); on limestone, los Guanitos, 7 mi E of Cabo Rojo, Pedernales, 13 Nov 1969, *Alain Liogier 16961b* (paratype: NY!, USF!).

**Notes:** The types or paratypes listed in the protologue for GH, IJ, P, and US have not been found.

*Omphalophthalma rubra* H. Karst., Fl. Columb. 2: 119, t. 163. 1866. = *Matelea rubra* (H. Karst.) Spellman & Morillo, Phytologia 34: 152. 1976.

**Protologue:** “Habitat litora maris Caribaei prope St. Martam [Colombia], “loc. not cited.

**Type(s):** St. Marta, New Granada, Herb. Karsten (holotype: LE [Sennikov, pers. comm.; n. v., not sent on loan due to budget constraints])

*Orthosia acuminata* Griseb., Cat. Pl. Cub. 175. 1866. = *Matelea acuminata* (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28: 225. 1941.

**Protologue:** “Cuba or. (*Wr. 2966*),” loc. not cited.

**Type(s):** Cuba, *Wright 2966*, 1860–1864 (lectotype: GH!, designated by Krings & Fantz (2006); isolectotypes: BM!, G!, HAC! [2 sheets], K!)

**Notes:** Krings & Fantz (2006) noted that sheets of *Wright 2966* (BM, G, GH, HAC, and K) bear white labels with the dates 1860–64. The mounted field ticket on the GH sheet reads: “*Asclepias* – Fl. (except the white stigma) green. Farallones San Andre Oct 27.” As *Wright 2966* (GH!) contains fifteen inflorescences and is in very good condition; it was designated as lectotype for *Orthosia acuminata* Griseb. by Krings & Fantz (2006). *Wright 2966* (G!) contains four inflorescences and is in superior condition to the HAC material. *Wright 2966* (BM!, G!, HAC!, K!) should be considered isolectotypes. See Krings & Fantz (2006) for additional discussion regarding their philosophy of typification of Wright specimens.

*Orthosia oblongata* Griseb., Cat. Pl. Cub. 176. 1866. = *Matelea oblongata* (Griseb.)

Woodson, Ann. Missouri Bot. Gard. 28: 226. 1941.

**Protologue:** “Cuba occ. (*Wr. 2967*),” loc. not cited.

**Type(s):** Cuba, *Wright 2967*, 1860–1864 (lectotype: GH!, designated by Krings & Fantz (2006); isolectotypes: BM!, G!, HAC!, K!, MO, S!).

**Notes:** Krings & Fantz (2006) noted that sheets of the original material for *O. oblongata*—at BM!, G!, GH!, HAC!, K!, MO, and S!—all bear white labels with the dates 1860–64. The mounted field ticket of *Wright 2967* (GH) reads: “*Asclepias* – Fl. green – a white speck at the tips of the segments. Stigma white. Loma de Ranjel June 17.” Field tickets do not accompany the other specimens. Krings & Fantz (2006) designated *Wright 2967* (GH) lectotype for *Orthosia oblongata* Griseb., considering the duplicates at G, HAC, K, MO, and S isolectotypes. *Wright 2967* (GH) is in good condition, with numerous inflorescences. See Krings & Fantz (2006) for additional discussion regarding their philosophy of typification of Wright specimens.

*Poicilla acuminata* (Griseb.) Schltr. in Urban, Symb. Antill. 5(3): 469. 1908. = *Matelea acuminata* (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28: 225. 1941.

See *Orthosia acuminata* Griseb.

*Poicilla costata* Urb., Symb. Antill. 6(1): 38. 1909. = *Matelea costata* (Urb.) Morillo, Anales Jard. Bot. Madrid 43: 239. 1986(1987).

**Protologue:** “Hab. in Jamaica juxta viam ad Wareka in Long Mountain ad latus australe, 200 m. alt., m. Nov. fl., m. Jun. fruct.: Harris n. 9590, 10006,” loc. not cited

**Type(s):** Jamaica, road to Wareka, Long Mountain, S side, twining and climbing over shrubs and trees, to a height of 25 feet, flowers greenish-yellow, stems full of milky juice, 19 Nov 1907 (fl), *W. Harris 10006* (lectotype: BM!, here designated; isolectotype: UCWI!); Jamaica, Long Mountain, S side, 600 feet altitude, a higher climber, 21 Jun 1907 (fr), *W. Harris 9590* (syntypes: NY!; UCWI!).

**Notes:** *Harris 9590* (NY) is annotated in Urban’s hand.

*Poicilla mollis* (Griseb.) Schltr. in Urban, Symb. Antill. 5(3): 470. 1908. = *Matelea mollis* (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28: 223. 1941.

See *Ibatia mollis* Griseb.

*Poicilla oblongata* (Griseb.) Schltr. in Urban, Symb. Antill. 5(3): 470. 1908. = *Matelea oblongata* (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28: 226. 1941.

See *Orthosia oblongata* Griseb.

*Poicilla ovatifolia* Griseb., Cat. Pl. Cub. 177. 1866. = *Matelea ovatifolia* (Griseb.)

Woodson, Ann. Missouri Bot. Gard. 28: 225. 1941.

**Protologue:** “Cuba or. (*Wr.* 2965),” loc. not cited

**Type(s):** Cuba, *Wright 2965* (lectotype: GOET!, designated by Krings & Fantz (2006);

syntypes: BM!, BREM!, G!, GH!, HAC!, K n. v., LE n. v., NY!, P!, S!, UC!)

**Notes:** As Krings & Fantz (2006) noted, no field tickets accompany the GOET specimen or any syntype, except the GH specimen. Accompanying field tickets of the GH specimen suggest that the sheet is comprised of at least two collections made at different times (Mar., June), although three fragments are mounted. The two fragments mounted on the right contain inflorescences; the fragment mounted on the left contains infructescences. Both field tickets refer to flowers with neither one mentioning fruits. Fruits are not described in Grisebach’s protologue and are not present on any other syntype beside the GH specimen. Except for the GOET specimen, collection labels of all other known specimens are white and bear the dates 1860–64. The GOET specimen bears a tan label with a printed date of 1860, although the zero appears to have been crossed out. It is heavily written on in Grisebach’s hand and is herein designated lectotype for *Poicilla ovatifolia* Griseb. The studied (and matching) dublicately-numbered material in other herbaria remain syntypes.

*Poicilla tamnifolia* Griseb., Cat. Pl. Cub. 176. 1866. = *Matelea tamnifolia* (Griseb.)

Woodson, Ann. Missouri Bot. Gard. 28: 225. 1941.

**Protologue:** “Cuba or., in monte Toro pr. Potosi (*Wr.*),” loc. not cited.

**Type(s):** Cuba, San José, 5 Oct, *Wright s.n.* (lectotype: GH!, here designated); *Wright s.n.* (syntype: NY! [fragment])

**Notes:** See discussion under *Gonolobus tigrinus* regarding problems of typification of Grisebach names based on Wright collections. Unfortunately, there is no extant Wright material corresponding to *Poicilla tamnifolia* at GOET. However, a specimen does exist at GH, which can be designated lectotype following Howard (1989a): Cuba, San José, 5 Oct, *Wright s.n.*

*Poicillopsis crispiflora* Urb., Feddes Repert. 19: 7. 1923. = *Matelea crispiflora* (Urb.) Jiménez, Rhodora 62: 238. 1960.

**Protologue:** “Haiti prope Furcy 1500 m alt., m. Sept. flor.: *Buch no. 1995*,” loc. not cited.

**Type(s):** Haiti, prope Furcy, im Gebüsch, Blth weiss, 1500 m alt., m. Sept. flor., *Buch no. 1995* (lectotype: IJ!, here designated)

**Notes:** *Buch 1995* consists of four flowers in two umbellate inflorescences and a few leaves on stems, though most are in a fragment pocket. The single additional collection of this species that matches the protologue is *Ekman H1933* (EHH n. v., K!, S!): Haiti, Morne de la Selle, Furcy, 1540m, in Buchs [sic] Botan. Garden, 17 Sept 1924. The sheets at K and S are in exceedingly good condition, bearing numerous leaves and flowers. The sheet at EHH has not been seen, but is listed here based on the catalogue provided by:  
[http://www.umce.ca/cours/martin/herbier\\_ekman/recherche.pl](http://www.umce.ca/cours/martin/herbier_ekman/recherche.pl) .

*Poicillopsis ovatifolia* (Griseb.) Schltr. in Urban, Symb. Antill. 7(3): 339. 1912. = *Matelea ovatifolia* (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28: 225. 1941.

See *Poicilla ovatifolia* Griseb.

*Poicillopsis tuerckheimii* Schltr. in Urban, Symb. Antill. 7(3): 339. 1912.

See *Matelea constanzana* Jiménez

*Ptycanthera berterii* Decne. in De Candolle, Prodr. 8: 606. 1844, nom. illeg.

**Protologue:** “S. Domingo (*Bertero*) [...] (v.s.h. DC.),”

**Type:** Hispaniola, ‘St. Domingue,’ *Bertero s.n.* (holotype: G-DC [IDC microfiche Candolle Prodromus Herbarium, fiche # 1543!]; isotype: P!).

**Notes:** The name *Ptycanthera berterii* Decne. is illegitimate as the nomenclatural type is the same as that of *Gonolobus pauciflorus* Spreng. (see above). Schlechter (1899) misapplied Decaisne’s name to *Orthosia acuminata* Griseb. (syn. *Matelea acuminata* (Griseb.) Woodson).

*Ptycanthera mollis* (Griseb.) Schltr. in Urban, Symb. Antill. 1(2): 280. 1899. = *Matelea mollis* (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28: 223. 1941.

See *Ibatia mollis* Griseb.

*Ptycanthera oblongata* (Griseb.) Schltr. in Urban, Symb. Antill. 1(2): 280. 1899. = *Matelea oblongata* (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28: 226. 1941.

See *Orthosia oblongata* Griseb.

*Ptycanthera ovatifolia* (Griseb.) Schltr. in Urban, Symb. Antill. 1(2): 279. 1899. = *Matelea ovatifolia* (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28: 225. 1941.

See *Poicilla ovatifolia* Griseb.

*Vincetoxicum acuminatum* (Griseb.) M. Gómez, Anales Acad. Ci. Med. Habana 23: 276. 1894. = *Matelea acuminata* (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28: 225. 1941.

See *Orthosia acuminata* Griseb.

*Vincetoxicum oblongatum* (Griseb.) M. Gómez, Anales Acad. Ci. Med. Habana 23: 276. 1894. = *Matelea oblongata* (Griseb.) Woodson, Ann. Missouri Bot. Gard. 28: 226. 1941.

See *Orthosia oblongata* Griseb.

*Vincetoxicum sintenisii* (Schltr.) Britton in Britton & Wilson, Sci. Surv. Porto Rico & Virgin Islands 6: 100. 1925. = *Matelea sintenisii* (Schltr.) Woodson, Ann. Missouri Bot. Gard. 28: 226. 1941.

See *Gonolobus sintenisii* Schltr.

*Vincetoxicum stephanotrichum* (Griseb.) Britton in Britton & Wilson, Sci. Surv. Porto Rico & Virgin Islands 6: 100. 1925.

See *Gonolobus stephanotrichus* Griseb.

*Vincetoxicum variifolia* (Schltr.) Britton in Britton & Wilson, Sci. Surv. Porto Rico & Virgin Islands 6: 100. 1925. = *Matelea variifolia* (Schltr.) Woodson, Ann. Missouri Bot. Gard. 28: 226. 1941.

See *Gonolobus variifolius* Schltr.

**Names of uncertain application.**---The following names includes those for which neither protologues nor types could be obtained, or for which the specimens do not belong in Gonolobinae. Names of the former category have long been placed in synonymy by authors of treatments of West Indian Gonolobinae (e.g., Schlechter, 1899; Alain, 1957).

*Gonolobus ottonis* C. Koch & Bouche, *Ind. Sem. Hort. Berol.* 13. 1855.

**Protologue:** unknown

**Type(s):** unknown.

**Notes:** Sometimes cited as *Gonolobus ottonis* Walp. (*Ann. Bot. Syst.* 5: 502. 1859.).

However, Walpers (1859) clearly cited *G. ottonis* C. Koch & Bouche and should not be considered author of a homonym if the Koch & Bouche name is indeed legitimate. Walpers (1859) also cited: 'Ex insula Cuba reportavit *Otto*.' However, no copy of the Koch & Bouche's protologue of *G. ottonis* could be obtained. Schlechter (1899) thought that the specimen collected by Otto (apparently formerly at B) was from Caracas, Venezuela, not from Cuba.

*Gonolobus oxyanthus* Turcz., *Bull. Soc. Imp. Naturalistes Moscou* 25(2): 318. 1852.

**Protologue:** "Venezuela, Funck 2," fide TROPICOS (protologue n. v.).

**Type(s):** Venezuela, 1845–1852, Funk 2 (G, n. v.; P, n. v.) fide TROPICOS

**Notes:** Fide Fontella & Schwarz (1981), a synonym of *Gonolobus rostratus* (Vahl) R. Br. ex Schult. (*Systema Vegetabilium* 6: 61. 1820). TROPICOS (23 Aug 2006) cited *Funk 2* (Venezuela) as the type, but a copy of the protologue could not be located. Specimens were not found on either of two visits to P.

*Gonolobus virescens* Desv. ex Ham., Prodr. Pl. Ind. Occid. 32. 1825.

**Protologue:** “Herb. Prof. Desvaux, Jamaica. (S. v.),” loc. not cited.

**Type(s):** “Jamaica,” *Desvaux s.n.* (holotype: P!).

**Notes:** Rendle (1936) considered *G. virescens* Desv. a *species incerta*. Schlechter (1899) noted that there was likely a label mix-up between *G. stapelioides* and *G. virescens*, and that the latter was likely collected from Tobago and not Jamaica. The morphology of the flowers of *Desvaux s.n.* (P) places it in Marsdenieae Benth., rather than Gonolobinae.

*Lachnostoma ovatum* Turcz., Bull. Soc. Imp. Naturalistes Moscou 25(2): 318. 1852.

**Protologue:** unknown

**Type(s):** unknown.

**Notes:** Cited as *L. ovata* and as a synonym for *Matelea ovatifolia* (Griseb.) Woodson by Alain (1957). Neither protologue, nor type could be located.

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TABLE 1. Authors and numbers of novelties at the species rank in Gonolobinae, including *Fischeria* and *Metalepis*, based on types from the West Indies.

<i>Author(s)</i>	<i>No. of spp. names published</i>	<i>Author(s)</i>	<i>No. of spp. names published</i>
Alain [Hno.], "A. H. Liogier"	8	Proctor, G. R.	1
Bertoloni, A.	1	Richard, A.	1
Britton, N. L. & P. G. Wilson	1	Schlechter, F. R. R.	9
Decaisne, J.	3	Spellman, D. L.	1
Ekman, E.	1	Sprengler, C. P. J.	2
Grisebach, A. H. R.	13	Urban, I.	9
Hamilton, W.	1	Vahl, M.	3
Jacquin, von, N.	1	Woodson, Jr., R. E.	3
Krings, A.	10		

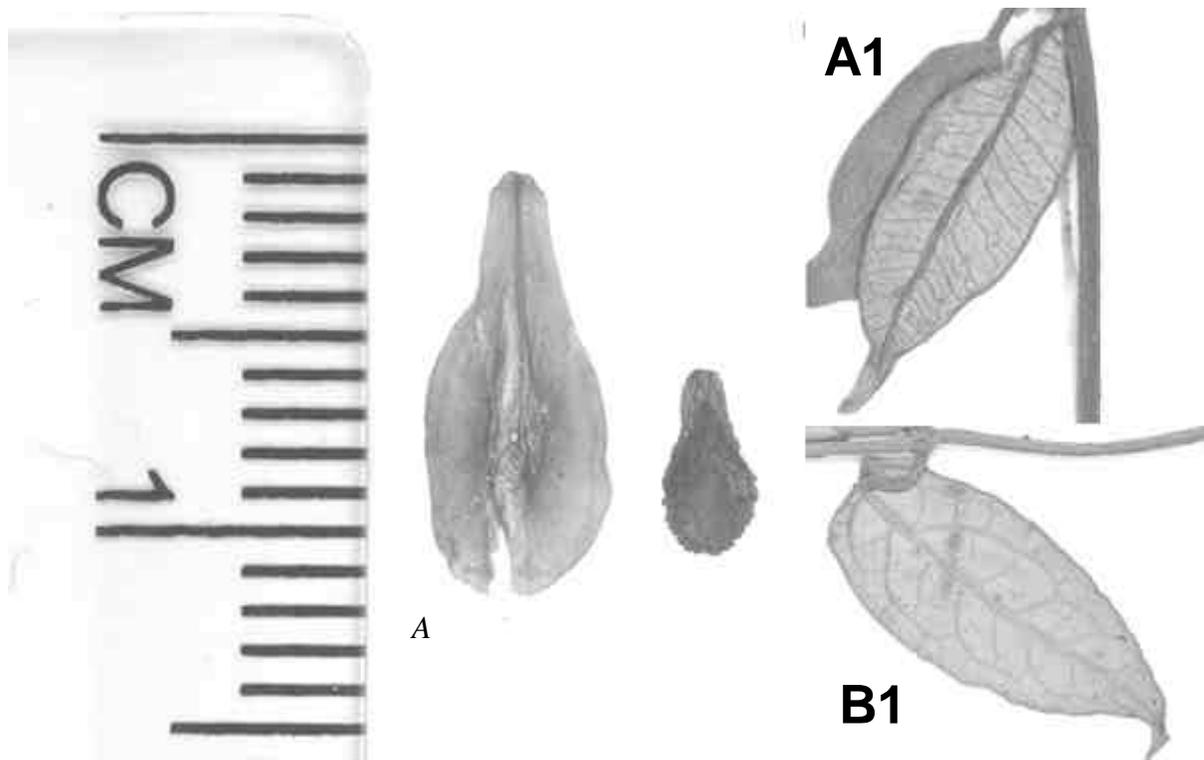


FIG. 1. Seeds and leaves: A-A1, *R. & E. Howard 8590* (GH) – species unknown; B-B1, *R. & E. Howard 8512* (NY, GH) – *Matelea annulata* Woodson ex Alain.

## **Additional studies in South American Gonolobinae**

## Chapter XV

**Two new species and three lectotypifications  
in the *Ibatia-Matelea* complex (Apocynaceae, Asclepiadoideae)  
from northern South America**

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Reproduced from: Krings, A. and A.C. Saville. Accepted, pending minor rev. *Syst. Bot.*  
Krings primarily wrote the manuscript, developing the key and describing *M. cumanensis*,  
*M. pacifica*, *M. rubra*, as well as gynostegial coronas and gynostegia for *M. fontana* and *M.*  
*maritima*. Under the direction and guidance of Krings, Saville provided the majority of  
descriptions for *M. fontana* and *M. maritima*, except for corona and gynostegium details,  
and contributed the exsiccatae for *M. maritima*.

**ABSTRACT.** Two new species of *Matelea* (Apocynaceae: Asclepiadoideae, Gonolobinae) are described from northern South America: *M. fontana* and *M. pacifica*. The species belong to the *Ibatia-Matelea* complex, but exhibit distinct differences in floral characters from previously known taxa, including the structure of gynostegial coronas. A key to members of the northern South American and West Indian *Ibatia-Matelea* complex is provided, including *M. cumanensis*, *M. maritima*, and *M. rubra*. *Asclepias maritimum*, *Cynanchum fimbriatum*, and *Ibatia muricata* are lectotypified.

**Keywords:** Gonolobinae, key, *Matelea fontana*, *Matelea pacifica*

*Matelea* Aubl. (Apocynaceae: Asclepiadoideae, Gonolobinae) is a New World genus estimated to comprise 20–200 species (Mabberley 1997; Stevens 2001). Over 100 species have been named and at least 56 combinations made since 1980 alone. The degree of variation in estimated species numbers is largely the result of still poorly known tropical taxa and differences regarding generic limits. The circumscription of *Matelea* and submerged genera, such as *Ibatia* Decne., has been particularly complicated. Unable to come to terms with the large variation in corona morphology, Woodson (1941) submerged thirty-six genera, including *Ibatia*, within *Matelea* (increasing its size from six to over 100 species). In the process, he erected sixteen informal subgenera. Woodson (1941) recognized members of ‘subgenus’ *Ibatia* by pollinia ‘more or less descending’ from the translator arms, corollas subcampanulate-rotate, faucal annuli lacking, and the ‘constituent segments’ of the gynostegial corona 3-lobed. In contrast to Woodson (1941), application of the terminology of Liede and Kunze (1993) would recognize the gynostegial coronas to be composed of an unlobed staminal segment (Cs) and a bilobed interstaminal segment (Ci)—at least for the core taxa surrounding the primarily West Indian *I. maritima* (Jacq.) Decne. To his ‘subgenus’ *Ibatia*, Woodson referred morphologically natural allies to *I. maritima*, such as northern South American *Omphalothalma rubra* H. Karst., as well as taxa of less immediately recognizable affinity such as Mexican *Rothrockia cordifolia* A. Gray. Based on shared similarities in the structure of corollas, gynostegial coronas, and terminal stylar head appendages, the complex that includes *M. maritima* (Jacq.) Woodson, also includes northern South American *M. cumanensis* (Willd. ex Schult.) W.D. Stevens (Morillo 1983). On-going study of subtribe Gonolobinae (Apocynaceae: Asclepiadoideae) has resulted in the discovery of two new species that appear to belong to this complex, here referred to

informally as the *Ibatia-Matelea* complex. The species are near *Matelea maritima*, but differ distinctly in a number of morphological characters. They appear to be restricted to northern South America, as are *M. cumanensis* (Colombia, Venezuela) and *M. rubra* (Colombia, Venezuela, Aruba, Bonaire, Curaçao). The two new species are described and illustrated below. Illustrations and amplified descriptions are also provided for *M. cumanensis*, *M. maritima*, and *M. rubra* to facilitate their recognition. Corona morphological terminology follows Liede and Kunze (1993) and Kunze (1995), although it is recognized that additional work may be needed to clarify issues of family-wide homology (see Endress and Bruyns 2000; Livshultz 2003). *Apocynum cumanense*, *Asclepias maritimum*, *Cynanchum fimbriatum*, and *Ibatia muricata* are lectotypified.

KEY TO THE *IBATIA-MATELEA* COMPLEX IN NORTHERN SOUTH AMERICA AND THE WEST INDIES

1. Base of Cs lobe (not the entire Cs segment) ca. > 1 mm higher than nadir of Ci lobe sinus; Ci not ligulate within; gynostegial stipe 1.28–1.35 mm tall; terminal stylar head appendage absent or reduced to ca. 0.1 mm, central rim of stylar head exhibiting five erect lobes, each ca. 0.24–0.26 mm tall ..... *M. rubra*
- 1'. Base of Cs lobe at same height as nadir of sinus of Ci lobes or below it; Ci ligulate within; gynostegial stipe < 0.35 mm tall or stipe absent; terminal stylar head appendage present, > 1mm tall, central rim of stylar head lacking erect lobes..... 2.

2. Corolla lobes white or cream, sometimes with lavender or purple striations; Ci 1.25–1.82 mm long, > 2.5 x as long as the Cs, lobed only about 13–50% from its apex to the apex of the C(is) tube.....*M. cumanensis*
- 2'. Corolla lobes greenish or greenish-yellow to greenish-red or deep purple-brown; Ci 0.5–0.65 mm long, < 1.5 x as long as the Cs, lobed completely from its apex to the apex of the C(is) tube..... 3.
3. Ci of two, narrowly elongate lobes, each half as wide or less as a Cs lobe, both lobes of the Ci somewhat longer than a Cs lobe.....*M. pacifica*
- 3'. Ci not as above ..... 4.
4. Corolla lobes deep purple-brown, adaxial surface sparsely (rarely moderately) pubescent, except for a dense ring of trichomes surrounding the gynostegial corona, trichomes abruptly reduced in size from those immediately surrounding the gynostegial corona to those on the adjoining adaxial surface, the former ca. 0.2 mm long, the latter ca. 0.03–0.08 mm long, corolla lobes 4.2–5.8 mm long; Ci bi-lobed, lobes slightly shorter to as long as Cs lobes, apices rounded; terminal appendage of stylar head distinctly bi-lobed.....*M. fontana*
- 4'. Corolla lobes green to yellowish-green (rarely reddish-green), adaxial surface densely pubescent, including a dense ring of trichomes surrounding the gynostegial corona, trichomes not appreciably reduced in size from those immediately surrounding the gynostegial corona to those on the adjoining adaxial surface, though gradually reduced in size from base of corolla to apex, trichomes ca. 0.13–0.2 mm long, corolla lobes 1.61–4.54 mm long; Ci variously lobed; terminal appendage of stylar head capitate.....*M. maritima*

*Matelea cumanensis* (Willd. ex Schult.) W.D. Stevens, *Phytologia* 64 (5): 335. 1988. (FIG.

1)

*Apocynum cumanense* Willd. ex Schult., *Syst. veg.* 4: 796. 1819 [Mar–Jun].— TYPE:  
VENEZUELA. In umbrosis Cumana, *Humboldt* (holotype: B-WILLD [digital image!])

*Cynanchum fimbriatum* Kunth, *Nov. Gen. Sp.* 3: 203, t. 234. 1819 [9 Jul]. *Metaplexis*  
*fimbriata* (Kunth) Spreng., *Syst. veg.* 1: 854. 1824. *Cynoctonum fimbriatum* (Kunth)  
Decne. in DC., *Prodr.* 8: 531. 1844. *Ibatia fimbriata* (Kunth) H. Karst., *Fl. Columb.* 2:  
113, t. 160, f. 3-6. 1865. *Vincetoxicum fimbriatum* (Kunth) Kuntze, *Revis. gen. pl.* 2:  
424. 1891. *Matelea fimbriata* (Kunth) Dugand, *Caldasia* 9: 436. 1966.— TYPE:  
Illustration in Kunth, *Nov. Gen. Sp.* 3: t. 234. 1819 [9 Jul]. (lectotype, here designated)

*Ibatia albiflora* H. Karst., *Fl. Columb.* 2: 113-114, t. 160, f. I. 1865. *Matelea albiflora*  
(H. Karst.) Dugand, *Caldasia* 9: 435. 1966.— TYPE: COLOMBIA. Magdalena: St. Marta,  
*Karsten s.n.* (holotype: LE, Sennikov, pers. comm, n.v.; isotype: NY!, W?)

Slender (woody?) vine. *Latex* unknown, presumably white. *Stems* pubescent, pubescence  
ubiquitous or in two lines, eglandular sharp trichomes ca. 1 mm long, retrorse or spreading,  
glandular capitate trichomes ca. 0.15 mm long. *Leaf blades* ovate to orbicular, 2.6–6.2 ×  
1.3–4.5 cm, adaxial surface densely pubescent, eglandular sharp trichomes ca. 0.6 mm  
long, spreading, somewhat denser on the midvein, abaxial surface tomentose, eglandular  
sharp trichomes spreading or curling, ca. 0.55 mm long, apex acute to acuminate, base  
cordate, margins entire, colleters 2–6, lanceoloid, 0.34–0.46 mm long; petioles 11–30.1 mm

long, eglandular sharp trichomes ca. 0.52 mm long, mostly retrorse-spreading, some antrorse-spreading, glandular capitate trichomes ca. 0.1 mm long, ubiquitous.

*Inflorescence* racemiform, peduncles to 5 mm long, eglandular sharp trichomes ca. 0.3 mm long, antrorse; pedicels 2.9–4.5 mm long, densely pubescent, eglandular sharp trichomes ca. 0.24 mm long, spreading to antrorse, glandular capitate trichomes ca. 0.06–0.08 mm long. *Calyx* 5-lobed, lobes oblong, lanceolate, or lance-oblong, 2.2–3.8 mm x 0.8–1 mm, adaxial surface glabrous, abaxial surface pubescent, eglandular sharp trichomes ca. 0.45–0.5 mm long, antrorse or spreading, apices obtuse or acute, margins entire, colleters 1 per sinus. *Corolla* white or cream, sometimes with lavender or purple striations (fide colectoris), 5-lobed, imbricate in bud, subcampanulate at base, tube ca. 1.7–3 x 1.8–2.6 mm, lobes lanceolate to lance-oblong, 4.8–6 x 1.7–2.1 mm, adaxial surface essentially glabrous except for some scattered trichomes and a dense ring of trichomes at base, eglandular sharp trichomes ca. 0.11 mm long, abaxial surface coarsely pubescent, eglandular sharp trichomes ca. 0.2 mm long, antrorse, apex obtuse, margins entire. *Faucal annulus* (Ca) apparently absent. *Gynostegial corona* of fused staminal (Cs) and interstaminal parts (Ci), tube ca. 0.6–1.2 mm tall, Cs apex a triangular lobe, papillate-pubescent up to and including the apex, Ci extending 1.25–1.82 mm beyond the C(is) tube, scattered papillate-pubescent mostly at the base, apex bi-lobed, lobes dissected 13–50% from the Ci apex to the apex of the C(is) tube, Ci ligulate basally within, two ridges emanating from the ligule evident well into the portion of the Ci that extends beyond the C(is) tube. *Stylar head* ca. 1.2 mm diam, not stipitate, anther guiderails apparently without appendages, laminar dorsal anther appendages (Cd) absent, terminal stylar head appendage

ca. 1.5 mm tall, distinctly bi-lobed, lobes ca. 0.75 mm long. *Pollinaria*: corpuscula ca. 0.15 mm long, pollinia more or less pendent, ovate, ca. 0.6 x 0.3 mm. *Follicles* unknown.

***Distribution and habitat***: *Matelea cumanensis* is presently known from Venezuela and Colombia. It has been collected primarily in dry, deciduous woodlands and forests.

***Etymology***: The epithet means “from Cumaná” (capital of Sucre, Venezuela).

***Additional specimens examined***: COLOMBIA. Specimen from rocky hill overlooking the sea at Playa Brava, 26 Oct 1898 or 1899, *H.H. Smith 1071* (NY [fl]).

VENEZUELA. **Aragua**: Parque Nacional Henri Pittier, Distr. Girardot, Ciénaga de Ocumare, entre 10° 28'–10° 29' N y 67° 48' – 67° 49' O, 0–200 msnm, trepadora, pétalos blancos, cerca del manglar, en bosque deciduo, 11 Jun 1986, *R. Ortiz. Q. 1029* (VEN [fl]); Carretera a Cuyagua, 4–5 km al NO del pueblo, bosque y matorral seco, m/m 300 m, trepadora heliófila, muy abundante en la zona, hojas verde claro en el haz, verde-glaucas en el envés, aterciopeladas en su aspecto y glandulosas, inflorescencias con 2–4 flores en ántesis simultáneas, corola blanco crema con estrias moradas hacia la base, “2/5/1982”, *G. Carnevali & H. Pivat 639* (VEN [fl]). **Sucre**: Península de Manare, quebrada seca con bosque enano tropofilo y espinares, Quebrada Manare, Playa Garrapata, al S de Manare, entre Punta Garrapata y Punta Aguirre, altura 0–15 m, 11 Sep 1973, *J.A. Steyermark, V. Carreño E. y B. José M. 108016* (VEN [fl]); Aguas Calientes, Km 12–15 de la carretera Cumaná–Cumanacoa, trepadora de flores blancas, “8-7-1970”, *L. Cumana 119* (VEN [fl]).

***Observations***: Stevens (1988) suggested that the pair of names *Apocynum cumanense* and *Cynanchum fimbriatum* were probably based on the same Humboldt and Bonpland collection, noting, as McVaugh (1955) had earlier pointed out, that names based on the sets at B and P often appeared independently and sometimes nearly simultaneously. Kunth,

who was describing plants primarily based on the set at P, and had access to portions of the Willdenow Herbarium at B, indicated that the pair of names referred to the same taxon (Nov. Gen. Sp. 3: 453. 1820). Unfortunately, neither Morillo (1983) nor Stevens (1988) located the type for *C. fimbriatum* (Venezuela. Sucre: “Crescit in umbrosis prope Cumana,” *Humboldt & Bonpland s.n.*). As we likewise could not locate a specimen, we choose the illustration in Kunth’s protologue to serve as lectotype.

Morillo (1983) suggested that *M. fimbriata* and *M. albiflora* likely were the same taxon, based on comparisons of the protologue and original illustration of the former and the protologue and type of the later. Stevens (1988) later agreed with this conclusion, as do we. Morillo (1983) provided an illustration of an apparently tuberculate follicle referred to *M. fimbriata*. However, we have not seen fruiting specimens and cannot provide an adequate description.

***Matelea fontana*** Saville & Krings, sp. nov. (FIG. 2).— TYPE: COLOMBIA. Magdalena:

Santa Marta, a twining vine to 5 ft, corolla deep purple-brown, open dry ravine, 5 mi N of Bonda, 100 ft, closely allied to no. 1672, but appears to be distinct, not only by its leaves and mode of growth (without long, leafless branches) but by the flower, only one seen, 27 Nov 1898 or 1899, *H.H. Smith 1673* (NY! [fl, fr-imm]).

Species nova *Mateleae* differt a *Matelea cumanense* (Willd. ex Schult.) W.D. Stevens, *M. maritima* (Jacq.) Woodson, *M. pacifica* Krings & Saville, et *M. rubra* (H. Karst.) Spellman & Morillo floribus atropurpureis, corollis insuper sparsim vel modice pubescentibus, trichomatibus abrupte abbreviatis, lobis 4.2–5.8 mm longis, appendicibus gynostegii bifidis.

Slender, woody vine. *Latex* white. *Stems* pubescent, pubescence ubiquitous or in two lines, eglandular sharp trichomes retrorse, ca. 0.6 mm long, glandular capitate trichomes ca. 0.05–0.1 mm long. *Leaf blades* oblong to ovate or orbicular, 3.6–8.6 x 1.8–7.6 cm, adaxial surface strigose, eglandular sharp trichomes ca. 0.5–0.8 mm long, antrorse, midvein pubescence denser and less strigose than on leaf surface, eglandular sharp trichomes ca. 0.4–0.6 mm long, antrorse, abaxial surface densely pubescent, eglandular sharp trichomes ca. 0.4–0.5 mm long, midrib pubescence dense, eglandular sharp trichomes ca. 0.5–0.6 mm long, antrorse, apex acute to acuminate, base cordate, margins entire; colleters 2–5, lanceoloid, 0.3–0.6 mm long; petioles 12.2–59.2 mm long, ubiquitously pubescent, eglandular sharp trichomes ca. 0.4–0.6 mm long, retrorse, glandular capitate trichomes ca. 0.1 mm long. *Inflorescence* racemiform, peduncles ca 1 mm long, densely pubescent, eglandular sharp trichomes ca. 0.3 mm long, antrorse, glandular-capitate trichomes absent; pedicels 2.5–4.1 mm long, densely pubescent, eglandular sharp trichomes ca. 0.3 mm long, antrorse. *Calyx* 5-lobed, lobes oblong, ca. 2.6 x 1.3 mm, adaxial surface glabrous, abaxial surface coarsely pubescent, eglandular sharp trichomes ca. 0.4–0.8 mm long, apex acute, margins entire, colleters 1 per sinus. *Corolla* deep purple-brown or maroon changing to green along the margins and apices (fide collectoris), 5-lobed, imbricate in bud, subcampanulate at base, tube ca. 1.1 x 2.1 mm, lobes ovate-lanceolate, 4.2–5.8 x 1.72–2.9 mm, adaxial surface sparsely pubescent, eglandular sharp trichomes ca. 0.03–0.08 mm long, antrorse, abaxial surface more densely pubescent, eglandular sharp trichomes ca. 0.3–0.4 mm long, antrorse, apex acute, margins entire. *Faucal annulus* (Ca) apparently absent. *Gynostegial corona* of fused staminal (Cs) and interstaminal parts (Ci), tube ca. 1.1–1.5

mm tall, Cs apex a triangular lobe, papillate pubescent up to and including the apex, Ci apically bi-lobed, each lobe essentially of similar dimension as a Cs lobe, extending ca. 0.5 mm beyond the apex of the C(is) tube, lateral margins dissected completely from the Ci apex to the apex of the C(is) tube, papillate-pubescent up to, but not including the apex, Ci ligulate basally within, two ridges emanating from the ligule up the C(is) tube. *Stylar head* ca. 2 mm diam, stipe absent, anther guiderails apparently without appendages, laminar dorsal anther appendages (Cd) absent, terminal stylar head appendage ca. 1.3–2.12 mm long, distinctly bi-lobed, apex papillate. *Pollinaria*: corpuscula ca. 0.4 mm long, caudicles present, pollinia more or less pendent, broadly elliptical, ca. 0.73 x 0.39 mm. *Follicles* ovate, ca. 3.4 x 2.4 cm (immature), densely pubescent, eglandular sharp trichomes ca. 0.9–1.2 mm long, tuberculate, tubercles capitate, 1.4–2.0 mm long, heads 1.7–2.9 mm diam.

***Distribution and habitat:*** *Matelea fontana* is currently known only from dry, coastal thickets in Colombia and Venezuela.

***Etymology:*** The bilobed nature of both the Ci and the terminal stylar head appendage abstractly resemble the bubbling up and falling action of a fountain of water.

***Additional specimens examined:*** COLOMBIA. **Magdalena:** Ciénaga, 25 Feb 1950, *R. Romero C. 2030* (NY [fl]); Santa Marta, twining vine, to 7 or 8 ft, moderately common in dry thickets below 500 ft, and especially near the coast, corolla deep purple or purple-brown, follicle ventricose, echinate about 2 in long (similar to that of no. 1673), flowers Aug–Nov, specimens were collected near Mamatoca, 100 ft, Sep 1898 or 1899, *H.H. Smith 1672* (NY [fl]); specimens collected 3 m E of Bonda, 4000 ft in dry thickets, a large number of examples show that the flowers differ constantly from those of no. 1673 but the

two agree in the form of the leaves and the long leafless shoots, no. 1672 was found near the same place on the same day, 19 Sep 1898 or 1899, *H.H. Smith 1672* (NY [fl]).

VENEZUELA. **Zulia**: Miranda, carretera Maracaibo-Altigracia, en el km 4 al norte del desvío de la carretera Maracaibo-Coro, en bosque seco al oeste de la carretera, trepadora en matas en margen del bosque, 4 m de largo, tallo beige, hojas aterciopeladas, casi gris en envés, corola verde fuera, dentro vino-tinto pasando a verde hacia los bordes y ápices de los lóbulos, corona de color crema, 8 Sep 1977, *G.S. Bunting 5408* (NY [fl]).

**Observations:** There appears to be some confusion between the labels of *Smith 1672* (two sheets) and *1673*. On one of the *Smith 1672* sheets, the label indicates that the vine was collected on the same day as *1673*, however on this sheet a date of 19 Sep is given, whereas on *Smith 1673*, 27 Nov is given.

*Mateleia maritima* (Jacq.) Woodson, Ann. Missouri Bot. Gard. 28: 222. 1941. (FIG. 3)

*Asclepias maritima* Jacq., Enum. syst. pl. 17. 1760. *Ibatia maritima* (Jacq.) Decne. in DC., Prodr. 8: 599. 1844.— TYPE: Herbar. Du Jacquin, 2 Insulae Caribaea. De Ponthieu (lectotype: BM!, here designated)

*Ibatia muricata* Griseb., Fl. Brit. W. I. 421. 1862.— TYPE: ANTIGUA. Cedar Hall, 1849, *Wullschlagel* (lectotype: M! [2 sheets], here designated)

Slender, woody vine. *Latex* white. *Stems* pubescent, pubescence ubiquitous or in two lines, eglandular sharp trichomes ca. 0.4–0.7 mm long, retrorse, glandular capitate trichomes ca. 0.07–0.1 mm long. *Leaf blades* ovate to oblong-ovate (orbicular), 1.2–10.5 x

0.7–9.8 cm, adaxial surface lightly pubescent, eglandular sharp trichomes ca. 0.2–0.6 mm long, antrorse, midvein pubescence denser than that of the surface, eglandular sharp trichomes ca. 0.4–0.6 mm long, antrorse, abaxial surface tomentose, eglandular sharp trichomes ca. 0.4–0.5 mm long, antrorse, midveins with eglandular sharp trichomes ca. 0.4–0.5 mm long, glandular capitate trichomes ca. 0.1–0.2 mm long, decreasing in density from base to apex, apex acute to acuminate, base cordate, margins entire, colleters 3–6, lanceoloid, ca. 0.3–0.5 mm long; petioles 8.1–72.3 mm long, ubiquitously pubescent, eglandular sharp trichomes ca. 0.5–0.7 mm long, antrorse, glandular capitate trichomes ca. 0.1–0.2 mm long. *Inflorescence* racemiform, peduncles ca. 1.12–1.9 mm long, pubescent, eglandular sharp trichomes ca. 0.3 mm long, antrorse; pedicels 0.6–4.1 mm long, densely pubescent, eglandular sharp trichomes ca. 0.3–0.5 mm long, antrorse. *Calyx* 5-lobed, lobes oblong-ovate to oblong ca. (1.1–)2.19–4.83 x 0.85–1.92 mm, adaxial surface glabrous, abaxial surface pubescent, eglandular sharp trichomes ca. 0.2–0.5 mm long, apices acute, margins entire, colleters 1(–2) per sinus. *Corolla* green to yellowish-green (rarely reddish-green) (fide colectoris), 5-lobed, imbricate in bud, subcampanulate at base, tube ca. 0.6–1 x 1.4–1.8 mm, lobes lance-oblong 1.61–4.54 x 1.42–3.56 mm, adaxial surface densely pubescent, trichomes eglandular sharp, white, ca. 0.2–0.3 mm long, antrorse, gradually reduced in length from corolla lobe base to apex, abaxial surface densely pubescent, eglandular sharp trichomes coarse, ca. 0.3–0.4 mm long, antrorse, apex obtuse or acute, margins entire. *Faucal annulus* (Ca) apparently absent. *Gynostegial corona* of fused staminal (Cs) and interstaminal parts (Ci), tube ca. 0.7–0.8 mm tall, papillate-pubescent, Cs apex a triangular lobe, papillate-pubescent up to and including the apex, Ci apically bi- or tri-lobed, lateral margins dissected completely from the Ci apex to the apex of the C(is)

tube, medial Ci lobe (if tri-lobed) smaller than the two lateral Ci lobes or of equal dimensions, papillate-pubescent up to, but not including the apex, Ci ligulate basally within, two ridges emanating from the ligule evident to about half way up the C(is) tube. *Stylar head* ca. 1.9–2.2 mm diam, not stipitate, anther guiderails apparently without appendages, laminar dorsal anther appendages (Cd) absent, terminal stylar head appendage ca. 1.13 mm tall, capitate, not distinctly bi-lobed. *Pollinaria*: corpuscula ca. 0.2 mm long, caudicles present, pollinia more or less pendent, ovate, ca. 0.6–0.7 mm x 0.28–0.31 mm. *Follicles* dark green (fide colectoris), lance-ovoid, 4.1–9.1 x 1.3–5.2 cm, unwinged, pubescent, tuberculate, each tubercle ca. 2.8–5.6 mm long, apex broadly capitate or irregularly swollen, ca. 0.7–2.9 mm diam. *Seeds* pyriform, plano-convex, 3.6–6 x 1.6–3.4 mm, both surfaces tuberculate, margins dentate.

***Distribution and habitat:*** *Matelea maritima* is currently known from throughout the Greater and Lesser Antilles to South America. It has been collected primarily in dry, scrubby, coastal thickets.

***Etymology:*** The epithet means “growing by the sea.”

***Additional specimens examined:*** ANEGADA. Swampy soil roadside, 31 May 1987, G. Proctor 43634 (FTG [fl], IJ[fl]).

ANTIGUA. 4-16 Feb 1913, J. Rose 3271 (GH [fr], US [fr]); **St. Mary:** Orange Valley, xerophytic brushlands, 17 Oct 1937, H. Box 1178 (BM [fl, fr-imm], US [fl]).

COLOMBIA. **Madgalena:** Salamanca, seaside roadside, 10 Dec 1966, R. Romero-Castañeda 10498 (NY [fl]).

DOMINICAN REPUBLIC. St. Joseph, scrub woodland roadside, 23 Aug 1965, C. Shillingford and W. Ernst 319 (MO [fl]); Mar 1978, A. and P. Liogier 27452 (JBSD [fl, fr],

NY [fr]). **Azua:** low hills, 17 Mar 1913, *J. Rose* 3970 (NY [fr], US [fr]); dry creek bed, 29 Aug 1946, *R. and E. Howard* 8656 (BM [fr-imm], GH [fr], MO [fr], NY-2 [fr, fr-imm]).

**Barahona:** Jun 1910, *P. Fuertes* 253 (A [fl, fr], BM [fl], E [fl], GH [fl], K [fl], MIN [fl], NY [fl], S [fl]); 1911, *P. Fuertes* 253 (G-2 [fl]); dry roadside scrub, 12 Apr 1985, *A. Gentry and M. Mejía* 50737 (MO [fr]). **La Altagracia:** Boca de Yuma, open thickets, 22 Aug 1968, *A. Liogier* 12271 (GH [fl], IJ [fl, fr], NY [fl, fr, fr-imm], US); Caldera Bay, 9 Feb 1975, *A. and P. Liogier* 22431 (MO [fr], NY [fr]); San Rafael, high forest, 27 August 1982, *R. Sauleda, D. Sauleda, M. Ragan, and D. Dodd* 7630 (USF [fl, fr]); maritime seasonal tropical forest, 19 March 2001, *D. Goldman* 1941 (BH [fl, fr-imm]). **La Romana:** grassy plain, 14 Jul 1981, *T. Zanoni, M. Mejia, C. Ramirez* 15438 (JBSD [fl, fr]). **Pedernales:** *Bertero* (MO [fl]); 24-27 Jul 1975, *A. and P. Liogier* 23176 (MO [fl], NY [fl]); 8 Feb 1986, *T. Zanoni, M. Mejia, and J. Pimentel* 36079 (NY [fr]). **Peravia:** 13 Oct 1981, *J. Czerwenka and S. Feucht* 374 (NY [fl, fr]); 23 Jul 1982, *T. Zanoni, M. Mejia, and J. Pimentel* 21995 (JBSD [fl, fr]). **San Cristóbal:** Grande Savana, grassland/dry woodland, 14 Jul 1965, *W. Ernst* 1889 (US [fl]). **Santiago:** in thickets, 15 Oct 1930, *E. Ekman* H16064 (S [fl]); 14 Apr 1949, *J. Jimenez* 1862 (US [fl]); Jaiquí Picado, hillside thickets, 23 May 1969, *A. Liogier* 15347 (NY [fl], US [fl]). **Santiago Rodriguez:** Monción, semi-arid pine region, 11 Nov 1929, *E. Valeur* 258 (G-2 [fl, fr-imm], MO[fl, fr-imm], NY [fl, fr, fr-imm], S [fr-imm]); Monción, semi arid pine region, 5 Jul 1931, *E. Valeur* 812 (US [fl], S [fl]); Monción, 8 Jan 1976, *A. and P. Liogier* 24668 (NY [fr]); Monción, 16 Apr 2002, *A. Veloz and B. Peguero* 2708 (JBSD [fr]).

GRENADA. wooded area, 7-25 Mar 1950, *R. Howard 10813* (GH [fr]). **Saint George:** Pointe Saline, 24 Feb-6 Mar 1950, *R. Howard 10549* (BM [fr]); Pointe Saline, 30 Oct-11 Dec 1957, *G. Proctor 17355* (A, BM, IJ, US [fl, fr]).

GRENADINES: wooded area, 7-25 Mar 1950, *R. Howard 10813* (BM [fr]). **Bequia Island:** Jun, *D. Joseph B324* (K [fl]). **Union Island:** Chatham Bay, 26 Mar 1933 (fr), *G. Cooper III 206* (NY [fr], US [fr]). GUADELOUPE. 1893, *P. Duss 2843* (NY [fl, fr]); 1 Sept 1980, *J. Jérémie 723* (A [fl, fr], NY [fl, fr]). **Basse-Terre:** 16 Feb 1934, *L. Rodriguez 2760* (A [fl]).

GUYANA. **Essequibo:** Darukoban Mountain, Jul 1989, *L.J. Gillepsie 1953a* (NY [fl]).

HAITI. Sep 1892, *Jaeger 198* (NY [st]); hillside, 1903, *G. Nash 995* (NY [fr]); fertile roadsides, 16 Jul 1924, *E. Ekman H923* (S [fr]); on fences, 14 Oct 1925, *E. Ekman H5104* (NY [fl, fr-imm], S [fl, fr]); riverside, 10 Dec 1925, *E. Ekman H5704* (IJ [st]); thickets, 15 May 1927, *E. Ekman H8126* (S [fl], US [fl]); riverside, 30 Jan 1929, *E. and G. Leonard 12700* (US [fr]). **Artibonite:** St. Marc, mountain side, 25-28 Feb 1920, *E. Leonard 2885* (US [fr]).

MARTINIQUE. *Hahn 1115* (BM [fl]); 1787, *Toeck 2* (C [fl, fr]); Case-Pilote, *P. Duss 1860* (NY [fl, fr]); Jan 1868, *L. Hahn 404* (K [fr]); 1868-1869, *L. Hahn 1115* (G [fl]); Oct 1867-1870, *M. Hahn 1115* (K [fl]); Case-Pilote, Oct 1867-1870, *M. Hahn 1115* (BM [fl], US [fl]).

MONTSERRAT. **Exclusion Zone:** Plymouth, trackside, 5 Feb 1959, *G. Proctor 19035* (A [fr], BM [fr], IJ [fr]).

PUERTO RICO. **Buck Island:** Jun 1969, *R. Woodbury 240* (MO [fr]). **Cayey:** dry thickets, 4 Nov 1989, *C. Taylor 9616* (MO [fr]). **Ceiba:** thickets, 31 Mar 1989, *A. and P.*

*Liogier, and L. Martorell* (NY [fl]). **Coamo**: 16 Dec 1885, *P. Sintenis* 3208 (US [fr]); 23 Nov 1899, *G. Goll* 750 (US [fl]); Coamo Springs, thickets, 19 Sep 1979, *A. and P. Liogier, L. Martorell* (NY [fl, fr]). **Culebra Island**: thickets, 3-12 Mar 1906, *N. Britton and W. Wheeler* 211 (NY [fr]). **Guanica**: rocky slope, 11-12 Mar 1913, *N. Britton and J. Shafer* (NY [fr], US [fr]); 9 Feb 1968, *R. Wagner* 1355 (A [fr]); 27 Sept 1968, *R. Wagner* 1660 (A [fl]); 20 Mar 1969, *R. Wagner* 1821 (A [fr]); roadside, 23 Sep 1982, *R. Sauleda, D. Sauleda, and M. Ragan* 7682 (USF [fl, fr]); dry rocky thicket, 4 Jun 1986 (fl), *G. Proctor* 41766 (IJ [fl], MO [fl], NY [fl]); 25 Nov 1988, *S. Guzman and F. Rodriguez* 95 (NY [fr]); dry tropical forest, 6 Jan 1991, *B. Boom* 10024 (MO [fr], NY [fr]); dry coastal forest, 3 Jan 1996, *L. Struwe and C. Specht* 1106 (NY [fr]). **Guayama**: 13 Oct 1885 *P. Sintenis* 2174 (GH [fl, fr-imm], US [fl, fr-imm]). **Mayagüez**: Desecheo Island, valley, 18-19 Feb 1914, *N. Britton, J. Cowell, and W. Hess* 1641 (NY [st], US [st]). **Ponce**: 16 Jul 1886, *Peñon* 3004 (S [fr]); 16 Jul 1886, *Peñon* 5004 (GH [fl, fr]). **Salinas**: thickets, 5 Jul 1987, *A. and P. Liogier, and L. Martorell* 36413 (NY [st]); disturbed dry scrub, 11 Jun 1993, *C. Taylor and R. Ross* 11146 (MO [fl, fr]). **Vieques Island**: Santa Maria, thicket, 2 Feb 1914 (fr), *J. Shafer* 2657 (NY [fr], US [fr]); 27 May 1978 (fl, fr), *Griffis and Brokx* 278 (NY [fl, fr]); thicket near strand and swamp, 11 Nov 1990, *G. Proctor* 46582 (FTG [fl], IJ [fl], US [fl]). **Yauco**: Susua, serrentine barrens, 28 Jun 1962, *Bro. Alain* 9251 (IJ [fl, fr]).

ST. BARTHÉLEMY. *A. von Goës* (S [fl]); 25 Apr 1945, *H. and M. Stehlé* 6770 (US [fl]); *Gustavia*, 26 Nov 1931, 20 (NY [fr]); Saline, 3 Jul 1938, 401 (NY [fl]).

ST. JOHN. 5 Feb 1913, *J. Rose* 3271 (NY [fr]); Bordeaux, hillside, 10-12 Feb 1913, *N. Britton and J. Shafer* 544 (NY [fr], US [fr]); center-line roadside, 27 Mar 1985, *P. Acevedo, R. Woodbury, and J. Earhart* 652 (NY [fr]); Reef Bay, open disturbed area, 22 Jun 1989, *P.*

*Acevedo-Rdgz* 2737 (NY [fl], US [fl]); Coral Bay, scrubby trailside, 29 Jan 1991, *P.*

*Acevedo-Rdgz* 4076 (NY [fl], US [fl]); Coral Bay, disturbed roadside, 4 Jan 1992, *P.*

*Acevedo-Rdgz* and *A. Siaca* 4674 (MO [fr], NY [fr]).

ST. THOMAS. Sep 1882, *Eggers* 736 (G [fl], GH [fl], WU [fl]); *Krebs* (H [fl], NY [fl]); coastal thicket, 31 Jan-4 Feb 1913, *N. and E. Britton, and J. Shafer* 178 (NY [fr], US [fr]).

ST. VINCENT. Mar 1890, *H. and G. Smith* 1300 (GH [fl]); dry forest, Jul-Oct 1889, *H. and G. Smith* 1300 (K [fl]); islet, Mar 1890, *H. and G. Smith* 1300 (NY [fl, fr-imm]).

TORTOLA. rocky hillside, 13-17 Feb 1913, *N. Britton and J. Shafer* 679 (NY [fr]); 1918, *W. Fishlock* T116 (K [fl]); Fish Bay, coastal hills, 28 Jun 1919, *W. Fishlock* 465 (NY [fl]); 26 May 1965, *W. D'Arcy* 69 (BM [fl]); Little Apple Bay, fences, 26 May 1965, *W. D'Arcy* 69A (MO [fl]); Little Apple Bay, 26 May 1965, *W. D'Arcy* 79B (A [fl]); Slaney Point, 27 Jul 1970, *W. D'Arcy* 4771 (MO [fl, fr]).

TRINIDAD. **Patos Island:** hillside, 13 Mar 1920, *N. Britton, T. Hazen, W. Mendelson* 529 (GH [fr]); roadside, 9 Jun 1929, *W. Broadway* 7220 (G [fl], K [st], MO [fl], S [fl], US [fl], Z [fl]); field near landing bay, 26 Jun 1932 (fl), *W. Broadway* 7220 (A [fl], S [fl]).

VENEZUELA. 1948, *A. Ferreller* 1041 (NY [fl]). **Anzoátegui:** 18 Aug 1961, *L. Aristeguieta* 4711 (NY [fl]); 18 Aug 1965, *G. Agostini* 527 (NY [fl]). **Aragua:** Marcaay, savanna, 17 Jul 1980, *H. Rodriguez* 1092 (NY [fl]). **Bolivar:** Las Nieves, carrizal-covered slope, 1-11 Feb 1961, *J. Steyermark* 88957 (NY [st]); Piar, tropical forest, Jul 1978, *F. Delascio and R. Liesner* 7116 (NY [fl], VEN [fl]); 26 Jul 1981 *Aymard, Stergios, and Mathiessen* 291 (VEN [fl]). **Guárico:** Calabozo, riverside, Jul 1960, *L. Aristeguieta* 4288 (NY [fl]). **Lara:** roadside, 23 Jan 1984, *P. Fryxell, and C. Burandt Jr.* 4333 (NY [fr]). **Miranda:** Macarao, 31 Aug 1924, *H. Pittier* 11562 (NY [fl]); Caserío Tomuso, 30 Oct

1971, *B. Manara s.n.* (NY [fr]); Montalbán, hills, 13 Sep 1975, *P. Berry 1336* (NY [fl]).

**Monagas:** Puerto La Cruz, wooded ravine, 22 Oct 1948, *B. Maguire, H. Kunhardt Jr., and L. Politi 27215* (NY [fr]); Santa Barbara, 22 Oct 1948 *B. Maguire, H. Kunhardt Jr., and L. Politi 27215* (NY [st]); 16 Jul 1972, *K. Dumont, G. Morillo, G. Samuels, and R. Cain VE-7720* (NY [fl]); roadside, 19 Jul 1972, *K. Dumont, G. Morillo, G. Samuels, and R. Cain VE-7788* (NY [fl]). **Sucre:** Bahía de Mochima, 5 Jul 1965, *L. Aristeguiteta and G. Agostini 5564a* (NY [st]); Gamero, tropical forest, 15 Sep 1973, *J. Steyermark, B. Manara, and G. Morillo 108523* (NY [st]); forested valley, 15 Sep 1973, *J. Steyermark, B. Manara, and G. Morillo 108676* (NY [fl]); savanna, 16 Sep 1973, *J. Steyermark, B. Manara, and G. Morillo 108462* (NY [fl, fr]); scrubby slopes, 2 Dec 1979, *J. Steyermark and R. Liesner 120973* (NY [fr]). **Trujillo:** 1854, *A. Fendler 1041* (NY, [fr]); Valera, gravelly slopes, 21 Nov 1922, *H. Pittier 10755* (NY [fl]); **Zulia:** Aricaua, thicket, 5 Jan-22 Feb 1923 *W. Broadway 349* (NY [fr-imm]).

**Observations:** Only a single sheet of *Asclepias maritima* Jacq. was located that could qualify as belonging to the original material. Eight fragments, all *Asclepias maritima*, are mounted on a single sheet held at BM and barcoded (BM000834432). A handwritten note on the top left of the back of the sheet reads “Herbar. Du Jacquin.” followed by “2 Insulae Caribaeae. De Ponthieu.” Based on the note, the fragments appear to represent two elements, but they cannot be delineated. A dehisced follicle is mounted along with leaves in relatively good condition and a few flowers in poor condition. Fruits and flowers are not mentioned by Jacquin in the protologue, and these elements may represent the collection later combined with the vegetative fragment used for the protologue. Considering that this

sheet appears to represent the only remaining collection of *Asclepias maritima* from the herbarium of Jacquin, it is here designated lectotype.

The following specimens were listed in the protologue of *Ibatia muricata* Griseb.: “Antigua, *Wullschl.*, Dominica!, *Imr.*; [Guadeloupe; Venezuela].” Their location of deposit was not cited. Although not identified as a type, the material at M is the only Wullschlagel specimen from Antigua found in the course of this study and is here designated lectotype of *Ibatia muricata*.

Whereas most members of the Gonolobinae in the West Indies are endemic to a single island, *Matelea maritima* is distributed throughout the region and into South America. Why this taxon is so broadly distributed while most other subtribe members in the area are narrow endemics remains unknown. Saville (2006) investigated whether additional taxa that may previously have been overlooked could be circumscribed within the *M. maritima* of prior authors. However, she found no correlation between geographical distribution and a number of morphological characters, including (1) shape of the terminal styler head appendage and gynostegial corona segments and (2) lengths/widths of petioles, leaves, sepals, corolla lobes, and follicles. The gynostegial corona of West Indian and northern South American populations appear rather plastic in that the Ci may be variously bi- or tri-lobed and medial Ci lobes, if present, may be as large as the two lateral Ci lobes, or significantly reduced. In a few instances, all three lobes of a Ci segment may be quite reduced and of similar dimensions. However, variation from bi- to tri-lobed Ci coronas exists within islands and none of the gynostegial corona variation could be correlated with distribution. The distribution of *M. maritima* could be explained by either intra- and inter-island gene flow, relatively recent colonization of the islands with respect to the origin of

the taxon, or slower rates of speciation, perhaps in part influenced by breadth of ecological niche and competitive ability. Additional genetic studies are sorely needed to understand the phylogeography of the taxon and to determine whether additional meaningful taxonomic delimitation is possible or necessary.

***Matelea pacifica*** Krings & Saville, sp. nov. (FIG. 4).— TYPE: VENEZUELA. Estado Mérida, Distr. Sucre, Las Gonzales-San José rd, near the village of Las Gonzales (ca. 20 km SW of Mérida), ca. 8 25 N, 71 20 W, ca. 800–1600 m, dry vegetation, liane with milky latex, older stems corky, flowers green, marked with purple in throat, fruit green with warty protuberances marked with white, 9–10 Nov 1990, *L.J. Dorr and L.C. Barnett* 7672 (holotype: NY! [fl, fr])

Species nova *Mateleae* differt a *Matelea cumanense* (Willd. ex Schult.) W.D. Stevens, *M. fontana* Saville & Krings, *M. maritima* (Jacq.) Woodson, et *M. rubra* (H. Karst.) Spellman & Morillo lobis corone interstaminalis lobis corone staminalis dimidio angustioribus, lobis corone interstaminalis longitudine coronam staminalem paulo superantibus, appendicibus gynostegii bifidis.

Slender, woody vine. *Latex* white. *Stems* densely pubescent, pubescence ubiquitous or in two lines where woody ridges developing, eglandular sharp trichomes retrorse or spreading, ca. 0.8 mm long, glandular capitate trichomes ca. 0.1 mm long, obscured by the dense long trichomes. *Leaf blades* ovate (1.7–)5.4–6.6 x (1–)3.2–5.1 cm, adaxial surface densely pubescent with eglandular, sharp trichomes, ca. 0.3 mm long, strigose-antrorse to

spreading, midvein more densely pubescent than surface, trichomes ca. 0.5 mm long, spreading, abaxial surface densely pubescent, eglandular sharp trichomes ca. 0.54 mm long, spreading, apex acute to short-acuminate, acumen to ca. 2.2 mm long, base cordate, margins entire; colleters 4–6, narrowly elongate-lanceoloid, 0.4–0.6 mm long; petioles 9.5–51 mm long, densely pubescent, pubescence ubiquitous, increasing somewhat in density toward the leaf blade, eglandular sharp trichomes to ca. 0.9 mm long, spreading or curling, glandular capitate trichomes ca. 0.3 mm long. *Inflorescence* racemiform, peduncles 1.6–3.5 mm long, densely pubescent, pubescence ubiquitous, eglandular sharp trichomes ca. 0.38 mm long, antrorse-spreading, glandular-capitate trichomes absent; pedicels 1.7–6.1 mm long, densely pubescent, pubescence ubiquitous, eglandular sharp trichomes ca. 0.35 mm long, spreading, glandular-capitate trichomes absent. *Calyx* 5-lobed, lobes lanceolate or lance-oblong, 2.7–3.4 × 0.7–0.9 mm, adaxial surface glabrous, abaxial surface densely pubescent, eglandular sharp trichomes ca. 0.45 mm long, antrorse, apex acute or obtuse, margins entire, colleters 1(–2) per sinus. *Corolla* pale purplish-red or green with maroon center (fide collectoris), 5-lobed, imbricate in bud, subcampanulate at base, tube ca. 2.3 × 2.3 mm, lobes lance-oblong 3.7–6.2 × 2.2–2.8 mm, adaxial surface densely pubescent, trichomes eglandular sharp, white, ca. 0.16–0.37 mm long, antrorse, gradually reduced in length from corolla lobe base to apex, abaxial surface densely pubescent, eglandular sharp trichomes coarse, ca. 0.35 mm long, antrorse, apex obtuse, margins entire. *Faucal annulus* (Ca) apparently absent. *Gynostegial corona* of fused staminal (Cs) and interstaminal parts (Ci), tube ca. 1.3 mm tall, papillate-pubescent primarily near the apex, Cs apex a triangular lobe, papillate-pubescent, Ci apically bi-lobed, lobed completely from its apex to the apex of the C(is) tube, lobes narrowly elongate, each half as wide or less as a Cs lobe, both lobes

of the Ci somewhat longer than a Cs lobe, ca. 0.65 mm, papillate-pubescent, Ci ligulate basally within, two ridges emanating from the ligule evident to about half way up the C(is) tube. *Stylar head* ca. 1.5 mm diam, stipe ca. 0.28 mm long, not toothed, anther guiderails apparently without appendages, laminar dorsal anther appendages (Cd) absent, terminal stylar head appendage ca. 1.6 mm tall, distinctly bilobed. *Pollinaria*: corpuscula ca. 0.18 mm long, caudicles present, pollinia more or less pendent, ovate, ca. 0.5 mm x 0.35 mm. *Follicles* lance-ovoid, ca. 4.7 x 1.5 cm (immature), pubescent, tuberculate, tubercles to ca. 1.7 mm long, broadly capitate. *Seeds* unknown.

***Distribution and habitat***: *Matelea pacifica* is presently unknown outside Estado Mérida, Venezuela. It has been found in arid areas in sandy soils.

***Etymology***: The relatively broadly obtuse apical lobe of the Cs combined with an adjoining bifid Ci lobe give an abstract appearance of a hand sign for “Peace.”

***Additional specimens examined***: VENEZUELA. **Mérida**: 36 km SW of Mérida along road to San Cristóbal, arid area, sandy soil, climber, leaves soft, herbaceous, dull, pale green, calyx pale green, corolla lobes pale purplish-red, pale green at the margin, stigma white, fruit ovoid with acuminate top, dull, pale green, with cork-topped protuberances [fruit not with specimen], 950 m elev., 30 Jul 1964, *F.J. Breteler 4069* (NY [fl]); Rastrojos secos, 18–20 km SO de Mérida, carretera Mérida-Estanques, 780 m snn, trepadora ramificada, tallos y hojas con olor desagradable, lobulus de la corola verdes con centros marron claro, corona verde, ginostegio cremoso, flores anormalmente grandes para la especie [det. *M. maritima* by the collector], 10 Oct 1979, *G. Morillo 8099* (VEN [fl]).

*Matelea rubra* (H. Karst.) Spellman & Morillo, *Phytologia* 34: 152. 1976. (FIG. 5)

*Omphalophthalma rubra* H. Karst., Fl. Columb. 2: 119-120, t. 163. 1866. *Matelea rubra* (H. Karst.) Aa & Stoffers, Proc. Kon. Ned. Akad. Wetensch., C 84(3): 309. 1981, nom. illeg.— TYPE: COLOMBIA. Magdalena: St. Marta, *Karsten s.n.* (holotype: LE, Sennikov, pers. comm., n.v.)

Slender, woody vine. *Latex* white. *Stems* pubescent, pubescence ubiquitous or in two lines where woody ridges developing, glandular capitate trichomes, ca. 0.1–0.3 mm long, eglandular sharp trichomes, ca. 0.4–0.7 mm long, retrorse. *Leaf blades* ovate to oblong-ovate, 2.1–8 x 1.2–7.3 cm, adaxial surface pubescent, eglandular sharp trichomes ca. 0.2–0.7 mm long, generally antrorse, midvein more densely pubescent than leaf surface, eglandular sharp trichomes ca. 0.1–0.7(–1.0) mm long, antrorse, abaxial surface densely pubescent, eglandular sharp trichomes ca. 0.4–0.7 mm long, midvein less densely pubescent than surface, apex acuminate or acute, base cordate, margins entire; colleters 2–5; petioles 9.9–58.1 mm long, densely pubescent, pubescence ubiquitous, eglandular sharp trichomes ca. 0.3–0.6 mm long, antrorse, sparser than glandular capitate trichomes, these ca. 0.1–0.2 mm long. *Inflorescence* racemiform, peduncles 1.5–3.1 mm long, densely pubescent, eglandular sharp trichomes ca. 0.3–0.4 mm long, antrorse-spreading, glandular capitate trichomes absent. *Calyx* 5-lobed, lobes oblong-ovate, ca. 2.6–4.1 x 1.0–1.5 mm, adaxial surface glabrous, abaxial surface very sparsely pubescent, eglandular sharp trichomes ca. 0.1–0.8 mm long, antrorse, apex acute, margins entire; colleters 1 per sinus. *Corolla* maroon, green with brown stripes, greenish-yellow and white (fide colectoris), 5-lobed, imbricate in bud, subcampanulate at base, tube ca. 0.6–1.7 x 0.6–0.7 mm, lobes ovate-lanceolate, 5.5–6.5 x 1.7–2.3 mm, adaxial surface glabrous with sparse pubescence at

apex, eglandular sharp trichomes ca. 0.2–0.4mm long, abaxial surface glabrate or very sparsely pubescent, eglandular trichomes ca. 0.14 mm long, apex obtuse, margins entire. *Faucal annulus* (Ca) apparently absent. *Gynostegial corona* of fused staminal (Cs) and interstaminal parts (Ci), tube ca. 1.3–2.4 mm tall, Cs apex a shallow, rounded lobe, ca. 0.2 mm tall, glabrous or papillate-pubescent near the apex, a single ridge leading from the base of the stipe to the base of the Cs within, Ci bi-lobed, lobes extending 2–3.8 mm beyond their medial sinus, glabrous, Ci not ligulate within. *Stylar head* ca. 2–2.6 mm diam, stipe 1.28–1.35 mm long, not toothed, anther guiderails apparently without appendages, laminar dorsal anther appendages (Cd) absent, terminal stylar head appendage absent or reduced to ca. 0.1 mm tall, central rim of stylar head exhibiting five erect lobes, each ca. 0.24–0.26 mm tall. *Pollinaria*: corpuscula ca. 0.3 mm long, caudicles present, pollinia more or less pendent, broadly ovate, ca. 0.66 x 0.46 mm. *Follicles* green and brown (fide colectoris), ovate, 6.3–6.9 x 1.9–3.9 cm, minutely pubescent, eglandular sharp trichomes ca. 0.1–0.2 mm long, tuberculate, tubercles 4.9–8.9mm long, color and pubescence as that of follicle surface, broadly capitate, apical swelling white, irregular, 2.0–6.6 mm diam. *Seeds* pyriform, plano-convex (or at least appearing so due to incurved margins), 4.1–4.3 x 2.1–2.5 mm, curved surface with a raised median ridge, both surfaces tuberculate, margins dentate.

***Distribution and habitat:*** *Matelea rubra* is currently known from Colombia, Venezuela, and the nearby islands Aruba, Bonaire, and Curaçao. It has been collected in subxerophytic associations on limestone.

***Etymology:*** The epithet means “red” and presumably refers to the coloration of the corolla lobes which were described as dark purple (“atropurpurea”) in the protologue.

*Additional specimens examined:* ARUBA. Savoneta, popular name: Maripompun, Kabez dimariku, climber, height: very long, color flower: white with red-brown, fruit: edible when green, 6-10 cm, Oct 1969, *Fr. M. Arnoldo-Broeders 3816* (A [fl]); Sewage treatment plant area, tough vine, flowers greenish-yellow and white; fruit green and brown, 17-21 Jan 1986, *R.A. Howard 20294* (A-2 [fl, fr], NY [fl, fr]); Hato plain, second limestone plateau near Hato-airport, next to dirt road in shrubby vegetation, liana, stem strongly voluble, dark brown with pale brown hairs, copious white latex present, older stem with strongly sulcate bark, whitish-pale brown, leaf grass green with rough indument, underside with velutinous indument, petiole pale green-dark brown, sepal pale green with white hairs, petal idem on the inner side, outside with dark brown stripes, staminodes white, translocator black-dark brown, stigma pale green, ovary yellow, fruits yellowish green, apex of the spines white, separate: fruits on spirit!, 9 Feb 1999, *A.S.J. van Proosdij, B.P. van de Riet, and S.A.L. Zander 597* (A [fl]); Hooiberg, N-hill, Scree hill, steep, growing in *Acacia* and *Caesalpinia*, liana, climbing up to 1 m height, stem later white, corky winged, copious latex present, leaf soft velutinous, dark green, calyx green, corolla greenish with brownish stripes, staminodes white, pollinia pinkish, stigma green, fruit grenada-like, green with wart-like appendages with white apices [sic], separate: fruits on spirit!, 16 Feb 1999, *A.S.J. van Proosdij, B.P. van de Riet, and S.A.L. Zander 667* (A [fl], NY [fl]).

BONAIRE. North-west of Goto Meer, 6 Nov 1952, *A.L. Stoffers 579* (A [fl]).

CURAÇAO. Christoffelberg, 26 Dec 1952, *A.L. Stoffers 1190* (A [fl]); Sint Joris, "Marie Pompoen," 9 Mar 1917, *H.H. Curran and M. Haman 238* (GH [fr]).

VENEZUELA. **Falcón:** Peninsula de Paraguana, Mun. Pueblo Nuevo, Reserva Biologica de Monte Cano, Sector El Recrea, proximidad pozos de agua rocosos (carsos), 11° 57' 11"

N, 69° 56' 33" O, alt. 90–140 m, trepadora, en bosque subxerofítico, secundario reciente, expuesta, 27 Nov 1988, *J. Castillo 218* (VEN [fl]). **Zulia:** Dtto. Maracaibo, en el Jardín Botánico de Maracaibo, espontáneo, bejuco con latex, corola de color vino tinto en su totalidad adax., corona blanca, fruto verde, excrecencias beige, ovoido obliquo, 7,8 cm x 3,9 cm, 19 Dec 1979, *G.S. Bunting 8509* (VEN [fl, fr]).

**Observations:** Morillo (1983) reports additional Venezuelan specimens of *M. rubra* at VEN, but these were not included in a loan recently sent to us: Carretera Maracaibo-Carora, entre km 5-7 SE de Sabana [...], *Bunting 5770* (VEN, n.v.); Falcón: Cardón, *van der Werff, Wingfield, and Ruiz 37* (VEN, n.v.); Zulia: Parque Yaguas, *Bunting and Galué 7930* (VEN, n.v.).

Although continental collections of *M. rubra* exhibit dark red corolla lobes, island collections of the species exhibit white or greenish corolla lobes that are striped. The two may represent two distinct varieties. Continental and island collections overlap in ranges of corolla lobe lengths, Cs lengths, and stylar head diameters.

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FIG. 1. *Matelea cumanensis*. A. Leaves and inflorescence. B. Sepal. C. Calyx colleter. D. Open flower. E. Gynostegial corona. F. Inner surface of gynostegial corona. G. Ligule at base of internal gynostegial corona surface. H. Bilobed terminal stylar head appendage. I. Pollinarium. Based on *Carnevali & Pivat 639* (VEN). Ci = interstaminal gynostegial corona segment; Co = corpusculum; Cs = staminal gynostegial corona segment; Po = pollinium.

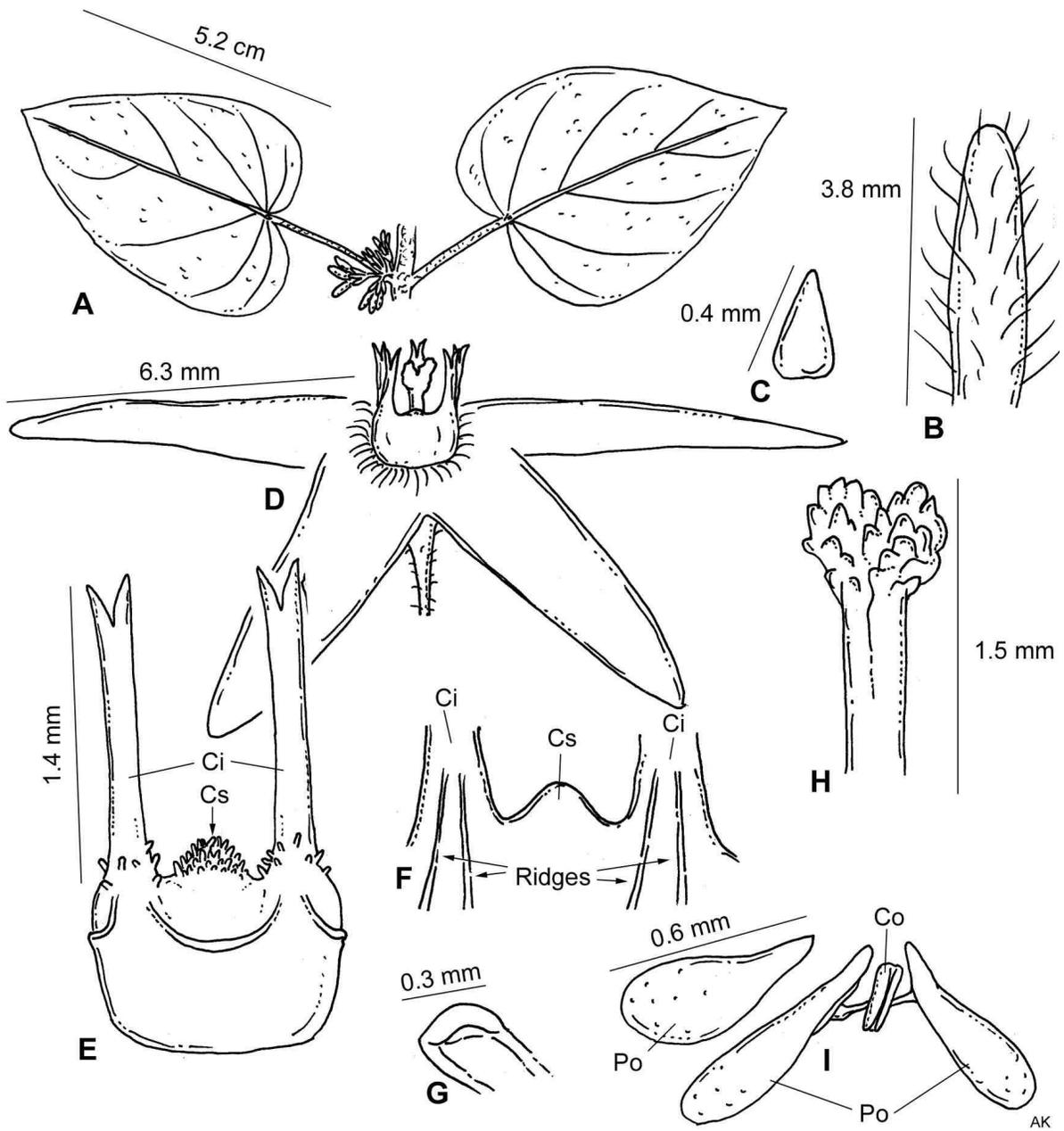


FIG. 2. *Matelea fontana*. A. Leaves and inflorescence. B. Open flower. Ci. Outer surface of gynostegial corona. Cii. Inner surface of gynostegial corona; note basal ligules. Ciii. Apex of gynostegial corona showing unlobed Cs and bilobed Ci. D. Pollinarium. Based on *Smith 1673* (NY). Ci = interstaminal gynostegial corona segment; Co = corpusculum; Cs = staminal gynostegial corona segment; Po = pollinium; Ta = terminal stylar head appendage.

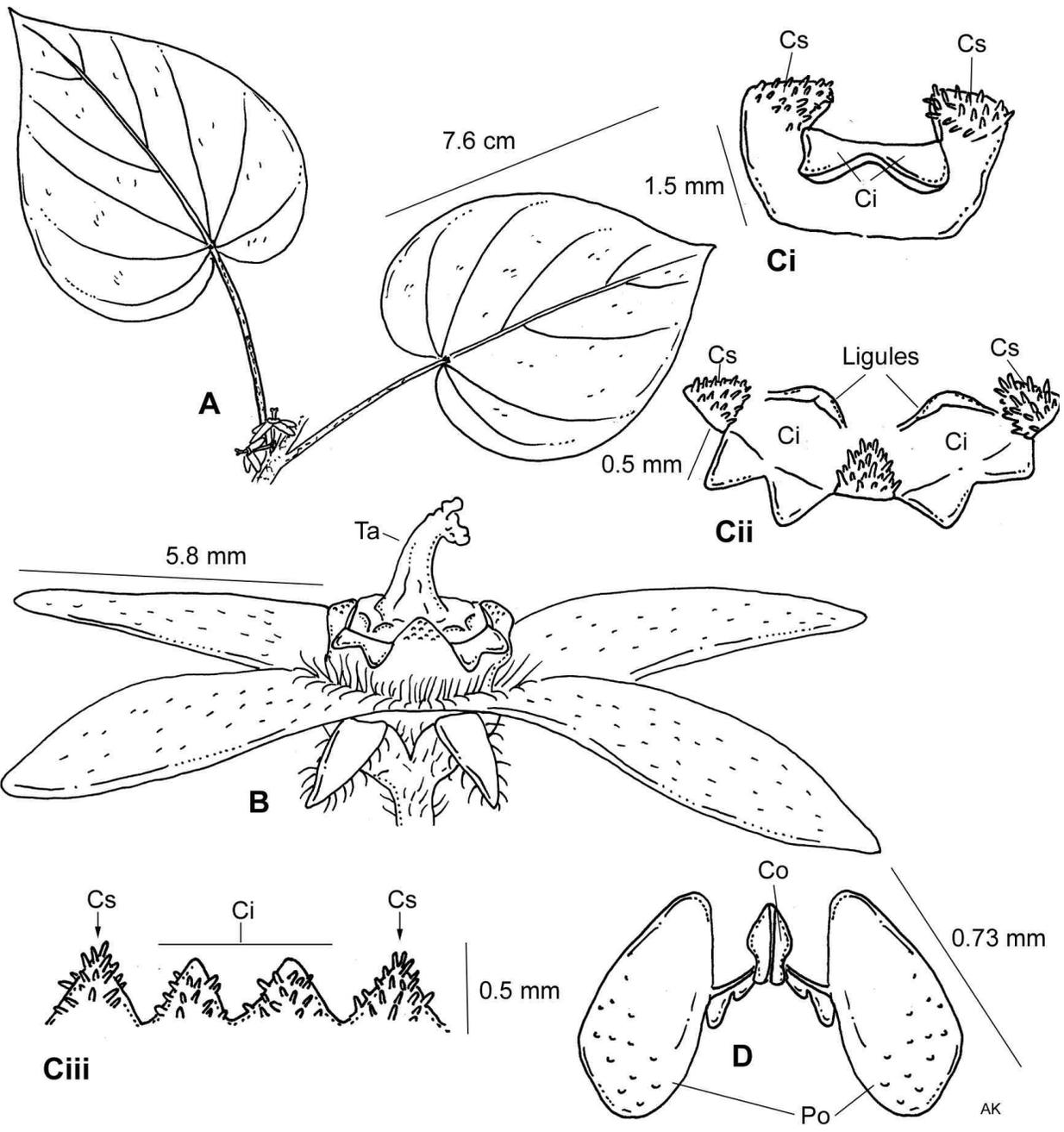


FIG. 3. *Matelea maritima*. A. Leaves and inflorescence. B. Open flower. Ci–Cv.

Gynostegial corona variation (inner surface with ligules shown). D. Pollinarium. E.

Follicle. Fi–iii. Plano-convex seed. A based on *Ekman 5104* (S); B & D based on

*Proctor 41760* (IJ); Ci based on *Goldman 1941* (BH), Cii on *Rodríguez 2760* ( ), Ciii on

*Proctor 17355* (GH), Civ on *Smith & Smith s.n.* (K), Cv on *Broadway 7220* (S); E

based on *Howard 10813* (BM); F based on *Sintenis 3004* (S). Ci = interstaminal

gynostegial corona segment; Co = corpusculum; Cs = staminal gynostegial corona

segment; Po = pollinium; Ta = terminal stylar head appendage.

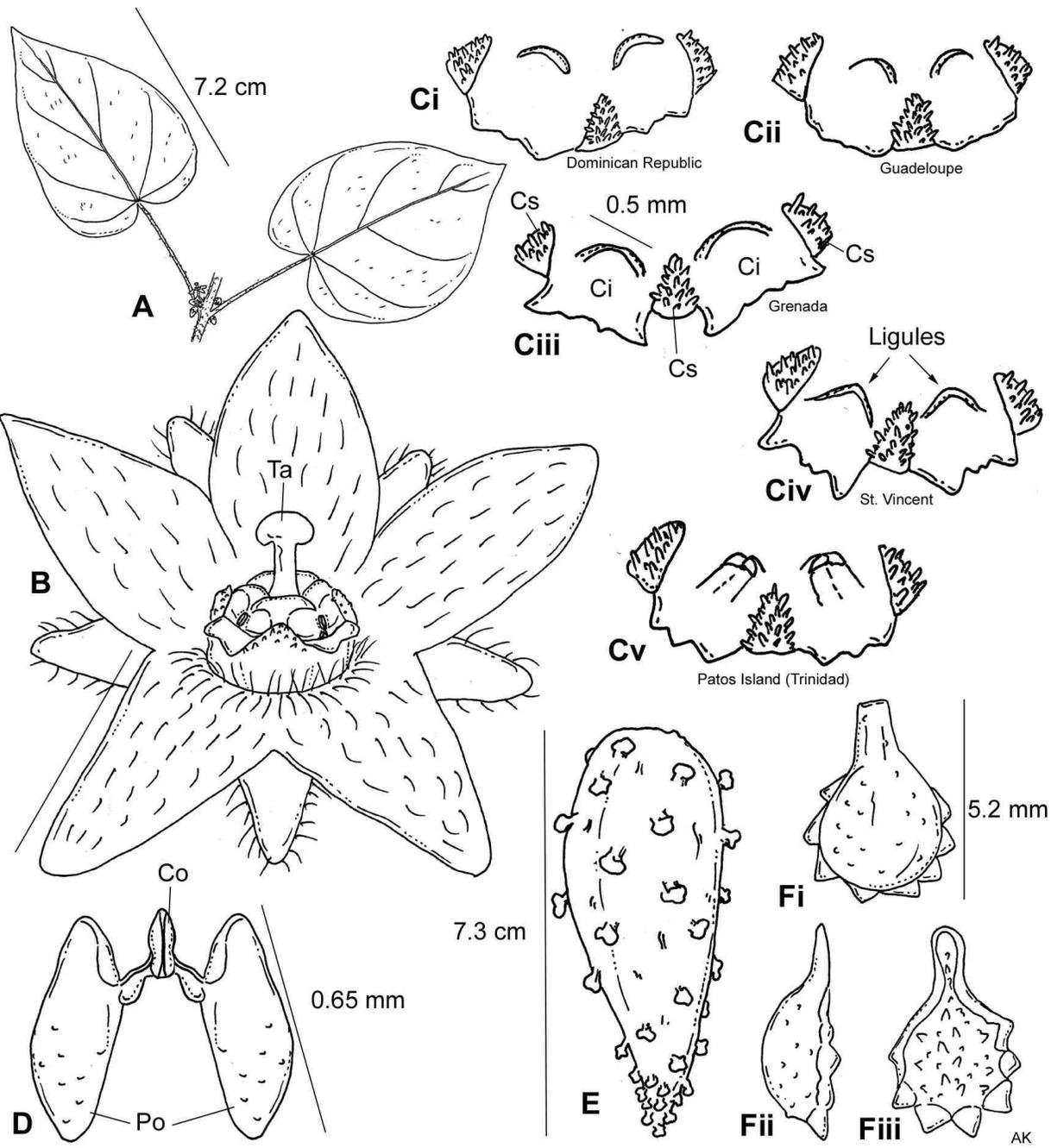
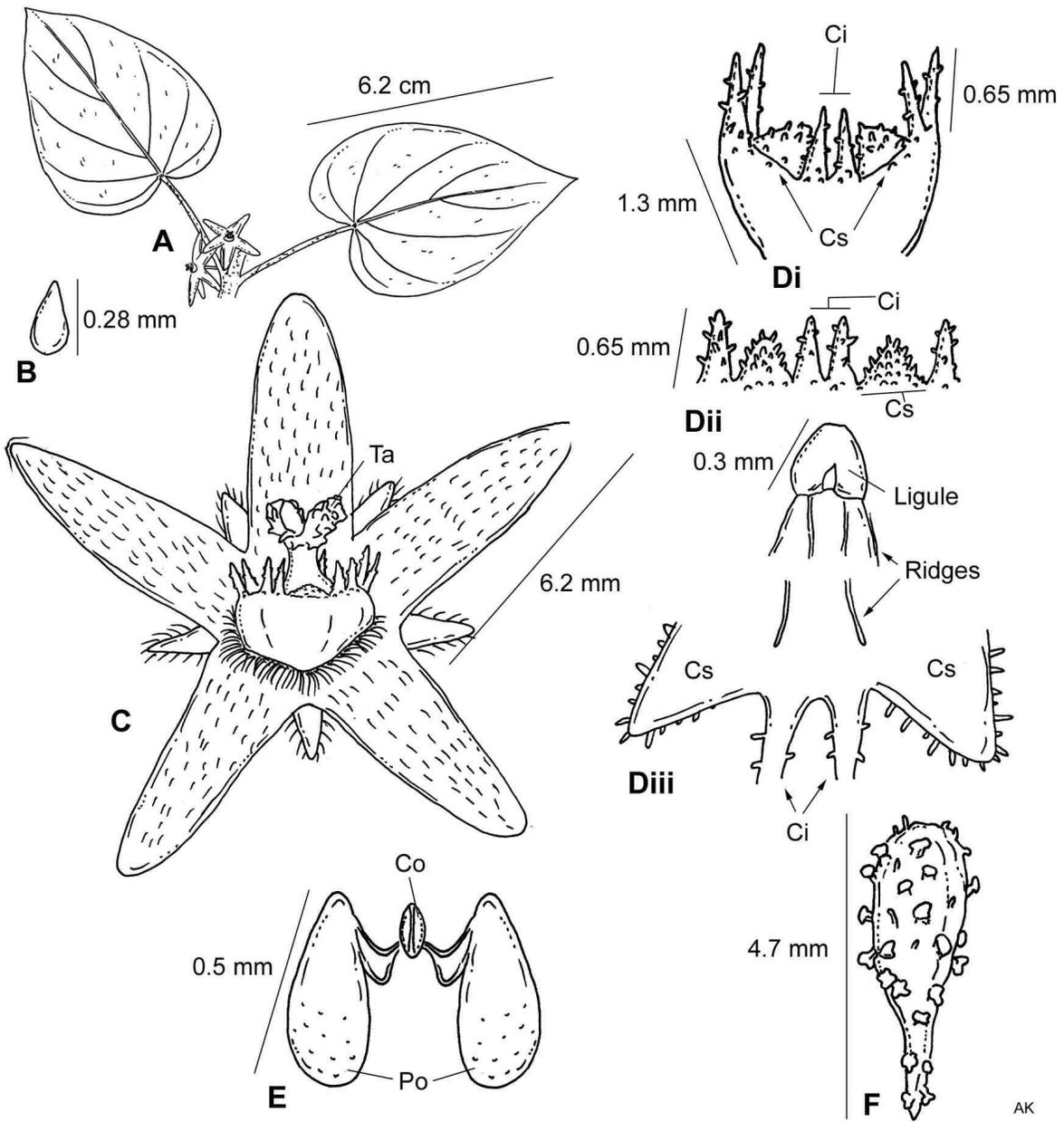


FIG. 4. *Matelea pacifica*. A. Leaves and inflorescence. B. Calyx colleter. C. Open flower. Di. Outer surface of gynostegial corona. Dii. Apex of gynostegial corona tube showing unlobed Cs and bilobed Ci. Diii. Inner surface of gynostegial corona showing basal ligule and ridges. E. Pollinarium. F. Follicle (immature). Based on *Dorr & Barnett 7672* (NY). Ci = interstaminal gynostegial corona segment; Co = corpusculum; Cs = staminal gynostegial corona segment; Po = pollinium; Ta = terminal stylar head appendage.



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FIG. 5. *Matelea rubra*. A. Leaves and inflorescence. B. Sepal. C. Calyx colleter. D. Open flower. E. Segment of gynostegial corona showing a reduced Cs flanked by half of each adjoining, deeply bifid Ci. F. Gynostegium showing edentate stipe, lack of terminal stylar head appendage, and five erect lobes on the central rim of the stylar head. G. Pollinarium. H. Follicle. ii–iii. Planoconvex seed. Based on *Howard 20294* (A, NY).  
Ci = interstaminal gynostegial corona segment; Co = corpusculum; Cs = staminal gynostegial corona segment; Po = pollinium; Ta = terminal stylar head appendage.

