Ph. D.

A REVISION OF MATELEA SUBGENUS DICTYANTHUS (APOCYNACEAE, SENSU LATO)

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A REVISION OF MATELEA SUBGENUS
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ABSTRACT

A REVISION OF MATELEA SUBGENUS DICTYANTHUS (APOCYNACEAE, SENSU LATO)

By

Warren Douglas Stevens

A revision of *Matelea* subgenus *Dictyanthus* (Gonolobeae) is provided. *Dictyanthus* can be distinguished from the rest of *Matelea* by having a digitate corona with the axes of the lobes entirely adnate to the corolla, simple inflorescences, a mixed indumentum with at least some of the trichomes glandular and at least some of the long trichomes uncinate, and follicles with thickish projections. *Dictyanthus* is here considered to be comprised of 10 species; two species, *Matelea macvaughiana* and *M. hamata*, are proposed as new. Another species, previously included in synonymy, is recognized and a new combination, *Matelea aenea*, proposed for it. Three species closely related to subgenus *Dictyanthus* are also treated. One of these, *Matelea altatensis*, was previously included in *Dictyanthus*. Another, *Matelea aspera*, is a new combination published as a result of this study and is the type species of subgenus *Pachystelma*, a taxon of uncertain status. The third, *Matelea sepicola*, is a new species published as a result of this study and is apparently most closely related to *M. aspera*. As a group, the three species can be distinguished from *Dictyanthus* especially by having corona lobes which are partially or entirely free from the corolla. A data-matrix is provided for subgenus *Dictyanthus*.

Also provided is a brief literature-based descriptive survey of Asclepiadoideae, especially Gonolobeae, and a summary of my own preliminary morphological and anatomical studies of the subfamily, especially with respect to the treated species. The stems of the treated species have inter-xylary phloem, a prominent pericyclic region defined by bundles of bast fibers, an endodermis represented by a starch sheath in young stems but not evident in older stems, and asymmetrical secondary xylem. Druses and branched, nonarticulated latex tubes occur in most tissues. The leaves have an unspecialized dorsiventral anatomy with a single palisade layer and anomocytic stomata. Only uniseriate trichomes occur and these can be glandular or nonglandular, straight or uncinate, and of varying lengths. Specialized glands occur on the stipular region, the base of the adaxial surface of the leaf blade, and the inside of the calyx tube below each sinus; because of their complex structure and specific sites, apparently homologous glands can be identified in related families. The inflorescences are interpetiolar helicoid cymes. The general morphology of the flower is that of Asclepiadoideae. Each corona lobe of Dictyanthus is produced by an enation from near the base of a filament.

Chromosome number data of Apocynaceae show a basic number of $x = 11$; about 97% of the genera and 86% of the species counted can have this number. Polyploidy occurs mainly in a few groups, but about 36% of the genera and 22% of the species counted can have polyploid numbers.

The relationships and distributions of the subfamilies of Apocynaceae and tribes of Asclepiadoideae are briefly discussed. Relationships within Matelea and within Dictyanthus are also discussed.

A REVISION OF MATELEA SUBGENUS DICTYANTHUS (APOCYNACEAE, SENSU LATO)

By

Warren Douglas Stevens

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Drs. Beaman, Rollin Baker, Aureal Cross, and S. N. Stephenson have reviewed various parts of this manuscript and have offered valuable suggestions.

Many other individuals have helped in various aspects of my work. Although not a complete list, I thank at least the following: Dr. Garrett Crow for examining a type specimen at the British Museum, Dr. Robert Cruden for two of the photographs used in this thesis, Dr. Melinda Denton for seeking out specific collection localities in Mexico and for briefly serving as my major professor, Dr. Richard Harris for examining my Latin diagnoses, Dr. Daniel Janzen for determining a collection of weevils, Dr. Rogers McVaugh for various kinds of help but especially for the use of his notes on the Sessé and Mociño collections, Dr. Lorin I. Nevling, Jr. for making available to me the Field Museum photographs of the Sessé and Mociño herbarium, and Dr. Willaim Tai for advice on microscopy as well as the use of his equipment.

And finally the one indispensable part of this study was the access to collections and I am indebted to the curators of the cited herbaria for allowing me to examine their material.

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INTRODUCTION

The genus *Dictyanthus* was described by Decaisne in de Candolle's *Prodromus* in 1844. The description was based on a Sessé and Mociño collection which had been distributed by Pavón. Judging from Decaisne's annotations, he had also seen Galeotti specimens of the type species, *Dictyanthus pavonii*, but he did not cite them in the protologue. A few years later, sometime in the late 1840's, *Dictyanthus pavonii* was introduced into European botanical gardens and became a relatively well-known plant. During this period the species was well illustrated in horticultural journals and was provided with several new names. Other than the addition of new names, the next treatment of the genus is that of Bentham and Hooker in their *Genera Plantarum* (1876). They considered the genus to be comprised of three to four Mexican species. Six years later, Hemsley (1882) treated the genus in *Biologia Centrali-Americana, Botany* and recognized four species, one of which he described as new. In Engler and Prantl's *Die natürlichen Pflanzenfamilien*, Schumann (1895) again considered *Dictyanthus* to be a Mexican genus of three to four species. The next treatment, that of Standley in his *Trees and Shrubs of Mexico* (1924), includes six species, one of which was described as new. Woodson (1941), in providing a generic revision of the North and Central American Asclepiadaceae, reduced *Dictyanthus* to a subgenus of *Matelea* and made new combinations for the ten species he recognized. These were simply listed,

with partial synonymy, to document the subgenus; there was no intent to provide a species-level revision. I am recognizing seven of the species Woodson listed, considering two of them as synonyms of other species, and removing one from the subgenus. Standley and Williams (1969) included the two Guatemalan species of this subgenus in their treatment of Asclepiadaceae in the *Flora of Guatemala*. This summarizes essentially the entire taxonomic history of *Dictyanthus* except for the descriptions of individual species. As can be seen, *Dictyanthus* has not been previously studied except as part of a consideration of the whole subfamily Asclepiadoideae. To date, no species have been added to or removed from Woodson's subgenus and no new species belonging to the group have been described since 1930.

Taxonomic neglect of one kind or another has been the fate of most asclepiads in tropical and subtropical North and Central America. A major problem is that the species tend to be poorly represented in herbaria. This is partially a reflection of the rarity of many species and partially the result of collecting biases. Many collectors tend to avoid the disturbed lowland forests which are relatively rich in asclepiads, to avoid collecting vines, and to avoid collecting groups, such as the asclepiads, which are not easily determinable. Except for the sorts of whole-subfamily studies mentioned above, and somewhat more detailed studies for species occurring within the United States, only three of the nine genera Woodson (1941) recognized in North and Central America have ever been revised for this region. The New World species of *Marsdenia* were revised by Rothe in 1915. Although the revision was well-done for the time, it is now almost totally out-of-date. Woodson (1954) revised *Asclepias*, probably the largest and certainly one of the

most difficult asclepiad genera in North and Central America. *Asclepias*, being primarily temperate and primarily in temperate habitats even in the tropics and not being a vine, is much better represented in herbaria than the other genera. Unfortunately, Woodson provided only a natural key to the species. Even with an illustration for each species, identifications of *Asclepias* are often tedious. *Sarcostemma*, as revised by Holm (1950), is the only asclepiad genus in which species can be readily identified. Although his key is again largely natural, the much smaller number of taxa, the use of more conspicuous and distinctive characters, and the generally better marked species make most determinations relatively easy.

It was in part because of this general taxonomic neglect that I originally began working with Asclepiadoideae. Also attractive were the possibilities for ecological study of the highly specialized insect pollination and insect predation of this group. The specific choice of *Matelea* subgenus *Dictyanthus* as my first project was influenced by several factors. Probably most important was the fact that the group was of such a size that the species could be considered in some detail, yet distinctive enough that one could be relatively certain of considering all the closely related species at once. Also, the ranges of the species were such that I could have a reasonable chance of examining all of them in the field. Also significant was the fact that the species tend to have large and attractive flowers, probably the largest of the New World Asclepiadoideae. This last fact has probably also been the cause for this group's being relatively well-collected, relative at least to the other viney asclepiads.

Using Woodson's ten species of the subgenus as a basis, I began the

study by gathering the pertinent literature and by examining the herbarium specimens at Harvard Herbaria, the Smithsonian Institution, the University of Michigan, and Michigan State University. In this way, the available material was sorted essentially into what I now consider to be 14 species (there was a little lumping and splitting in this original sorting). These sorted elements were considered to include all of the subgenus Dictyanthus plus the most closely related species. On closer examination, one of the species, Matelea congesta (Decaisne in de Candolle) Woodson, proved to be only superficially similar and not actually closely related to the others. Therefore, it is not included in this revision. The remaining thirteen species are treated, ten as belonging to subgenus Dictyanthus and three not assigned to a subgenus; the status of the three unassigned species is discussed in the section on Relationships.

With these reasonably good concepts of the taxa and specific collection localities, about three months were spent in Mexico and Guatemala collecting Matelea. Before Dictyanthus was chosen as a specific project, I spent three months in Mexico with a University of Michigan expedition; during this trip there was ample opportunity to collect asclepiads and several collections which proved to be important to the study were made. After the taxonomic treatment was largely finished, an additional one-month trip was made to western Mexico to fill certain gaps in my material. As has been my practice since the beginning of my field work, considerably more than herbarium specimens are collected when an asclepiad is found (and members of certain other groups as well). Of major importance has been the collection of spirit-preserved flowers. Asclepiad flowers, especially when large or fleshy, are

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drastically deformed by pressing and drying and no amount of soaking or boiling will restore their original shape (cf. Drapalik, 1970). Besides spirit-preserved flowers, also collected, as feasible, were anatomically preserved materials, insects either feeding on the plants or visiting the flowers, information on local names and uses (little has been contributed in this regard), and living plants or seeds. In summary, of the 14 species originally considered, 13 have been seen in the field, spirit-preserved flowers have been collected of 12, and 10 have been successfully cultivated.

In addition to my own collections, I felt it necessary to examine as many herbarium specimens as reasonably possible. In this regard, loans or other information were solicited from a total of 46 herbaria and specimens were actually received from 35. For the 13 treated species, about 880 specimens, representing 341 separate collections, have been examined.

The major result of this work is the essentially classical taxonomic revision presented in the Taxonomic Treatment. The descriptions, thus the resulting differences and similarities among the taxa, were derived almost entirely from the population of herbarium specimens examined. In this sense, the resulting taxonomy would probably not have differed significantly if no field work had been done. The major difference is that I probably would not have been inclined to distinguish between _Matelea_ _aenea_ and _M_. _yucatanensis_ without having examined living plants. It should also be mentioned that additional field work may in some cases provide justification for further taxonomic distinctions; these are discussed under the appropriate headings. However, having examined a variety of material, especially spirit-preserved flowers and livi

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living plants, I believe that I have a much better understanding of the taxa, their inter-relationships, and their relationship to the rest of Matelea than would have been possible from herbarium specimens alone. This understanding is at least partially expressed in the section on Relationships. The section on General Description is, in part, a brief literature-based survey of Asclepiadoideae, especially Gonolobeae, and, in part, a summary of my own preliminary morphological and anatomical studies of the subfamily, especially with respect to those species included in the Taxonomic Treatment.

During the course of this study a number of specific questions regarding the ecology and taxonomy of this group of species have become apparent. My contribution to the understanding of Apocynaceae will be relatively small if my future work is not directed toward these problems as well as toward additional revisionary studies within the family. A considerable body of material, information, and inspiration has accumulated from my field, herbarium, and literature studies and I sincerely hope I will be able to continue studying this most interesting family.

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GENERAL DESCRIPTION

Morphology and anatomy

Roots

The roots of most species of *Matelea* with perennial woody stems are diffuse and fibrous. The more herbaceous species, especially of subgenus *Chthamalia*, typically have fleshier and less diffuse root systems, probably associated with the increased importance of the roots as storage structures. The strictly erect species of subgenus *Pherotrichis*, which are probably ill-placed in the genus *Matelea*, are exceptional in having a few thick, fusiform roots. The roots of subgenus *Dictyanthus* are diffuse and fibrous. The roots are least woody in the two species, *Matelea ceratopetala* (Figure 1D) and *M. standleyana*, which often have thin, nearly herbaceous, horizontal rhizomes which are little more than stems with adventitious roots. The other species of subgenus *Dictyanthus* appear to develop prominently woody taproots and secondary roots (Figure 1A-C). When exposed on the surface, these woody roots develop fissured corky bark similar to that of the stem.

The stem anatomy of Asclepiadoideae has seldom been studied. Scott and Sargent (1893) and Groom (1893) studied the aerial roots of *Dischidia rafflesiana*. Francke (1927) studied the exodermis of 12 species, including examples from the various habit types within the subfamily. In their classic study on internal phloem, Scott and Brebner (1891) included discussions of about ten species of Apocynaceae;

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they discussed in some detail the root and root-stem transition of a species of Asclepias. Mayberry (1938) briefly described the anatomy of three North American species of Asclepias. He found the roots of all three species to have a suberized hypodermis (=exodermis) and an endodermis, this forming a continuous cylinder in two species and a broken cylinder in the third. The xylem was in a triarch arrangement in one species, tetrarch in the second, and forming a solid strand in the third. The cortex was filled with starch grains and oil globules and there were conspicuous calcium oxalate crystals in the cortex of two species. As far as I am aware, the roots have never been examined for a species of Gonolobeae. I have not examined the root anatomy of Matelea.

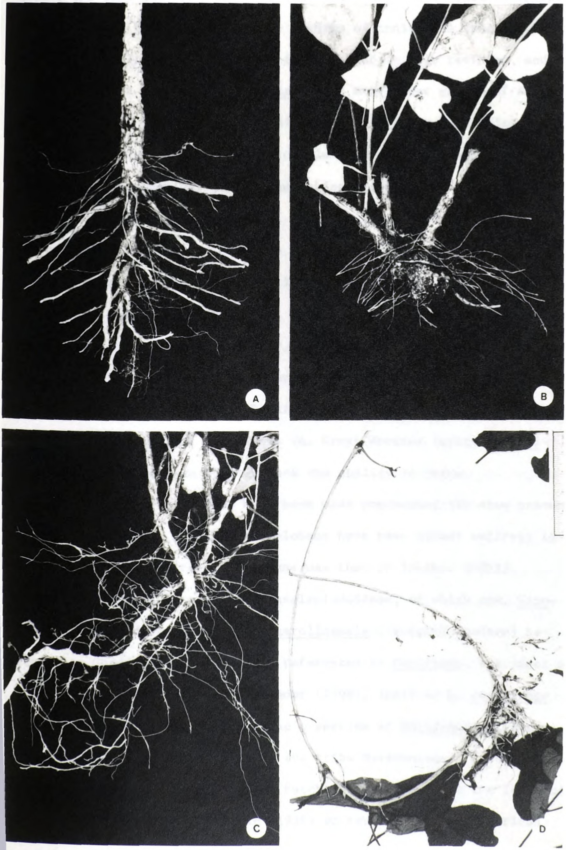
Demeter (1923) studied the mycorrhizal associations of several north-temperate, herbaceous species of Apocynaceae. It would be interesting to know how widely the phenomenon of mycorrhizal associations occurs in the family, especially among the epiphytic species.

Stems

The perennial stems of Matelea vary from distinctly woody to nearly herbaceous and from aerial to ground-level or below. This aspect of the plants is often ignored by collectors and it is thus often difficult to evaluate the habit of a given species. The most common type of perennial stem for the species of this revision is aerial and woody, but four species perennate from ground-level woody or fleshy caudices (two other species can have woody caudices in addition to aerial woody stems) and two species can have thin, nearly herbaceous, rhizomes. Representative examples of the basal parts of Matelea subgenus Dictyanthus are shown in Figure 1. These summarize the types of perennial

Figure 1. Representative basal parts of Matelea subgenus Dictyanthus (x ca 0.5).

A. erect woody stem, Matelea aenea, Stevens 1145 (MSC); B. woody caudex, M. dictyantha, Stevens 1311 (MSC); C. atypical form with elongate rhizome, M. dictyantha, Stevens 1311 (MSC); D. thin, nearly herbaceous rhizome, M. ceratopetala, Harmon & Dwyer 3230 (MO).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stems, and thus the habits, occurring in the species of this revision. Other examples are included in the figures of individual species within the Taxonomic Treatment. The species included in this revision, and apparently most of the rest of *Matelea* and many other genera of Asclepiadoideae, are notable for the thick, fissured corky bark which develops on the woody stems. This feature is often useful, especially for the more robust species, in distinguishing between the annual and perennial stems.

The annual stems of *Matelea* are predominantly twining but can also be erect or procumbent. Although in natural conditions certain species of subgenus *Dictyanthus* are almost always erect, they all seem to have the capability to twine when under favorable conditions, especially in the greenhouse. There are, however, species within Woodson's concept of *Matelea*, e.g. *M. balbisii* (Decaisne *in* de Candolle) Woodson (subgenus *Pherotrichis*) and *M. caudata* (A. Gray) Woodson (subgenus *Heliostemma*), which seem to totally lack the ability to twine.

A number of contributions have been made concerning the stem anatomy of Asclepiadoideae, but again Gonolobeae have been almost entirely ignored. The most comprehensive study was that of Treiber (1891). Treiber considered 59 species of Asclepiadoideae, of which one, *Gonolobus hirsutus* Michaux (=*Matelea carolinensis* [Jacquin] Woodson) belonged to Gonolobeae. Most early references to *Gonolobus*, e.g. most of those in Treiber (1891) and Solereder (1908), apply to *G. condurango* Triana, which was later found to be a species of *Marsdenia*, *M. condurango* Reichenbach f., which is in the tribe Marsdenieae. Other notable references include the studies by Puech (1912a, 1912b) on the leafless species of Madagascar, by Zemke (1939) on several succulent African

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species, by Scott and Brebner (1891) on internal phloem, by Mayberry (1938) on Asclepias, and by Singh (1943) on the inter- and extra-xylary phloem of Leptadenia. The laticifers have been studied in some detail by Chauveaud (1891) and Schaffstein (1932). The following summary of the stem anatomy is based on these studies as well as the information provided in Metcalfe and Chalk (1950) and Solereder (1908).

The most significant features of the stem anatomy of Asclepiadoideae are: 1) the presence of both inter- and extra-xylary phloem, both as bicollateral bundles and in the vascular cylinder; the inter-xylary phloem of the vascular cylinder may be in discrete bundles or in a continuous ring and may or may not be produced by a separate cambium (intra-xylary phloem also occurs in some species); 2) the presence of branched, nonarticulated or occasionally articulated latex tubes, apparently throughout most tissues; 3) the presence of druses in most tissues, these probably of calcium oxalate (cf. Esau, 1965, p. 29); 4) a prominent pericyclic region defined by a ring of bast fibers, these either separate or organized into bundles; 5) a well-defined endodermis; and 6) the superficial origin of the bark, either epidermally or subepidermally. Although I have not considered wood anatomy in any detail, the vessels of the viney species can be summarized as having simple perforations, bordered pits, and very wide lumina.

The species considered in this revision conform to the general description above. Representative thin-sections are illustrated in Figures 2 and 3[1]. The vascular tissue of the stem hardly passes

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[1] All thin-sections used in this study are from material killed and fixed in 50% FAA, dehydrated through a standard TBA series, embedded in paraffin, sectioned at ten microns on a rotary microtome, and stained in safranin-fast green, all procedures after Sass (1958). All figures of thin-sections were photographed on a Zeiss photomicroscope.

Figure 2. Representative stem thin-sections of *Matelea sepicola* and *M. dictyantha*.

A. transverse section of pedicel of small flower bud, *Matelea dictyantha*, x 150; B. transverse section of young stem, *M. sepicola*, x 35; C. transverse section of young stem, note inter-xylary (iph) and extra-xylary (eph) phloem, *M. sepicola*, x 120; D. longitudinal section through primary and early secondary xylem of very young stem, *M. sepicola*, x 250.

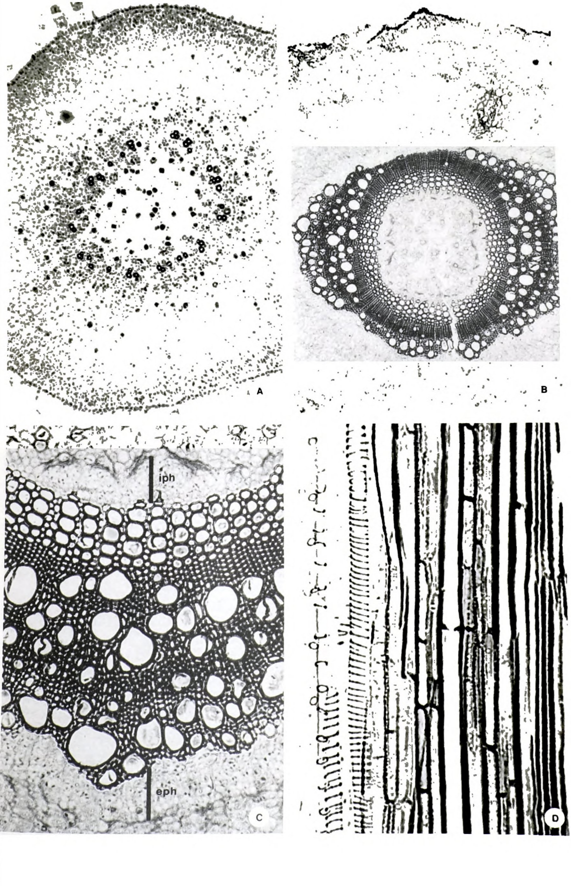
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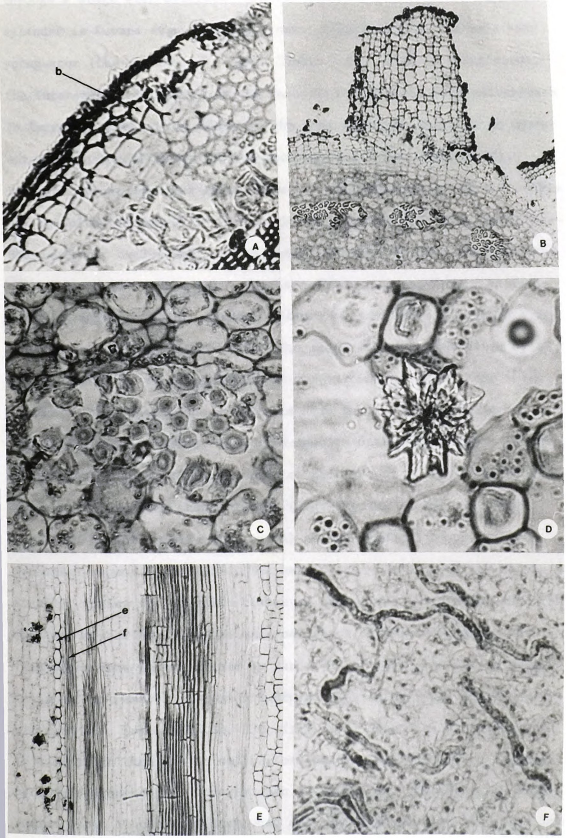
Figure 3. Representative stem thin-sections of Matelea and Hoya.

A. transverse section of very young stem, note subepidermal initiation of bark (b), Matelea sepicola, x 225; B. transverse section of young stem, note bundles of bast fibers and proliferation of bark, M. sepicola, x 70; C. transverse section of a single bundle of bast fibers, M. sepicola, x 305; D. transverse section of pith of young stem showing a druse, M. sepicola, x 530; E. longitudinal section of young stem, note endodermis (e) outside of fibers (f), Hoya obovata Decaisne in de Candolle, x 55; F. transverse section of receptacle of small flower bud, with branched, nonarticulated latex tubes, M. dictyantha, x 395.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through a stage with discrete vascular bundles; a continuous vascular cylinder is formed even in young stems. Figure 2A illustrates a very young stem (the pedicel of a small flower bud). Even in young stems, the inter-xylary phloem is in the form of a continuous ring and appears to increase little in quantity as the stem enlarges; there is no apparent cambium specifically for the inter-xylary phloem (Figure 2C). Branched, nonarticulated latex tubes are conspicuous in both the cortex and the pith (Figure 3F). Within the stem, the latex tubes branch predominantly or exclusively at the nodes. Druses are also common in the pith (Figure 3E) and cortex. The bast fibers are completely unlignified and aggregated into bundles (Figure 3C) and these bundles are organized into a ring (Figure 2B). The endodermis is represented by a starch sheath in young stems but is not evident in older stems. In contrast, the conspicuous endodermis said to be characteristic of Asclepiadoideae is illustrated by a species of Hoya in Figure 3E. The parenchyma of the cortex, and to a certain extent of the pith, of older stems is filled with starch grains (e.g. Figures 3C and 3E). Bark is initiated subepidermally (Figure 3A) and is produced in quantity on perennial stems (Figure 3B). The secondary xylem is produced asymmetrically, giving the vascular tissue an oval shape (Figure 2B), but this does not appear to alter the external shape of even old stems; this same phenomenon was described by Handa (1936) for a species of Marsdenia and is possibly a common feature. The ontogeny of the tracheary elements (cf. Esau, 1965, p. 232, fig. 11.4) from annular thickenings to helical thickenings to scalariform pitting and finally to circular pitting (bordered pits) can be seen in Figure 2D. Vessels with wide lumina occur in the secondary wood and, although no very old stems have been s

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been sectioned, appear to have a weakly-developed ring-porous arrangement (Figure 2B).

Leaves

The leaves of Matelea, as well as other Gonolobeae and almost all Asclepiadoideae, are opposite in arrangement. Depending on the source consulted, the group is considered either to be exstipulate (e.g. Cronquist, 1968) or to have minute stipules (e.g. Lawrence, 1951). I have never observed typical laminar stipules in Asclepiadoideae, but the stipular region usually has a fringe of glands (colleters) and/or trichomes (Figure 5E). A similar situation also occurs in Plumerioideae and Apocynoideae, of which Standley and Williams (1969) state: "Members of this family [Apocynaceae, s.s.] are usually said to be without stipules, however stipules or stipular vestiges are often present. Interpetiolar stipules much like those in some Rubiaceae are often found . . . ." Boke (1947) interprets these stipular glands as vestigial stipules. All the species of this revision have well-developed petioles and basically ovate leaf blades with lobate bases and mostly acuminate to attenuate apices. The terminology used for the description of the leaves is that of Hickey (1973). This terminology has the advantages of being comprehensive, similar to current usage, and generally with precise definitions. Although not specified by Hickey, I measured the length of the blade from the attachment of the petiole to the apex, that is, the length of the midrib. This seems more precise than including the prominent basal lobes and does not alter the basic leaf shape (the widest part of the leaf is often below the attachment of the petiole). It should also be noted that the leaf measurements were always based on the largest leaf of a specimen.

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Although the leaf development is probably not truly heteroblastic, there is often a marked difference in leaf size and shape along the stem, especially associated with the erect habit. The largest leaves are typically near the middle of the annual growth; the lower leaves tend to be smaller, broader, and with broader sinuses and more abrupt apices and the upper leaves tend to be smaller, narrower, and with narrower sinuses and longer apices. Even when measuring only the largest leaves, the resulting size and shape ranges are still quite large. This is probably in part a reflection of the natural variability of the species but is certainly also influenced by differences in habitat, maturity of the specimens, and the fact that herbarium specimens often do not have the section of stem bearing the largest leaves. The leaves of Asclepiadoideae always have entire margins, but certain species, including some treated here, can have a ragged appearance due to the multicellular bases of the long trichomes. The placement of the glands (colleters) on the leaf presents something of a problem with respect to Hickey's terminology. I have tentatively referred to the position as acropetiolar, but they are actually on the adaxial surface of the midrib (and sometimes also on the first lateral veins) at the base of the blade. Hickey provides no term which specifically describes this position, which occurs on most Asclepiadoideae and some Apocynoideae (e.g. Mandevilla), nor for the similar position of being scattered along the midrib, which occurs in some Apocynoideae.

The leaf venation has not been carefully described according to Hickey's terminology. Although this is to be desired and the terminology seems clear, I am inclined to believe that it should be done by someone familiar with a broad range of venation types. For instance,

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it is not clear to me how the basic venation pattern should be described. The basic pattern is probably brochidodromous, but the first pair or two of lateral veins are often fully as large, both in the amount of leaf surface they supply and in their thickness and number of subdivisions, as the midrib and are often congested into virtually a palmate arrangement (Figure 5F). This pattern could just as well be called actinodromous (basal, perfect, reticulate). Someone interested in comparing angiosperm venation patterns could most likely profit more from examining the leaves I have studied than from my descriptions of them. The degree to which the veins, including the higher-order veins, are raised from the lower leaf surface is one conspicuous feature of the venation that does vary within the species I examined. The extremes are illustrated in Figures 4E and 4F. This feature varies somewhat with habitat but is still often of diagnostic value. I have not measured leaf thickness, but two species, Matelea altatensis and M. aspera, appear to have thinner than average leaves and a strong tendency to wilt. Matelea altatensis, and to a certain extent M. aspera, tend to grow in arid environments and this may be one adaptation to reduce transpirational water loss. A practical consequence of this is that the herbarium specimens of these two species often have poorly-pressed leaves. The herbarium specimen in Figure 29 is about the best-pressed example of Matelea altatensis.

The terminology of leaf surfaces is according to Stearn (1966). The only significant variation is that in some species the surface is smooth while in others it is pusticulate (Figure 4A-D). I have not determined the anatomical basis for the pusticulations, but I suspect that they mark the sites of large druses. The pusticulations have some

Figure 4. Leaf surfaces of <u>Matelea</u> subgenus <u>Dictyanthus</u>.

A. adaxial leaf surface of <u>Matelea standleyana</u>, <u>Stevens 1392</u> (MSC), smooth, x ca 65; B. abaxial surface of <u>M. standleyana</u>, <u>Stevens 1392</u> (MSC), smooth, x ca 65; C. adaxial surface of <u>M. pavonii</u>, <u>Stevens 1435</u> (MSC), pusticulate, x ca 65; D. abaxial surface of <u>M. pavonii</u>, <u>Stevens 1435</u> (MSC), pusticulate, x ca 65; E. abaxial surface of <u>M. dictyantha</u>, <u>Stevens 1311</u> (MSC), veins raised, x 4; F. abaxial surface of <u>M. standleyana</u>, <u>Stevens 1392</u> (MSC), veins not raised, x 4.

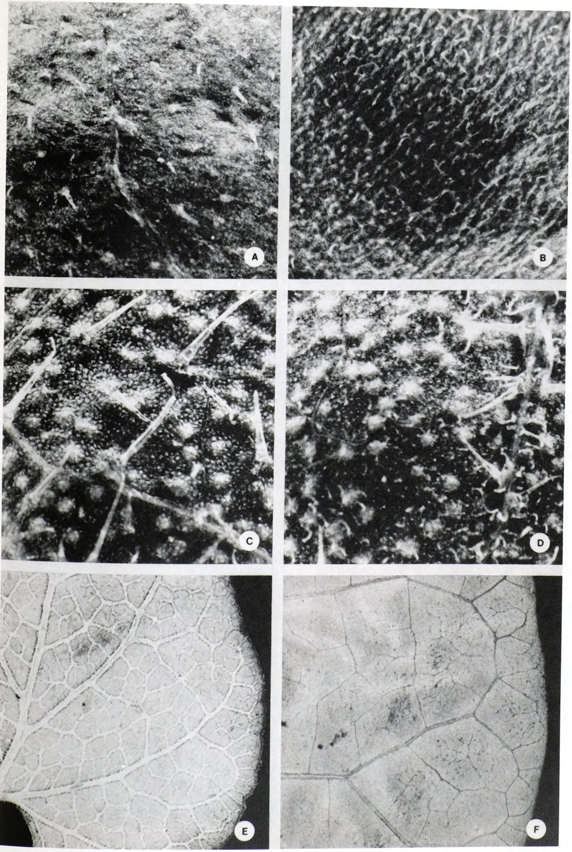
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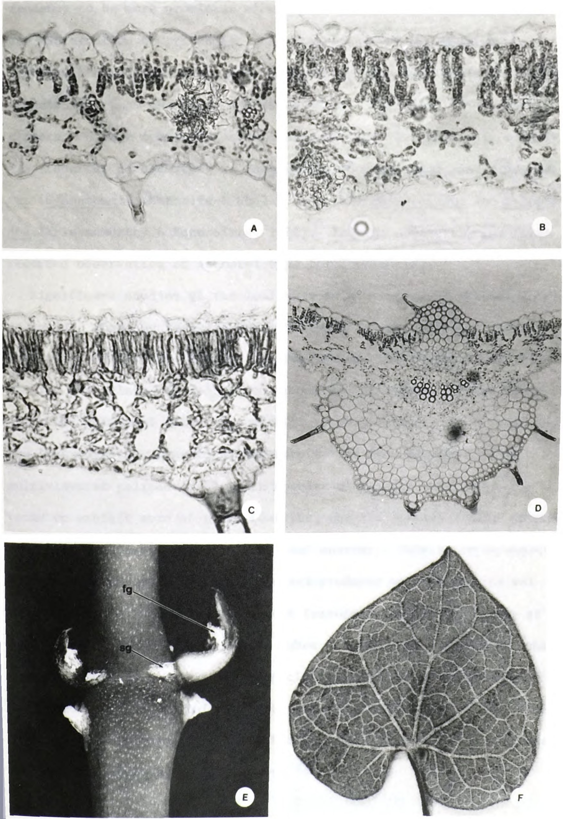
Figure 5. Leaf features of *Matelea* and *Hoya*.

A. thin-section of blade, note large complex druse, *Matelea sepicola*, x 30; B. thin-section of blade, *M. hemsleyana*, x 30; C. thin-section of blade, base of long trichome in lower right corner, *M. obovata* (H.B.K.) Woodson, x 30; D. transverse section of major vein, *M. sepicola*, x 9; E. young node of *Hoya obovata* Decaisne *in* de Candolle, note stipular (sg) and foliar (fg) glands, structures immediately below leaves are adventituous roots, x ca 3; F. adaxial leaf surface showing major veins, *M. tuberosa*, *Stevens 1458* (MSC), x ca 2.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tendency to be more prominent along veins and have no relationship to the distribution of trichomes. The stomata are of the anomocytic (ranunculaceous) type; the cells surrounding the guard cells are indistinguishable from the other epidermal cells. Paracytic (rubiaceous) stomata are more common in Asclepiadoideae, but the anomocytic type is also recorded as occurring in Sarcostemma, Solenostemma, and Vincetoxicum [Cynanchum?] (Metcalfe & Chalk, 1950) and Heterostemma and Tylophora (Krishnamurthy & Kannabiran, 1970). This is apparently the first recorded observation of stomatal type for Gonolobeae.

Significant studies of the leaf anatomy of members of Asclepiadoideae include those by Vesque (1885), Trochain (1932), Mayberry (1938), and Nolan (1966). The primary specializations considered by these studies are related to epiphytic and xerophytic habits. Among these are thick epidermal walls or cuticles, stomata equally distributed on the leaf surfaces, centric arrangement of the leaf mesophyll, and multi-layered palisades. Certain species of Matelea will likely be found to exhibit some of these features, but the species I have considered have relatively unspecialized leaf anatomy. This is to be expected because the leaves are deciduous and produced only during the wet season. Figure 5A-D illustrates some features of the leaf anatomy of Matelea. As with the stems, latex tubes and druses are present in the leaves. Consistent with their unspecialized nature, the epidermal cell walls and cuticles are thin, the stomata are predominantly on the abaxial surface, the mesophyll is distinctly dorsiventral, and the palisade is single-layered and loosely packed.

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Only two types of trichomes are known to occur in Asclepiadoideae, unicellular and uniseriate. The complex structures variously known as glandular shaggy hairs, glands, squamellae, denticles, and colleters are not true trichomes and are considered separately. The uniseriate trichomes of Asclepiadoideae can have several modifications and these have systematic significance in at least some cases. Among the species I have considered and perhaps in the whole tribe Gonolobeae, only uniseriate trichomes occur and their various forms definitely have systematic significance. I have not critically examined these modifications in a broad enough selection of Gonolobeae to establish a satisfactory classification of the types, but this will certainly be necessary to adequately understand and describe the relationships within the tribe.

To describe the indumentum of the species treated in this revision, I have used the convention of referring to all trichomes as short, glandular, or long, and these terms are modified as appropriate.

Short trichomes are considered to be those less than 0.1 mm long; they are mostly about 0.05 mm long. They are few-celled, not accompanied by specialized epidermal cells, and mostly straight (but sometimes have a hooked terminal cell). Except on the inner surface of the corolla, short trichomes are almost always mixed with long trichomes and often also with glandular trichomes. The short trichomes of the inner surface of the corolla, when present, are always unmixed and have a distinctive form; they have from one to a few small basal cells and one larger fusiform terminal cell. When dried, the short trichomes of the inner surface of the corolla typically have a glassy appearance.

Glandular trichomes are about the same length as short trichomes but

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are inflated in the middle. They are not surrounded by specialized epidermal cells. In dried specimens, the inflated part almost always collapses and presents the appearance of a capitate glandular trichome, but when fresh, these trichomes always have a straight or hooked apiculum. The inflated part is thin-walled and presumably the contents could be released by diffusion or by mechanical damage, but I have seen no evidence of anything being actively secreted from them. I have called these trichomes glandular because they have that appearance on dried specimens and they have almost always been referred to as such.

Long trichomes are considered to be those more than 0.1 mm long; they are mostly one to three or four millimeters long but can be somewhat shorter, especially when without accompanying short and glandular trichomes. When long trichomes occur alone, they are often of two discrete lengths, giving a mixed indumentum of long trichomes. Long trichomes are several-celled and, depending on the species and the part of the plant, the terminal cell can be hooked (uncinate) or straight. The epidermal cells surrounding the long trichomes are modified into a raised ring or collar; this basal collar can be quite prominent, especially on the leaf blade.

Woodson (1941) partially justified the separation of Gonolobus from Matelea on the basis of the indumentum, Matelea typically having a mixed indumentum of long plus glandular trichomes and Gonolobus typically having an unmixed indumentum lacking the glandular trichomes. Within Matelea, the nature of the trichomes, especially the glandular trichomes, varies considerably. Uncinate long trichomes apparently occur on only a few species of Matelea other than those treated in this revision. The systematic importance of trichomes is further discussed in the

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section on Relationships. The possible adaptive significance of the indumentum of the species of this revision is discussed in the section on Ecology and Distribution.

Glands (colleters)

The identity and occurrence of these structures has been very much confused in the literature. The term "trichome" is normally applied to epidermal appendages and the term "emergence" is used for appendages which involve subepidermal tissues (Uphof, 1962; Esau, 1965). Carlquist (1959) further implies that a trichome should be the product of a single protodermal initial. The distinction between trichomes and emergences is, however, not always clear (Uphof, 1962; Esau, 1965); this is especially true when a normal trichome is raised upon an emergence. It is perhaps for this reason that various types of structures fitting the definition of emergences are often considered to be trichomes. Uphof (1962, pp. 25-26) states, "It does not seem right that the stinging hairs of *Urtica* are, in the same way as the prickles of *Rosa* and those on the fruits of *Aesculus* and *Datura*, regarded as emergences, simply because in these stinging hairs too the subepidermal cells take part in the development." But neither does it seem right that the glandular structures of Apocynaceae be regarded as trichomes. Metcalfe and Chalk (1950) refer to the glandular structures of Asclepiadaceae as "glandular shaggy hairs" and do not include Asclepiadaceae in their list of "Families in which only unicellular or uniseriate hairs have been found," in which it would certainly be included if the glandular structures were not considered to be hairs. Esau (1965, p. 309), in discussing secretory structures, refers to "emergences such as the shaggy hairs of *Nerium* [Apocynoideae]" in the text, but

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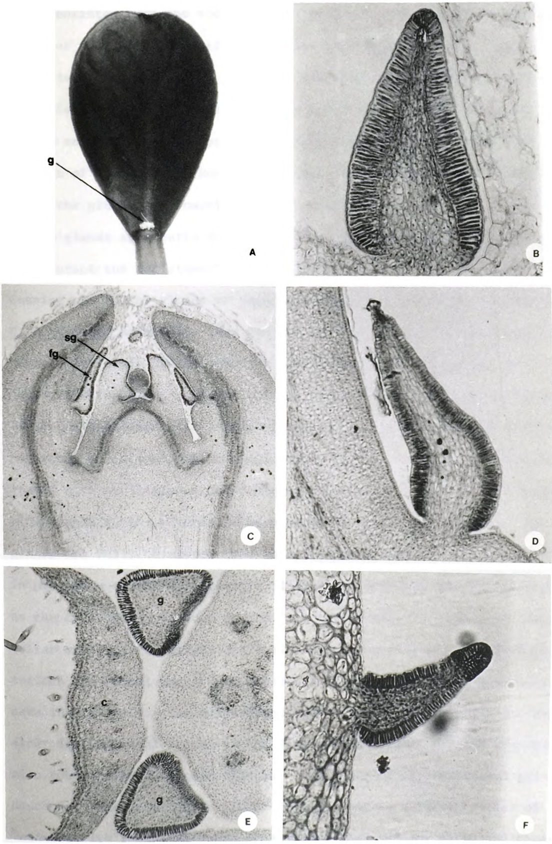
in the text (Fig. 13.1) labels them as "multicellular glandular trichomes." Besides the terms already mentioned, these structures have been called, in Apocynaceae, squamellae when they occur on the calyx (Woodson & Moore, 1938; Holm, 1950; Woodson, 1954; Safwat, 1962) and stipular glands, glandular emergences, foliar glands, denticles, and glands when they occur on the leaves or on the stipular area (Rothe, 1915; Woodson & Moore, 1938; Holm, 1950; Woodson, 1954; Leach, 1970). The almost certainly homologous structures of the Rubiaceae have been termed colleters (cf. Anderson, 1972). In this treatment I have simply referred to the structures as glands, but a more specific term would be desirable.

Whatever they may be called, these structures have a very distinctive morphology, anatomy, and distribution on the plant. Their phylogenetic distribution and function appear to be consistent as well. Figure 7 illustrates the glands of Matelea and Hoya. Developmentally, they appear to be initiated in the subepidermal tissues and form finger-shaped projections covered by a single epidermal layer. When fully developed, the glands are generally one to two millimeters long and obliquely conical; there is a solid core of cells which are generally somewhat smaller and more tightly packed than the subepidermal tissues with which they are continuous and somewhat elongated with the axis of the gland. The epidermal cells are palisade-like, much larger than the adjacent epidermal cells, densely staining, and with the nuclei situated near their bases. Normal epidermal cells typically extend somewhat up the base of the gland, making the gland shortly-stalked. In all the examples I have examined from Asclepiadoideae, the glands are especially peculiar in that the tip is somehow chemically

Figure 6. Representative glands of *Matelea* and *Hoya*.

A. young leaf showing glands (g) at base of adaxial surface of blade, *Hoya obovata*, x 1; B. longitudinal section of calyx gland, *Matelea hemsleyana*, x 200; C. longitudinal section of shoot apex, note how leaf (fg) and stipular (sg) glands enclose apical meristem (see also Figure 5E), *H. obovata*, x 35; D. longitudinal section of leaf gland, note secretion and differentiated tip, *H. obovata*, x 85; E. transverse section of calyx lobe (cl) and glands (g) of a young flower bud, *M. dictyantha*, x 90; F. longitudinal section of leaf gland, note differentiated tip, *M. hemsleyana*, x 140.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differentiated from the body; the tip is hardly, if at all, morphologically or anatomically distinct, but has a slightly different color when living and distinctly different staining characteristics in safranin-fast green. In Asclepiadoideae I have not observed vascular tissue entering or even approaching these glands, but in some other members of Apocynaceae (Woodson & Moore, 1938) and Rubiaceae (Anderson, 1972) the glands are sometimes vascularized.

The glands apparently function in secreting substances which coat and protect the meristematic tissues. Rothe (1915, p. 359), in discussing the foliar glands of Marsdenia notes, "An lebendem Material von M. cundurango Rchb. fil. fand ich bei meinen anatomischen Untersuchungen, dass diese Drüsen schon in der Knospe im Verhältnis zu den jungen Blattanlagen ausserordentlich gross und schon an den Knospe anliegenden Blättchen voll entwickelt sind." Metcalfe and Chalk (1950) note that the stipular glands (glandular shaggy hairs) coat the young leaves with mucilaginous and resinous material. Both of these observations apply to the material I have examined in Asclepiadoideae. The glands are fully developed (and thus relatively large) and functional in proximity to the meristematic tissues and appear to become inactive as the surrounding tissues mature. As can be seen in Figure 6C, the foliar and stipular glands, in their opposite positions, essentially enclose the apical meristem. Traces of the glandular secretion can be seen in Figure 6D. The calyx glands are also relatively large in the early developmental stages of the flower buds (Figure 6E) and probably also coat the meristematic tissues. One piece of circumstantial evidence for this function in flower buds is that in several species of Secamone with the calyx lobes arranged so that two are outer and three are i

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are inner, only the three inner lobes are supplied with glands (Safwat, 1962). Rothe's (1915) suggestion that the glands were extrafloral nectaries which attracted ants as a defense against herbivors was quite enlightened for his era but is unlikely because the glands only appear to be active on very young tissues where they would be inaccessible to the ants. I have never observed significant numbers of ants on an asclepiad, but Rothe's suggestion might be considered with respect to the myrmecophytic species of Dischidia (Asclepiadoideae).

In Asclepiadoideae glands can be found in three specific sites on the plants and they are nearly universal in their occurrence. The three sites are the base of the adaxial surface of the leaf blade, the stipular area, and the adaxial surface of the calyx tube. The only exceptions of which I am aware are that the glands are also found on the apices of the leaves of the myrmecophytic species of Dischidia (Scott & Sargent, 1893), they are missing from the leaf blades of a few broad-leaved species, are often missing from the leaf blades of species with reduced and caducous leaves, and are missing from the stipular region of many of the stem-succulent species. The presence or absence of stipular glands is sometimes of taxonomic significance in the succulent species of Ceropegieae (Leach, 1970; Dyer, 1971). In the other subfamilies of Apocynaceae, glands are not as universal as in Asclepiadoideae, but are found on the same places on the plants (except that they are sometimes also scattered along the petiole and midrib of the leaf in Apocynoideae). The peculiar structure and positions of these glands should make it possible to identify truly homologous glands in other families, and they could therefore have some interesting phylogenetic implications. In this regard, it would probably be useful to have a speci

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specific descriptive term for this type of gland, but I would not like to propose one until the matter has been further studied. The term colleter, a "name given by HANSTEIN to those glands which secrete either mucilage, resin, or a mixture of the two, and which start their secreting activity at a very early moment" (Uphof, 1962, p. 174) is perhaps the best available term, but as currently used includes nonhomologous structures. Metcalfe and Chalk (1950) list 31 families as having glandular shaggy hairs, but again these are almost certainly not all homologous. In the list, Asclepiadaceae are incorrectly noted as having these glands "infrequent or rare" when, in fact, they are much more common in Asclepiadoideae than in Apocynaceae (_s.s._), for which they are listed as "especially common." From Metcalfe and Chalk's list and family descriptions, there are several other possible examples of homologous glands. As mentioned above, the glands of Rubiaceae are almost certainly homologous with those of Apocynaceae (_s.l._). Other notable possibilities include _Bartonia_ and _Obolaria_ of Gentianaceae, _Fagraea_ and _Strychnos_ of Loganiaceae, and _Calonyction_ and _Ipomoea_ of Convolvulaceae (referred to as extrafloral nectaries). The distribution of these glands is an especially interesting subject with definite phylogenetic implications and warrants further study.

Inflorescence

The asclepiad inflorescence has been a source of interest since the earliest botanical writings. Students, both metaphysical and scientific, have speculated on its pecularities to the point where it is hard to imagine a novel hypothesis being proposed. The earlier literature is well summarized by Nolan (1967) and more recent pertinent contributions have been made by Brunaud (1968a, 1968b, 1968c, 1968d, 1969a,

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1969b, 1970a, 1970b, 1971a, 1971b), Jonsson (1968a, 1968b), and Nolan (1969). The major peculiarity of the inflorescence is that it is interpetiolar and not subtended by any structure. Apparently related to this is the fact that at the flowering nodes one leaf subtends a "strong" bud while the opposite leaf subtends a "weak" bud. The phyllotaxy of the leaves, the "weak" and "strong" buds, and the inflorescences (which side and which axil they are closest to) are related. Nolan, through extensive anatomical studies, concludes that the peduncle and shoot apex are produced by a true dichotomy and thus are independent of subtending structures. Tomlinson et al. (1970) apparently accept this as the only known example of a true dichotomy among dicots. Nolan's suggestion that this is a primitive character and that the asclepiads have evolved separately from the rest of the dicots, separate even from Apocynaceae (s.s.), warrants no consideration. I will not attempt to evaluate the competing theories. The easily observed morphological features of the species treated in this thesis are briefly described below.

All the species treated, and apparently all Asclepiadeae, have interpetiolar helicoid cymes. Nolan (1967) is probably the first contemporary botanist to refer to the inflorescence as a helicoid cyme, but that is a perfectly accurate descriptive term in this case. Nolan's (1967, figure 122) diagram of a flowering shoot with inflorescences ("inflorescence-units," Nolan considers the whole flowering shoot to be the inflorescence proper) essentially fits my observations. The peduncle produces a single terminal pedicel subtended by a single bract. The bud in the axil of this bract continues to develop and again terminates with a pedicel ("major pedicel"), this time subtended

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by two bracts. From the axil of one bract a pedicel ("minor pedicel") is produced and from the axil of the other bract a shoot (= inflorescence axis) is produced which again terminates in a "major pedicel" subtended by two bracts, one axil giving rise to a "minor pedicel" and the other the inflorescence axis, and so on. In a given inflorescence, the inflorescence axis is consistently produced from the axis of the right or left bract, thus producing a right- or left-handed helix. An intriguing observation of Nolan's is that the inflorescences of successive nodes are enantiomorphic. They are enantiomorphic not only in the direction of the helix, but also in the sequence of initiation of the calyx lobes; in the right-handed (clockwise) helices, the terminal flowers (produced by the "major pedicels") have their calyx lobes initiated in a clockwise order, and the lateral flowers (produced by the "minor pedicels") have their calyx lobes initiated in a counterclockwise order. In the left-handed helices, the reverse is true. In some species, e.g. Asclepias syriaca, Nolan found the (apparent) helicoid cyme condensed into a virtual umbel. In the species treated in this thesis which produce many flowers, e.g. Matelea sepicola, the inflorescence axis becomes considerably thicker than the peduncle and is covered with the scars of the pedicels and bracts, but still conforms to a tight helix.

One exception to Nolan's scheme occurs in the three species treated here which can produce compound inflorescences. The compound inflorescence occurs when one of the "minor pedicels" is replaced by an additional inflorescence axis. See Figure 30C for an example. This can happen from one to several times in an inflorescence. The observation that subgenus Dictyanthus produces only simple inflorescences is of some

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some diagnostic value. A more troublesome exception is when an inflorescence is reduced to a single flower which lacks the subtending bract (see Figure 19D for an example) which at least topologically separates the peduncle from the pedicel. Another exception occurs when the peduncle is branched below the level of the first bract (see Figure 33C). I offer no explanations for these exceptions but the phenomena are obviously significant in evaluating the nature of the asclepiad inflorescence.

Flowers

The asclepiad flower can be described as actinomorphic, 5-merous, sympetalous, with epipetalous stamens completely connate laterally and adnate to the style apex, and with two carpels which are separate except at the apex and have essentially superior ovaries. The gynostegium can be loosely referred to as the androecium plus the style apex but the corolla, below the insertion of the stamens, forms at least the base of the structure. A "corona" is often present and is typically produced by enations from the filaments (no longer readily identifiable in the gynostegium), but sometimes other parts of the gynostegium or even the corolla are involved. At least in Dictyanthus, the corona lobes are distinct enough from the rest of the gynostegium to be described as separate structures. Despite this apparently simple description, the flowers are actually much too complicated to be discussed in any significant detail here. I will restrict the following paragraphs to a brief discussion of the most important features, especially as they apply to Matelea subgenus Dictyanthus. The description should be prefaced, however, by noting that Gonolobeae have been as much ignored with respect to their floral morphology and anatomy as

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with the previously discussed topics; there is no study directly involved with Gonolobeae, but the most useful references include those by Corry (1884), Demeter (1922), Deshpande and Joneja (1962), Drapalik (1970), Frye (1902), Mulay et al. (1965), Payer (1857), Rao and Ganguli (1963), Safwat (1962), Woodson (1933), and Woodson and Moore (1938). Figures 7-10 demonstrate various floral features of the treated species.

Calyx. The calyx of *Dictyanthus* is 5-lobed nearly to the base and is always green. During development of the flower bud, the calyx lobes are relatively large and erect (Figure 7A). The calyx thus encloses the rest of the bud without actually clasping around the corolla. The shape of the lobes has been described in the same way as the shape of the leaves, that is, according to Hickey (1973). The calyx lobes are typically provided with an indumentum on the outside and are glabrous inside. The calyx vasculature varies considerably in Apocynaceae (Woodson & Moore, 1938; Safwat, 1962); *Dictyanthus* is of the 1-trace, 1-gap type. Each trace trifurcates almost immediately and the adjacent lateral branches typically join to form a ring of vascular tissue which gives rise to sevaral major veins to each calyx lobe. Within the calyx, slightly below each sinus, is one or occasionally two glands. As described above, these glands apparently function in producing a protective secretion for the developing bud.

Corolla. The corolla of *Dictyanthus* is most often relatively large and distinctly campanulate. In nearly mature flower buds the corolla is plane or slightly concave on top and strikingly drum-shaped, hence the name of one of the synonymous genera, *Tympananthe*. I have described the shape of the corolla tube as "convoluted" in the literal

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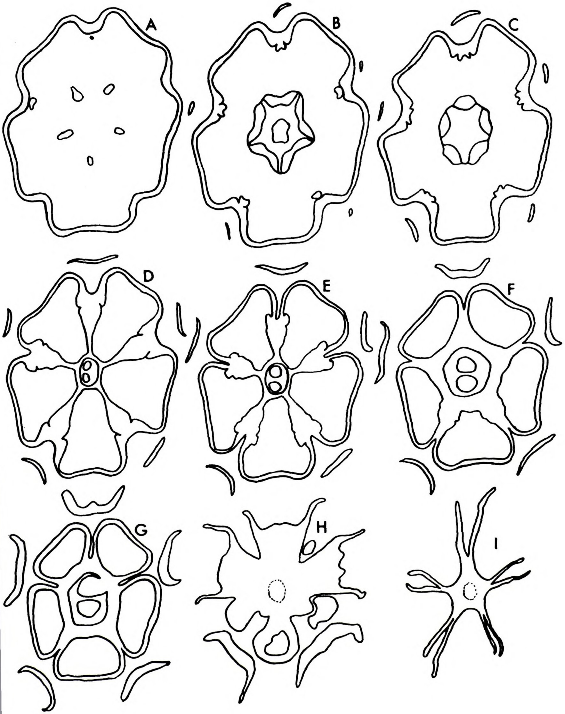
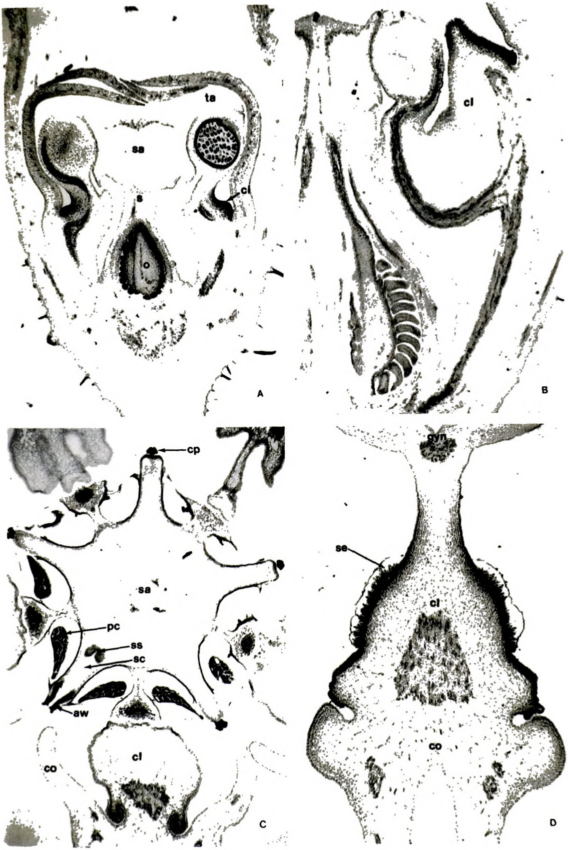


Figure 7. Outline of floral structures of Matelea dictyantha as seen in serial transverse sections.

Outlines of sections ca 1 mm apart, a nearly mature flower bud, ca x 6, from A near top of flower to I near base.

Figure 8. Representative flower thin-sections of *Matelea sepicola*, *M. hemsleyana* and *M. dictyantha*.

A. longitudinal section of young flower bud, note epipetalous stamens with initials of corona lobes (ci) and terminal appendages (ta) overlapping style apex (sa), one style (s) and one ovary (o) visible in this plane, *Matelea sepicola*, x 40; B. longitudinal section of nearly mature flower bud, corona lobe (cl) fully formed, both styles and ovaries visible in this plane, *M. sepicola*, x 40; C. transverse section of nearly mature flower bud, note corona lobes (cl) and adjacent wings of corolla (co), style apex (sa), corpuscula (cp), essentially horizontal pollen sacs (pc), anther wings (aw), stigmatic chamber (sc), and stigmatic surface (ss), refer to Figure 7, especially B and C, for orientation, *M. hemsleyana*, x 40; D. transverse section of corona lobe of nearly mature flower at level of nectary, corona lobe axis (cl) adnate to corolla (co) and adnate by a wall to gynostegium proper (gyn), secretory epidermis (se) of nectary on sides of lobe, refer to Figure 7E for orientation, *M. dictyantha* x 45.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sense of the word rather than in the conventional botanical sense (the aestivation is actually best described as imbricate). In transverse section (Figure 7), the corolla tube is convoluted because the parts which are adnate to the corona are drawn in toward the gynostegium while the alternating parts are bulged out (more or less saccate). The bulged out parts in some cases actually meet behind (outside of) the drawn in parts. Woodson (1941) states that, "The only really unique feature of Dictyanthus is that the faucal callus, or annulus, of the corolla is digitate, as are the segments of the corona." Woodson may have been referring to the overall shape of the corolla tube, but the corolla is not specialized, either anatomically or morphologically, in such a way that there is a structure which could be identified as a faucal annulus or callus. There are, however, good faucal annuli in other Gonolobeae. In two species of Dictyanthus, Matelea tuberosa and M. hemsleyana, the base of the corolla, lateral to the corona lobes, becomes somewhat winged, separating the bases of the sacs (or bulges) from the gynostegium (Figure 8C). Woodson also states, in his key to the subgenera of Matelea, that Dictyanthus has corolla lobes which are "sharply revolute" and "essentially glabrous within." The former is often but not always true and the latter is true for only one of the ten species. The margin of the corolla limb, as well as the lobes, is also often sharply revolute. The indumentum of the inner surface of the corolla is always of short trichomes but its distribution is of onsiderable diagnostic value. The pattern of markings within the coolla is also of considerable diagnostic value. In order to more preisely describe the pattern of indumentum and markings within the coolla, I have divided the corolla into the tube, the limb, and the

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lobes, rather than the more conventional tube and limb. The two corolla measurements used are the length, from the base to a sinus, and the length of the lobes, from the tip to a sinus to sinus line. The individual lobes are 1-trace, 1-gap structures and the pattern of markings, when present, follows the pattern of the major veins.

Gynostegium. The gynostegium is composed of the connate stamens plus the adnate style apex and, at the base, the corolla tube (see Figure 7F-G). In anatomically prepared material the identity of the various structures is relatively easy to determine. In *Dictyanthus*, at least, the corona is always the product of one enation from near the base of each filament; developmentally, these enations bulge out and push their way against and up the corolla and become completely adnate (Figure 8A-B). The vascular bundle of each filament is carried along with the bulge and forms a prominent loop (Figure 8B). A thin wall or partition typically connects the corona lobe to the body of the gynostegium (Figures 7D-F and 8B and D), which is generally stipitate. The bases of the corona lobes themselves become connate in eight of the ten species. The corona is the most variable and difficult asclepiad structure, especially so in *Matelea*. The seven most specialized species of *Dictyanthus* have nectaries on the corona lobes. The nectaries are located on the sides of the lobes near the base, are often ringed with distinctive colors, and are composed of palisade-like secretory epidermal cells (Figure 8D). *Matelea tuberosa* and *M. hemsleyana* appear not to have nectaries and the poor condition of the flowers of *M. hamata* make it impossible to determine whether or not it has them. On the gynostegium (excluding the corona lobes) there are wings or alae which correspond, at least in position, to the lateral margins of adj

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adjacent anthers (Figure 8C). The wings perform the dual, but related, functions of guiding the legs or hairs of the pollinating insects to the corpuscula, which attach the pollen sacs to the insect, and subsequently in guiding the pollen sacs to the stigmatic, or alar, chambers (Figure 8C). The wings and stigmatic chambers are not as well formed as, for instance, with Asclepias, but at any rate the style apex is stigmatic only in the five spots corresponding to the stigmatic chambers (Figure 8C). The structures referred to as "terminal anther appendages" correspond to apical prolongations of the connectives; they are laminar and partly to completely overlie the top of the style apex (Figure 8A). The tip of the style apex can become variously elaborated. In Dictyanthus the tip varies only from concave to apiculate, but is of some diagnostic value.

Pollinia. A pollinium is, in one form or another, a coherent mass of pollen which is transferred by a pollination vector as a unit. Pollinia have evolved independently at least three times. Some species of Acacia (Fabaceae) have evolved a sort of pollinium, but pollinia only become highly developed in Apocynaceae and Orchidaceae. In Apocynaceae rudimentary pollinia are found in a few species of Plumerioideae and Apocynoideae, more specialized pollinia are found in Periplocoideae and Secamonoideae, and highly specialized pollinia are found in Asclepiadoideae. Orchidaceae exhibit a similar phylogenetically correlated series of pollinium specializations. Only two loculi of each anther are fertile in Asclepiadoideae. Secretions from the style apex, and perhaps from the anthers as well, aid in fusing the pollen into a solid mass and form the translator arms, or caudicles, and the corpuscula, or glands. One corpusculum is formed at the apex of each pair of anther win

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wings. A translator arm connects each side of a corpusculum to the nearest pollen mass, or pollen sac. A pollinium proper, then, is composed of a corpusculum, two translator arms, and half the pollen of the two adjacent anthers, or two pollen sacs. A pollinium is removed when some part of an insect, often a hair, is caught between the anther wings and pulled up to the corpusculum. The corpusculum has a narrow slit which is confluent with the slit between the anther wings and, because of the decreasing width of the slit, fastens itself to the insect. When the corpusculum is removed by an insect, the pair of pollen sacs is carried along. When the insect visits another flower the pollen sac can be caught between the anther wings and deposited in the stigmatic chamber. In *Asclepias* the broken translator arm has been observed to remove another corpusculum, forming chains of pollinia. Studies pertinent to the pollinia of Asclepiadoideae include those by Brown (1833), Corry (1883), Dop (1902, 1903), Galil and Zeroni (1969), Guignard (1903), Liskens and Suren (1969), Richharia (1934), and Volk (1949).

The tribes of Asclepiadoideae are essentially defined on the basis of pollinium characters: Asclepiadeae have pendulous pollinia (that is, with the corpuscula borne above the pollen sacs) with uniformly fertile pollen sacs, Ceropegieae have erect pollinia with pollen sacs having a sterile, hyaline margin, Marsdenieae have erect pollinia with uniformly fertile pollen sacs, and Gonolobeae have more or less horizontal pollinia (see Figure 8C) with pollen sacs having a sterile, hyaline section associated with the attachment of the translator arm. In Gonolobeae the sterile, hyaline part of the pollen sac is usually distinctly concave or excavated on one side and the translator arms are

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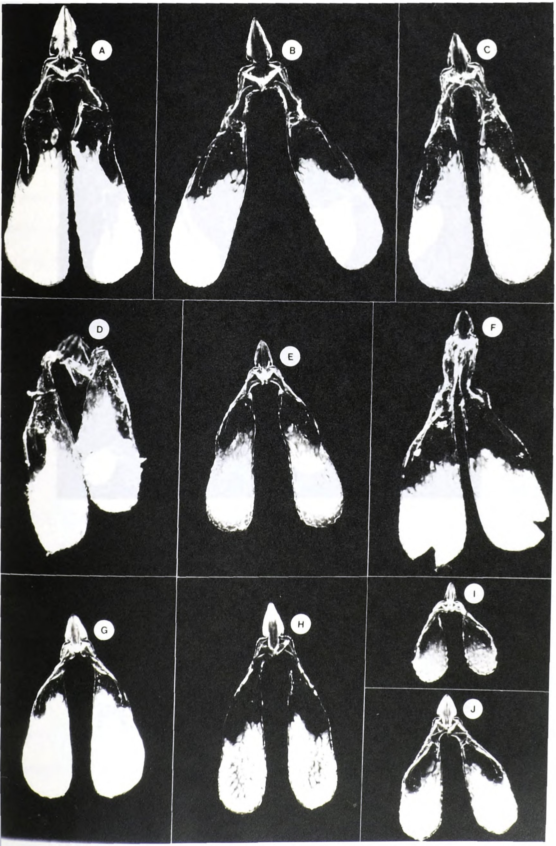
often broad and flat. The pollinia of *Matelea* fit this general description but there is still considerable variation in size, shape, and orientation. In order to adequately organize the pollinium variation within the genus it will be essential to have a set of well-defined and readily comparable descriptive terms, but I have not seen enough of the variation to attempt this. Pollen sacs of *Dictyanthus* can be generally described as obliquely obovate and the corpuscula sagittate. The pollinia of *Dictyanthus* are shown in Figure 9 and those of four related species in Figure 10. The pollinium measurements given in the Taxonomic Treatment were determined with an ocular micrometer on an epi-illumination apparatus; the measurements were of wet material in the orientation they assume when removed.

Ovaries. In all Asclepiadoideae, the gynoecium is composed of two pistils which are separate below but fused at the style apices (Figure 8B); this condition is probably unique to Apocynaceae. As mentioned above, the style apex is stigmatic only in five lateral sites alternate with the anthers. Hypothetically, one pollen sac placed in one stigmatic chamber should result in the complete fertilization of the ovules in one ovary. A second pollen sac, if placed in an appropriate stigmatic chamber, should result in the second ovary being fertilized. In fact, the number of ovaries actually maturing into fruits appears to be controlled by factors in addition to pollination (see Moore, 1946, for a discussion relative to *Asclepias*). Some genera regularly have both ovaries maturing into fruits but most have only one. I have never seen two mature follicles produced by a single flower of *Dictyanthus*. Apocynaceae are generally considered to have superior ovaries with marginal placentation. Baum (1949) and Safwat (1962), among others, have

Figure 9. Pollinia of Matelea subgenus Dictyanthus, epi-illumination photographs, x 37.

A. Matelea standleyana, Stevens 1392 (MSC); B. M. ceratopetala, Stevens 1245 (MSC); C. M. pavonii, Stevens 1462 (MSC); D. M. hamata, Langlassé 257 (US); E. M. yucatanensis, Stevens C-158, a cultivated plant of Stevens 1168 (MSC); F. M. macvaughiana, Faberge s.n. (TEX); G. M. aenea, Stevens C-157A, a cultivated plant of Stevens 1145 (MSC); H. M. dictyantha, Stevens 1343 (MSC); I. M. hemsleyana, Stevens C-162, a cultivated plant of Stevens 1399 (MSC); J. M. tuberosa, Stevens 1468 (MSC).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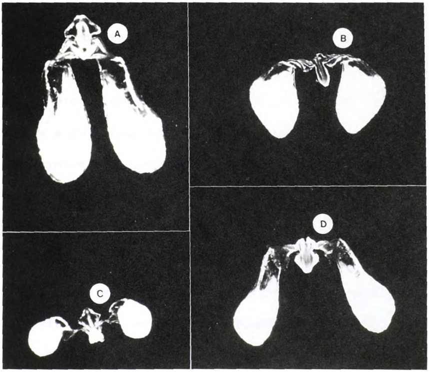

Figure 10. Pollinia of four species of Matelea related to Matelea subgenus Dictyanthus, epi-illumination photographs, x 37.

A. Matelea aspera, Stevens 1296 (MSC); B. M. sepicola, Stevens 2038 (MSC); C. M. congesta, Stevens 1462 (MSC); D. M. altatensis, Stevens 2062 (MSC).

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noted that the placentation in their material was actually submarginal; the placentation in *Dictyanthus* also appears to be submarginal. It has likewise repeatedly been repeatedly shown that various members of the family have so-called subinferior ovaries (e.g. Woodson & Moore, 1938; Safwat, 1962). The ovaries of *Dictyanthus* also bear ovules somewhat down into the receptacular tissue and on that account could likely be termed subinferior. This may seem to be of minor consequence, but the potential for producing inferior ovaries is important in evaluating the relationships within Gentianales and related orders. There have been numerous embryological investigations of asclepiads; see Davis (1966) for a nearly complete bibliography.

Fruits and seeds

With a few minor exceptions, Asclepiadoideae always produce fruits which are follicles and seeds which are apically comose. The follicles can become quite woody, as with some species of *Marsdenia*, or greatly inflated, as with *Calotropis*, and the surface can be variously ornamented. *Matelea*, excluding *Macroscepis*, which should stand as a good genus, and *Matelea viridiflora* (Meyer) Woodson, which is better placed in *Gonolobus*, has follicles which are either smooth or equipped with one or another sort of projection. It appears that follicle characteristics are taxonomically useful but little attention has been given them. I suspect that Woodson's (1941) subgeneric classification of *Matelea* would have been different had he known more about the different types of follicles. Woodson can hardly be faulted in this case though because the follicles are poorly known in general. In many asclepiad species the fruits mature long after the plant has finished flowering; these plants generally flower near the middle of the wet season,

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especially July-August, but the follicles are not mature until the middle of the dry season, mostly February-March. Two related problems result from this. The first is that fruiting collections often cannot be correlated with flowering collections of the same species and sit undetermined in herbaria. The related problem is that collectors tend to avoid fruiting specimens when they realize that they are probably not determinable. The fruits of many species are still unknown. *Matelea pavonii*, for instance, is the most common species of *Dictyanthus*, yet mature fruits and seeds are unknown for this species. I have examined about 70 collections and nearly 200 sheets of this species and have seen one immature follicle and three old, dehisced follicles from the previous season. This is also, at least in part, an indication that species such as *Matelea pavonii* produce relatively few fruits. Seeds are, of course, even more poorly known than fruits. There is little basis for judging the systematic importance of seed characters but they have been described in the Taxonomic Treatment as well as possible on the basis of the available material. Fruits and seeds were collected whenever possible and when the seeds were viable attempts were made to grow the plants to flowering. Through this cultivation, I have been able to make certain flower-fruit correlations, as for instance with *Matelea prosthecidiscus* Woodson (Stevens, 1975). As fruiting specimens become more determinable, follicle characteristics will probably take on greater importance in the taxonomy of *Matelea*.

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Cytology

Although several cytological features could be considered, only chromosome number data are presented here. Table 1 summarizes these data. The table has been compiled primarily from Federov (1969) and Moore (1973, 1974), but a few counts have been derived from other sources. It is important to note that these data are presented in digested, not literal, form. Chromosome data are especially difficult to deal with because a certain, probably significant, number of the recorded counts are inaccurate, either because of faulty taxonomy or faulty counting, or are insignificant for other reasons. Since the data are summarized basically at the tribal level, taxonomy is probably not a significant problem here. Many of the counts, however, are suspect, especially those from the older literature. I have attempted to minimize this problem by evaluating the probable credibility of individual counts. The decisions were admittedly arbitrary in some cases, but I believe this has clarified rather than altered the results. Most likely to be eliminated were old counts which differed from more recent and more reasonable counts. Still, some species appear to have more than one possible number and these have been included; the totals of the individual counts, therefore, are somewhat higher than the totals of the genera and species. The few infraspecific taxa counted have been treated as species. For convenience, meiotic counts have been converted to the mitotic equivalent. Counts of artificial polyploids and hybrids have been mostly eliminated. There are undoubtedly some spurious counts still included and possibly some legitimate counts have been eliminated but the resulting table gives at least a general overview of the chromosome number data of Apocynaceae.

Table 1. Chromosome numbers of Apocynaceae (see text for explanation).

Subfamily - Tribe Genera Species Modified

Table 1. Chromosome numbers of Apocynaceae (see text for explanation).

Subfamily - Tribe	Genera	Species	Modified summary of counts (2n)																
			8	16	18	20	22	24	32	33	36	40	44	46	66	72	88	92	100+
Plumerioideae																			
Carisseae	9	15																	
Genera							9						1						
Species							14						1						
Tabernaemontaneae	5	16																	
Genera							5			1									
Species							16			1									
Plumerieae	9	22																	
Genera				3	1	1	4	1	3		1		1	1			1	1	
Species				4	1	1	7	1	3		4		1	3			1	1	
Rauwolfieae	2	10																	
Genera							1				1		1		1		1		1
Species							4				1		5		1		1		1
Allamandeae	1	5																	
Genera					1														
Species					5														
Cerbereae	3	6																	
Genera					1	1	1				1	1	1			1			
Species					1	2	1				1	1	1			1			
Apocynoideae																			
Nerieae	10	15																	
Genera				1		2	9												
Species				1		20	13												

Table 1 (continued)

Table 1 (continued)

Subfamily - Tribe	Genera	Species	Modified summary of counts (2n)																
			8	16	18	20	22	24	32	33	36	40	44	46	66	72	88	92	100+
Parsonsieae	5	18																	
Genera				1	1	2	1												
Species				1	14	2	1												
Apocyneae	3	7																	
Genera				1		1	1	1											
Species				3		1	3	1											
Ichnocarpeae	3	3																	
Genera						1	2												
Species						1	2												
Periplocoideae	5	7																	
Genera			1				2	2											
Species			1				4	2											
Secamonoideae	1	1																	
Genera							1												
Species							1												
Asclepiadoideae																			
Asclepiadeae	12	54																	
Genera				1		1	12	2					1						
Species				1		1	48	2					3						
Marsdenieae	5	6																	
Genera							5												
Species							6												

Table 1 (continued)

Subfamily - Tribe	Genera	Species	Modified summary of counts (2n)																
			8	16	18	20	22	24	32	33	36	40	44	46	66	72	88	92	100+
Ceropegieae	15	170																	
Genera							14			2			7		2				1
Species							126			6			36		3				1
Gonolobeae	1	1																	
Genera							1												
Species							1												
Totals	89	356																	
Genera			1	7	4	9	68	6	3	3	3	1	12	1	3	1	2	1	2
Species			1	10	21	28	247	6	3	7	6	1	47	3	4	1	2	1	2

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The subfamilies and tribes used are according to Wagenitz (1964) except Cerberoideae has been treated as a tribe of Plumerioideae and Secamoneae has been treated as a subfamily. Refer to the section on Relationships for a discussion of the subfamilies. No counts have been reported for Chilocarpeae, Ambelanieae, and Skytantheae, all in subfamily Plumerioideae.

Two obvious conclusions can be made from the data in Table 1. The more significant of these is that the primary basic number for the family is most probably $x = 11$. About 97% of the genera and 86% of the species have this number ($2n = 22, 33, 44, 66, 88$) on the basis of recorded counts (but, as mentioned above, some species have more than one recorded number). Six of the tribes or subfamilies have only $x = 11$ reported and only one (Allamandeae, with the single genus Allamanda) lacks a report with $x = 11$. The apparently secondary basic numbers ($x = 8, 9, 10$, and possibly 12 and 23) could be derived from the primary basic number. This is the same conclusion reached by Roy Tapadar (1964) in a study of Apocynaceae in the strict sense. It can also be seen that polyploidy has had some influence on chromosomal evolution in this family. About 36% of the genera and 22% of the species can be assumed to be of polyploid origin. Polyploidy occurs especially in Plumerieae, Rauwolfieae, Cerbereae, and Ceropegieae. Polyploids are unknown in nine of the tribes or subfamilies with recorded counts.

The most anomalous count is $2n = 8$ for Cryptolepis buchanani Roemer & Schultes (Mulay et al., 1965) in Periplocoideae. This count was made both meiotically and mitotically and there is no good reason to doubt it, but the number is unusual enough that confirmation is much to be desired. Most of the related families have basic numbers similar to

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those of Apocynaceae and to my knowledge only *Gelsemium rankinii* Small ($2\underline{n} = 8$) of Loganiaceae has a number this low. Since it is unlikely that either the number or the species is especially primitive within the family, the number must have been derived through reduction. If this is true, it should be expected that some intermediate numbers will be found in Periplocoideae.

This family, as well as most other primarily tropical families, is poorly known cytologically. Although nearly 10% of the species have recorded chromosome counts, the majority of the counts are from temperate representatives and from the horticulturally important (and consequently taxonomically inflated) stapeliads (Ceropegieae, in part). There is, for instance, but a single recorded count for the nearly 300 species of Gonolobeae. This count is recorded for a species treated in this thesis, *Matelea ceratopetala*. The count was made in 1934 and it is very likely that the species was actually *Matelea dictyantha*.

Distribution

Apocynaceae are essentially tropical in distribution but there are a few well-known temperate genera, especially *Apocynum* and *Asclepias*. Of the five subfamilies recognized here, three (Plumerioideae, Apocynoideae, and Asclepiadoideae) are widespread and two (Periplocoideae and Secamonoideae) are restricted to the Old World. Of the four tribes of Asclepiadoideae, two (Asclepiadeae and Marsdenieae) are widespread, one (Ceropegieae) is restricted to the Old World, and one (Gonolobeae) is restricted to the New World. Asclepiadoideae are the most specialized and can be assumed to be derived from Apocynoideae which can in turn be derived from Plumerioideae; Periplocoideae and Secamonoideae are

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usually considered to be intermediate stages of specialization between Apocynoideae and Asclepiadoideae (cf. Good, 1956). Raven and Axelrod (1974) suggest that the subfamilies and some of the tribes of Apocynaceae were probably differentiated when South America and Africa were closer together. Assuming that the continents have moved in the manner summarized by Raven and Axelrod, this must have been true for the three widespread subfamilies and even for some of their tribes and more broadly circumscribed genera, especially when it is considered that there are very few "weedy" species in the family and Asclepiadoideae, in particular and despite their comose seeds, are generally unsuccessful at migrating to islands (cf. Good, 1952). Since the essentials of the distributional patterns of the subfamilies and tribes are relatively well-known and there are not likely to be any great revelations in the understanding of their phylogenetic relationships, any explanations for their distributions must be based on existing information. Some aspects of the distributions can undoubtedly be explained by overland migrations across the existing continents and by long distance dispersal, but in the face of current theories and accumulating data it would be a mistake not to attempt to correlate the modern distributions with the historical arrangements of the landmasses. Although the arguments can become circular, the viability of including continental movement as a factor in distributions can be tested by examining the distributions of many groups of organisms and taking into account such factors as time of origin, dispersibility, and ecological requirements. Biogeographical models including continental movement will be acceptable in the degree to which they fit the geological facts and successfully explain the distributions of a variety of organisms.

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Periplocoideae are widespread in the warmer parts of the Old World, occupying nearly all the landmasses, except isolated islands, between latitudes 40° N and 40° S (Good, 1952). On the basis of the distributions of the least specialized genera and the total numbers of genera and species, it would appear that Periplocoideae are basically an African group. Furthermore, many of the distinctive vegetative specializations found in the subfamily are adaptive to arid environments. The periplocoid pollinia, at least theoretically, can be thought of as evolutionary intermediates between those of Apocynoideae and Plumerioideae on one hand and Secamonoideae and Asclepiadoideae on the other, but they are in their own way highly, sometimes even bizarrely, specialized and not at all functional intermediates, but functional equivalents of the asclepiadoid and secamonoid pollinia. Although I have never seen it suggested, my basic reaction is that Periplocoideae do not represent evolutionary intermediates but are a separate evolutionary line. The line could have had its origin in Apocynoideae near that of Secamonoideae-Asclepiadoideae or it could have had quite a distinct origin within either Apocynoideae or Plumerioideae. If this separate origin is, in fact, the case, it is easy to speculate that Periplocoideae differentiated in Africa after it had become well-separated from South America, possibly associated with the increasing aridity which commenced in the Miocene (cf. Raven & Axelrod, 1975). The Asian distribution of Periplocoideae is largely the result of a few widespread genera and could be accounted for by dispersal from Africa northward and eastward into Asia and subsequently southward into Australasia. The Australasian range south of about 10° S latitude is the result of a single genus, <u>Gymnanthera</u> (Good, 1952). This is all

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extremely speculative, of course, but would, among other things, explain the absence of Periplocoideae from the New World.

Secamonoideae, on the other hand, almost certainly represent an intermediate evolutionary step toward the more highly specialized Asclepiadoideae and must have differentiated at least concurrently with the tribes Asclepiadeae and Marsdenieae, or while migration between South America and Africa was still possible. Although not directly explaining its absence from South America, it should be noted that the subfamily is small and not particularly diverse. It is normally divided into at least three genera with a total of about 150 species, which are best represented in Africa and Madagascar. The genera are separated mainly on the basis of differences in the style apex and there is reason to believe that the variation is best represented as comprising a single genus (Stevens, 1971). Whether represented by one genus or by three or more, the group currently appears to exhibit little evolutionary potential. A group of this type could be supposed to have either been eliminated from South America or to have had a limited distribution while Africa and South America were closer.

It is not unreasonable to assume that Ceropegieae and Gonolobeae differentiated after South America and Africa were isolated from each other. Ceropegieae, with their striking xeromorphic adaptations, very likely differentiated in Africa in response to increasing aridity. Gonolobeae, with which I am most concerned here, are not easily assessed. The major problem is that they are poorly known and understood. It is possible to identify certain species or groups of species as being derived on the basis of highly specialized features; the subgenera _Labidostelma_ and _Dictyanthus_ of _Matelea_, for instance, could be

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considered rather advanced in the tribe because of their highly specialized corona lobes. Other than with such specific examples I have little idea about what is primitive or advanced in the tribe. Likewise, I have no idea from which group the tribe may have evolved or where it may have evolved. Essentially by default, the tribe can be guessed to have differentiated in South America from something like Marsdenieae or Asclepiadeae. Raven and Axelrod (1974) indicate that although there are a few temperate North American genera, most genera of North and Central American Apocynaceae are South American in origin. Matelea is too poorly known, both as to the relationships within the genus and the numbers and distributions of species, especially in South America, to provide evidence either for or against a South American origin. The major center of diversity of Matelea in North and Central America is apparently in the area of Chiapas and Guatemala (cf. Williams, 1968) and the diversity decreases significantly southeastward in Central America, but remains relatively high northward through most of Mexico. Alternatively, Gonolobeae could have had a tropical North American origin and, either because of its time of origin or its tropical nature, did not disperse more widely in Laurasia. The South American and perhaps even the temperate North American parts of the range would then be considered relatively recent.

Subgenus Dictyanthus ranges from Nicaragua northward to Veracruz on the east side of Mexico and southern Sonora on the west side. The three other related species treated here fall within this range except one extends a little farther north in Sonora. I have seen no South American species which appear to be closely related to this group; the closest affinities I can detect are with Mexican species. Of the two

most generalized species of Dictyanthus, one forms the northernmost extension of the range and the other nearly equals the southernmost extension.

Ecology

Matelea subgenus Dictyanthus, as with the majority of tropical asclepiads, tends to occupy low, open, seasonally dry forests and the adjacent grasslands. Since most are vines which do not grow particularly tall, they are not often found in taller forests except in openings. The species, as a group, occur from sea level up to about 2250 m; only Matelea pavonii (mostly 650-1750 m) and M. dictyantha (1250-2250 m) normally occur above 1500 m. Most of the species are apparently tolerant of a variety of substrates; Matelea dictyantha is at least commonly associated with limestone and the two species on the Yucatán Peninsula occur only on limestone-derived soils. Flowering normally starts in June or July and is completed by September or October. The Yucatán species are the earliest-flowering and Matelea tuberosa, from northwestern Mexico, is the latest.

Despite the amount of time spent in the field, the pollination biology of Dictyanthus remains essentially a mystery. I have seen many examples of pollinator activity on tropical species of Asclepias, Cynanchum, and Sarcostemma (Asclepiadeae) and Marsdenia (Marsdenieae), but almost never on Gonolobeae. Admittedly I have been more concerned with collecting good material of as many species as possible in various parts of their ranges than observing individual populations in detail. A realistic study of gonoloboid pollination biology will require a different type of effort. This is one case where taxonomic and

ecological investigations are not particularly compatible, at least not when the level of taxonomy at which I am working and the logistic problems of field work in tropical America are taken into consideration. This is unfortunate because the selective pressures giving rise to the elaborate floral features of Dictyanthus are, of course, related to pollination, both in attracting insects to the flowers and in manipulating their behavior in such a way that pollination can take place. My best guess is that Dictyanthus is pollinated by dipterans. This suggestion is based on the flower colors and color patterns, on the fact that at least one of the species, Matelea standleyana, produces a faint foetid odor, and on the small amount of nectar which is openly presented. The flower colors are mostly dull shades of red, brown, purple, and yellowish-green and are organized into intricate patterns, features often associated with dipteran pollination, as are foetid odors. The open placement of the nectaries, on the sides of the corona lobes, is compatible with the mostly small feeding organs of dipterans. Nectar does not normally accumulate in the flower, probably because of evaporation, but a small drop can be seen to form if the flower is placed in a moist chamber for a few hours. Drapalik (1970) found that the southeastern United States species of Matelea were pollinated by small flies.

Because of the occurrence of certain kinds of compounds, especially cardenolides (cardiac glycosides), asclepiads are often toxic to, and thus protected from, general predators. At the same time, however, certain groups of insects have become specialized predators of asclepiads and assimilate the poisonous compounds as part of their own defense mechanisms. This is a fascinating aspect of asclepiad biology,

but again one to which I have contributed little and which is not discussed here. As well as possible, I have noted in the Taxonomic Treatment the occurrence and type of predation observable on collected specimens and from field observations. I hope eventually to be able to identify the groups of insects which utilize Matelea as a host.

Trichomes appear to have special ecological significance in the species treated here. Valuable reviews on the ecological aspects of trichomes are provided by Uphof (1962) and Levin (1973). These authors provide numerous examples of both speculation and experimentation on the roles of plant trichomes. Although I am not providing experimental evidence, the indumentum is such a prominent aspect of the species that a short discussion seems appropriate. The type and density of trichomes varies somewhat both between and within the taxa, but they are always dense on the young parts of the shoot tips. Uphof (1962) lists the following as possible functions of dense trichomes on vulnerable plant parts: protection against excessive water loss by transpiration, insulation against marked temperature changes, protection against the blocking of stomata by rain or dew, protection against strong irradiation, and mechanical protection. On mature parts, the density of trichomes has been repeatedly demonstrated to influence the type and degree of insect predation. In the case of the species of this revision, the hooked, or uncinate, long trichomes are especially significant. Hooked hairs of vines often aid in climbing (Uphof, 1962), but this is not the case with these species because, with the exception of Matelea aenea and M. yucatanensis, hooked hairs are not found on the internodes (the long straight hairs of the stems are often somewhat reflexed and could be of some benefit in this regard), but are found on

various other parts. Levin (1973) gives several examples where hooked trichomes have been shown to be a specific defense against herbivorous insects, especially soft-bodied insects which are likely to be punctured as well as snared by the legs. The example by Gilbert (1971) where the hooked trichomes of _Passiflora_ _adenopoda_ snared and punctured the larvae of heliconiine butterflies, specific predators of _Passiflora_ (Ehrlich & Raven, 1964), is especially interesting because certain lepidopteran groups are among the most successful asclepiad predators. It is more difficult to suggest a function for the glandular trichomes of _Matelea_. If they actually have a defensive function, they must contain some chemical deterrent to insects. Since the glandular trichomes are not secreting visible substances from their cells, they could be secreting volatile deterrents or they could contain nonvolatile substances which serve as gustatory repellents (Levin, 1973). In this regard, it should be remembered, as Levin notes, that insects often have chemoreceptors on their legs as well as on their mouthparts and do not necessarily need to commence feeding to be chemically repelled. It should be possible to test some of these possible defense funtions by experimentation with natural asclepiad predators.

RELATIONSHIPS

Family-subfamily

Although the phylogeny of angiosperms is still largely speculative, and current students differ somewhat in their interpretations, there are many examples where the relationships seem undeniable. It seems clear that the phyletically large and diverse Loganiaceae (in the broad sense but excluding Buddlejaceae) are the remains of an evolutionary line that has produced several modern groups. Loganiaceae can and have been divided into a number of smaller families, and these probably represent lines which have maintained more of the primitive characters and have been generally less successful. Lines which have diverged farther and been more successful are represented by Gentianaceae, Apocynaceae (in the broad sense), and Rubiaceae. Menyanthaceae, Buddlejaceae, Oleaceae, and perhaps Caprifoliaceae (excluding *Sambucus* and *Viburnum*) may also be derived directly from proto-loganiaceous ancestors, but the relationships seem less clear. To substantiate my own speculations on this subject would require a discussion of characters which is hardly appropriate here. The discussion would be hindered at any rate by the lack of data on the nature and distribution of some of the most important characters. Suffice it to say that I believe Loganiaceae (*s.l.*), Apocynaceae (*s.l.*), Gentianaceae, and Rubiaceae are intimately related and have their common origin best represented in modern Loganiaceae and

that there are very likely other families directly but somewhat more distantly related.

A question more pertinent to this thesis is whether or not Asclepiadaceae should be separated from Apocynaceae. If we ignore the fact that some of the more primitive members of Apocynaceae (s.s.) are hardly distinct from Loganiaceae (s.l.), almost everyone, with the possible exception of Nolan (1967), would agree that what is represented by Apocynaceae and Asclepiadaceae (including Periplocaceae) is a single taxon at some classificatory level; the cumulative similarities within this group far outweigh the differences. The major subdivisions within the group are also generally agreed upon and these can be easily arranged into a linear sequence based on the degree of specialization for entomophily, though this does not necessarily represent a phylogenetic sequence. The question resolves to whether or not this obviously natural group, which can be divided into several well-defined and probably natural subgroups, should be divided into two or more families. Robert Brown (1810) was the first to separate Asclepiadaceae from Apocynaceae. Since that time it has become traditional to recognize at least these two families; only Hallier (1912) and more recently Thorne (1968), among leading phylogenists, have recombined the two. Even some of the phylogenists who accept the distinction, however, admit that it is arbitrary. Cronquist (1968), for instance, states ". . . there is a step by step gradation of characters, so that the line between the two families is only arbitrary established." I have no basic objection, however, in arbitrarily delimiting families and hence I cannot agree with Thorne's (1973) justifying the recognition of a single family on the basis of the width of the gap between the two classically recognized

families. One need only compare current phylogenetic systems to realize that it is still difficult to put families into their proper order; it is even more difficult to compare families on the basis of the phyletic gaps between them. My contention that this group is best represented as a single family is, nonetheless, partially based on phyletic gaps, but only on gaps <u>within</u> the group, and ignoring how these gaps may compare with those separating other families. As I evaluate the group, five distinct subgroups can be recognized. The largest of the gaps among them is that which separates the two classically recognized subfamilies of Apocynaceae (Plumerioideae and Apocynoideae). If I have correctly evaluated the subgroups and their distinctions, then the classical separation of the two families inaccurately describes the relationships within the whole group. There are three more or less interrelated choices in remedying the situation. The first would be to continue to recognize two families, but to redefine them by raising Plumerioideae to family rank and adding Asclepiadaceae to Apocynaceae for the second family. This distinction between the two families would still be arbitrary, but would more accurately represent their relationship. The second choice would raise Plumerioideae to family rank and would also raise some of the other subgroups to families as well, up to a total of five families. This tendency has already been partially indicated by the often recognized family Periplocaceae. The last choice, and the one I obviously prefer, is to recognize but a single family, this with five subfamilies. The difference between recognizing one family with five subfamilies and recognizing five separate families cannot be objectively evaluated; this is primarily a matter of individual preference and convention, and I am more comfortable with a single

family. The family Apocynaceae as I conceive it then, is comprised of the subfamilies Plumerioideae, Apocynoideae, Periplocoideae, Secamonoideae, and Asclepiadoideae.

A second objection I have to the classical distinction between Apocynaceae and Asclepiadaceae is the implication it carries that the latter is monophyletically derived from the former. While the subfamilies recognized here are probably natural and may actually represent a single line of evolution, it would be difficult on the basis of current knowledge to argue that they are derived from one another in a linear sequence. The most advanced members of Apocynoideae and Periplocoideae, for instance, are much too specialized to give rise to the succeeding subfamilies. It would not be surprising, as mentioned above, to find that Periplocoideae had a separate origin, within either Plumerioideae or Apocynoideae, from that of Secamonoideae and Asclepiadoideae. The recognition of a single family with five subfamilies implies only that the group, as a whole, had a single origin.

It is significant to add that the two most comprehensive studies of the floral anatomy of the group, those of Demeter (1922) and Safwat (1962), both concluded that the group is best represented as a single family. Safwat's conclusion is essentially identical with my own. The closing paragraph of his summary is as follows:

> In view of the present study, as well as from investigations of others, I am inclined to believe that phylogeny is better portrayed by combining Asclepiadaceae and Apocynaceae into a single family and re-subdividing the group into five subfamilies according to the degree and kind of specialization of the translator apparatus and the relationship between the pollen tetrads to one another at the time of maturity, thus: Plumerioideae, Echitoideae (or Apocynoideae), Periplocoideae, Secamonoideae and Asclepiadoideae.

Thorne's (1968) treatment differs only in the recognition of an additional subfamily, Cerberoideae. This follows Wagenitz (1964) and I cannot evaluate this further subdivision of Plumerioideae at this time.

In summary, my recognition of Apocynaceae in the broad sense, while contrary to most current interpretations, is neither without precedent nor without justification. I plan in the future and in a more appropriate place to provide additional justification on the basis of a careful evaluation of a broad range of characters.

Tribe-genus

The subfamily with which this thesis is most concerned is Asclepiadoideae. It is most often, and I tentatively think most accurately, divided into four tribes: Asclepiadeae, Marsdenieae (=Tylophoreae), Ceropegieae (including Stapelieae), and Gonolobeae. Each of these tribes is relatively specialized in one way or another and I can only generally speculate on their interrelationships. Asclepiadeae and Marsdenieae are the larger (ignoring the extreme splitting of the stapeliads) and the more widespread of the tribes (both tribes as well as several of their constituent genera occur in both the Old and New Worlds). Ceropegieae tend to occupy arid areas and exhibit a strong tendency towards succulence, culminating in the remarkable stem-succulent stapeliads. Ceropegieae are apparently derived from Marsdenieae, with which they are sometimes combined (e.g. Good, 1952), and are restricted to the Old World. Gonolobeae have the smallest number of genera and species and are restricted to the New World. The affinities of Gonolobeae to the other tribes are still unclear to me.

Woodson (1941) recognized three genera of Gonolobeae in America:

Matelea, Gonolobus, and Fischeria. Although Woodson did not at the time consider the South American species, it is clear from the broad circumscription of the genera, especially Matelea, and from his later work on South American asclepiads, that he would have recognized few, if any, additional genera of Gonolobeae. I would recognize a few additional genera, but Woodson's concepts of Matelea and Gonolobus still clearly form the core of the tribe.

Subgenus-species

Even if the most discordant elements are removed, Matelea probably still contains nearly 200 species, or roughly two-thirds of the species of Gonolobeae. Woodson (1941) divided the genus into a number of not entirely satisfactory subgenera and sections, many of which had been previously recognized as genera. While I do not pretend to understand all the complexities of the genus, I can vaguely recognize a large group composed of species of the following of Woodson's subgenera: Dictyanthus, Pachystelma, at least part of Chthamalia, and parts of Macroscepis, Heliostemma, and Matelea. The tendencies I see represented in this group are to have a corona, lobed or unlobed, which is composed of a single series of enations which are connate laterally and adnate to the corolla, to have a distinctly mixed indumentum which often has at least some of the trichomes uncinate, and to have follicles which are tuberculate. The species of Dictyanthus, as well as the other three species treated here, have strongly lobed corollas and otherwise fit the above tendencies quite well.

As may be surmised from reading this thesis, Woodson was prone to making errors of detail in his taxonomic work. The value of his

revolutionarily conservative approach to generic limits of the asclepiads has, nevertheless, been repeatedly confirmed (at least in large part). Woodson was "very reluctant to merge *Dictyanthus* with *Matelea*" but chose to do so in large part because *M. altatensis* provided "a very suggestive link with either *Pachystelma* or *Eumatelea*, according to one's viewpoint at a particular time." Although I do not agree with the circumscription of some of his subgenera, including *Pachystelma* and "*Eumatelea*," and have, on technical grounds, removed *Matelea altatensis* from subgenus *Dictyanthus*, I still believe *Dictyanthus* is inextricably linked to the larger concept of *Matelea* and is best kept in the genus. The virtue of Woodson's conservative concept is thus reaffirmed. I have defined *Dictyanthus*, as nearly as possible, in the same manner as Woodson, which was the same as the generic concept. In a natural key to the current subgenera of *Matelea*, *Dictyanthus* could be identified as having digitate corona lobes with their axes entirely adnate to the corolla, simple inflorescences, a mixed indumentum with at least some of the trichomes glandular and at least some of the long trichomes uncinate, and narrowly fusiform follicles with thickish projections. The "faucal annulus" Woodson refers to in describing *Dictyanthus* simply does not exist. Pollinium characters are apparently important, though not as overwhelmingly important as Woodson supposed, but they have not been uniformly enough described to be of much use at this time.

Dictyanthus could be redefined, either to exclude *Matelea hemsleyana* and *M. tuberosa* or to include additional related species, especially the three treated here, but I think it best not to consider doing this until more of the related species are studied. *Dictyanthus*, or any of the other subgenera, is best circumscribed in the context of all the

related subgenera. Most of the genus is not yet well enough studied to provide this kind of perspective. This is essentially my basis for not assigning the three non-Dictyanthus species treated here to any existing subgenus. With respect to a broader study of the genus, it should be noted that there will need to be a better set of descriptive terms for the coronas, trichomes, and pollinia to make the descriptions more comparable.

Within Matelea subgenus Dictyanthus, the relationships, on a subjective basis, seem relatively clear. Evolutionary changes in Matelea are most strikingly exhibited in the shape of the floral structures, particularly the coronas. The changes that take place in the shape of these structures, while of paramount importance in reproductive biology, are not particularly suited to objective measurement and, in fact, almost defy description. In order to employ an objective technique, these characters would need to be described and properly weighted (non-floral characters can in no sense have the same evolutionary significance as floral characters in the asclepiads). Rather than attempting to employ an objective technique and then comparing the results with my subjective evaluations, I will simply summarize the relationships as I see them.

Subgenus Dictyanthus, if defined in the strictest reasonable sense, would include seven species (species number four through ten in the Taxonomic Treatment). Among these, Matelea aenea and M. yucatanensis are the most closely related and obviously derived from something like the other five; these two are unique enough in several respects that they may have been isolated for some time and show no special affinities with any particular one of the other five. On a character by

character basis, however, they would be most similar to *Matelea dictyantha*, which is, incidentally, the only other species which commonly occurs on limestone-derived soils. The remaining five species are all closely related, but among them *Matelea pavonii* and *M. ceratopetala* form the closest pair, *M. macvaughiana* is only a little more distantly related, and *M. standleyana* and *M. dictyantha* slightly more distant. Although *Matelea pavonii* should not be considered directly ancestral to the other six species, they may have been derived from something similar to it. This species appear to be the most generalized and variable member of the seven core species of *Dictyanthus* and is also the most common and widespread.

When circumscribed somewhat more broadly, as done here, *Dictyanthus* includes three additional species (species number one through three in the Taxonomic Treatment). *Matelea hemsleyana* and *M. tuberosa* are relatively distant from the seven species described above and definitely more generalized. These two, especially *Matelea hemsleyana*, appear to be intermediate between *Dictyanthus* in the strictest sense and the rest of *Matelea*. *Matelea hamata* apparently bridges the gap between *M. tuberosa* and *M. hemsleyana* and the seven species noted above. Unfortunately it is very poorly known and additional collections are much to be desired. As hinted above, these subgroups could be taken into account, both in defining the subgenus and introducing additional infrageneric categories, but this is pointless outside a broader study of *Matelea*.

TAXONOMIC TREATMENT

Matelea *subgenus* Dictyanthus

Matelea subgenus *Dictyanthus* (Decaisne *in* de Candolle) Woodson, Ann. Missouri Bot. Gard. 28: 236-237. 1941.

Dictyanthus Decaisne *in* de Candolle, Prodr. 8: 605. 1844. Type species: *Dictyanthus pavonii* Decaisne *in* de Candolle.

Tympananthe Hasskarl, Flora 47: 258-259. 1847. Type species: *Tympananthe suberosa* Hasskarl.

Rytidoloma Turczaninow, Bull. Soc. Imp. Naturalistes Moscou 25(2): 319-320. 1852. Type species: *Rytidoloma reticulatum* Turczaninow.

Plants erect, trailing, or twining, herbaceous or woody, with or without a woody or fleshy caudex. Woody parts typically with thick, fissured, corky bark. Indumentum variable and often mixed; trichomes multicellular, uniseriate, simple, straight or uncinate, of three general types: short nonglandular, short glandular, and long nonglandular. Leaves ovate in general outline, apices mostly acuminate to attenuate, bases lobate, with acropetiolar glands; exstipulate but with an interpetiolar finge of long trichomes and glands. Inflorescence extra-axillary, a condensed, simple, helicoid cyme or reduced to a single flower with or without an apparent peduncle. Calyx 5-lobed nearly to the base, with one or two glands below each sinus within. Corolla deeply to shallowly campanulate; tube convoluted, with raised

parts opposite corona lobes and sacs formed between them. Corona digitately 5-lobed, lobes connate below or not, adnate to gynostegium and adnate for their entire length to corolla. Gynostegium stipitate, apex pentagonal and concave to apiculate, terminal anther appendages covering margin of apex. Corpusculum sagittate; translators winged, hardly distinct from pollen sacs; pollen sacs flattened, excavated and hyaline along upper margin, obliquely obovate. Follicles fusiform, with few to numerous, thick to thin, straight to arcuate projections. Seeds obovate, flattened, with a raised, smooth or radially grooved, entire or toothed margin, surface otherwise verrucate to rugose, light to dark brown; with a white apical coma. Includes species number 1-10.

Matelea *subgenus unassigned*

For a discussion of the status of these species, consult the section on Relationships. Includes species number 11-13. As a group, these species differ from subgenus *Dictyanthus* as follows.

Plants always twining. Inflorescence simple or more often compound. Corolla urceolate or shallowly campanulate; tube convoluted or not. Corona lobes partially or entirely free from corolla. Gynostegium apex slightly or not at all convex, terminal anther appendages covering from nearly half to the entire apex. Pollen sacs tending to be smaller, broader, and more angular than those of subgenus *Dictyanthus*.

Notes on characters used in Taxonomic Treatment

For more detailed discussions, consult the appropriate sections under Morphology and anatomy. The most critical points are listed below.

(1) The description of the indumentum has been simplified and, to a certain extent, generalized by the convention of referring to all trichomes as either short, glandular, or long and modifying these terms as appropriate. These trichomes are all uniseriate and multicellular and can have straight or uncinate tips. Short trichomes are less than 0.1 mm long, typically about 0.05 mm. Short trichomes on the inner surface of the corolla, when present, are somewhat different in form and have a glassy appearance when dried. Glandular trichomes are the same length to slightly shorter than the short trichomes, with which they are almost always mixed, and have a short stalk, an inflated middle, and a short apiculum. The glandular trichomes are probably not actually secretory, but the inflated part typically collapses on drying, giving these the appearance of normal capitate glandular trichomes. Long trichomes are more than 0.1 mm long, typically much more. The maximum length of long trichomes is given only for the stem; they tend to be somewhat shorter on other structures. When only long trichomes are present on a structure, as is often the case with the leaf blade, they often occur in two discrete lengths, giving much the same appearance as mixed long and short trichomes.

(2) The terminology used for describing the surfaces of the leaves and seeds is according to Stearn (1966).

(3) The leaves are described essentially according to Hickey (1973). The same terminology is employed to described the shape of the bracts, calyx lobes, and corolla lobe apices. The leaf length has been considered to be the length of the midrib. In all cases the leaves are described on the basis of the largest leaf of each specimen examined. The largest leaves, especially on specimens of the erect species, tend

to be near the middle of the stems; the lower leaves tend to be broader and the upper leaves tend to be narrower. Even using this method, the leaves are markedly variable in size and shape.

(4) The inflorescence and floral characters are described only on the basis of examples in anthesis. The bracts are described on the basis of the largest bract of each inflorescence. The first bract (opposite the first flower) tends to be the largest and the subsequent bracts somewhat smaller.

(5) For descriptive purposes, I have considered the corolla lobes to be distinct from the limb. The corolla, then, is composed of the tube, the limb, and the lobes. The descriptions of flower colors have been much simplified. In general, only the basic color pattern of the corolla has been described. This color pattern applies only to the inner surface of the corolla and considerable care should be exercised in attempting to discern the pattern by examining the outside of pressed flowers.

(6) Measurements of pollinia are taken in lateral view, that is, the depth or thickness is ignored, and in the normal orientation they assume when removed. The length of the pollen sac is taken from the point of attachment of the corpusculum to the tip, including, therefore, the translator arms or caudicles. This has been done because in most species of Gonolobeae there is no sharp demarcation of the translator arms from the pollen sacs.

Artificial key to species

1. Corolla tube with parallel vertical lines, these only occasionally with a few cross-connections (sometimes difficult to see in the small urceolate corolla of *M. sepicola*)
    2. Corolla lobes less than 8 mm long; corona lobes less than 4 mm long, not basally connate
        3. Corolla deeply campanulate or tubular, with dense short trichomes on limb and lobes within, corolla tube much exceeding corona lobes . . . . 2. *M. tuberosa*
        3. Corolla urceolate, entirely glabrous within, corona lobes equalling corolla tube . . . . 12. *M. sepicola*
    2. Corolla lobes more than 8 mm long; corona lobes more than 4 mm long, basally connate
        4. Corolla base-sinus length more than 12.5 mm, with a narrow band of short trichomes around corona lobes within; long trichomes of peduncles and pedicels mostly uncinate; twining woody vines without thickened caudices 4. *M. pavonii*
        4. Corolla base-sinus length less than 12.5 mm, glabrous around corona lobes within; long trichomes of peduncles and pedicels straight; erect or weakly twining herbaceous vines with thickened caudices . . . . . . 5. *M. macvaughiana*
1. Corolla tube with circular lines, distinct reticulations, or without a distinct pattern
    5. Corolla entirely glabrous within; corona lobes basally connate and forming a distinct cup; inflorescence bracts more than 1.5 mm long, elliptic in general shape . . . 3. *M. hamata*

5. Corolla with dense short trichomes within, at least on limb; corona lobes basally connate or not but not forming a distinct cup; inflorescence bracts less than 1.5 mm wide, linear or ovate in general shape

  6. Corona lobes spathulate, with prominent, glistening, purplish-black, deeply rugose tips; long trichomes of internodes uncinate; plants of Yucatán Peninsula

    7. Corolla lobes 7-12 mm long, length to width (sinus-sinus) ratio greater than 0.80, margins revolute, limb and lobes plane or slightly reflexed; corolla densely grayish-purple-reticulated . . . . . . 10. *M. yucatanensis*

    7. Corolla lobes 5-9 mm long, length to width (sinus-sinus) ratio less than 0.80, margins not revolute, limb and lobes ascending; corolla yellowish-green when fresh, sometimes drying darker and somewhat reticulated 9. *M. aenea*

  6. Corona lobes of various shapes but never modified as above; long trichomes of internodes rarely uncinate; plants not of the Yucatán Peninsula

    8. Corolla campanulate, base to sinus length 7 mm or greater, margins strongly revolute; corona lobes more than 4.5 mm long, linear to linear-spathulate, adnate to corolla; inflorescence a simple cyme

      9. Corolla tube with circular lines . . . 6. *M. standleyana*

      9. Corolla tube with a reticulate pattern or without a distinct pattern

10. Gynostegium apex apiculate; corona lobes 8 mm long or longer; twining vines without thickened caudices; plants from southeast of the Isthmus of Tehuantepec . . . . 7. _M_. _ceratopetala_

10. Gynostegium apex shallowly concave; corona lobes 8 mm long or shorter; erect or weakly twining vines, mostly from thickened caudices; plants from northwest of the Isthmus of Tehuantepec . . . . 8. _M_. _dictyantha_

8. Corolla shallowly campanulate to nearly rotate, base to sinus length 11 mm or less, margins slightly or not at all revolute; corona lobes less than 4.5 mm long, shape various but not linear or linear-spathulate, adnate to corolla or not; inflorescence a simple or compound cyme

11. Peduncles 4 mm long or shorter; pedicels 5 mm long or shorter; inflorescence a simple cyme; leaf blades 34 mm long or shorter; erect or weakly twining vines with thickened caudices . . . . 1. _M_. _hemsleyana_

11. Peduncles 3 mm long or longer; pedicels 5 mm long or longer; inflorescence a simple or more often a compound cyme; leaf blades 31 mm long or longer; twining vines mostly without thickened caudices

12. Corona lobes triangular in outline, not inflated, adherent to corolla to tip; corolla distinctly convoluted; plants of Sinaloa and Sonora . . . . . 11. _M_. _altatensis_

12. Corona lobes ovate in outline, inflated, free from corolla above; corolla only very slightly convoluted; plants from Jalisco and Veracruz to Nicaragua 13. _M_. _aspera_

Species treatments (subgenus Dictyanthus)

1. Matelea hemsleyana Woodson, Ann. Missouri Bot. Gard. 28: 237. 1941, based on Dictyanthus parviflorus Hemsley.

Dictyanthus parviflorus Hemsley, Biol. Centr. Am. Bot. 2: 329. 1882, non Matelea parviflora (Torrey) Woodson. Lectotype: Ghiesbreght 663 (K? not seen, lectotype; GH! MO! NY! isolectotypes). Syntype: Ghiesbreght s.n. (K! syntype; GH! L! P! probable isosyntypes).

Dictyanthus prostratus Brandegee, Univ. Calif. Publ. Bot. 7: 329. 1920, non Matelea prostrata (Willdenow) Woodson. Type: Purpus 8411 p.p.[1] (UC! holotype; GH! MO! NY! US, 2 specimens! VT! isotypes).

Matelea diffusa Woodson, Ann. Missouri Bot. Gard. 28: 236. 1941, based on Dictyanthus prostratus Brandegee.

Plants erect to trailing or rarely weakly twining. Stems 20-60 (-90) cm long, with a woody caudex to 4 cm long and 2 cm wide, this with thin to thick corky bark, also often with short woody stems above caudex, these with or without corky bark, otherwise herbaceous and lacking bark, with dense short and glandular trichomes and sparse to dense, mostly straight long trichomes to 3 mm long. Leaf blade ovate to very-wide-ovate, 13-34 mm long, 13-36 mm wide, with mostly uncinate long trichomes and also often with scattered glandular trichomes below,

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[1] The use of p.p. (pro parte) indicates cases where different taxa are represented on different sheets with the same collection number or where sheets with the same collection number are given different collection data, i.e., those cases where normal collection practices would indicate different collection numbers. Cases of more than one taxon on one sheet, i.e., mixed collections, are mentioned parenthetically where judged significant.

surface smooth, smaller veins sharply raised below, apex acuminate to attenuate or rarely obtuse, base lobate, lobes overlapping to divergent, with 2-6 (-8) acropetiolar glands, margin often somewhat thickened and revolute; petiole 7-18 (-26) mm long, with dense short and glandular trichomes and sparse to dense, mostly uncinate long trichomes. Inflorescence a simple cyme; peduncle 1-4 mm long, with dense short and glandular trichomes and sparse to dense, straight or uncinate long trichomes; bracts linear or lorate to lanceolate, 2-4 mm long, with indumentum of leaf or nearly glabrous; pedicel 3-5 mm long, with indumentum of peduncle. Calyx lobes narrow-ovate or occasionally lanceolate, 4-6 mm long, 1.5-2.5 mm wide, apex acute to attenuate, with one gland below each sinus, abaxial surface with scattered glandular trichomes and scattered to dense, straight or uncinate long trichomes, adaxial surface glabrous. Corolla shallowly campanulate, base to sinus length 3-6 mm, limb not distinct, margin slightly revolute; lobes (3-) 4-6 (-7) mm long, apex acute or occasionally rounded, plane or slightly reflexed at tip, margin slightly revolute; glabrous within except with dense short trichomes on limb and lobes and these sometimes extending down raised ridges within tube, indumentum on outside of straight long trichomes or sometimes limb and lobes nearly glabrous; tube convoluted, with raised parts opposite corona lobes, forming shallow pockets between them, with corona lobes in distinct pockets in bases of raised parts; moderately to densely brownish-purple-reticulated, becoming pale purple on and around corona lobes. Corona lobes 1.0-1.5 mm long, basically short-spathulate with an acute apex, main axis adnate to corolla and adaxially adnate to gynostegium, upper surface with a narrow ridge which extends as a short spur to edge of gynostegium. Gynostegium

1.0-1.5 mm high and 1.5-2.0 mm wide at apex, short-stipitate, apex convex and slightly bilobed, terminal anther appendages covering margin of apex. Corpusculum 0.18-0.22 mm long, 0.08-0.10 mm wide, pollen sacs 0.58-0.91 mm long, 0.26-0.34 mm wide. Follicles fusiform, 48-70 mm long, 10-18 mm wide, green with white markings, glabrous or with sparse short and glandular trichomes, with 28-54 projections, these to 2 mm long, arcuate and somewhat reflexed proximally, straight and leaning forward distally. Seeds obovate, ca 4 mm long, ca 3 mm wide, with a raised margin, this irregularly toothed distally, inside this margin slightly convex on one side and slightly concave on opposite side, both sides verrucate, concave side with a narrow ridge from apex to near center, apparently light brown; coma ca 25 mm long. Figure 11.

DISTRIBUTION AND ECOLOGY. Found in Michoacán, state of México, Morelos, Veracruz, Chiapas, Guatemala, and El Salvador. Figure 12. The gap in the range at the Isthmus of Tehuantepec is as expected on the basis of elevation, but the absence of collections from Puebla and northern Oaxaca is more difficult to explain. Although parts of this region are too arid and parts are on limestone or dolomite, substrates not yet known for this species, there should be suitable habitats. Perhaps additional collecting in this area will show a more continuous distribution. Collected at elevations of from somewhat below 800 m to nearly 2600 m, but mostly 1000-1500 m. From the meager data on edaphic conditions, Matelea hemsleyana can grow at least on volcanic cinder and rocky clay soils. Found growing on slopes and hills, mostly in grasslands, but sometimes in open pine-oak forests. Flowering mostly June-September, but flowering specimens also collected once each in April and November. Specimens with mature-sized fruits collected

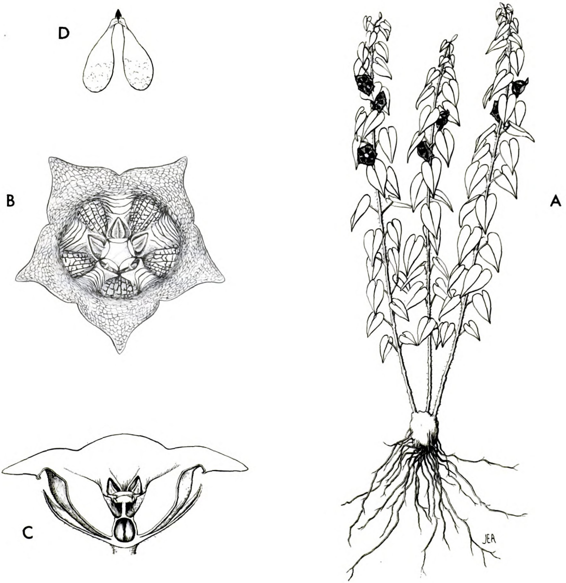

Figure 11. Matelea hemsleyana (drawn from Stevens C-162, a cultivated specimen of Stevens 1399).

A. habit, x 0.6; B-C. flowers, x 4.6; D. pollinium, x 35.

August-December.

The only grazing insect damage observed was a few chewed leaves on Dressler & Jones 252. Hemsley 4471 and some specimens of Pringle 13112 have a number of their flower buds modified into galls, these probably being caused by parasitic dipterans.

COMMON NAMES AND LOCAL USES. Steyermark 32972 gives the local name chinuna and Steyermark 50732 gives the local name pegapega; both these collections are from Guatemala. Calderón 1017, from El Salvador, gives the local name yulpate. No local uses were found.

DISCUSSION. In combining what Woodson considered to be two species, I was left with two names which were equivalent with respect to priority. My choice is simply arbitrary, but does agree with the priority of the original epithets under Dictyanthus. The lectotypification of Matelea hemsleyana, however, was more of a problem. The part of the protologue referring to specimens reads, "Mexico, Cuernavaca and Chiapas (Ghiesbreght, 663.) Hb. Kew." At first glance, it would seem that the type, and thus the holotype, is designated as Ghiesbreght 663 at K, but by indicating both Cuernavaca and Chiapas, he was implying that he had seen specimens from both localities. Further, I have seen Ghiesbreght specimens from both localities. Specimens of Ghiesbreght 663 (GH, MO, NY) bear a printed label with, "Chiapas, etc.: coll. Dr. Ghiesbreght ann. 1864-70." and the specimen at GH bears an additional hand-written label with more detailed collection data, including a locality apparently in Chiapas. The other Ghiesbreght specimens of this species (GH, K, L, P) are unnumbered and bear the printed label, "MEXIQUE, Province d`Oaxaca. M. Ghiesbreght, 1842." The K specimen of Ghiesbreght s.n. has, as is often the case, the, "province d`Oaxaca" crossed out and

replaced with, "Cuernavaca," apparently in Decaisne's hand. I can only conclude that specimens of both collections were seen by Hemsley and that he implicitly cited both in the protologue, thus requiring lectotypification. Since the rest of the protologue gives no details which would indicate Hemsley's intent, I believe Ghiesbreght 663 is less ambiguous as a lectotype than Ghiesbreght s.n. Unfortunately, I have seen only the latter represented by a specimen at K; whether the former exists there or not, I still believe it is a preferable lectotype. Additionally, though it does not affect the choice of a lectotype, there are two elements within the species which may eventually warrant recognition, as discussed below, and the Ghiesbreght collections represent both elements. It is therefore especially important to the stability of the nomenclature that the type of this name be fixed.

There is also a potential source of confusion as to the type of Dictyanthus prostratus. There are at least two collections of this species bearing the type number, Purpus 8411. One is from Acaxónica (Aug 1919) and the other is from Barranca de Panoaya (Sep 1920). One additional specimen with this number bears the date 1920 and no locality data. This problem apparently results from the fact that the Purpus collections were not numbered chronologically as collected, but rather much later (Sousa S., 1969, p. 15). The protologue, however, specifically gives the type locality as Acasonica [Acaxónica] and the accession number at UC which corresponds to that specimen. The Barranca de Panoaya collection was not mentioned in the protologue and therefore has no status as a type.

The plants of this species collected from the part of the range centered around the state of Morelos differ somewhat from the plants in

the rest of the range. Woodson, according to his annotations, considered the Morelos plants to be *Matelea hemsleyana* and the others *M. diffusa*. Standley and Williams (1969) also considered the plants from southern Mexico to El Salvador to be *Matelea diffusa*, but perhaps without seriously considering the plants from Morelos. Standley (1924) considered the two species to be synonymous. The plants from around Morelos tend to be shorter and more erect, to have thicker caudices, larger, more distinctly veined leaves, larger flowers (to nearly twice as large), and proportionately longer corona lobes. In describing *Dictyanthus prostratus* (=*Matelea diffusa*), Brandegee considered it to be different from *D. parviflorus* (=*M. hemsleyana*) in having, "five minute scales attached to the middle of the gynostegium representing an inner corona." I have found no such character. The "scales" to which he referred were most likely the remains of the attachments of the coona lobes to the gynostegium, which are typically torn free when the flower is flattened. Despite the differences described above, I have found no character or set of characters which will faithfully differentiate the two elements. It may well be that further collection of adequately preserved material will demonstrate that some level of taxonomic recognition is preferable, but on the basis of the currently available material, I do not believe that it is warranted.

SPECIMENS EXAMINED. *MEXICO*. MICHOACAN: Morelia, Cerro Azúl, 2300 m, Nov 1911 (fl), *Arsène s.n.* (G); ca 20 mi S of Uruapan on Hwy 37, 3300 ft, 7 Sep, year not given (fl), *Oliver et al. 865* (MO). MEXICO: Dist. Temascaltepec, Cajones, 2580 m, 15 Sep 1932 (fl), *Hinton 1690* (G, K, MO, NY, US); Dist. Temascaltepec, Vigas, 1080 m, 15 July 1933 (sterile), *Hinton 4328* (GH, MICH, NY, UC, US); Dist. Temascaltepec,

Ixtapan, 1000 m, 2 Aug 1933 (fl), *Hinton 4471* (G, MO, NY, US); Dist. Temascaltepec, Carboneras, 20 Aug 1935 (fl), *Hinton 8008* (GH, MO, NY, 2 specimens, PH, US, WTU); 5 km al SW de Temascaltepec, sobre la carretera a Tejupilco, 1900 m, 4 Sep 1965 (fl), *Rzedowski 20823* (ENCB). MORELOS: Cuernavaca [written above "Province d'Oaxaca" of printed label of K specimen], without date (fl), *Ghiesbreght s.n.*, syntype of *Dictyanthus parviflorus* (GH, K, L, P; not necessarily all of the same collection); Cuernavaca, hillsides, 5000 ft, 28 July 1896 (apparently fl) and 18 Sep 1896 (apparently fl & fr), *Pringle 6376* (BKL, CAS, ENCB, F, G, 3 specimens, GH, ISC, K, MASS, MEXU, MINN, MO, MSC, ND, NY, P, PH, UC, US, 2 specimens, VT); plains near Cuernavaca, 5000 ft, 10 Sep 1903 (fl & fr), *Pringle 11627* (F, L); hillsides near Cuernavaca, 5000 ft, 20 July 1904 (fl), *Pringle 13112* (ARIZ, CAS, F, GH, L, MICH, MO, MSC, PH, SMU, US, VT); Cuernavaca, 14 Aug 1906 (fl), *Pringle s.n.* (VT). VERACRUZ: region of San Andrés Tuxtla, Cerro Mono Blanco, NW of Catemaco, 2 Sep 1953 (fl), *Dressler & Jones 252* (MICH, MO, NY, UC, US); Acanoxica or Acasonica [Acaxónica], Aug 1919 (fl), *Purpus 8411 p.p.*, type of *Dictyanthus prostratus* (GH, MO, NY, UC, US, 2 specimens, VT); Barranca de Panoaya, Sep 1920 (fl), *Purpus 8411 p.p.* (ARIZ, DS); without precise locality, 1920 (fl), *Purpus 8411 p.p.* (UC); Cerro de las Animas, near Playa Azúl on Lago de Catemaco, 8 Aug 1971 (sterile), *Stevens 1399* (MSC). CHIAPAS: Mpio. of Tenejapa, paraje of Mahben Chauk, slopes along Ala Shashib River below Habenal, 3300 ft, 15 July 1964 (fl), *Breedlove 6475* (DS); Mpio. of Tenejapa, paraje of Mahben Chauk, slopes near Habenal, 3500 ft, 26 Nov 1964 (fr), *Breedlove 7639* (DS, F); Mpio. of Ixtapa, 26 mi S of Bochil along rd to Tuxtla Gutiérrez, 3800 ft, 7 Aug 1967 (fl), *Clarke 107* (DS); "les montagnes pres de

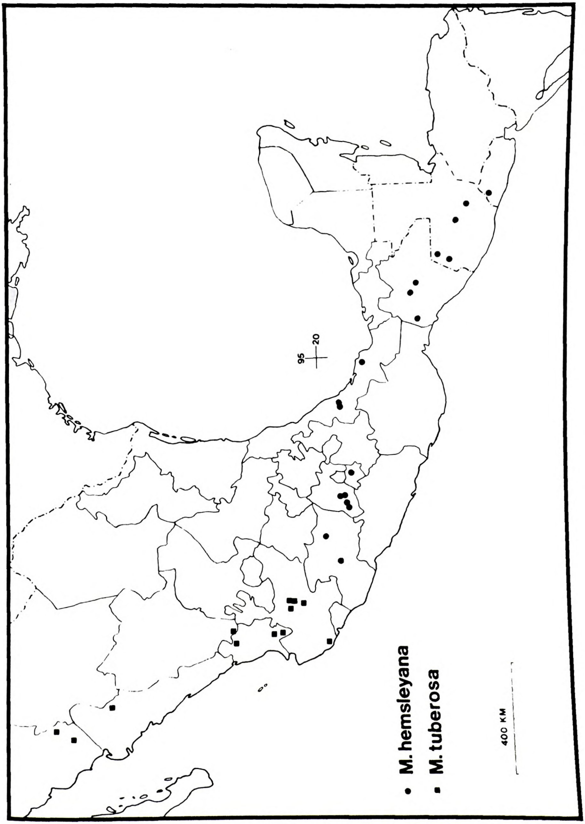

Figure 12. Distribution of Matelea hemsleyana and M. tuberosa.

village indien de Cancunc" [?Cancuc, Mpio. Chilon], June, year not given (fl), *Ghiesbreght 663*, lectotype of *Dictyanthus parviflorus* (GH, MO, NY); rocky mountain slopes, Monserrate, June 1925 (fl), *Purpus 206* (US); Hacienda Monserrate, Sep 1923 (fl), *Purpus 9075* (F, GH, MEXU, MO, NY, US); near Hacienda Monserrate, Sep 1923 (fl), *Purpus 9077* (UC); without precise locality, Sep 1923 (fl), *Purpus s.n.* (UC); mountains E of Monserrate, June, year not given (fl), *Purpus 10631* (UC, US); Mpio. of Tenejapa, paraje of Oshewits, slopes, 3500 ft, 10 Apr 1968 (fl), *Ton 4033* (DS). STATE UNKNOWN: without date (fl), *Sessé, Mociño, et al. 837* (F, fragment of MA specimen, MA, not seen, photo from F neg. 41468 of MA specimen at MSC). *GUATEMALA*. BAJA VERAPAZ: 12 km SW of Granados, slopes above Río Montagua, 2 Sep 1970 (fl), *Harmon & Dwyer 4208* (MO). JALAPA: Montaña Durazno, 2 mi E of San Pedro Piñula, open slopes of cuesta, 1400-1900 m, 10 Dec 1939 (fr), *Steyermark 32972* (F). HUEHUETENANGO: slopes between San Ildefonso Ixtahuacán and Cuilco, 1350-1600 m, 16 Aug 1942 (fl), *Steyermark 50732* (F, MO); between Nentón and Las Palmas, via Yalisjao, Rincón Chiquite, Chiaquial, Guaxacaná, in Sierra de los Cuchumatanes, 800-1200 m, 30 Aug 1942 (fl & fr), *Steyermark 51624* (F, US). *EL SALVADOR*. SANTA ANA: near Chalchuapa, 1922 (fl), *Calderón 1017* (US).

2. *Matelea tuberosa* (Robinson) Woodson, Ann. Missouri Bot. Gard. 28: 237. 1941.

Dictyanthus tuberosus Robinson, Daedalus 27: 180-181. 1891/1892 [1893]. Lectotype: *Pringle 3568* (GH! lectotype; F! VT! isolectotypes). Syntype: *Palmer 251* (GH! syntype; ENCB! G! K! MO! ND! NY, 3 specimens! P! PH! US! isosyntypes).

Plants erect to trailing or sometimes weakly twining. Stems 10-70 (-100) cm long, with a woody caudex to 5 cm long and 3 cm wide, this with thick corky bark, otherwise typically herbaceous and lacking bark (rarely subshrubs with erect, branched woody stems), with dense short trichomes, very sparse glandular trichomes, and sparse to dense, mostly straight long trichomes to 2 mm long. Leaf blade ovate to very-wide-ovate, 17-45 mm long, 17-40 mm wide, with mostly uncinate long trichomes, surface smooth, smaller veins sharply raised below, apex acuminate to attenuate, base lobate, lobes mostly convergent to descending, with 3-6 (-9) acropetiolar glands, margin often somewhat thickened and revolute; petiole 7-31 mm long, with dense short trichomes, very sparse glandular trichomes, and sparse to dense, mostly uncinate long trichomes. Inflorescence a simple cyme; peduncle 0.5-9.0 mm long, with dense short trichomes, very sparse glandular trichomes, and sparse to dense, straight or uncinate long trichomes; bracts linear or lorate to lanceolate, 2-8 mm long, with mostly uncinate long trichomes; pedicel 4-5 mm long, with indumentum of peduncle. Calyx lobes lanceolate to narrow-ovate or elliptic, 5-9 mm long, 1.5-3.5 mm wide, apex acute to attenuate, with one gland below each sinus, abaxial surface with sparse to dense, straight or uncinate long trichomes, adaxial surface glabrous. Corolla deeply campanulate, base to sinus length 6-10 mm, limb revolute; lobes 2.5-6.0 mm long, apex acute, slightly to strongly reflexed, margin revolute; glabrous within except with dense short trichomes on limb and lobes, indumentum outside of short trichomes on tube and straight or uncinate long trichomes on limb and lobes, occasionally a few long trichomes scattered along tube and occasionally distal third of lobes glabrous; with a pair of ridges within tube opposite each

corona lobe, ridges of adjacent pairs almost coming together at base and forming pockets at base of corolla, with corona lobes in distinct pockets in bases of furrows between the paired ridges; within tube with fine grayish-brown vertical lines, limb densely grayish-brown-reticulated. Corona lobes ca 2 mm long (but borne distinctly above base of corolla), shape elaborate but basically sagittate in outline, main axis adnate to corolla and adnate to gynostegium by a thin wall. Gynostegium ca 2 mm high and ca 2 mm wide at apex, stipitate, apex broadly and shallowly concave, with corpuscula as high points, and slightly convex and bilobed in center, terminal anther appendages covering margin of apex. Corpusculum 0.14-0.22 mm long, 0.08-0.13 mm wide, pollen sacs 0.63-0.86 mm long, 0.29-0.37 mm wide. Follicles fusiform, 55-65 mm long, 11-19 mm wide, mottled light and dark green, with scattered short and long trichomes, with 50-110 arcuate projections to 2 mm long. Seeds obovate, nearly circular, 5.5-6.0 mm long, 4.5-5.0 mm wide, with a raised, radially grooved margin, this entire to shallowly toothed distally, inside this margin slightly convex and verrucate on both sides, one side with a narrow ridge from apex to near center, light brown; coma ca 25 mm long. Figure 13.

DISTRIBUTION AND ECOLOGY. Collected from southern Sonora to southern Jalisco at elevations of 500-1600 m. Figure 12. Growing in open oak and pine-oak forests and adjacent grasslands, usually in shallow, red clay soil. Flowering specimens have been collected from late July to early October and the one specimen with mature seeds was collected in March.

Three collections, Pennell 19544, Rose 2009, and Stevens 1458, have specimens with from a few to most of the flower buds developing into

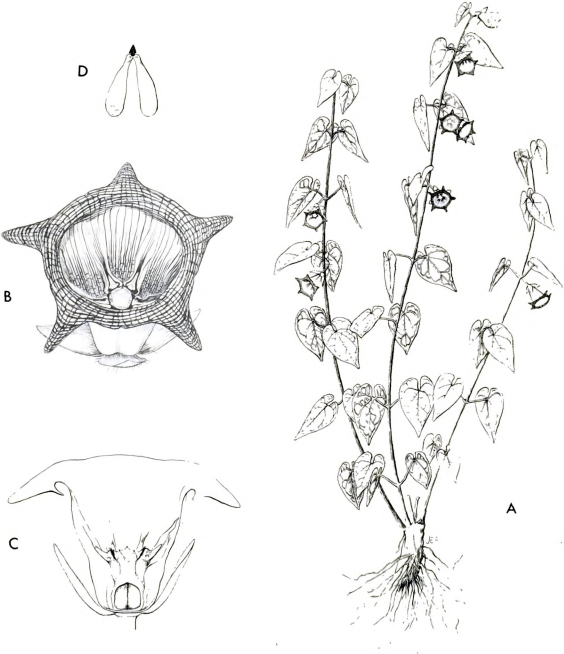

Figure 13. Matelea tuberosa (drawn from Stevens C-163 and C-164, cultivated specimens of Stevens 1458 and 1473, respectively and Stevens 1473).

A. habit, x 0.6; B-C. flowers, x 4.6; D. pollinium, x 24.

galls. On Stevens 1458 these galls contain larvae and nearly mature pupae of an undetermined dipteran. No other examples of insect damage have been found. One undetermined bee was collected visiting the flowers of Stevens 1458, but no pollinia were found attached. Although this insect is of the appropriate size to be a pollinator, the flowers do not appear to produce anything of food value, a common requirement of bee pollination. The actual pollinating insects of this species will only be determined by careful field study.

COMMON NAMES AND LOCAL USES. The label of one collection from Sinaloa, Gentry 6554, indicates the use of the name bonete. No other names or uses have been found.

DISCUSSION. In describing Dictyanthus tuberosus, Robinson discussed both the Palmer and Pringle specimens in the protologue, but it is clear from both the format and from the purpose of the publication, that of describing new species based on Pringle collections, that he intended the Pringle specimen to be the type. The lectotypification is based on this clear but unspecified intent. The name Dictyanthus stapeliiflorus was misapplied to specimens of Palmer 251 by Gray (in Watson, 1887) and Woodson perpetuated the error in his annotations.

The nearly tubular corolla of this species readily distinguishes it from the other species of this subgenus and as far as I am aware is unique in the genus Matelea. It may well be an adaptation to a distinctly different type of pollinator.

SPECIMENS EXAMINED. MEXICO. SONORA: ridge S of Arroyo Gochico and E of San Bernardo, 750-900 m, 5-9 Aug 1935 (fl), Pennell 19544 (PH, US); Sierra de Alamos, 15 Mar 1910 (fr), Rose 12863 (US). SINALOA: Quebrado de Mansana, Sierra Surotato, ca 4000-4500 ft, 10-14 Sep 1941

(fl), *Gentry 6554* (ARIZ, DS, GH, MICH, MO, NY, PH). DURANGO: Sierra Madre [between Santa Teresa, Nayarit, and Huazamota in extreme SW Durango, according to Goldman, 1951, p. 144], 13 Aug 1897 (fl), *Rose 3468* (US), *3473* (US). NAYARIT: Km 870, 22 mi SE of Tepic on Hwy 15, 1150 m, 21 Sep 1966 (fl), *Anderson & Laskowski 3692* (MICH), 26 Aug 1957 (fl), *McVaugh 16393* (MICH), *16393A* (MICH); foothills of Sierra Madre, between San Blasito and Aguacate, 5 Aug 1897 (fl), *Rose 2009* (GH, MO, NY, US); ca 10 mi SE of Ahuacatlán along rd to Barranca del Oro, 26 Aug 1971 (fl), *Stevens 1458* (MSC); ca 18 mi SE of Tepic along Hwy 15, 26 Aug 1971 (fl), *Stevens 1473* (MSC). JALISCO: 5 mi S of Guadalajara, 5000 ft, 12 Aug 1947 (fl), *Barkley et al. 7499* (F, 2 specimens, TEX); without precise locality and date (fl), *Diguet s.n.* (P, 2 specimens); rocky mountainsides near El Molino (ca 25 mi SW of Guadalajara), overlooking Acatlán and the basin of Laguna de Atotonilco, 1650 m, 10 Oct 1952 (fr), *McVaugh 13278* (MICH); 3 mi above (S of) La Huerta, rd to Barra de Navidad, 500-550 m, 3 Oct 1960 (fl), *McVaugh 19834* (MICH); Guadalajara, in ravines, [15 July-3 Aug, according to McVaugh, 1956, p. 215] 1886 (fl), *Palmer 251*, syntype of *Dictyanthus tuberosus* (ENCB, G, GH, K, MO, ND, NY, 3 specimens, P, PH, US); slopes of barranca near Guadalajara, 10 Sep 1891 (fl), *Pringle 3568*, lectotype of *Dictyanthus tuberosus* (F, 1 specimen and 1 photo from F neg. 51448 of F specimen, GH, VT); slopes near Guadalajara, 15 Aug 1893 (fl), *Pringle 4482* (BKL, F, G, 3 specimens, GH, ISC, MASS, MEXU, MICH, MO, MSC, ND, NY, P, PH, UC, US, VT); Baños del Padre, Sierra de la Venta, 33 km al W de Guadalajara, 1600 m, 30 July 1967 (fl), *Villarreal de Puga 853* (ENCB); 22 mi SE of Tequila, 17 Aug 1961 (fl), *Waterfall 16368* (MO). STATE UNKNOWN: without date (fl), *Sessé, Mociño, et al. 3584* (MA, not seen, photo from

F neg. 41469 at MSC).

3. Matelea hamata W. D. Stevens, sp. nov. Type: Langlassé 257 (US! holotype; GH! P! isotypes).

Matelea hamata W. D. Stevens; a speciebus ceteris subgeneris Dictyanthi pagina interiore corollae glabra et corona cupulata lobis brevibus (circa 1 mm) corollae adnatis clare distinguenda.

Plants apparently twining vines. Lower stems and basal parts unknown, upper stems with moderately dense short and glandular trichomes and sparse straight long trichomes to 1.5 mm long, these mostly broken off. Leaf blade narrow-ovate to ovate, 74-84 mm long, 49-73 mm wide, with sparse to dense uncinate long trichomes, surface smooth to minutely pusticulate, apex acute to attenuate or obtuse, base lobate, lobes slightly convergent to divergent, with 4-9 acropetiolar glands, margin somewhat thickened and revolute; petiole 38-40 mm long, with moderately dense short and glandular trichomes and sparse, mostly uncinate long trichomes. Inflorescence an elongate but apparently simple, few-flowered cyme; peduncle 20-53 mm long, with indumentum of stem; bracts narrow-elliptic to elliptic, 7-10 mm long, with indumentum of leaf; pedicel 23-26 mm long, with indumentum of stem. Calyx lobes elliptic, 11-14 mm long, 4.5-6.5 mm wide, apex acute to acuminate, with one gland below each sinus, abaxial surface with moderately dense, straight or uncinate long trichomes, adaxial surface glabrous. Corolla campanulate, base to sinus length 13-15 mm, limb broad, apparently plane; lobes 9-11 mm long, apex obtuse or rounded, orientation unknown, apparently not revolute; glabrous within, indumentum on outside of dense

short trichomes and also moderately dense long trichomes on limb and lobes; tube shallowly convoluted, with a pair of ridges opposite and a shallow pit alternate with each corona lobe; with fine, faint, reticulated lines within tube, limb with fine, distinct circular lines, these becoming reticulated on lobes, these lines said to be green on a yellowish-white background (Langlassé 257). Corona lobes connate and forming a cup ca 2 mm deep, lobe tips subulate and extending ca 1 mm above rim of cup, cup adnate to corolla and lobe tips adnate to corolla between paired ridges, adnate to gynostegium by a thin wall opposite each lobe tip, each wall with a distinct fleshy hump near center of upper margin. Gynostegium ca 3 mm high and ca 3 mm wide at apex, stipitate, apex broadly and shallowly concave with corpuscula as high points, terminal anther appendages apparently covering margin of apex. Corpusculum ca 0.23 mm long, ca 0.18 mm wide, pollen sacs ca 1.49 mm long, ca 0.42 mm wide. Fruit and seeds unknown. Figures 14 and 15.

DISTRIBUTION AND ECOLOGY. Known only from the type collection from lowland southwestern Guerrero. Figure 16. According to the label, growing in clayey soil. Flowering specimen collected on 29 July. Some leaves on one specimen have been chewed or otherwise damaged.

COMMON NAMES AND LOCAL USES. None known.

DISCUSSION. This is the least known species of subgenus Dictyanthus but perhaps the most interesting. In many ways it is intermediate between Matelea hemsleyana and M. tuberosa on one hand and the other seven species of the subgenus on the other. The overall aspect of the plant, the general size and shape of the corolla, the fact that the corona lobes are connate, and the size and shape of the pollinia are essentially comparable to the larger group of species. The corona

Figure 14. Holotype of <u>Matelea</u> <u>hamata</u>.

Matelea hamata W D Stevens, ined
HOLOTYPE
Det. by Warren Douglas Stevens 1974
MICHIGAN STATE UNIVERSITY HERBARIUM

385809

UNITED STATES NATIONAL HERBARIUM.
DEPOSITED IN THE SMITHSONIAN INSTITUTION
E. LANGLASSÉ, HERBORISATIONS AU MEXIQUE
ETATS DE MICHOACAN ET DE GUERRERO

No 257. Dictyanthus stapeliaeflorus Reichenb. ?

Localité : La Union

Altitude : 50 m. Époque : 23.III.98

Obs. : Tige grimpante. Fleurs brun pourpre, rayées de vert
Cal. rugueux

Nom indigène :

Figure 15. Inflorescence of holotype of Matelea hamata.

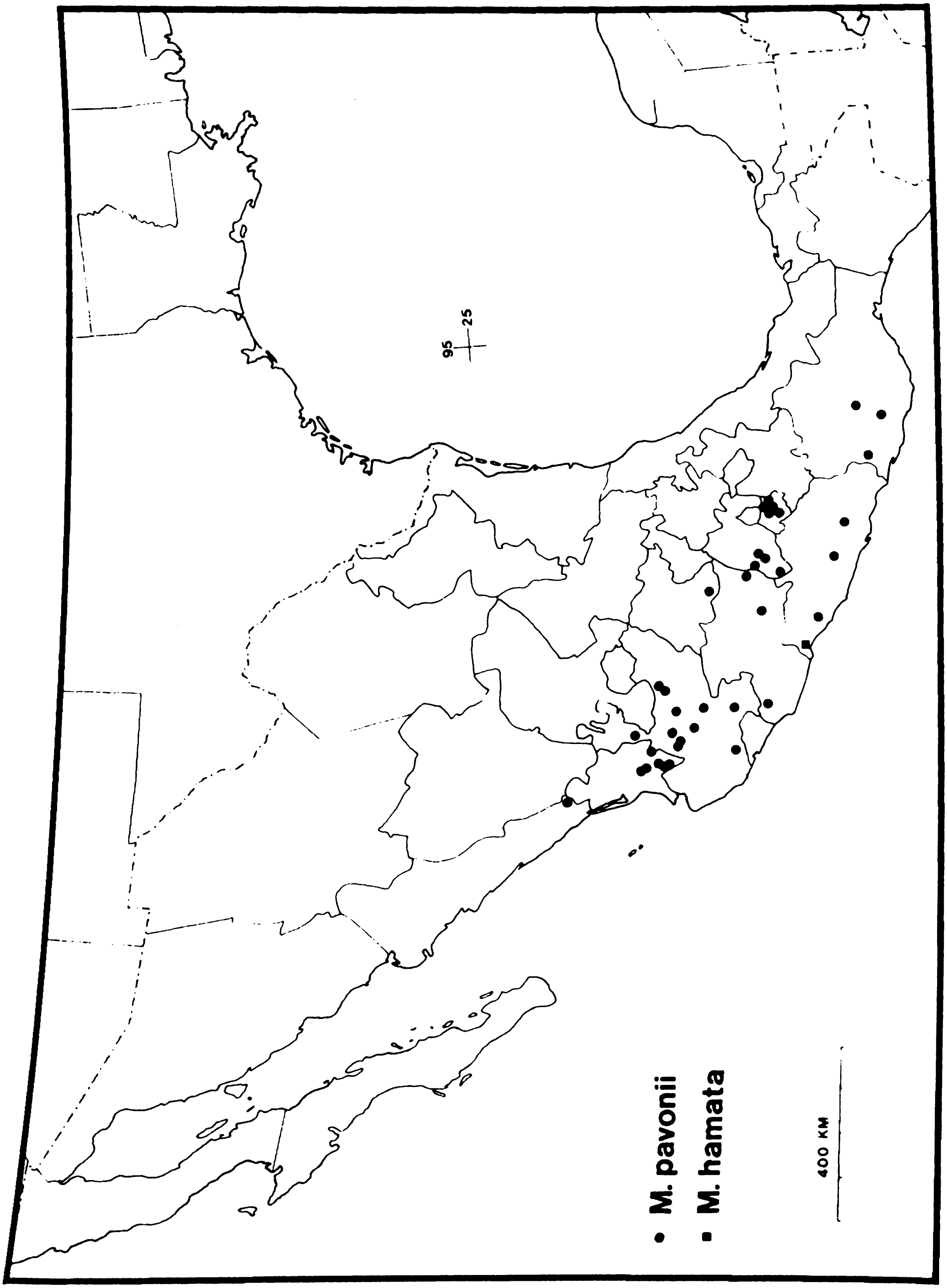

Figure 16. Distribution of Matelea hamata and M. pavonii.

lobes, in this case the tips of the lobes, are more comparable in size, shape, and method of adnation to the corolla to Matelea hemsleyana and M. tuberosa. The extent to which the corona forms a cupulate structure is, however, unique. Also unique are the large, nearly foliaceous bracts, the large elliptic calyx lobes, the broad, apparently plane corolla limb, and the relatively short and blunt corolla lobes.

The type locality of this species, La Unión, Guerrero, can be identified with some certainty because of the work of McVaugh (1951), but has been essentially inaccessible. The coastal lowland near the mouth of the Río Balsas is apparently poorly collected. Although most maps show a road to La Unión, on 2 August 1971, I was able to travel only about half the 25-30 miles between Zihuatenejo and La Unión before being stopped by an unfinished bridge. The area I was able to travel was heavily grazed thorn scrub. Perhaps when the locality becomes accessible, there will be some intact vegetation remaining and this most interesting species can be better known.

The holotype of this species previously had been tentatively determined as Dictyanthus stapeliiflorus. See the discussion of this name under Matelea pavonii.

SPECIMENS EXAMINED. MEXICO. GUERRERO: La Unión, 50 m, 29 July 1898 (fl), Langlassé 257, type of Matelea hamata (GH, P, US).

4. Matelea pavonii (Decaisne in de Candolle) Woodson, Ann. Missouri Bot. Gard. 28: 237. 1941.

Dictyanthus pavonii Decaisne in de Candolle, Prodr. 8: 605. 1844. Type: "Pavón" [Sessé, Mociño, et al. s.n.] (FI, not seen, holotype; P, fragment of holotype!).

Stapelia campanulata Pavón *ex* Decaisne *in* de Candolle, Prodr. 8: 605. 1844. pro syn.

Tympananthe suberosa Hasskarl, Flora 47: 258-259. 1847. Type: unknown.

Dictyanthus campanulatus Reichenbach, Selectis e Seminario Horti Academici Dresdenis 4. 1850 [Linnaea 24: 207. 1851]. nom. superfl. Type: unknown.

[?] *Dictyanthus stapeliiflorus* Reichenbach, *l.c.* Type: unknown.

[?] *Matelea stapeliiflora* (Reichenbach) Woodson, Ann. Missouri Bot. Gard. 28: 237. 1941.

Stapelia campanulata Sessé & Mociño, Pl. Nov. Hisp. 41. 1888. Type: unknown [*Sessé*, *Mociño*, *et al.* *s.n.*, from mountains of Mazatlán, Guerrero].

Plants twining vines. Stems woody below, with thick or occasionally thin corky bark, herbaceous and lacking bark above, with sparse to dense short and glandular trichomes and sparse to dense, straight or uncinate long trichomes to 1.5 mm long, these brittle and often missing from specimens. Leaf blade ovate to wide-ovate or rarely very-wide-ovate, (49-) 60-128 mm long, 29-100 mm wide, indumentum of sparse to dense uncinate long trichomes, surface pusticulate to minutely pusticulate or occasionally nearly smooth, smaller veins occasionally slightly raised below, apex acuminate to attenuate, base lobate or very rarely cordate, lobes mostly descending to widely divergent, with (0-) 1-6 (-11) acropetiolar glands, margin often slightly thickened and revolute; petiole (16-) 22-65 (-81) mm long, with indumentum of stem. Inflorescence a simple cyme; peduncle 9-60 (-90) mm long, with indumentum of stem or occasionally long trichomes absent; bracts lanceolate or occasionally lorate, narrow-oblong, very-narrow-elliptic, narrow-ovate, or ovate, 4-13 mm long, with sparse to dense short and uncinate long trichomes or sometimes nearly glabrous; pedicel (7-) 10-25 (-32) mm long, with indumentum of stem or occasionally long trichomes absent. Calyx lobes lanceolate to narrow-ovate or rarely ovate, 9-18 mm long, 3-6 (-9) mm wide, apex attenuate, with one gland below each sinus, abaxial surface with sparse to moderately dense uncinate long trichomes, adaxial surface glabrous. Corolla campanulate, base to sinus length 13-25 mm, limb revolute; lobes 11-25 mm long, apex rounded or occasionally acute or obtuse, plane to slightly reflexed, margin revolute; glabrous within except with moderately dense short trichomes around corona lobes and on limb and lobes, indumentum on outside of very sparse to dense uncinate long trichomes except lobes distally to entirely glabrous; tube convoluted with raised parts opposite corona lobes and deep sacs formed between them; with purple, brown, or red vertical lines within tube, these lines becoming finer and circular on base of limb and finely to densely reticulated on distal part of limb and on lobes. Corona lobes 7-13 mm long, linear to linear-spathulate in outline, connate at base, adnate to corolla and adnate by a thin wall to gynostegium, this wall continuing as a narrow ridge nearly the length of the lobe and often with one (or rarely two) distinct teeth on upper margin. Gynostegium 3-6 (-7) mm high and 3.0-4.5 mm wide at apex, stipitate, apex apiculate, the apiculum 0.5-1.5 mm long, slightly shorter than to slightly exceeding corpuscula, appearing to be papillate when dried, terminal anther appendages covering margin of apex. Corpusculum 0.31-0.38 mm long, 0.12-0.18 mm wide, pollen sacs 1.45-1.62

mm long, 0.42-0.48 mm wide. Follicles fusiform, ca 70-73 mm long, ca 22 mm wide, color unknown, with dense short trichomes, with 29-44 projections, these thick, straight or occasionally slightly arcuate, to 4 mm long. Seeds unknown. Figure 17.

DISTRIBUTION AND ECOLOGY. Collected from southernmost Sinaloa to Oaxaca. Figure 16. Found mostly at elevations of 900-2000 m, but also once at 2500 m and three times at about 600-750 m. Mostly occurring in mountainous areas where pine-oak forests occupy the more exposed sites and tropical deciduous forests occupy the more protected slopes and barrancas. Found in either vegetation type, especially in disturbed places. Apparently tolerant of a variety of substrates, including limestone, lava, weathered metamorphics, and alluvium. Flowering primarily July-September but flowering specimens also collected twice in June and once each in October and November. Mature fruits unknown, but one immature fruit collected in July and two collections made in August have old dehisced fruits, probably from the previous season.

The following collections have significant chewing insect damage to the leaves: *Burch 5270*, *Feddema 782*, *Ghiesbreght s.n.* (Oaxaca), *Hinton 4590*, *13275*, *14481*, *15061*, *Lyonnet 1033*, *Matuda et al. 26961*, *McVaugh 17340*, *Mexia 589*, *Palmer 113*, *Pringle 2994*, *Rose 1645*, *1699*, *Stevens 1375*, *1435*, *1453*, and *Wilbur & Wilbur 2079*. Large lepidopteran larvae were found to be causing the damage on *Stevens 1435*.

COMMON NAMES AND LOCAL USES. In Nayarit the names *boneta de diablo* (*Collins & Kempton 33*) and *hiedra del monte* (*Mexia 589*) have been noted. The name *atuz* has been used in the state of México (*Hinton 8014* and *8201*) for this species as well as for certain other asclepiads (cf. Stevens, in press). No local uses have been noted.

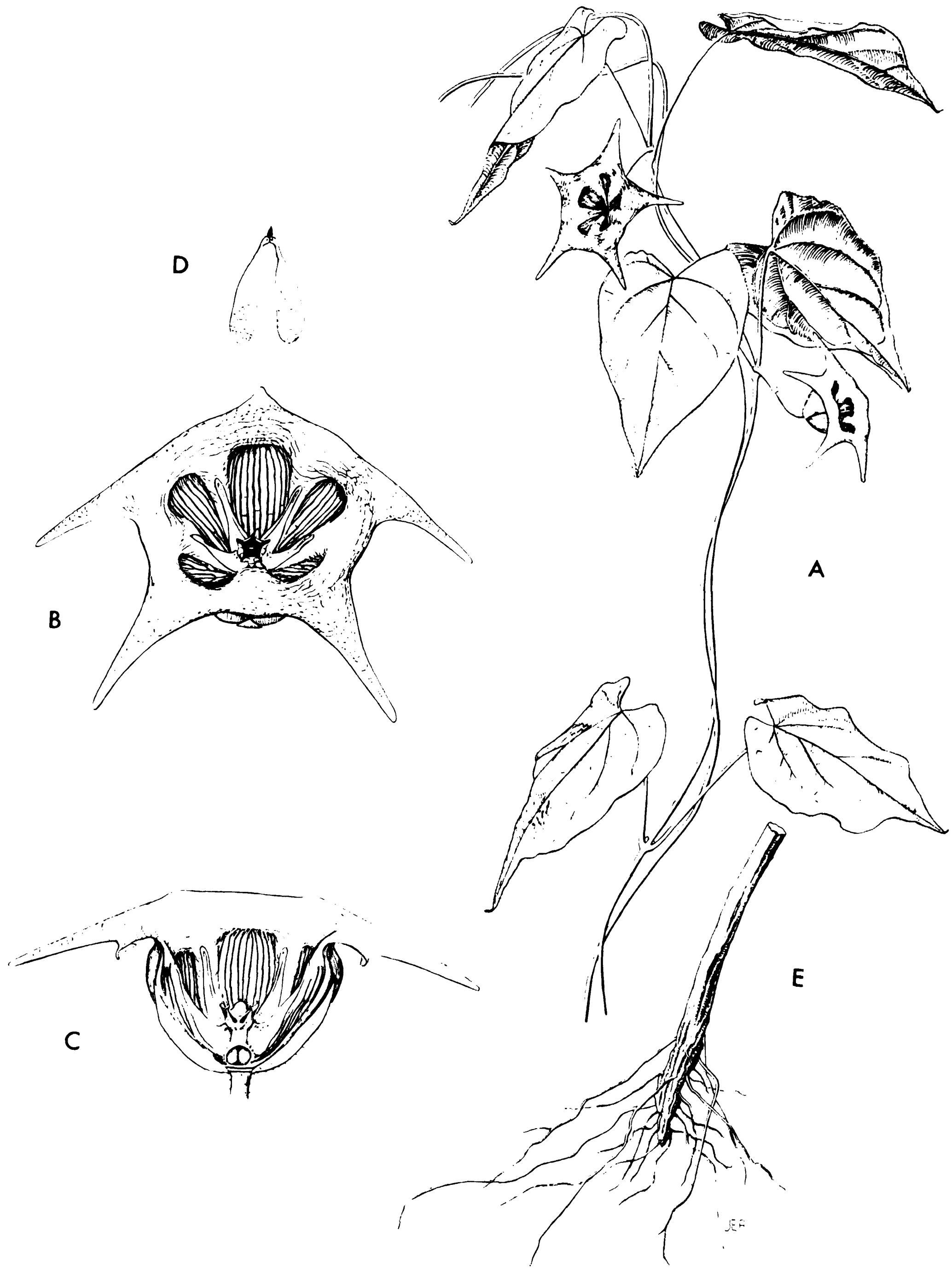

Figure 17. Matelea pavonii (A-D drawn from Stevens C-160, a cultivated specimen of Stevens 1375, and E from Stevens 1427).

A. section of flowering stem, x 0.6; B-C. flowers, x 1.7; D. pollinium, x 12; E. base of stem, x 0.6.

DISCUSSION. Although there can be no question as to the proper name of this, the type species of Dictyanthus, the treatment of the Sessé and Mociño names and specimens has considerably complicated the synonymy. Between 1787 and 1803, Martin Sessé, José Mariano Mociño, and a few collaborators made about 8,000 collections of plants in North and Central America. The history of these collections and the associated manuscripts and paintings is too complicated to be described here, and, in fact, much of the story remains unknown. Although there have been a number of contributions on the subject (see Stafleu, 1967, p. 444, for a partial listing of references), there remains to be a good summary of the available information. Dr. Rogers McVaugh has kindly made available to me his unpublished notes and manuscripts on the subject and my summary pertaining to this species is based largely on those accounts. Also critical were the pertinent Field Museum photographs of the Sessé and Mociño herbarium at Madrid, which were made available to me by Dr. Lorin I. Nevling, Jr. In many respects, Sessé and Mociño must have been astute collectors because six (five of which were undescribed at the time) of the thirteen species treated here are represented in their collections. Until my own collections, which were specifically directed toward these species, only Pringle had collected as many of the species; he also collected six species. A summary of the Sessé and Mociño specimens relating to Matelea pavonii is provided in Table 2. A curious aspect of this summary is that two of the herbarium numbers, 3580 and 3581, are mixtures of Matelea pavonii and M. standleyana. Since these species are not known to be sympatric, the mixing probably occurred at some stage of herbarium handling. After both Sessé and Mociño had died, Pavón apparently distributed (sold?) specimens from

Table 2. Sessé and Mociño collections pertinent to *Matelea pavonii*.

S & M Herb. no.	Herb.	F neg. no.*	S & M label names	Woodson's dets.	Dets. according to this treatment
829	MA	41470	*Stapelia campanulata*	*Matelea pavonii*	not determinable from photo, probably not subgenus *Dictyanthus*, perhaps not *Matelea*
835	MA	41471	*Cynanchum violaceum*	*M. pavonii*	probably at least in part *M. pavonii*
838	F	-----	---------------	*M. pavonii*	*M. pavonii*
838	MA	41472	*C. campanulatum*	*M. pavonii*	*M. pavonii*
1253	MA	41473	*C. campanulatum* & *C. punctatum*	*M. pavonii*	*M. standleyana*
3580	F	-----	---------------	*M. pavonii*	*M. standleyana*
3580	MA	41474	*S. campanulata*	*M. pavonii*	*M. pavonii*
3581	F	-----	---------------	*M. pavonii*	*M. pavonii* plus *M. standleyana*
3581	MA	41475	*C. campanulatum*	*M. pavonii*	*M. pavonii* plus *M. standleyana*
s.n.	FI	-----	*S. campanulata*	----------	*M. pavonii* (not seen)
s.n.	P	-----	---------------	----------	*M. pavonii*

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* photos at MSC

their herbarium. It was upon one of these specimens that Decaisne based his genus Dictyanthus. The specimen was in the Webb herbarium, which at the time was in Paris (now at FI), but Decaisne kept a fragment which is now at P. I have not seen the specimen at FI, but Dr. McVaugh has examined it. Decaisne attributed the specimen and the label name, Stapelia campanulata, to Pavón. The name was actually a Sessé and Mociño name and was published posthumously in their Plantae Novae Hispaniae (1888). In that publication both a locality, mountains of Mazatlán, Guerrero, and a plate, "Fl. Mex. Ic. 255," are cited, but these cannot be associated with any particular one of the Sessé and Mociño herbarium numbers or with the specimen distributed by Pavón. The plate is apparently the same as de Candolle plate 804 (labelled "255"), which is at G (F neg. 30763). A small line drawing taken from the flowers of de Candolle plate 804 is also at G (F neg. 30406) and is labelled Eurybia stapeliaeflora. This may or may not have been a Sessé and Mociño name, but was never published.

Reichenbach added to the proliferation of names by describing Dictyanthus campanulatus and D. stapeliiflorus. The former, apparently as an early attempt to apply the idea of priority, is a superfluous name, citing "Stapelia campanulata Pavon. D. Pavonii DC. prodr. Tympananthe suberosa Haskarl." Dictyanthus stapeliiflorus is a most problematical name. Reichenbach described both these species from plants growing in a botanical garden in Dresden. The plants were grown from seeds collected in Mexico, at the foot of the Sierra Madre, near Durango. Apparently no specimens were collected and neither description is alone adequate for identifying the species, but both could apply to Matelea pavonii. This source area, if accurate, would be more appropriate for

Matelea pavonii than for any other of the larger-flowered species of subgenus *Dictyanthus*. Partly on the basis of this very weak evidence and partly because of a later reference (Anon., 1857), I have tentatively considered *Dictyanthus stapeliiflorus* to be synonymous with *Matelea pavonii*. This second reference purports to provide the first illustration of *Dictyanthus stapeliiflorus*. It is implied, but not stated, that the illustration, taken from a living plant, is from the original material. Considering that the plant was apparently also growing in a German botanical garden and only seven years had passed since Reichenbach's description, it could well have been from the original material. The illustration does not precisely fit any species I have seen, but most resembles *Matelea pavonii*. It is conceivable that this represents a distinct species which has never been recollected, but, in the absence of specimens, I prefer to consider it an atypical representative of the variable *Matelea pavonii*. Although Woodson (1941) made a new combination, *Matelea stapeliiflora*, I cannot be certain as to what he intended the name to apply. In some cases he annotated specimens of *Matelea tuberosa* with this name, probably following Gray's misapplication (in Watson, 1887). In one other case, Woodson applied the name to a specimen of *Matelea yucatanensis*, a duplicate of which he properly determined. He also almost certainly had examined the specimen of *Langlassé 257* at US which had been tentatively determined as *Dictyanthus stapeliiflorus*, but which I am describing as a new species, *Matelea hamata*. Standley (1924) apparently (but tentatively) described the equivalent of my *Matelea hamata* under *Dictyanthus stapeliiflorus* and this may well have been Woodson's concept of the species.

In the late 1840's this species was introduced into European botanical gardens and was apparently a popular plant for about 10 years. During this period at least six illustrations, mostly colored plates, were published in horticultural journals (Anon., 1852; Anon. & Beaton, 1852; Morren, 1852; Planchon & Van Houtte, 1852-1853; Anon., 1853; Anon., 1857). These plants probably originated from one or two introductions, but little reliable information was provided.

This is easily the most common species of subgenus Dictyanthus and exhibits considerable floral variation. The most conspicuous variation is in the background color of the corolla and in the color and density of corolla reticulations. The basic color pattern, however, is essentially constant. The presence or absence of teeth on the wall from the corona lobe to the gynostegium appears to have some geographical basis. Untoothed specimens occur throughout the range, but all the toothed specimens occur in Jalisco and northward. In some populations, examples can be found with prominent teeth, with small teeth, and with no teeth.

I have tentatively, and with some misgivings, included McVaugh 15826 with this species, but it has been neither mapped nor included in the description. This collection most likely represents an undescribed species related to Matelea pavonii. Besides a unique and distinctive pattern of reticulations on the corolla, the peduncles and pedicels are both about 2 mm long, or about one fourth to one fifth as long as the smallest measurements for Matelea pavonii. The bracts and calyx lobes are comparably smaller while the measurements for the corolla, corona, and gynostegium are within the lower limits of those for Matelea pavonii. Vegetatively, the specimen is essentially similar to Matelea pavonii. Considering the large number of specimens of Matelea pavonii

which I was able to examine, these differences are obviously significant. The specimen itself is well-prepared and as adequate as any for descriptive purposes. If the plant were as distinctive as Matelea hamata, of which I have less adequate material, I would not hesitate to describe it, but because of the similarity of McVaugh 15826 to Matelea pavonii, I have placed the specimen here for now. Additional material, especially living or spirit-preserved material should preferably be examined before the species is described. I have twice attempted to recollect this plant and in both cases was unable to find my way to the precise locality.

SPECIMENS EXAMINED. MEXICO. SINALOA: between Rosario and Colomas [Colomos], 13 July 1897 (fl), Rose 1645 (US); near Colomas [Colomos], 16 July 1897 (fl), Rose 1699 (MO, US), 20 July 1897 (fl), Rose 3222 [?] (US). NAYARIT: slopes of arroyos below SE slope of Cerro San Juan, ca 2 mi W of bull ring in Tepic, 12 Aug 1959 (fl), Bell & Duke 16649 (MO); Fresno, 2 Oct 1923 (fl), Collins & Kempton 33 (US, 2 specimens); mountains 10 mi SE of Ahuacatlán on rd to Barranca del Oro, slopes S of divide, 1100-1300 m, 11-12 Aug 1959 (fl), Feddema 378 (MICH); slopes and barrancas leading down to lake NE of Santa María del Oro, ca 1000 m, 18-20 Aug 1959 (fl), Feddema 782 (MICH); Arroyo de la Fundición, 5 mi SE of Ahuacatlán on rd to Barranca del Oro, steep ravine with small permanent stream, 1300 m, 25 Aug 1957 (fl), McVaugh 16349 (MICH); rd from Tepic to Calexicillo [Calixcillo], 1000 m, 13 Sep 1926 (fl), Mexia 589 (A, CAS, F, GH, UC, US); NW of Tepic, 900-950 m, 18-19 Aug 1935 (fl), Pennell 19842 (MEXU, MICH, NY, PH, US); ca 5 mi SE of Ahuacatlán along rd to Barranca del Oro, along a small stream, 25 Aug 1971 (fl), Stevens 1453 (MSC). GUANAJUATO: Arumbaro [?Acambaro], Sep, year not given (fl), *Ghiesbreght 220* (P), without date (fl), *Ghiesbreght s.n.* (K). JALISCO: Volcán Tequila, 7.4 mi from summit on rd from Tequila, 1900 m, 11 Aug 1968 (fl), *Anderson & Anderson 5146* (MICH); 1/3 mi SE of Etzatlán at end of narrow rd to factory-like ruin, ca 1500 m, 18 Sep 1966 (fl), *Anderson & Laskowski 3659* (MICH); Valle de Ahualulco, Aug 1887 (fl), *Bárcena 536* (MEXU); Hwy 80 ca 13 km S of Cocula, ca 1800 m, 5 Sep 1971 (fl), *Burch 5270* (MO, MSC, USF); Ruta 15, Km 121-122, ca 43 km NW of Magdalena, near Jalisco-Nayarit border, 10 Sep 1974 (fl), *Cruden 2153* (MSC); Río Verde, near Yahualica, 1372 m, 22 July 1961 (fl), *Detling 8455* (MICH); without precise locality and date (fl), *Diquet* [*Diguet*] *s.n.* (NY, 2 specimens, P, US); Huejotitlán, July 1912 (fl), *Diguet s.n.* (MICH, mixed with *Matelea macvaughiana*); barranca of Río Verde, ca 20 mi N of Tepatitlán on rd to Yahualica, ca 1450 m, 27-28 Aug 1958 (fl), *McVaugh 17340* (MICH); Baranca [La Barranca], near Guadalajara, 16-23 June 1886 (fl), *Palmer 113* (G, GH); Barranca near Guadalajara, 27 Sep 1889 (fl), *Pringle 2994* (GH, VT), 11 Sep 1891 (fl), *s.n.* (F), 20 July 1893 (fl), *4468* (BKL, F, G, GH, MEXU, MICH, MO, MSC, ND, NY, P, PH, UC, US, VT); bluffs of the barranca of Guadalajara, 5000 ft, 28 July 1902 (fl), *Pringle 11020* (F, GH, K, L, MICH, MO, NY, PH, US, VT); Mpio. de San Martín de Bolaños, 3 km al NW de El Platanar, 1500 m, 2 Sep 1968 (fl), *Rzedowski 26243* (ENCB, MICH); ca 5.3 mi N of Tecalitlán along Hwy 110, 17 Aug 1971 (fl), *Stevens 1427* (MSC); barranca of Río Verde, ca 0.5 mi SW of bridge on rd from Tepalitlán to Yahualica, 21 Aug 1971 (fl), *Stevens 1435* (MSC); Cerro de Tequila, cerca de Tequila, 2500 m, 11 Aug 1968 (fl), *Villarreal de Puga 1651* (ENCB); trail between Chante and Mamantlán ca 15 mi SSE of Autlán, 4500 ft, 1 Aug 1949 (fl), *Wilbur & Wilbur 2079* (MICH); slopes facing the

Pacific, 10 mi S of Autlán, 5300 ft, 6 Aug 1949 (fl), *Wilbur & Wilbur 2155* (MICH). COLIMA: steep ravines in gorge of Río Cihuatlán, near bridge 13 mi N of Santiago, 200-300 m, 27 July 1957 (fl), *McVaugh 15826* (MICH). MICHOACAN: Inés [Santa Inés], Aug-Nov 1840 [?1837] (fl), *Galeotti 1394* (P); Dist. Zitacuaro, Zitacuaro-Jungapeo, 1850 m, 23 Sep 1938 (fl), *Hinton 13275* (ARIZ, DS, ILL, MICH, MO, NY, PH, POM, TEX, US, WTU); Dist. Coalcomán, Pto. Zarzamora, 5 Aug 1939 (fl), *Hinton 15061* (ARIZ, MO, NY, 2 specimens, PH, US, WTU). MEXICO: Dist. Temascaltepec, Chorrera, 1230 m, 29 Aug 1932 (fl), *Hinton 1498* (P); Dist. Temascaltepec, Luvianos, barranca, 26 Aug 1933 (fl), *Hinton 4590* (ARIZ, G, 2 specimens, NY, US); Dist. Temascaltepec, Cañitas, barranca, 3 July 1935 (fl), *Hinton 8014* (GH, K, MO, NY, US); Dist. Temascaltepec, Rincón del Carmen, barranca, 21 Aug 1935 (fl), *Hinton 8201* (CAS, MO, US); Valle de Bravo, carretera entre Valle de Bravo y Colorín, 1500 m, 31 Aug 1952 (fl), *Matuda et al. 26961* (NY); Cerro de Los Capulines, Palmar Chico, 1100 m, 26 Aug 1954 (fl), *Matuda et al. 31345* (US). MORELOS: Cañon de Lobos, 20 km al ESE de Cuernavaca sobre la carretera a Cuantla, en el fondo del cañon, 1320 m, 6 Aug 1967 (fl), *Flores C. 12* (ENCB); ca 8 mi E of Cuernavaca along rd to Tepoztlán, 17-19 Aug 1952 (fl), *Gentry & Fox 12017* (MICH); Cuernavaca, without date (fl), *Ghiesbreght s.n.* (P, 3 specimens, not necessarily the same collection); "pres de Cuernavaca," Sep [?], year not given (fl), *Ghiesbreght ex JDP 37* (P, mixed with *Matelea dictyantha*); Cuernavaca [?], without date (fl), *Ghiesbreght ex JDP 38* (P); canyon at Cuernavaca, 4500 ft, 10 July 1941 (fl), *Leavenworth & Leavenworth 917* (F); Xochitepec, Sep 1934 (fl), *Lyonnet 1033* (US, 2 specimens); Cuernavaca, Sep 1946 (fl), *Martínez 15116* (MO); along rivulets in Chapultepec, E of Cuernavaca, 1500 m, 25 Aug 1935 (fl), *Nagel 8038* (GH); Tlayacapan, 23 Sep 1956 (fl), *Paray 2114* (ENCB); barranca near Cuernavaca, 5000 ft, 23 July 1896 (fl), *Pringle 7364* (F, ISC, MEXU); near Cuernavaca, 8 Sep 1903 (fl), *Rose 6858* (US), 12-13 Sep 1905 (fl), *10229* (US); ca 4.5 mi E of Ocotepec on rd from Cuernavaca to Tepoztlán, 4 Aug 1971 (fl), *Stevens 1375* (MSC). GUERRERO: Dist. Montes de Oca, Vallecitos, 11 July 1937 (fl), *Hinton 10592* (GH, US); Dist. Mina, Campo Morado-Otatlán, 1000 m, 24 July 1939 (fl), *Hinton 14481* (ARIZ, GH, MO, NY, 2 specimens, PH, TEX, US, WTU); Acahuizotla, 1000 m, 27 Aug 1960 (fl), *Kruse 523* (ENCB). OAXACA: Dist. Zimatlán, San Pablo Cuatro Venados, 2000 m, 22 June 1925 (fl), *Conzatti 4628* (US); without precise locality and date (fl), *Ghiesbreght s.n.* (F, GH, L, P, 5 specimens, 1 mixed with *Matelea dictyantha*, US; not necessarily all of the same collection, probably actually collected at Cuernavaca, Morelos); Cerro Espino, 650 m, Nov 1917 (fl), *Reko s.n.* (MEXU); along Hwy 131 ca 3.6 mi N of river bridge near Juchatenango, 27 July 1971 (fl), *Stevens 1362* (MSC). STATE UNKNOWN: plant cultivated in an English greenhouse, source unknown, 1897 or before (fl), *Park s.n.* (K); without locality and date (fl), *Sessé, Mociño et al. 835* (MA, not seen, photo from F neg. 41471 at MSC), *838* (F, fragment, MA, not seen, photo from F neg. 41472 at MSC), *3580 p.p.* (MA, not seen, photo from F neg. 41474 at MSC; F specimen of this number is *Matelea standleyana*), *3581* (F, MA, not seen, photo from F neg. 41475 at MSC; both specimens mixed with *Matelea standleyana*), *s.n.* ["Pavon"], type of *Dictyanthus pavonii* (FI, not seen, P, fragment); apparently a greenhouse-cultivated specimen, "horti Rougemont," "Patria: Nova Hispania," 14 July 1861 (fl), collector not given (NY).

5. Matelea macvaughiana W. D. Stevens, sp. nov. Type: Pringle 8629 (MSC! holotype; ENCB! F! G, 4 specimens! GH! L, 2 specimens! MEXU! MO! NY! P! PH, 2 specimens! POM! UC! US, 2 specimens! VT! isotypes).

Matelea macvaughiana W. D. Stevens; M. pavonii affinis, a qua imprimis differt caulibus annuis erectis vel leniter volubilibus et caudice perenni ligneo, pagina folii laevi, pedunculis plerumque brevioribus (0-16 mm), trichomatibus longis pedunculorum et pedicellorum rectis, tubo corollae breviore (9-12 mm e basi ad sinum), dentibus lateralibus loborum coronae duobus parvis et prominentiis folliculorum numerosioribus.

Plants erect to occasionally twining. Stems 20-85 cm long, with an herbaceous or woody caudex to 4 cm long and 2 cm wide, this with thin to moderately thick corky bark, occasionally with short woody stems above caudex, these with or without thin corky bark, herbaceous and lacking bark above, with dense short trichomes, sparse to dense glandular trichomes, and sparse to dense straight long trichomes to 3 mm long, these thin and often broken off on lower and older stems. Leaf blade ovate to wide-ovate or rarely narrow-ovate or very-wide-ovate, 30-95 mm long, 21-72 mm wide, with sparse to dense uncinate long trichomes, surface smooth, smaller veins sharply raised below, apex acuminate to attenuate, base lobate, lobes mostly descending to widely divergent, with 2-6 (-8) acropetiolar glands, margin often somewhat thickened and revolute; petiole 9-37 (-48) mm long, with dense short trichomes, sparse to dense glandular trichomes, and sparse to dense uncinate long trichomes. Inflorescence a simple cyme or often reduced to a single flower, this with or rarely apparently without a rudimentary peduncle (as indicated by the presence of a bract, Figure 19D); peduncle absent-16 mm long, with indumentum of stem or occasionally with long trichomes nearly absent; bracts linear to lorate or lanceolate, (2-) 4-7 mm long, abaxial surface with dense short trichomes, sparse to dense glandular trichomes, and sparse to dense, straight or uncinate long trichomes, adaxial surface glabrous or with scattered short trichomes distally; pedicel (5.5-) 8-20 mm long, with indumentum of peduncle. Calyx lobes lanceolate to narrow-ovate, 8-12 mm long, 3.0-4.5 mm wide, apex attenuate, with one or occasionally two glands below each sinus, abaxial surface with dense short trichomes, sparse to dense glandular trichomes, and sparse to dense, straight or uncinate long trichomes, adaxial surface glabrous. Corolla campanulate, base to sinus length 9-12 mm, limb revolute; lobes 9-17 mm long, apex rounded or occasionally obtuse, plane, margin revolute; glabrous within except limb and lobes with moderately dense to dense short trichomes, indumentum outside of dense short trichomes on tube and limb and sparse to moderately dense uncinate long trichomes on limb and lobes; tube convoluted with raised parts opposite corona lobes and sacs formed between them; with gray or black vertical lines within tube, these becoming circular on base of limb and reticulated on distal part of limb and on lobes. Corona lobes (6-) 7-9 (-10) mm long, linear to linear-spathulate in outline, connate at base, adnate to corolla and adnate by a thin wall to gynostegium, this wall continuing as a narrow ridge about half the length of the lobe, and with a pair of small teeth lateral to the upper margin near center. Gynostegium (2.5-) 3-4 mm high and (3-) 4-5 mm wide at apex, stipitate, apex broadly convex or nearly apiculate, the center apparently slightly shorter than to equaling the corpuscula, terminal anther appendages covering margin of apex. Corpusculum 0.23-0.26 mm long, 0.12-0.15 mm wide, pollen sacs 1.46-1.68 mm long, 0.43-0.49 mm wide. Follicles fusiform, ca 83 mm long, ca 20 mm wide, striped light and dark green, with dense short and glandular trichomes, with 118-144 arcuate projections to 3 mm long. Seeds obovate, 5.5-6.0 mm long, ca 4.5 mm wide, with a raised, faintly radially grooved margin, this entire or weakly toothed distally, inside this margin both sides flat or slightly convex, both sides verrucate to rugose, one side with a slight ridge from apex to near center, light brown; coma 25-30 mm long. Figures 18 and 19.

DISTRIBUTION AND ECOLOGY. The known collection localities are essentially centered in the region of Lago de Chapala at elevations of about 1600 m. Figure 20. Apparently growing in seasonally wet meadows and grasslands or, in the case of McVaugh 24934, in a somewhat drier roadside thicket. The erect or weakly twining habit and ground-level perennating parts are consistent with this open type of vegetation. The color positive from which Figure 19B was made is thought to have been taken 6-7 km southwest of Unión de Tula, Jalisco (Robert Cruden, pers. comm.), significantly southwest of the known localities, but apparently no specimens were taken. Flowering July-August. Specimens with mature-sized fruits collected in December.

A few specimens of Pringle 8629 have a little chewing insect damage on the leaves.

COMMON NAMES AND LOCAL USES. None known.

DISCUSSION. This species is named in honor of Dr. Rogers McVaugh for his major contributions to the flora of the part of Mexico in which

Figure 18. Isotype of *Matelea* *macvaughiana* (VT).

Matelea macvaughiana W.D. Stevens ined

ISOTYPE

Det. by Warren Douglas Stevens 1974

MICHIGAN STATE UNIVERSITY HERBARIUM

C. G. PRINGLE,

PLANTÆ MEXICANÆ.

1902.

STATE OF JALISCO—

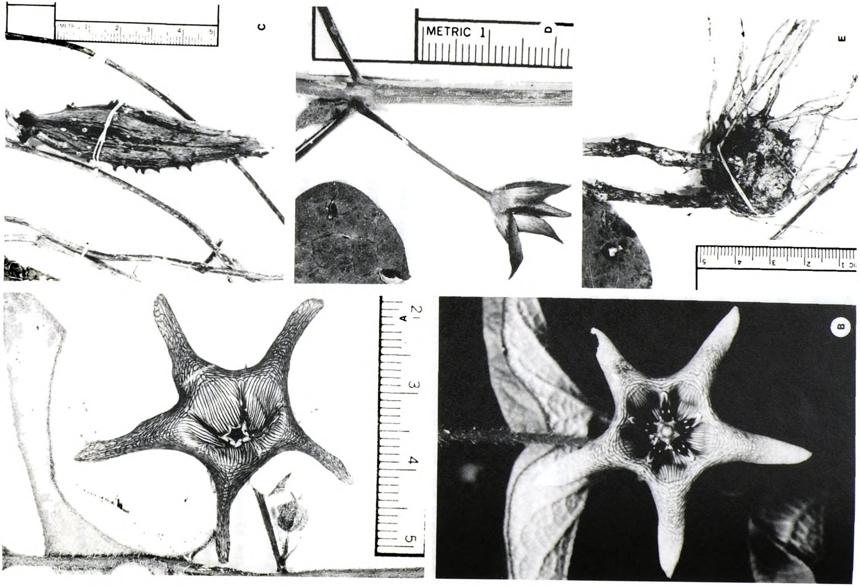
8629 Dictyanthus reticulatus, B. & H.

Moist slopes near Guadalajara.

5. August

Figure 19. Representative features of _Matelea_ _macvaughiana_.

A. pressed flower, _Pringle_ _8629_ (US); B. flower in living state, negative taken from color positive, courtesy of Dr. Robert W. Cruden, ca same scale as A; C. fruit, _McVaugh_ _24934_ (MICH); D. inflorescence reduced to a single flower (past anthesis), without a bract to indicate the presence of a peduncle (contrast with more typical inflorescence of A), _Pringle_ _8629_ (VT); E. caudex, _McVaugh_ _24934_ (MICH).


C
METRIC 1
D
E
A
B

this species is found, not the least of which are the many fine specimens of *Matelea* which have resulted from his years of study in this region.

It is something of a quirk that this species requires description. Woodson recognized the species, but according to his annotation of the MO specimen of *Pringle 8629*, considered it to be *Matelea dictyantha* Woodson, a new name based on *Rytidoloma reticulatum* Turczaninow (see the synonmymy of *M. dictyantha*). This apparently resulted from the fact that the two Pringle collections of this species were misdetermined as *Dictyanthus reticulatus* (Turczaninow) Bentham & Hooker f. *ex* Hemsley (actually "*Dictyanthus reticulatus* Turcz. (ex char.)" in the case of *Pringle 5431* and "*Dictyanthus reticulatus* B. & H." in the case of *Pringle 8629*). Woodson, in providing the new name, cited both the basionym and Turczaninow's type, *Jurgensen 692*, leaving no question as to the application of the name. *Jurgensen 692*, which Woodson apparently never examined, represents another species of *Matelea*, a species which Woodson did not recognize, but which must nevertheless bear his name, *M. dictyantha*. This left the species he did recognize without a description or name, which are herewith provided.

This species is likely to be confused with *Matelea pavonii* because of the similarity of the shape and color pattern of the corolla, but it is amply distinct. *Matelea macvaughiana* differs most prominently from *M. pavonii* by having a caudex, an erect or weakly twining habit, straight rather than uncinate long trichomes on several structures, smaller flowers on more reduced inflorescences, paired lateral teeth on the corona lobes, a lack of indumentum around the corona lobes, and the more numerous and arcuate projections on the follicles.

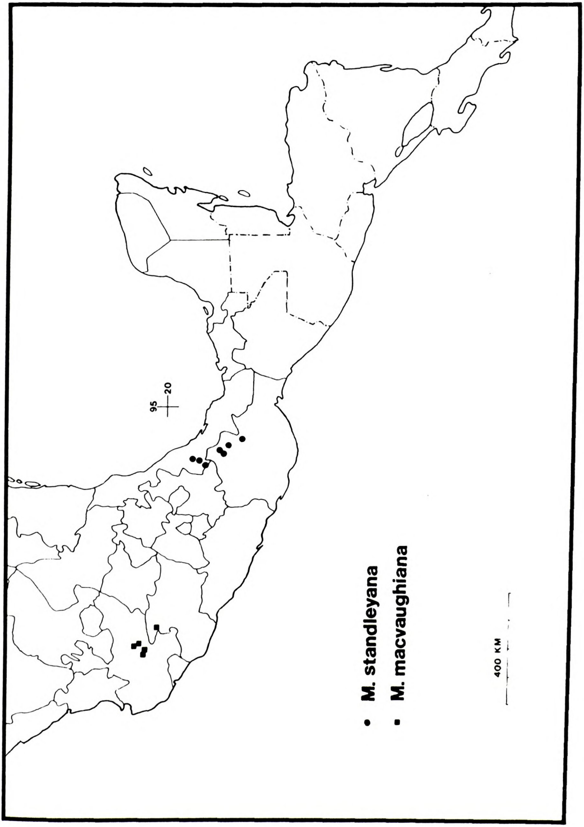


Figure 20. Distribution of *Matelea macvaughiana* and *M. standleyana*.

SPECIMENS EXAMINED. *MEXICO*. JALISCO: Huejotitán, July 1912 (fl), *Diguet s.n.* (MICH, 2 specimens, 1 mixed with *Matelea pavonii*, P, US); ranch near Coyula (near Tonalá) ca 12 mi E of Guadalajara, July 1963 (fl), *Faberge s.n.* (TEX); wet seepage area 23 mi S of Guadalajara on Hwy 15, 5300 ft, 13 July 1963 (fl), *Molseed & Rice 220* (ARIZ, MEXU, MICH, MO, NY, UC); wet meadows near Guadalajara [El Castillo, according to Davis, 1936, p. 118], 22 Aug 1893 (fl), *Pringle 5431* (GH, VT); moist slopes near Guadalajara [between El Castillo and Juanacatlán, op. cit., p. 199], 5 Aug 1902 (fl), *Pringle 8629*, type of *Matelea macvaughiana* (ENCB, F, G, 4 specimens, GH, L, 2 specimens, MEXU, MO, MSC, NY, P, PH, 2 specimens, POM, UC, US, 2 specimens, VT). MICHOACAN: cultivated fields 6-7 km N of Jaripo, rdside thickets, 1600 m, 1 Dec 1970 (fr), *McVaugh 24934* (MICH, MSC).

6. *Matelea standleyana* Woodson, Ann. Missouri Bot. Gard. 28: 237. 1941, based on *Dictyanthus tigrinus* Conzatti & Standley.

Dictyanthus tigrinus Conzatti & Standley *in* Standley, Contr. U.S. Natl. Herb. 23: 1183-1184. 1924, *non Matelea tigrina* (Grisebach) Woodson. Type: *Conzatti 3760* (US! holotype; GH! isotype).

Plants twining vines. Stems herbaceous and lacking bark or sometimes rhizomes slightly woody and with thin corky bark, rhizomes thin, horizontal, stem indumentum of sparse to dense short and glandular trichomes and sparse to very sparse straight long trichomes to 1.5 mm long, these very brittle and mostly missing from specimens. Leaf blade wide-ovate to very-wide-ovate or occasionally ovate, 48-104 mm long,

36-102 mm wide, indumentum of sparse uncinate long trichomes above and dense uncinate short trichomes below, surface smooth, apex acuminate to attenuate, base lobate, lobes mostly convergent to descending, with 1-7 acropetiolar glands; petiole 35-112 mm long, with sparse to dense short and glandular trichomes and sparse to very sparse, straight or uncinate long trichomes. Inflorescence a simple cyme; peduncle 5-18 (-25) mm long, with indumentum of stem or often with long trichomes absent; bracts linear to lanceolate, 2-6 mm long, with dense short and sparse straight long trichomes; pedicel 7-16 mm long, with indumentum of stem. Calyx lobes narrow-ovate or occasionally lanceolate or ovate, (8.5-) 12-18 mm long, 4.0-6.5 mm wide, apex attenuate, with one gland below each sinus, abaxial surface with dense short trichomes, margin also with sparse straight or uncinate long trichomes, adaxial surface glabrous. Corolla deeply campanulate, base to sinus length (14-) 17-31 mm, limb revolute; lobes 17-28 mm long, apex acute, plane to reflexed, margin revolute; glabrous within except with moderately dense to dense short trichomes on lobes, limb, and around corona lobes, indumentum on outside of sparse to dense short trichomes; tube convoluted with raised parts opposite corona lobes and sacs formed between them; with thick, brownish-red, circular lines within tube, these becoming thinner and reticulated on distal part of limb and on lobes. Corona lobes 9-13 mm long, linear in outline, connate at base, adnate to corolla and adnate by a thin wall to gynostegium. Gynostegium (3-) 4-5 mm high and 3.0-4.5 mm wide at apex, stipitate, apex with a blunt projection (formed from apices of anther wings) below each corpusculum and exceeding them laterally, apex convex with tip flattened and slightly bilobed and slightly exceeding corpuscula, terminal anther appendages covering ca one third of apex. Corpusculum 0.48-0.55 mm long, 0.23-0.28 mm wide, pollen sacs 1.54-1.88 mm long, 0.45-0.63 mm wide. Mature follicles unknown, immature follicles fusiform, to 85 mm long, to 28 mm wide, apparently green, with dense short trichomes, with ca 50 thick, straight projections to 7 mm long. Seeds unknown. Figure 21.

DISTRIBUTION AND ECOLOGY. Apparently restricted to northern Oaxaca and adjacent Veracruz at elevations up to ca 900 m. Figure 20. Apparently a plant of moist thickets. Flowering specimens collected mainly in August, but also once each in June and late October. The one immature fruit was collected in August. Santos 2318 and Smith 595 show apparent chewing insect damage to the leaves. No pollination activity was observed but the flowers of a greenhouse-grown specimen were noted to produce a faint foetid odor in late afternoon, suggesting possible dipteran pollination.

COMMON NAMES AND LOCAL USES. None known.

DISCUSSION. Despite the number of collections, this is a poorly known species. Most of the collections are inadequately labelled and several are difficult to locate on maps with certainty. My collection, from near the type locality, is the only one obtained since 1943. This species is readily identifiable because of the large, deeply campanulate corolla with circular markings inside the tube. This is likely the largest-flowered species of New World Asclepiadoideae. Well-formed leaves of this species are, along with those of Matelea pavonii, the largest of the subgenus and have uniquely angled sinuses.

For a discussion of the Sessé and Mociño collections of this species, see the discussion under Matelea pavonii.

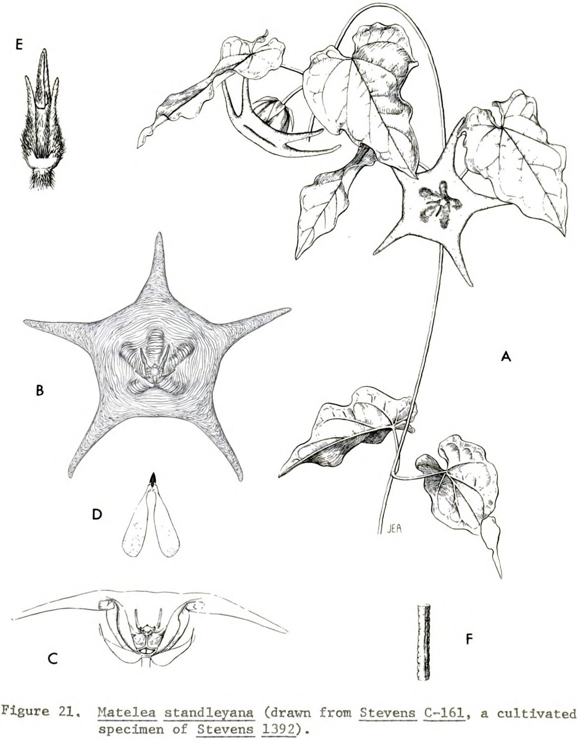


Figure 21. Matelea standleyana (drawn from Stevens C-161, a cultivated specimen of Stevens 1392).

A. section of flowering stem, x 0.6; B-C. flowers, x 1.2; D. pollinium, x 12; E. fertile shoot apex, x 6; F. section of old stem, x 0.6.

SPECIMENS EXAMINED. *MEXICO*. VERACRUZ: Córdoba, 16 Aug 1907 (fl), *Arsène 4799* (L); Mirador, June 1856 (fl), *Botteri s.n.* (US); "In remetis Miradoris Sarton," 1857 (fl), *Keck 5* (US); Córdoba, 16 Aug 1882 (fl), *Kerber 35* (G, 2 specimens, MICH, P); Ejido de Manzanares, 1-4 km NW of Campo Experimental de Hule, El Palmar, Zongolica, 1-5 Aug 1943 (fl), *Santos 2318* (MICH). OAXACA: Dist. Tuxtepec, de La Laguna de Ojitlán, 350 m, 31 Oct 1919 (fl), *Conzatti 3760*, type of *Dictyanthus tigrinus* (GH, US); Petlapa, 3000 ft, 184? (fl), *Galeotti 1563* (P, 3 specimens); Dist. Tuxtepec, en la montaña de Jacatepec, 22 m, 16 Aug 1940 (fl), *Martínez-Calderón 111* (A, UC, US); Ixcatlán, 850 ft, 19 Aug 1895 (fl & fr), *Smith 595* (GH); ca 29.7 mi W of Tuxtepec along rd to Ixcatlán, near where it branches from rd to Jalapa de Díaz, 7 Aug 1971 (fl), *Stevens 1392* (MSC). STATE UNKNOWN: Trapiche, Aug 1842 (fl), *Liebmann 12053* (F, 3 specimens, US); without locality and date (fl), *Sessé*, *Mociño*, *et al*. *1253* (MA, not seen, photo from F neg. 41473 at MSC), *3580 p.p.* (F, MA, not seen, photo from F neg. 41474 of MA specimen at MSC; MA specimen partly or completely *Matelea pavonii*), *3581* (F, MA, not seen, photo from F neg. 41475 at MSC; both specimens mixed with *Matelea pavonii*); without locality and date (fl), Herb. M.-E. Moricand (G).

7. *Matelea ceratopetala* (J. D. Smith) Woodson, Ann. Missouri Bot. Gard. 28: 236. 1941.

Dictyanthus ceratopetalus J. D. Smith, Bot. Gaz. (Crafordsville) 18: 208. 1893. Type: *Heyde & Lux ex J. D. Smith 3999* (US! holotype; G! GH! K! NY! US! isotypes).

Plants twining or occasionally trailing or erect. Stems 25-55 cm long when erect, woody and with thin to thick corky bark below or occasionally entirely herbaceous, otherwise herbaceous and lacking bark, with dense short trichomes, sparse to dense glandular trichomes, and very sparse to moderately dense, mostly straight long trichomes to 2 mm long. Leaf blade ovate to very-wide-ovate, 25-63 mm long, 15-55 mm wide, indumentum above of sparse or occasionally dense, straight or uncinate long trichomes and occasionally also sparse short trichomes, or rarely glabrous, indumentum below of dense short and sparse straight or uncinate long trichomes, surface smooth, smaller veins often moderately to sharply raised below, apex acute to attenuate, base lobate, lobes mostly convergent, with 1-4 (-7) acropetiolar glands, margin often somewhat thickened and revolute; petiole 13-60 (-70) mm long, with dense short trichomes, sparse to dense glandular trichomes, and very sparse to moderately dense, mostly uncinate long trichomes. Inflorescence a simple cyme or sometimes reduced to a single flower but always with a distinct peduncle; peduncle 1-15 (-27) mm long, with dense short trichomes, sparse to dense glandular trichomes, and very sparse to moderately dense, straight or uncinate long trichomes; bracts linear to lanceolate, 3-5 (-7) mm long, abaxial surface with short, glandular, and long trichomes, adaxial surface with short and occasionally also scattered long trichomes; pedicel 3-12 (-15) mm long, sometimes accrescent in fruit, with indumentum of peduncle. Calyx lobes narrow-ovate or occasionally lanceolate, 9-13 mm long, 3.5-6.0 mm wide, apex acute or attenuate, with one gland below each sinus, abaxial surface with scattered straight or uncinate long trichomes, adaxial surface glabrous. Corolla campanulate, base to sinus length 12-20 mm, limb revolute; lobes 11-18 mm long, apex acute, plane to reflexed, margin revolute; glabrous within except with scattered short trichomes on lobes, limb, and around corona lobes, indumentum on outside of sparse to dense short and scattered long trichomes; tube convoluted with raised parts opposite corona lobes and deep sacs formed between them; brownish- or reddish-purple-reticulated, reticulations wider within tube. Corona lobes 8-11 mm long, linear-spathulate in outline, connate at base, adnate to corolla and adnate by a thin wall to gynostegium, this wall with a distinct tooth near center of upper margin. Gynostegium 3.5-5.5 mm high and 3.0-4.5 mm wide at apex, stipitate, apex apiculate, apiculum 1-2 mm high and exceeding corpuscula, terminal anther appendages covering margin of apex. Corpusculum 0.41-0.46 mm long, 0.18-0.22 mm wide, pollen sacs 1.52-1.63 mm long, 0.40-0.49 mm wide. Follicles fusiform, 75-90 (-103) mm long, 20-27 mm wide, striped green and light green or white, with short and glandular trichomes, with (36-) 48-60 straight or occasionally arcuate projections to 7 mm long. Seeds obovate, ca 4.5 mm long and 2.5-3.5 mm wide, with a raised, radially grooved margin, this weakly toothed distally, inside this margin convex and verrucate on one side, concave and verrucate to rugose on opposite side, concave side with a slight ridge extending ca 1 mm from apex, dark brown; coma 20-30 mm long. Figure 22.

ECOLOGY AND DISTRIBUTION. Collected from southern Guatemala to northern Nicaragua, mostly at elevations of 800-1000 m but occasionally up to 1360 m and down to near sea level. Figure 23. Apparently not found in forests but rather in moist or dry fields, thickets, fencerows, streamsides, and roadsides. Mostly associated with rocky volcanic soils but once noted as occurring on a salt flat. Flowering mostly

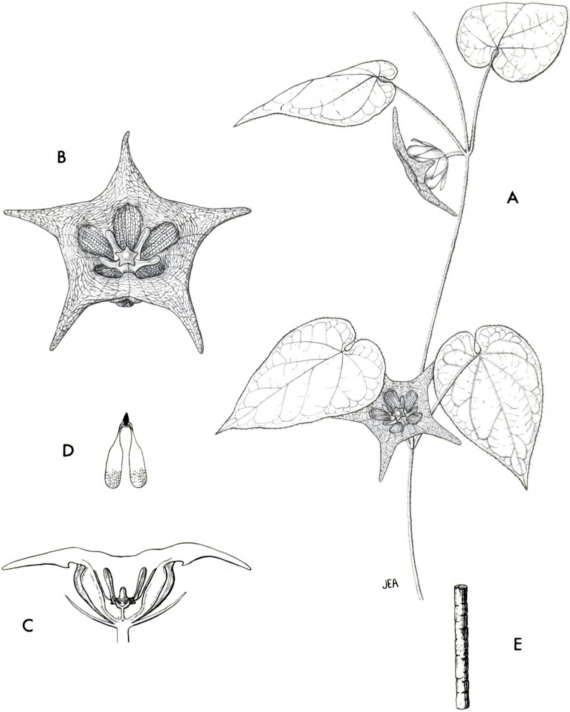


Figure 22. <u>Matelea ceratopetala</u> (drawn from <u>Stevens 1245</u>).

A. section of flowering stem, x 0.6; B-C. flowers, x 1.2; D. pollinium, x 12; E. section of old stem, x 0.6.

mid-July to early October but as early as June and as late as November. Collected with mature-sized fruits from mid-September to December.

The following collections showed significant chewing insect damage to the leaves of at least some of the specimens: *Molina R. 4053*, *22511*, *Standley 12709*, *26902*, and *Stevens 1245*. In one case a lepidopteran larva was pressed on the leaf and this is likely the kind of insect causing all the damage noted here.

COMMON NAMES AND LOCAL USES. The following names have been applied to the fruits of this species, which are cooked and eaten when young: *cochita* (*Standley 76325*), *cochitos* (*Standley 75729*), *corazon de loro* (*Moreles R. 1293*), *cuchampel* (*Standley et al. 547*), *chanchitos* (*Molina R. 1084*), *chununa* (*Standley 76678* and *White 5243*). The names *sombreros* and *sombreritos* (*Standley 76662*) apply to the flowers. "Leoncia picuda" is written on the label of the Châvez collection but I do not know the intent of this entry.

DISCUSSION. Until now, the plants I consider to be *Matelea dictyantha* have been included in this taxon. The two species are actually quite distinct and, in fact, *Matelea ceratopetala* has its closest affinities with *M. pavonii*. For a further discussion of this problem, see the discussion under *Matelea dictyantha*.

Matuda 1778 is only tentatively included under this species and is neither mapped nor included in the description. It differs in several respects but probably would still key to this species. The most significant differences are 1) it is outside the otherwise known range of the species, but would not be an unrealistic extension of the range, 2) the calyx lobes are larger and proportionately wider than those on any other specimen of this species, 3) the corolla is as large as the

largest measurements for this species, 4) the corolla reticulations are thinner and more widely and uniformly spaced than in any other specimen, 5) the thin wall of the corona lobe apparently lacks a tooth, and 6) the apiculum of the gynostegium apex is less than 1 mm long and is apparently exceeded by the corpuscula. In some ways these characters approach *Matelea pavonii* but 1) it is also out of the known range of that species and represents a less likely range extension, 2) the leaves are not pusticulate and in general size and shape much more nearly resemble those of *M. ceratopetala*, 3) the peduncle is too short, and 4) the pattern of lines within the corolla tube is reticulate rather than of parallel vertical lines. The single specimen of *Matuda 1778* has but one open flower and I consider it inadequate for a more definite taxonomic disposition at this time. I attempted to recollect this plant in 1971, but the lack of wet season roads prevented an effective search. Additional searches for *Dictyanthus* in southern Chiapas and southwestern Guatemala are much to be desired and may help clarify the status of this specimen.

SPECIMENS EXAMINED. *MEXICO*. CHIAPAS: Fca, Fuarez, Esc. [?Escuintla], 12 Aug 1937 (fl), *Matuda 1778* (MICH). *GUATEMALA*. ESCUINTLA: SE of Escuintla, 7 Sep 1964 (fl), *Elias et al. 800* (MO): Puerto de S. José, 5 m, Nov 1929 (fl), *Morales R. 1293* (F). JALAPA: vicinity of Jalapa, ca 1360 m, 7-18 Nov 1940 (fl), *Standley 76662* (F), 7-18 Nov 1940 (fr), *76678* (F); Finca El Ingenio, 3900 ft, 27-28 Sep 1944 (fl), *White 5243* (MICH). JUTIAPA: vicinity of Jutiapa, ca 850 m, 24 Oct-5 Nov 1940 (fl), *Standley 75105* (CAS, F, MO), 24 Oct-5 Nov 1940 (fr), *75729* (F), *76325* (F, MO); potreros between Trapiche Vargas and Asunción Mita, 500-600 m, 15 Nov 1939 (fr), *Steyermark 31786* (F). SANTA ROSA:

Km 38, 16 km NW of Barberena, 22 July 1970 (fl), Harmon & Dwyer 3230 (UMO); Santa Rosa, 3000 ft, Aug 1892 (fl), Heyde & Lux ex J. D. Smith 3999, type of Dictyanthus ceratopetalus (G, GH, K, NY, US, 2 specimens); 12 km NNE of Barberena, ca 3 km from Santa Rosa de Lima, 15 July 1971 (fl), Stevens 1245 (MSC). DEPARTMENT UNKNOWN: near Rosario, 16 Aug 1860 (fl), Hayes s.n. (GH). EL SALVADOR. LA LIBERTAD: Km 14 de la carretera hacia La Libertad, 8 July 1957 (fl), Lagos 810 (USF). SAN SALVADOR: San Salvador, June 1922 (fl), Calderón 824 (US). HONDURAS. EL PARAISO: drainage of Río Yeguare (ca 87°W, 14°N), Llano de Lizapa, 900 m, 24 Aug 1948 (fl), Molina R. 1084 (F, MO, US); drainage of Río Yeguare (ca 87°W, 14°N), entre Mata Indio y Lizapa, 950 m, 25 July 1951 (fl), Molina R. 4053 (F, GH); drainage of Río Yeguare (ca 87°W, 14°N), Río Lizapa, 1000 m, 19 Sep 1951 (fl), Molina R. 4121 (F, GH); Las Casitas, 950 m, 4 Dec 1946 (fl & fr), Standley et al. 547 (F); along Río Yeguare near Casitas, 900 m, 4 Dec 1946 (fr), Williams & Molina R. 11068 (MO). MORAZAN: drainage of Río Yeguare (ca 87°W, 14°N), Jicarito River, 2600 ft, 15 July 1948 (fl), Glassman 1902 (F, ILL, MIN, NY); Río Guacerique between Los Laureles and Las Tapias, NW of Tegucigalpa, 1000 m, 4 Nov 1966 (fl & fr), Molina R. 18618 (F, G, GH, NY); small streamside ca 2 km S of EAP campus, El Zamorano, Aug 1960 (fl), Pfeifer 1633 (US); along Río Yeguare, E of El Zamorano, ca 750 m, Sep-Dec 1948 (fl & fr), Standley 12709 (F, P); along rd from El Zamorano toward San Antonio de Oriente, 825-950 m, Sep-Nov 1948 (fl), Standley 13671 (F); vicinity of El Zamorano, near Rastro, 800-850 m, 5 Aug 1949 (fl), Standley 22152 (F, MO, US); along road from El Zamorano toward San Antonio de Oriente, 825-950 m, 9 Aug 1949 (fl), Standley 22377 (F); W of El Zamorano, along trail from Río de la Orilla to El Pedregal,

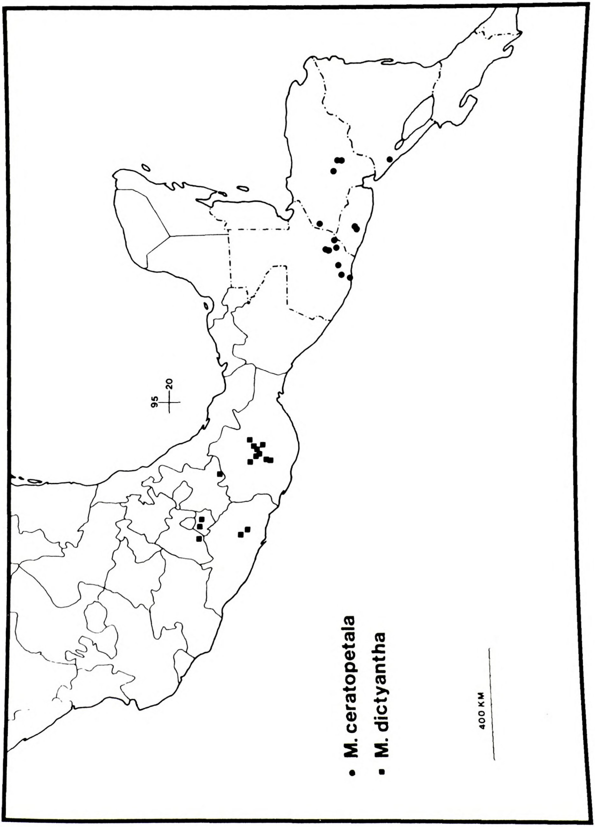


Figure 23. Distribution of *Matelea ceratopetala* and *M. dictyantha*.

800-900 m, 6 Aug 1949 (fl), *Standley 22683* (F); vicinity of El Zamorano, rd toward Chagüite, ca 800 m, 30 Sep 1950 (fl), *Standley 26902* (F, GH, US); Zamorano, 800 m, Aug, year not given (fl), *Valerio R. 63* (F); Santa Inés, 850 m, Aug 1943 (fl), *Valerio R. 413* (F); El Pedregal, 800 m, 18 Sep 1943 (fr), *Valerio R. 874* (F); Río Yeguare, 800 m, 32 [!] Sep 1943 (fl), *Valerio R. 985* (F); Zamorano, 800 m, 4 Oct 1943 (fl), *Valerio R. 1082* (F), 25 July 1945 (fl), *Valerio R. 3140* (F, MO); along Santa Clara Creek, Zamorano Valley, 850 m, 9 Oct 1946 (fl), *Williams & Molina R. 10569* (F, MO). OCOTEPEQUE: along rd, vicinity of Antiguo Ocotepeque, 800 m, 31 Aug 1968 (fl), *Molina R. 22511* (F, NY). *NICARAGUA*. CHINANDEGA: vicinity of Chichigalpa, ca 90 m, 12-18 July 1947 (fl), *Standley 11388* (F). DEPARTMENT UNKNOWN: "Leoncia picuda," 8 Oct 1927 (fl), *Chaves* [*Chávez*] *315* (US).

8. *Matelea dictyantha* Woodson, Ann. Missouri Bot. Gard. 28: 236. 1941, based on *Rytidoloma reticulatum* Turczaninow.

Rytidoloma reticulatum Turczaninow, Bull. Soc. Imp. Naturalistes Moscou 25(2): 319-320. 1852, *non Matelea reticulata* (Engelmann *ex* A. Gray) Woodson. Type: *Jurgensen 692* (K! probable isotype).

Dictyanthus reticulatus (Turczaninow) Bentham & Hooker f. *ex* Hemsley, Biol. Centr. Am. Bot. 2: 329. 1882.

Plants erect to trailing or twining. Stems 15-70 (-150+) cm long, with a woody caudex to 5 cm long and 3 cm wide, this with thin to thick corky bark, or occasionally with an elongate woody rhizome, also often with woody stems above caudex or rhizome, these usually with thin corky

bark and up to ca 5 cm long but occasionally up to 20 cm long, otherwise herbaceous and lacking bark, with dense short and glandular trichomes and sparse to dense, mostly straight long trichomes to 3 mm long. Leaf blade wide-ovate to very-wide-ovate, 26-62 (-103) mm long, 24-52 (-76) mm wide, with uncinate long trichomes and also often glandular trichomes on veins below, surface smooth, smaller veins sharply raised below, apex acute to attenuate or rarely obtuse, base lobate, lobes mostly convergent to descending, with 1-6 (-8) acropetiolar glands, margin often somewhat thickened and revolute; petiole (11-) 14-34 (-57) mm long, with dense short and glandular trichomes and sparse to dense uncinate long trichomes. Inflorescence a simple cyme or sometimes reduced to a single flower with or apparently without a rudimentary peduncle; peduncle absent-10 mm long, with indumentum of petiole; bracts linear to lanceolate, 2.5-7.0 mm long, abaxial surface with indumentum of stem, adaxial surface glabrous; pedicel 5-12 (-16) mm long, sometimes markedly accrescent in fruit, with indumentum of stem. Calyx lobes narrow-ovate or occasionally lanceolate or ovate, 6-11 mm long, 2.5-6.0 mm wide, apex acute to attenuate, with one gland below each sinus or occasionally these somewhat above sinus near margin of lobe, abaxial surface with indumentum of stem, adaxial surface glabrous. Corolla campanulate, base to sinus length (7-) 9-16 mm, limb revolute; lobes 8-14 mm long, apex acute or sometimes rounded, plane to strongly reflexed, margin revolute; glabrous within except with sparse to dense short trichomes around corona lobes and on limb and bases of lobes or sometimes over whole surface of lobes, indumentum on outside of short trichomes and occasionally also with long trichomes on limb and bases of lobes or occasionally tube and tips of lobes nearly glabrous; tube

convoluted with raised parts opposite corona lobes and deep sacs formed between them; faintly to densely grayish-purple-reticulated, reticulations wider within tube. Corona lobes (5-) 6-8 mm long, linear in outline with a raised margin, adnate to corolla and adnate by a thin wall to gynostegium, connate at base, wall to gynostegium continuing as a narrow ridge nearly the length of lobe. Gynostegium 3-4 mm high and 3.0-3.5 mm wide at apex, stipitate, apex broadly and shallowly concave with corpuscula as high points, terminal anther appendages covering margin of apex. Corpusculum 0.22-0.35 mm long, 0.09-0.17 mm wide, pollen sacs 1.17-1.45 mm long, 0.29-0.38 mm wide. Follicles fusiform, (45-) 55-70 mm long, 10-22 mm wide, light green with a few dark green stripes, with short and glandular trichomes, with (30-) 50-110 straight to arcuate projections to 3 mm long. Seeds obovate, ca 5.5 mm long and 4.0-4.5 mm wide, with a raised, radially grooved margin, this weakly toothed distally, inside this margin flat or slightly concave and verrucate on one side, convex and verrucate on opposite side, flat side with slight ridge from apex to near center, light brown to brown; coma 25-30 mm long. Figures 24 and 25.

DISTRIBUTION AND ECOLOGY. Collected in the mountains of four more or less discrete areas: around Cuernavaca (Morelos and adjacent state of México), around Chilpancingo (Guerrero), around Oaxaca (Oaxaca), and in southwestern Puebla. Figure 23. Found at elevations of about 1500-2500 m. About a third of the collections are noted as being on or associated with limestone and many of the other localities are in limestone areas, but it cannot be determined at this time if the species is restricted to this substrate. Mostly found in low, open oak, pine, or pine-oak forests, especially where disturbed. Flowering mid-June to

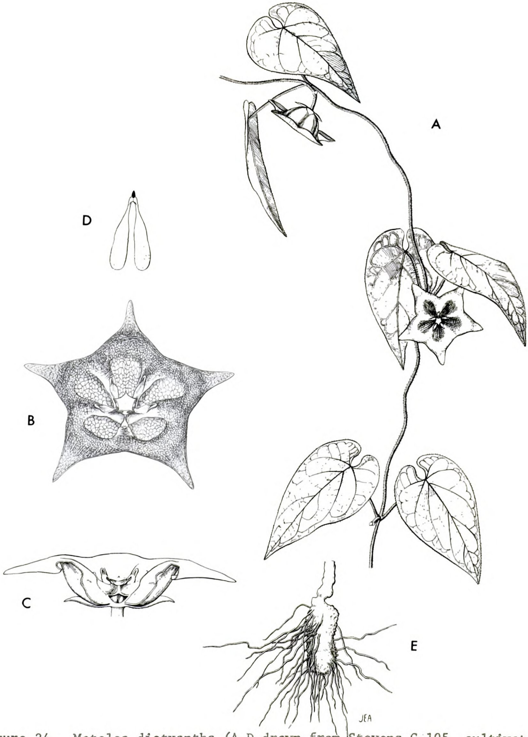
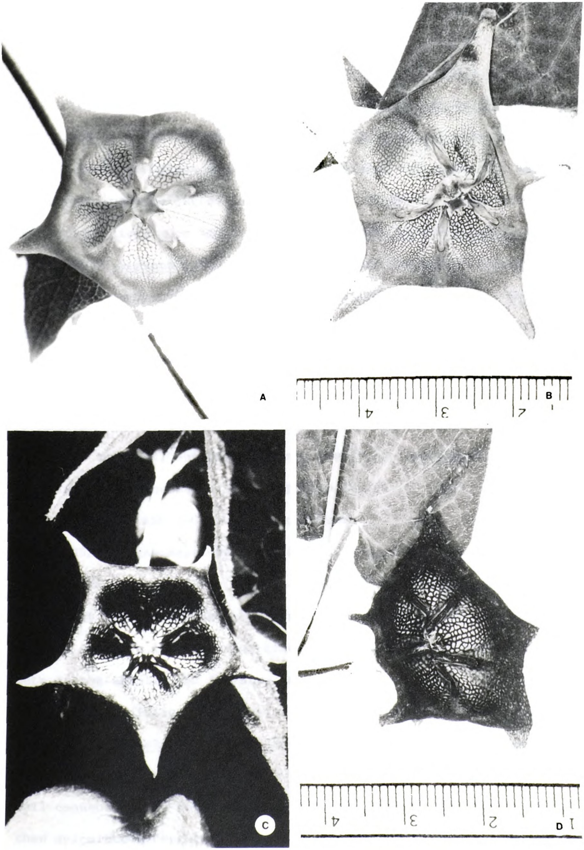


Figure 24. Matelea dictyantha (A-D drawn from Stevens C-105, cultivated specimens of Graham 1231, and E from Stevens 1311).

A. section of flowering stem, x 0.6; B-C. flowers, x 1.7; D. pollinium, x 18; E. caudex, x 0.6.

Figure 25. Regional variation of *Matelea dictyantha*.

A-B represent plants from Morelos and Guerrero and C-D represent plants from Oaxaca, all scales approximately equal. A. *Stevens C-105* (greenhouse-grown plant of *Graham 1231*); B. *Rose 11065* (US); C. copy negative taken from color positive, courtesy of Dr. Robert Cruden; D. *Iltis et al. 1198* (WIS).


A
B
4
3
2
1
C
D
4
3
2
1

mid-September. Mature-sized fruits collected August-December, but with mature seeds only in December.

Four of my collections from Oaxaca (*Stevens 1203*, *1311*, *1344*, *1346*) have a few insect-chewed leaves and *Graham 1231*, *Iltis et al. 1204*, and *Rose 11065* have some of the flower buds forming galls. The galls were removed from the Graham specimen at the time of collection (by me) and the insects were collected as they emerged. They are an undetermined dipteran species. One adult cerambycid beetle, probably *Tetraopes*, was collected on *Stevens 1311*. The larvae of many species of *Tetraopes* live in the stems and rhizomes of *Asclepias* (Chemsak, 1963). *Matelea dictyantha* as well as the other species of *Matelea* with thick rhizomes or caudices might be suitable hosts for *Tetraopes* but I have no direct evidence of this.

Most plants of *Stevens 1311* were infected with a rust. Associated with the rust, but probably only feeding on the fungal spores or secretions, were numerous small dipteran larvae.

COMMON NAMES AND LOCAL USES. None known.

DISCUSSION. As mentioned in the discussion under *Matelea macvaughiana*, Woodson provided the epithet for *M. dictyantha* quite by accident. He did not distinguish between this species and *Matelea ceratopetala*, a species to which it bears some resemblance in the shape and color pattern of the corolla and the size and shape of the leaves but from which it is clearly distinct. The major characteristics distinguishing this species from *Matelea ceratopetala* include the woody caudex and predominantly shorter habit, the smaller flowers, the lack of a tooth on the wall connecting the corona lobe to the gynostegium, the concave rather than apiculate gynostegium apex, and the smaller follicles with smaller

and more numerous projections. The geographic ranges of the two species are also distinct. The distinctiveness of this species from Matelea ceratopetala has been noted on two specimens, Conzatti 2168 at F (unsigned and undated) and Pringle 4768 at GH (J. M. Greenman, 18 Sep 1890). Standley (1924) considered Rytidoloma reticulatum to be synonymous with Matelea pavonii.

The holotype for the Turczaninow name has not yet been located. It may be at CWU (Charkow University, U.S.S.R.), to which was given the Turczaninow herbarium after his death, but I have not attempted to borrow their material. The one specimen of Jurgensen 692 which has been examined is at K and is probably an isotype. The form of Turczaninow's protologue (1852, pp. 319-320) has also led to some confusion. The apparent generic description is actually a description of the genus and its single species and cites Jurgensen 692. Immediately following the genus-species description is the entry, "18. R. reticulatum. Altera species hujus generis, quantum e flore unico, Ptino corrupto, dijudicare possum, adest in collectione Galeottiana ex Oaxaca sub n. 1563." This led Langman (1964, p. 748) to state that Rytidoloma reticulatum was based on a Galeotti collection. Turczaninow was actually indicating that he recognized another species in his new genus, but he neither named nor described it. Galeotti 1563 is indeed a different species, Matelea standleyana.

As with Matelea hemsleyana, two distinctive elements of this species can be recognized, but I do not believe they warrant taxonomic recognition of the basis of currently available material. The flowers of the Morelos-Guerrero element of this species tend to be larger, more shallowly campanulate, and much lighter in color than the Puebla-Oaxaca

element (Figure 25). In this case the ranges are apparently distinct but I have found no non-subjective way of describing the difference in dried specimens. Perhaps with additional spirit-preserved collections and specimens with descriptions of the flower colors, taxonomic recognition will become more feasible. In this connection, the specimens of Ghiesbreght s.n. from province d`Oaxaca are of the Morelos-Guerrero type and were most likely collected at Cuernavaca, Morelos (this mixing of labels apparently occurred often with Ghiesbreght specimens). It is also interesting to note that the distribution of this species largely resembles that of *Crusea calcicola* (Anderson, 1972), another species growing on calcareous soils.

SPECIMENS EXAMINED. MEXICO. MEXICO: 4 mi S of Ixtapan on Hwy 55, 16 Aug 1972 (fl), Dunn et al. 20451 (MSC, UMO); cercania de Ixtapan de la Sal, 1800 m, 16 Aug 1953 (fl), Matuda et al. 28802 (MO). MORELOS: "pres de Cuernavaca," Sep [?], year not given (fl), Ghiesbreght ex JDP 37 (P, mixed with *Matelea pavonii*); near Yautepec, 12-13 July 1905 (fl), Rose 8568 (US); near Cuernavaca, 14 Aug 1906 (fl & fr), Rose 11065 (GH, NY, US). GUERRERO: Mpio. de Chilpancingo, camino al Cerro Alquitrân, cerca de Mazatlân, 1500 m, 5 July 1966 (fl), Châvez 16 (ENCB); hill S of Chilpancingo, 5.7 mi S of S entrance to town on Hwy 95, 20 Aug 1972 (fl), Dunn et al. 20508 (MSC, UMO); small rocky mountain valley 14 mi from Mex. 95 on rd to Chichihualco, 26 Oct 1970 (fr), Graham 1231 (MICH); Mpio. de Chilpancingo, veriente E del Cerro Alquitrân, cerca de Mazatlân, 1500 m, 5 July 1966 (fl), Rzedowski 22677 (ENCB, MICH, MSC, WIS). PUEBLA: Cerro de Castillo, near Coatepe [Coatepec], July 1907 (fl), Purpus 2620 (F, GH, MO, NY, UC, US); cerros near San Luis, July 1907 (fl), Purpus 2620A (UC). OAXACA: Valley of

Etla, July 1895 (fl), *Alvarez ex L. C. Smith 470* (GH); lower slopes of Cerro San Felipe, S side, above town of San Felipe del Agua, 1700-2000 m, 20 July 1968 (fl), *Anderson & Anderson 4856* (MICH); Dist. Centro, Hacienda de Guadalupe, 1600 m, 14 June 1908 (fl), *Conzatti 2168* (F); Cañada de San Gabriel Etla, 1930 m, 8 Aug 1897 (fl), *Conzatti & Gonzalez 219* (GH); Sierra, 7000-8000 ft, 184? (fl), *Galeotti 1567 p.p.* (US); Yavezia [Santa María Yavesía], 184? (fl), *Galeotti 1567 p.p.* (P); without precise locality and date (fl), probably actually from Cuernavaca, Morelos, *Ghiesbreght s.n.* (K, P, mixed with *Matelea pavonii*); base of Cerro San Felipe, ca 9-11 km NNE of Oaxaca, along rd from San Felipe, ca 2000 m, 21 Aug 1960 (fl & fr), *Iltis et al. 1198* (WIS, 4 specimens), 21 Aug 1960 (fl), *1204* (MEXU, MICH, MO, UC, WIS, 2 specimens); "Sierra San Pedro Nolasco, Talea, etc.," 1843-1844 (fl), *Jurgensen 692*, type of *Rytidoloma reticulatum* (K); Valley of Oaxaca, 5100-5800 ft, 8 Sep 1894 (fl), *Nelson 1247* (US); Valley of Oaxaca, 5000-5300 ft, 20 Sep 1894 (fl), *Nelson 1296* (US); hills above Oaxaca, 6000 ft, 6 Aug 1894 (apparently fl & fr), 26 Dec 1894 (apparently fr), *Pringle 4768* (BKL, ENCB, F, G, 3 specimens, GH, ISC, MASS, MEXU, MICH, MIN, MO, MSC, ND, NY, P, PH, UC, US, VT); near city of Oaxaca, 16-21 June 1899 (fl), *Rose 4615* (US); 9 km al S de Sola de Vega, sobre la carretera a Puerto Escondito, 1600 m, 30 Sep 1965 (fr), *Rzedowski 21370* (ENCB); along rd to microwave tower ca 3.6 mi S of Matatlán on Hwy 190, ca 1 mi S of Km 595, 6 July 1971 (fl), *Stevens 1203* (MSC), 22 July 1971 (fl), *Stevens 1311* (MSC); ca 5.8 mi N of Telixlahuaca along Hwy 131, 25 July 1971 (fl), *Stevens 1343* (MSC); ca 3.8 mi NE of Sola de Vega along Hwy 131, 26 July 1971 (fl), *Stevens 1344* (MSC); ca 4.9 mi SW of Sola de Vega along Hwy 131, 26 July 1971 (fl), *Stevens 1346* (MSC). STATE

UNKNOWN: "Eugenio," "Sierra de la Cruz," "Vera Cruz to Orizaba," 1 Aug 1853 (fl), Müller 1108 (K, NY).

9. *Matelea aenea* (Woodson) W. D. Stevens, comb. nov.

Dictyanthus aeneus Woodson, Amer. J. Bot. 22: 691, pl. 1, fig. 4. 1935. Type: *Steere 3005* (MO! holotype; MICH! isotype).

Plants twining vines. Stems woody below, with thin to thick corky bark, herbaceous and lacking bark above, with dense short and glandular trichomes and dense uncinate long trichomes to 2.5 mm long. Leaf blade wide-ovate to very-wide-ovate or occasionally ovate, 35-98 mm long, 26-70 mm wide, indumentum of uncinate long trichomes and also glandular trichomes on veins below, surface smooth, apex acute to acuminate, base lobate, lobes convergent to widely divergent, with 4-11 acropetiolar glands, margin often crispate; petiole 21-62 mm long, with indumentum of stem. Inflorescence a simple cyme; peduncle 4-11 mm long, with indumentum of stem; bracts linear to lanceolate, 3-4 mm long, with indumentum of stem or occasionally glabrous on adaxial surface; pedicel ca 4 mm long, with indumentum of stem. Calyx lobes lanceolate to narrow-ovate, 6-9 mm long, 2.0-4.5 mm wide, apex acute to attenuate, with one or occasionally two glands below each sinus, abaxial surface with dense short, glandular, and uncinate long trichomes, adaxial surface glabrous. Corolla campanulate, base to sinus length (6-) 8-12 mm, limb ascending to nearly plane, not revolute; lobes 5-9 mm long, length to width (sinus-sinus) ratio 0.67-0.78, apex acute or rounded, ascending to slightly reflexed at tip, margin not revolute; glabrous within except with dense short trichomes on limb and lobes, indumentum on

outside of short, glandular, and uncinate long trichomes; tube convoluted with raised parts opposite corona lobes and deep sacs formed between them; pale yellowish-green, sometimes with faint reticulations, these often drying darker. Corona lobes 6-8 mm long, linear-spathulate in outline, with tip deeply rugose and glistening purplish-black, otherwise yellowish-green or tinted purple, connate at base, adnate to corolla and adnate by a thin wall to gynostegium, this wall continuing as a narrow ridge nearly the length of lobe. Gynostegium ca 3 mm high and ca 2.5 mm wide at apex, stipitate, apex broadly and shallowly concave with corpuscula as high points and occasionally also slightly convex in center, terminal anther appendages hardly covering margin of apex. Corpusculum 0.21-0.28 mm long, 0.12-0.15 mm wide, pollen sacs 1.08-1.18 mm long, 0.35-0.37 mm wide. Young follicles with short projections, mature specimens unknown on specimens but said to be 10-15 cm long and "tuberculosa" (Flores 1). Seeds unknown on specimens but said to be comose (Flores 1). Figure 26.

DISTRIBUTION AND ECOLOGY. Collected only in the vicinity of Progreso, on the tip of the Yucatán Peninsula, at near sea level. Figure 27. Growing in low scrub vegetation in thin, limestone derived soils, apparently where not particularly saline. Collected in flower June-August and in December.

The only insect damage found was a few chewed leaves on Stevens 1145.

COMMON NAMES AND LOCAL USES. Gaumer 1173 p.p. gives the name xbockin. Flores 1 gives the common names cabeza de cocodrilo, apparently referring to the follicles, and mata chivo on the label as well as an attached note as follows: "Parece ser la Philiverta Lindeleana.

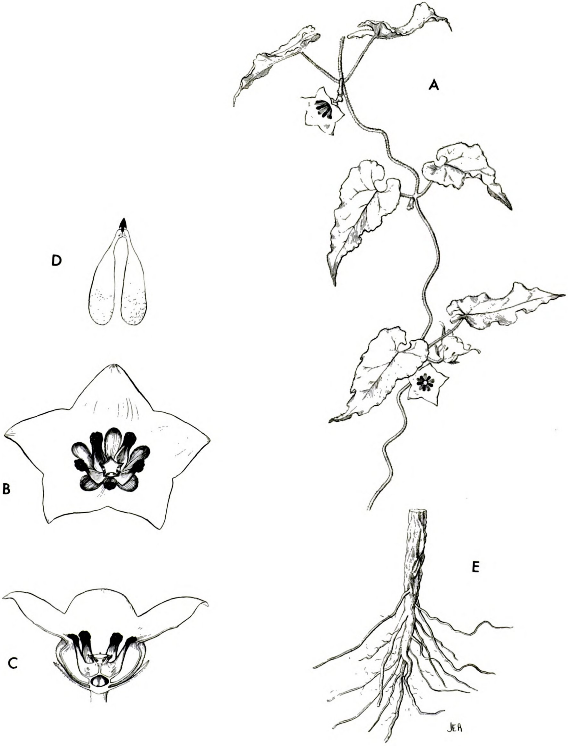


Figure 26. *Matelea aenea* (A–D drawn from *Stevens C-157*, cultivated specimens of *Stevens 1145*, and E from *Stevens 1145*).

A. section of flowering stem, x 0.6; B–C. flowers, x 2.3; D. pollinium, x 24; E. base of stem, x 0.6.

Apoccinia silvestre que abunda en el camino del ferrocarril de via angusto, algunos le dicen mata chivo porque aunque la come el ganado, sus hojas trituradas y molidas en la comida matân â los Perros, lo mismo que â los chivos que las comen. Su fruto de 10 a 15 ctms. es una câpsula tuberculosa y lechosa cuando verde, sus granos llevan pelos largos." It is unfortunate that more collectors do not make such useful and interesting observations.

DISCUSSION. See also the discussion under Matelea yucatanensis. In describing Dictyanthus aeneus, Woodson (1935) summarized the differences as follows: " T. aeneus differs from T. yucatanensis Standl. [sic] superficially in the smaller and more shortly petiolate leaves with paler color and hispidulous or strigillose surfaces, and smaller, paler corollas with a more pronounced campanulate tube. Structural differences of the corolla and corona are conspicuous as well." Later, Woodson (1941) considered the species to be synonymous with Matelea yucatanensis (Standley) Woodson and so annotated the type specimen. I concur with his original recognition of Dictyanthus aeneus, but unfortunately his characters are not particularly diagnostic and, in fact, his drawing of the flower (Woodson, 1935, p. 1, fig. 4a) has the shape of Matelea yucatanensis and the size of M. aenea. The best characters for separating the two species are most easily observable in fresh flowers. The corolla limb and lobes of Matelea yucatanensis form essentially a right angle with the tube and have revolute margins while those of M. aenea are ascending and do not have revolute margins. (Under greenhouse conditions, Matelea aenea occasionally produces flowers which have slightly revolute margins and lobes which are not strongly ascending.) This difference can often still be seen in dried

specimens when, ironically, they are not carefully pressed. The corolla color is also strikingly different in fresh flowers, yellowish-green with faint reticulations in Matelea aenea and densely grayish-purple-reticulated in M. yucatanensis. Unfortunately, Matelea aenea sometimes darkens in drying and the difference is partially obscured. The floral characters which are most dependable in pressed specimens are the size and shape of the corolla lobes, but even with these the flowers often require boiling to be accurately measured. As noted in the descriptions, Matelea aenea has shorter and proportionately wider corolla lobes. There seem to be certain vegetative differences as well, but the variation within each species is large and there are too few specimens to make possible any meaningful conclusions. Matelea aenea tends to have denser long trichomes on the vegetative parts and smaller, wider, more crispate, and less purple-pigmented leaves. Finally, it can be seen in Figure 27 that the ranges of the two species seem to be allopatric; Matelea aenea appears to be restricted to the coastal area immediately around Progreso, while M. yucatanensis is found at scattered, more inland, localities. Both species are too poorly collected, however, to support much conjecture on their relative distributions.

As can be partially noted in the descriptions and Figures 9, 26, and 28, the pollen sacs of the two species differ somewhat in size and shape. More specifically, the pollen sacs of Matelea aenea have a mean length of 1.13 mm (1.08-1.18) and a mean width of 0.36 mm (0.35-0.37) while those of M. yucatanensis have a mean length of 1.18 mm (1.11-1.26) and a mean width of 0.33 mm (0.28-0.35). The mean length to width ratio of Matelea aenea is 3.18 (3.04-3.35) and that of M.

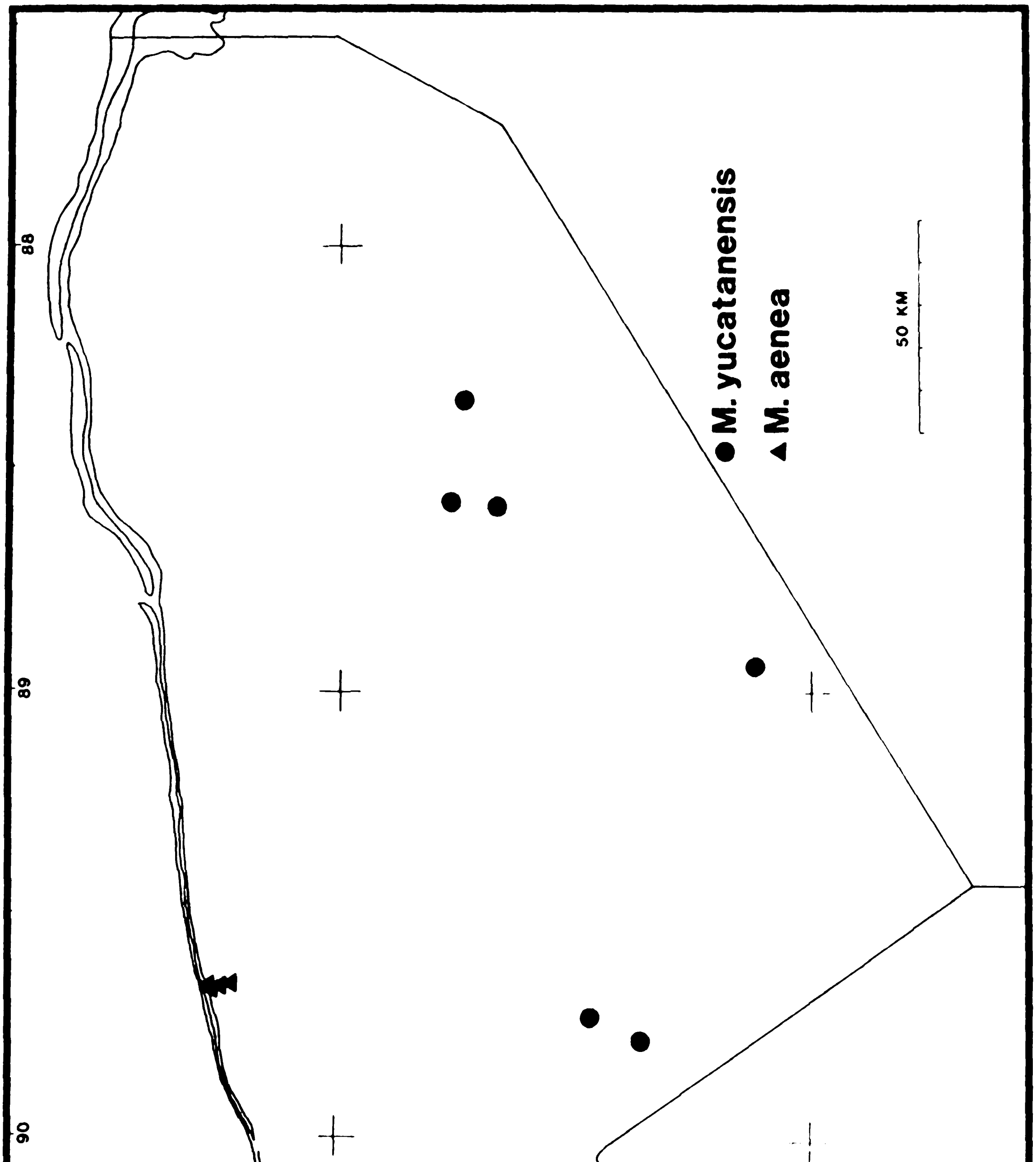


Figure 27. Distribution of *Matelea aenea* and *M. yucatanensis*.

yucatanensis is 3.56 (3.20-4.22). Of the several potential isolating mechanisms directly associated with pollination, one of the most easily detectable is a change in pollen sac shape which makes hybridization mechanically difficult or impossible. Holm (1950) found that closely related species of Sarcostemma with sympatric or contiguous ranges had markedly different pollen sac shapes. Although the differences in this case are not great and are based on a very inadequate sample, it is interesting to speculate that changing pollen sac shape is a factor in the divergence of these two closely related species.

SPECIMENS EXAMINED. MEXICO. YUCATAN: Progreso, along railroad near port, Dec 1932 (fl), Flores 1 (F); Progreso, without date (fl), Gaumer 1173 p.p. (F, GH, NY); Progreso, Km 31, Mérida rd, 21 July 1938 (fl), Lundell & Lundell 8012 (MICH); Progreso, 11-15 Aug 1932 (fl), Steere 3005, type of Dictyanthus aeneus (MICH, MO); at Km 28 on rd from Mérida to Progreso, 28 June 1971 (fl), Stevens 1145 (MSC).

10. Matelea yucatanensis (Standley) Woodson, Ann. Missouri Bot. Gard. 28: 237. 1941.

Dictyanthus yucatanensis Standley, Publ. Field Columbian Mus., Bot. Ser. 8: 37. 1930. Type: Gaumer 933 (F! holotype; G! fragment of holotype).

Plants twining vines. Stems woody below, with thin to thick corky bark, herbaceous and lacking bark above, with dense short and glandular trichomes and dense uncinate long trichomes to 2.5 mm long. Leaf blade ovate to wide-ovate or occasionally very-wide-ovate, (39-) 45-95 mm long, 24-81 mm wide, indumentum of uncinate long trichomes and also

glandular trichomes on veins below, surface smooth, apex acuminate to attenuate, base lobate, lobes mostly convergent to descending, with 4-10 acropetiolar glands, margin often crispate; petiole (22-) 42-57 (-82) mm long, with indumentum of stem. Inflorescence a simple cyme; peduncle 2-9 mm long, with indumentum of stem; bracts linear to lanceolate, 3-5 mm long, with indumentum of stem or sometimes with long trichomes on margin only and glabrous on adaxial surface; pedicel 3-5 (-7) mm long, with indumentum of stem. Calyx lobes lanceolate to narrow-ovate, 7-10 mm long, 2.0-3.5 mm wide, apex acute to attenuate, with one gland below each sinus, abaxial surface with scattered short trichomes, dense glandular trichomes, and scattered uncinate long trichomes or occasionally nearly glabrous, adaxial surface glabrous. Corolla campanulate, base to sinus length (7-) 10-11 mm, limb plane, revolute; lobes 7-12 mm long, length to width (sinus-sinus) ratio 0.83-1.20, apex acute, plane or slightly reflexed at tip, margin revolute; glabrous within except with sparse to dense short trichomes on limb and lobes, indumentum on outside of short, glandular, and uncinate long trichomes; tube convoluted with raised parts opposite corona lobes and forming deep sacs between them; densely grayish-purple-reticulated, reticulations wider in tube. Corona lobes (4-) 5-7 mm long, linear-spathulate in outline, with tip deeply rugose and glistening purplish-black, otherwise deep purple, connate at base, adnate to corolla and adnate by a thin wall to gynostegium, this wall continuing as a narrow ridge nearly the length of lobe. Gynostegium 3.0-3.5 mm high and 2.5-3.0 mm wide at apex, stipitate, apex broadly and shallowly concave with corpuscula as high points and occasionally also slightly convex in center, terminal anther appendages hardly covering margin of apex. Corpusculum

0.24-0.26 mm long, 0.12-0.15 mm wide, pollen sacs 1.11-1.26 mm long, 0.28-0.35 mm wide. Follicles fusiform, ca 95 mm long, ca 15 mm wide, finely mottled green and white, with scattered short and glandular trichomes, with ca 55 thick projections to 4 mm long. Seeds obovate, ca 4.5 mm long, ca 3.5 mm wide, with a raised, faintly radially grooved margin, this entire, inside this margin essentially flat on one side and convex on the other side, both sides deeply verrucate to deeply rugose, dark brown; coma ca 35 mm long. Figure 28.

DISTRIBUTION AND ECOLOGY. The identifiable collection localities are scattered in inland areas of the state of Yucatán at elevations probably well below 200 m. Figure 27. Almost certainly to be expected in the adjacent areas of Campeche and Quintana Roo. Growing in low forests and second growth and probably always in limestone-derived soils. Collected flowering June-July.

Three collections, Lundell & Lundell 7885, Steere 2120, and Stevens 1168, have insect damage to the leaves, probably caused by large lepidopteran larvae, but none of these insects have been found.

COMMON NAMES AND LOCAL USES. The only information available is the name boochin given on the label of Gaumer 933.

DISCUSSION. Most closely related to Matelea aenea. For a comparison of the two species, see the discussion under Matelea aenea. These two species form a distinct unit morphologically, and are geographically isolated from the other species of subgenus Dictyanthus. They are obviously related to the several species grouped with Matelea pavonii but have no clear affinities with any one of the species. Their most conspicuous innovation, besides occupying a unique region (Yucatán Peninsula) and a unique environment (karst limestone), is the highly

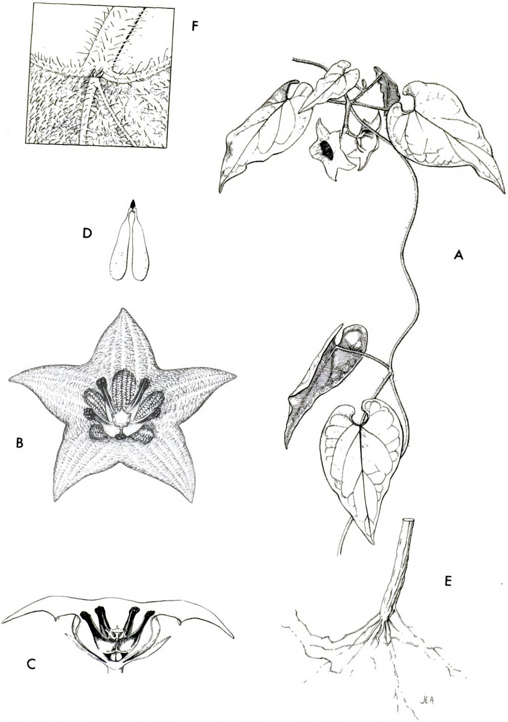


Figure 28. *Matelea yucatanensis* (drawn from Stevens C-158, a cultivated specimen of Stevens 1168).

A. section of flowering stem, x 0.6; B-C. flowers, x 2.3; D. pollinium, x 18; E. base of stem, x 0.6; F. base of adaxial surface of leaf blade, showing acropetiolar glands, x 6.

modified tip of the corona lobe. These tips glisten as if they were wet but apparently produce no secretion. They may function as a "pseudo-nectary" in the attraction of pollinators, probably dipterans. It should be noted, however, that the sides of the corona lobes are secretory in apparently the same manner as the species grouped with *Matelea pavonii*. The "pseudo-nectaries" then, may function as a visual attractant or may have some other function, such as producing an olfactory attractant, but the major attractant is probably still the nectar produced by the corona lobes. These two species are also unique in having predominantly uncinate long trichomes on the internodes, the other species considered here having either entirely straight or only occasionally a few uncinate long trichomes on the internodes.

SPECIMENS EXAMINED. *MEXICO*. YUCATAN: without precise locality and date (fl), *Gaumer 933*, type of *Dictyanthus yucatanensis* (F, G, fragment of F specimen); Buena Vista Xbac, without date (fl), *Gaumer 1173 p.p.* (F, 2 specimens); Chichankanab, without date (fl), *Gaumer 1544* (F), *1968* (F, GH); without precise locality and date (fl), *Gaumer et al. 803* (MICH); Chichên Itzá, near Xocenpich, June-July 1938 (fl), *Lundell & Lundell 7885* (MEXU, MICH); Chichên Itzá, 13 June 1932 (fl), *Steere 1294* (MICH); Chichên Itzá, near Xnaba cenote, 25 June 1932 (fl), *Steere 1548* (MICH, 2 specimens); Chichên Itzá, 25 June 1932 (fl), *Steere 1621 p.p.* (MICH), 29 June 1932 (fl), *Steere 1621 p.p.* (MICH, MO); Uxmal, 20-21 July 1932 (fl), *Steere 2082* (MICH); Muna, on high ridge, 22-23 July 1932 (fl), *Steere 2120* (MICH, MO); Peto, 26-27 July 1932 (fl), *Steere 2208* (MICH); along rd from Dzitás to Valladolid, ca 4.0 mi NW of Uayma, 1 July 1971 (fl), *Stevens 1168* (MSC); greenhouse-grown specimen of *Stevens 1168*, Aug 1974 (fr), *Stevens C-158-3* (MSC).

Species treatments (subgenus unassigned)

11. *Matelea altatensis* (Brandegee) Woodson, Ann. Missouri Bot. Gard. 28: 236. 1941.

Gonolobus altatensis Brandegee, Zoe 5: 244. 1908. Type: *Brandegee s.n.*, 10 Sep 1904 (UC! holotype; MO, 2 specimens, fragments of holotype!).

Plants twining vines. Stems woody below, with thin to thick corky bark, sometimes with a weakly developed woody caudex with thick corky bark, herbaceous and lacking bark above, with sparse to dense short, glandular, and long trichomes, the long trichomes to 3 mm long and mostly straight. Leaf blade wide-ovate or rarely very-wide-ovate, (35-) 45-75 (-87) mm long, (25-) 35-77 mm wide, with sparse glandular trichomes and sparse to occasionally dense, mostly uncinate long trichomes, surface pusticulate, especially above, apex acute to attenuate, base lobate, lobes mostly convergent, with (0-) 2-5 acropetiolar glands, margin occasionally somewhat thickened and revolute; petiole 25-52 mm long, with sparse to dense short, glandular, and long trichomes, long trichomes mostly uncinate. Inflorescence a simple or more often a compound cyme; primary peduncle (15-) 30-135 mm long, with sparse to dense short, glandular, and long trichomes, long trichomes straight or uncinate; bracts linear to lanceolate, 1.5-4.0 mm long, with indumentum of leaf; pedicel (6-) 12-28 mm long, with indumentum of peduncle. Calyx lobes lanceolate to ovate or occasionally elliptic, (2-) 4-6 mm long, 1.5-2.5 mm wide, apex acute to attenuate, with one gland below each sinus, abaxial surface with sparse glandular trichomes and sparse to dense, mostly uncinate long trichomes, adaxial surface

glabrous or with scattered glandular trichomes. Corolla shallowly campanulate, nearly rotate, base to sinus length 4-6 mm, limb not distinct, margin slightly or not at all revolute; lobes (2-) 4-7 mm long, apex acute to obtuse or rounded, slightly reflexed, margins slightly revolute; indumentum within of dense short trichomes except glabrous between corona lobes and especially dense around corona lobes and in a line above them, indumentum on outside of glandular and straight long trichomes, occasionally distal half of lobes nearly glabrous; tube convoluted, with raised parts opposite corona lobes and shallow pockets formed between them, with corona lobes in distinct pockets in bases of raised parts; pale greenish-white or sometimes also tinted yellowish, especially at base, with very faint to moderately dark green reticulations, mostly drying pale brown. Corona lobes ca 2 mm long, basically triangular in outline above, appressed side to side, adnate to gynostegium and adherent but not adnate to corolla. Gynostegium ca 2 mm high and ca 2 mm wide at apex, not markedly stipitate, apex plane or slightly convex, with a low ridge from each corpusculum to center, this formed from adjacent margins of terminal anther appendages which nearly or completely cover apex. Corpusculum 0.20-0.26 mm long, 0.15-0.18 mm wide, pollen sacs 0.78-0.88 mm long, 0.28-0.35 mm wide. Follicles fusiform, with a distinct basal flange on one side and apex often long and thin, 60-100 mm long, 13-20 mm wide, striped and mottled light and dark green, glabrous or with sparse short trichomes, with 18-34 (-44) arcuate to hooked projections to 8 mm long. Seeds obovate, 4-5 mm long, ca 2 mm wide, with a raised margin, this coarsely toothed, especially distally, inside this margin slightly convex and sparsely verrucate on one side, the other side slightly concave, verrucate, and with a narrow

ridge from apex to near center, dark brown; coma ca 35 mm long. Figures 29 and 30.

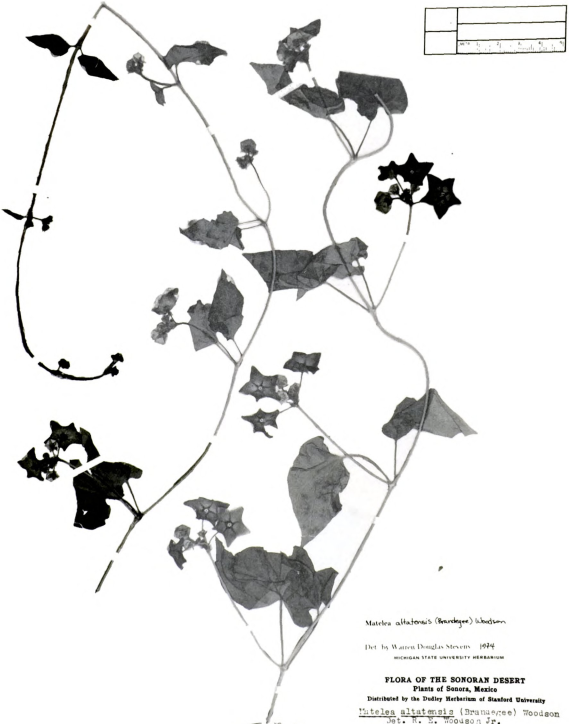
DISTRIBUTION AND ECOLOGY. *Matelea altatensis* has been collected from northern Sonora to central Sinaloa, but is to be expected farther south, southern Sinaloa being rather poorly collected. Figure 31. Most of the collections have been on the coastal plain at elevations of less than 50 m, but the northernmost localities are more inland and apparently up to about 500 m. This species is found in dry thorn forest in heavy clay soils or occasionally in sandy washes. Flowering specimens have been collected from late July to mid-September. Two collections with nearly mature fruits were made in September, and one specimen with completely mature fruits was made in February.

Only two of the 12 collections of this species have been made since the 1940's and it is probably not at all common. Particularly with the increased development of irrigation systems, the coastal plains of this part of Mexico are rapidly being cleared for agricultural purposes, especially for growing cotton. Suitable habitats for *Matelea altatensis* are already difficult to find near highways. Although the true abundance of this species cannot be known until its range is better explored, it may well be endangered.

Small orange lepidopteran larvae were found feeding on the flowers of *Stevens 2062*. These have not been reared or identified. A few other specimens showed similar damage to the flowers but no insect damage to the foliage has been found.

COMMON NAMES AND LOCAL USES. The only information available comes from the label on the specimen collected by Tays in 1912, which gives the local name *maguey* and the note, "young tender pods are eaten raw by

Figure 29. Representative specimen of *Matelea altatensis* (*Wiggins & Rollins 140*, A).



Matelea altatensis (Brandegee) Woodson

Det. by Warren Douglas Stevens 1974
MICHIGAN STATE UNIVERSITY HERBARIUM

FLORA OF THE SONORAN DESERT
Plants of Sonora, Mexico
Distributed by the Dudley Herbarium of Stanford University

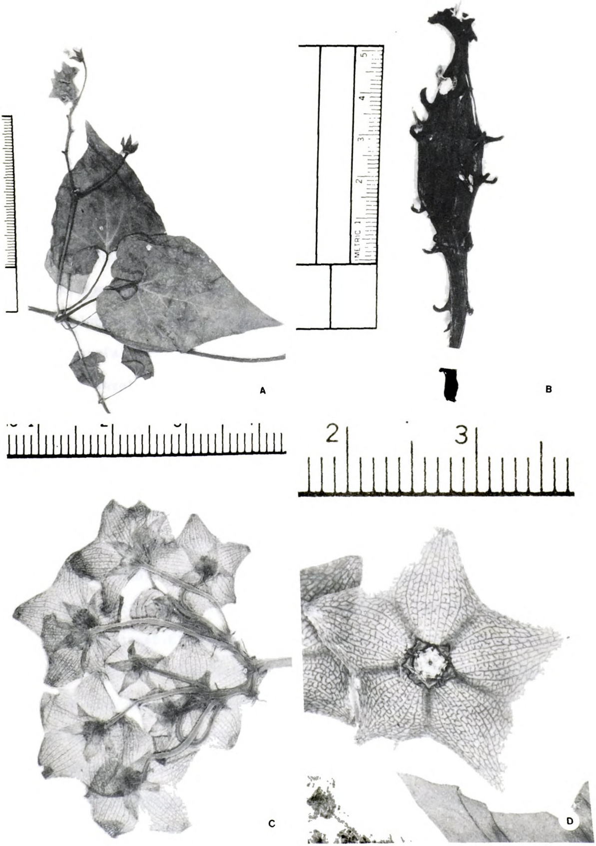
Matelea altatensis (Brandegee) Woodson
Det. R. E. Woodson Jr.

Vine, woody at base, climbing 15 to 20 ft. over *Acacia*; fls. yellowish-green; leaves very thin; llano, 27 miles west of Hermosillo on the road to Kino Bay. Alt. 720 ft.

IRA L. WIGGINS & REED C. ROLLINS 140 28 August, 1941

Figure 30. Representative features of Matelea altatensis.

A. leaves and old inflorescence, Stevens 2062 (MSC); B. fruit, Wiggins & Rollins 259 (MO); C. inflorescence, Wiggins & Rollins 140 (ARIZ); D. flower, Wiggins & Rollins 140 (A).


A
METRIC 1
2
3
4
5
B
2
3
C
D

the natives."

DISCUSSION. Although Woodson (1941) included this species in his subgenus Dictyanthus, it lacks the major character that has been used to distinguish the group, the adnation of the digitate corona lobes to the corolla. The corona lobes of this species (in size, shape, and position) are much like those of Matelea tuberosa and M. hemsleyana, but in these species the corona lobes are adnate for their full length to the corolla. The corona lobes of Matelea altatensis are appressed to or perhaps even connivent with the corolla and it may be a small step to complete adnation. I have made a preliminary examination of the developmental stages of Matelea hemsleyana and it will be interesting to carefully study the three species together to see if there are any basic developmental differences. Three other characters can more readily be used to distinguish this species from subgenus Dictyanthus. (1) This is the only species considered here in which the terminal anther appendages essentially cover the style apex. In dried flowers these appendages often shrink somewhat, leaving an uncovered spot in the center, but because of the drying become white and easily observable (Figure 30D). In fresh flowers the appendages are translucent and more difficult to see. (2) Also unique among the species considered is the distinct basal flange on one side of the follicle (Figure 30B). (3) This species differs from those I have included in Dictyanthus, but compares with the other two species I am treating but have not included, in having an inflorescence which is, or at least can become, a compound rather than a simple cyme. Although this species could be added to subgenus Pachystelma, I prefer not to make a descision until the status of that subgenus is better understood.

Within the geographic range of *Matelea altatensis*, there are two species of *Matelea* not treated here which could be confused with it in fruiting condition. *Matelea pringlei* (A. Gray) Woodson, which may actually be restricted to Baja California, differs in having longer, thinner, and straight rather than arcuate projections on the follicles and the follicles lack the basal flange. *Matelea caudata* (A. Gray) Woodson differs in having shorter and thicker follicles which again lack the basal flange. *Matelea caudata* also tends to be shrubby rather than viney.

SPECIMENS EXAMINED. *MEXICO*. SONORA: Torres, 6 Feb 1903 (fr), *Coville 1627* (US); 0.2 mi N of Km marker 2231 and ca 0.2 mi N of side rd to Querobabi, Hwy 15, 28 July 1969 (fl), *Mason 2895* (ARIZ, CAS, NY); Bacum Station, near Río Yaqui, 30-40 m, 7 Sep 1935 (fl), *Pennell 20207* (GH, MICH, NY, PH, US); ca 2.2 mi NE of Hwy 15, ca 6.9 mi SE of Ciudad Obregon, 12 Sep 1973 (fl & fr), *Stevens 2062* (MSC); 27 mi W of Hermosillo on rd to Kino Bay, 720 ft, 28 Aug 1941 (fl), *Wiggins & Rollins 140* (A, ARIZ, DS, MO, ND, NY, TEX, UC, US); 5 mi N of Suhuoral, 18 mi W of El Camino Nacional (Hermosillo-Guaymas), 3 Sep 1941 (fl & fr), *Wiggins & Rollins 259* (A, ARIZ, DS, MO, 2 specimens, ND, NY, UC, US). SINALOA: vicinity of Culiacan, Yerba Buena, 10 Sep 1904 (fl), *Brandegee s.n.*, type of *Gonolobus altatensis* (MO, 2 specimens, fragments of UC specimen, UC); Culiacan, 17 Sep 1904 (fl), *Brandegee s.n.* (POM); Culiacan and vicinity, volcanic cerro and valley, 150-500 ft, Sep 1944 (fl), *Gentry 7065* (GH); Maraton, 12 mi W of Culiacan, 100 ft, 21 Sep 1944 (fl), *Gentry 7086* (GH, MICH, NY); Los Mochis, July 1912 (fl), *Tays s.n.* (US). STATE UNKNOWN: without locality and date (fl), *Sessé*, *Mociño*, *et al. 1301* (F, fragment, MA, not seen, photo from F neg. 41451 at

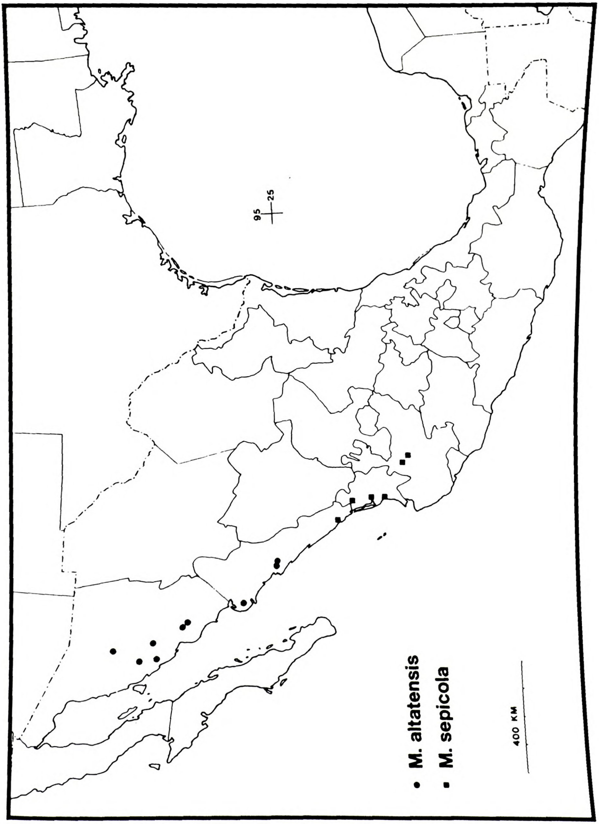


Figure 31. Distribution of Matelea altatensis and M. sepicola.

MSC), 3570 (F, fragment, MA, not seen, photo from F neg. 41452 at MSC).

12. Matelea sepicola W. D. Stevens, Phytologia 32: 387-392. 1975. Type: Stevens 1436 (MSC! holotype).

Plants twining vines. Stems essentially herbaceous and lacking bark except with a woody caudex with thick corky bark, with dense short and glandular trichomes and moderately dense to dense, mostly straight long trichomes to 3 mm long. Leaf blade wide-ovate or occasionally ovate or very-wide-ovate, 35-85 (-105) mm long, 23-85 mm wide, indumentum of dense, or occasionally sparse above, uncinate long trichomes, surface pusticulate to minutely pusticulate or occasionally nearly smooth, smaller veins often slightly to sharply raised below, apex acuminate to attenuate, base lobate, lobes convergent to divergent, with 0-3 (-5) acropetiolar glands, margin often slightly thickened and revolute; petiole (19-) 28-72 (-88) mm long, with dense short and glandular trichomes and sparse to dense, mostly uncinate long trichomes. Inflorescence a simple or more often a compound cyme; primary peduncle mostly 2-4 mm long, but occasionally with an inflorescence branch originating at or near the base of the apparent peduncle (Figure 33C), with dense short and glandular trichomes and moderately dense to very sparse, straight or uncinate long trichomes, or occasionally long trichomes absent; bracts linear to lorate or lanceolate, 1-2 mm long, abaxial surface with dense short and glandular trichomes and moderately dense to dense, straight or uncinate long trichomes, adaxial surface glabrous; pedicel 1.5-3.5 mm long, with indumentum of peduncle. Calyx lobes narrow-ovate, 3-5 mm long, 1.5-2.5 mm wide, apex attenuate, with

one gland below each sinus, abaxial surface with sparse to moderately dense uncinate long trichomes, adaxial surface glabrous. Corolla urceolate, base to sinus length 3-5 mm, limb slightly reflexed and slightly revolute; lobes 2.5-4.5 mm long, apex acute to obtuse, slightly reflexed and slightly revolute; glabrous within, indumentum outside of moderately dense straight long trichomes on limb and lobes; tube with a pair of ridges inside opposite each corona lobe; with reddish-brown vertical lines within tube, these becoming circular and reticulated on limb and lobes but partially obscured by the green or greenish-brown background. Corona lobes 1.5-3.0 mm long, shape elaborate but basically thickly laminar and rhombic in lateral view, adnate or tightly connivent along axis to corolla (between ridges) for part of length but tip free above, adnate to gynostegium along axis by a narrow wall, loosely to tightly appressed side to side, lateral tips sometimes slightly thickened, giving lobes a trilobed appearance from above. Gynostegium 1.5-3.0 mm high and 1.5-2.0 mm wide at apex, slightly stipitate, apex broadly and shallowly concave and slightly convex and bilobed in center, corpuscula slightly exceeding convex center, terminal anther appendages covering nearly half of apex. Corpusculum 0.20-0.25 mm long, 0.08-0.09 mm wide, pollen sacs 0.62-0.72 mm long, 0.34-0.43 mm wide. Follicles fusiform, (44-) 54-74 mm long, 12-20 mm wide, green with white stripes, with dense short trichomes and occasionally with very sparse glandular trichomes, with 22-37 (-48) projections, these thick, straight or arcuate, to 4 mm long. Mature seeds unknown; immature seeds obovate, to 4 mm long, to 3 mm wide, irregularly toothed distally, both sides verrucate to rugose, dark brown; coma to 30 mm long. Figures 32 and 33.

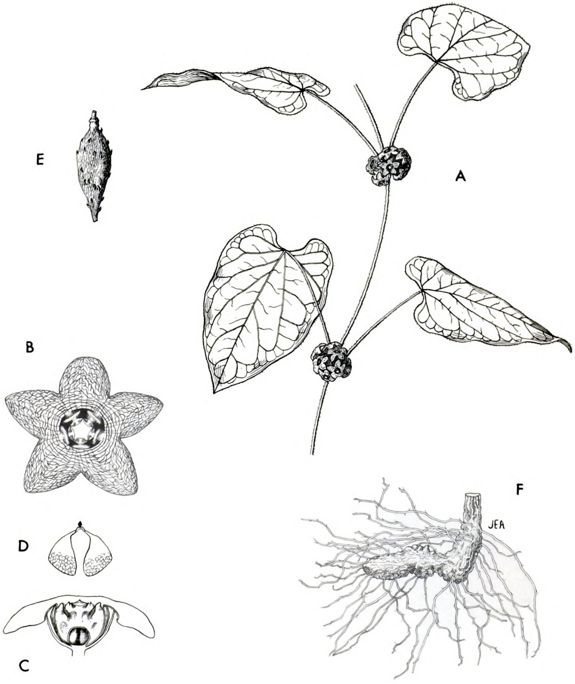
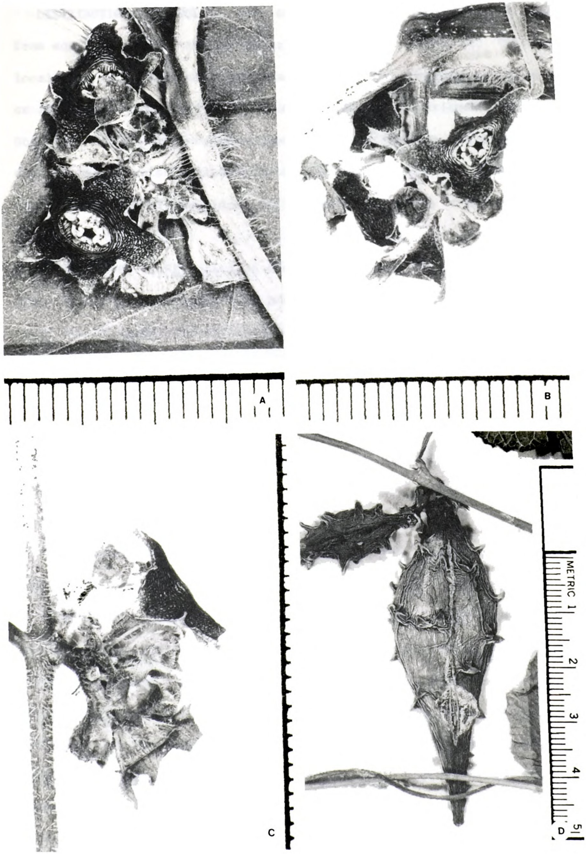


Figure 32. Matelea sepicola (drawn from Stevens 1436).

A. section of flowering stem, x 0.6; B-C. flowers, x 3.5;
D. pollinium, x 24; E. fruit, x 0.6; F. caudex, x 0.6.

Figure 33. Representative features of Matelea sepicola.

A. inflorescence, note parallel vertical lines within corolla, Stevens 1436 (MSC); B. inflorescence, note method of adnation of corona lobes, Stevens 1436 (MSC); C. inflorescence, one petiole removed, note inflorescence branch originating near base of apparent peduncle, Stevens 1895 (MSC); D. immature fruit, Pringle 5439 (F).


A
B
METRIC 1
2
3
4
5
C
D

DISTRIBUTION AND ECOLOGY. The six known collection localities range from southern Sinaloa through Nayarit to Jalisco. Figure 31. The four localities in Nayarit and Sinaloa are apparently at elevations of 30 m or less and the two in Jalisco at about 1300 m. Flowering August-October. Mature-sized fruits collected in September and November and old, dehisced fruits collected in June and September. The known habitats are fencerows, roadsides, and thickets, hence the origin of the epithet.

A few leaves of Stevens 1436 and 2038 had minor chewing insect damage. One fruit of Pringle 5439 had the seeds partially eaten but I could not determine whether this occurred before or after the specimen was collected. No pollination activity was observed but this species appears to produce significantly more nectar than the other species considered and also appears to produce more fruits, only one of the seven collections lacked fruits in some stage of development. A higher level of seed production might be expected from a species occupying such an ephemeral habitat.

COMMON NAMES AND LOCAL USES. The label of Mexia 1060 notes the name taquarinde for this species. No other names or uses are known.

DISCUSSION. Woodson recognized this as an undescribed species by his undated annotation "Matelea (Macroscepis) n.sp." on Ferris 5506 at DS, but annotated another collection, Pringle 5439 at F, as Matelea reticulata (Engelmann) Woodson, probably because the label determination was "Gonolobus reticulatus, Engelm., (with short peduncles)." Matelea reticulata is quite a different species both in morphology (Woodson [1941] placed it in his subgenus "Eumatelea") and in range, being found in northeastern Mexico and adjacent United States. As

certainly as this species is distinct from _Matelea_ _reticulata_, it also does not belong to subgenus _Macroscepis_, even as Woodson (1941) conceived it. The six species Woodson referred to _Macroscepis_ form an unnatural assemblage of which the type element probably deserves generic status. There are at least two other distinct groups represented in the subgenus, but all the other species are probably appropriately placed in the genus _Matelea_. _Matelea_ _sepicola_ appears to have closer affinities with subgenus _Dictyanthus_ than with any species Woodson included in _Macroscepis_. Despite the differences in corolla shape, urceolate rather than campanulate, and the proportionately broader corona lobes, the flowers are much like those of _Dictyanthus_, especially with respect to the position and mode of adnation of the corona lobes. The vegetative features, including the indumentum, and the nature of the fruit are identical with those of _Dictyanthus_ and distinct from most of the rest of _Matelea_. Until _Matelea_ is better studied, I prefer not to assign this species to any of Woodson's subgenera.

SPECIMENS EXAMINED. _MEXICO_. SINALOA: ca 2.0 mi SW of Hwy 15 along rd to Chametla, ca 5 mi S of Rosario, 10 Sep 1973 (fl & fr), _Stevens_ _2038_ (MSC). NAYARIT: vicinity of San Blas, first hill on old Spanish rd to Tepic, 13 Oct 1925 (fl), _Ferris_ _5506_ (DS, US); Tuxpan, Palapar Redondo [labelled as state of Jalisco], 20 m, 6 Nov 1926 (fr), _Mexia_ _1060_ (UC); Acaponeta, 23-30 June 1897 (fr), _Rose_ _3122_ (US). JALISCO: hills near Tequila, 26 Sep 1893 (fl & fr), _Pringle_ _5439_ (F, MO, US); ca 6.9 mi SW of Hwy 15 along rd to Ameca, near dirt rd leading N, 23 Aug 1971 (fl), _Stevens_ _1436_, type of _Matelea_ _sepicola_ (MSC), 2 Sep 1973 (fl), _1895_ (MSC).

13. Matelea aspera (Miller) W. D. Stevens, Phytologia 32: 396. 1975.

Cynanchum asperum Miller, Gard. Dict., ed. 8, no. 6. 1768. Type: Houstoun s.n. (BM, not seen, holotype, photos from BH neg. 5251 at MICH! & US!).

Gonolobus littoralis Decaisne in de Candolle, Prodr. 8: 596. 1844. Type: Galeotti 1545 (P! holotype; G! isotype, F! fragment of G isotype! photo from F neg. 26924 of G isotype at MO!).

Vincetoxicum littorale (Decaisne in de Candolle) Standley, Contr. U. S. Natl. Herb. 23: 1188. 1924.

Vincetoxicum megacarphum Brandegee, Univ. Calif. Publ. Bot. 4: 381. 1913. Type: Purpus 6014 (UC! holotype; F! G, 2 specimens, 1 a fragment of F specimen! GH! MO, 3 specimens, 2 are fragments, probably of UC specimen! NY! P! isotypes).

Matelea megacarpha (Brandegee) Woodson, Ann. Missouri Bot. Gard. 28: 236. 1941.

Pachystelma cordatum Brandegee, Univ. Calif. Publ. Bot. 7: 330. 1920. Lectotype: Purpus 8508 [UC no. 204968, not Purpus 8008 of protologue] (UC! lectotype, mixed with sterile Matelea sp.).

Dictyanthus brachistanthus Standley, Publ. Field Columbian Mus., Bot. Ser. 8: 38. 1930. Lectotype: Heyde & Lux ex J. D. Smith 6346 (F! lectotype, mixed with sterile, probably apocynaceous, vine, photo from F neg. 51447 of F specimen at F!; G! GH, mixed collection! K! MO! NY! US, 2 specimens, 1 a mixed collection! isolectotypes).

Plants twining vines. Stems woody and with thick corky bark below, at least at the base, herbaceous and lacking bark above, with dense short and glandular trichomes and dense to essentially absent, mostly straight long trichomes to 2 mm long. Leaf blade ovate to wide-ovate or occasionally narrow-ovate or very-wide-ovate, 31-98 (-122) mm long, 18-75 (-102) mm wide, indumentum above of sparse to moderately dense uncinate long trichomes and short trichomes on major veins, indumentum below of moderately dense to dense uncinate long trichomes, surface pusticulate to smooth, smaller veins slightly raised below or not, apex acuminate to attenuate, base lobate, lobes convergent to widely divergent, with 2-8 acropetiolar glands, margin often slightly thickened and revolute; petiole 15-70 mm long, with dense short and glandular trichomes and dense to essentially absent, mostly uncinate long trichomes. Inflorescence a simple or more often a compound cyme; primary peduncle 3-31 (-65) mm long, with dense short and glandular trichomes and dense to essentially absent, straight or uncinate long trichomes; bracts linear to lanceolate or lorate, 2-5 (-6) mm long, abaxial surface with dense short and straight or uncinate long trichomes, adaxial surface with sparse short trichomes or glabrous; pedicel 5-13 mm long, with indumentum of peduncle. Calyx lobes lanceolate to narrow-ovate or rarely ovate, (3.5-) 5-10 mm long, (1-) 2.0-3.5 (-4) mm wide, apex attenuate, one or occasionally two glands below each sinus, abaxial surface with sparse to dense straight or uncinate long trichomes, surface often pusticulate, adaxial surface glabrous. Corolla shallowly campanulate, nearly rotate, base to sinus length 4-9 (-11) mm, limb broad, hardly distinct from short tube, margin slightly revolute; lobes 3.5-8.0 mm long, apex rounded or occasionally acute or obtuse, plane to somewhat

reflexed, margin slightly revolute; indumentum within of dense, very small short trichomes except glabrous at base between corona lobes and especially dense in lines above corona lobes, glabrous outside or with sparse to moderately dense short and sparse straight long trichomes on distal part of limb and bases of lobes, with shallow pockets alternate with corona lobes; background color very pale green (drying cream-white) to deep brownish-green, reticulations from essentially absent on palest backgrounds to dense on darker backgrounds, reticulations purple to brownish-purple. Corona lobes (1.5-) 2-3 (-4) mm long, ovate in outline from above, inflated, with a small tooth on inner surface, lower half adnate to corolla, free above, adnate to base of gynostegium, connate at base and forming a fleshy disc partially distinct from lobes. Gynostegium (1.5-) 2-3 (-3.5) mm high and (1.5-) 2-3 mm wide at apex, slightly and shortly stipitate, anther wings prominent, apex essentially flat, terminal anther appendages covering ca half of apex. Corpusculum 0.23-0.29 mm long, 0.20-0.26 mm wide, pollen sacs 0.89-1.04 mm long, 0.34-0.43 mm wide. Follicles fusiform, 62-87 (-113) mm long, 12-18 (-27) mm wide, apparently dark purplish-red or nearly black when mature but drying to lighter colors, with moderately dense to dense short trichomes, with 18-34 (-46) projections, these straight or slightly arcuate, mostly thick and blunt, to 5 or rarely even 7 mm long. Seeds obovate, 4-5 mm long, 2.0-3.5 mm wide, with a raised, radially grooved margin, this entire or irregularly toothed, especially distally, one side convex and shallowly to deeply verrucate to rugose, other side concave and deeply rugose, with a shallow ridge from apex to near center, dark brown; coma 25-30 mm long. Figure 34.

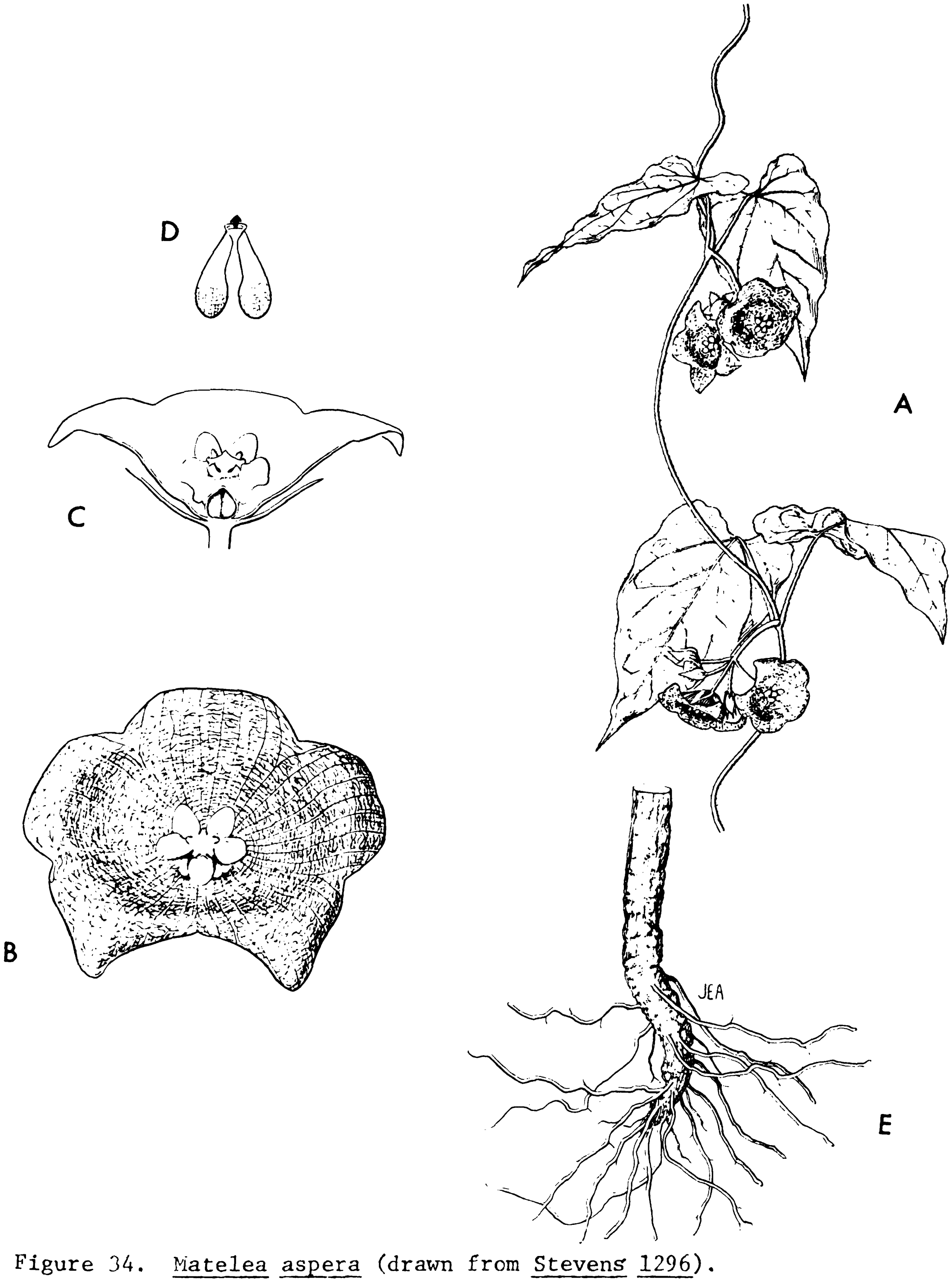


Figure 34. Matelea aspera (drawn from Stevens 1296).

A. section of flowering stem, x 0.6; B-C. flowers, x 2.3; D. pollinium, x 18; E. base of stem, x 1.2.

DISTRIBUTION AND ECOLOGY. Occurring from Jalisco and Colima southeastward to central Nicaragua. Figure 35. The areas where this species has been collected are rather widely spaced northwest of the Isthmus of Tehuantepec but are more continuous southeastward. Found from sea level to about 1000 m. Tolerant of a variety of substrates, including limestone derived soils and beach sands, and a variety of communities, including pine forests at the highest elevations, but most commonly collected in disturbed thorn forests with clay soils. Flowering mostly June to October, but collected flowering once in December and once in February. Considering the number of collections of this species, I doubt the validity of the isolated flowering date in February, especially since the specimens concerned appear to be in early stages of flowering. The later flowering dates tend to be from plants of southeast of the Isthmus of Tehuantepec. Mature-sized fruits collected July-March.

The following collections showed significant chewing insect damage to the leaves: *Davidse & Pohl 2407*, *Emrick 224*, *Heyde & Lux ex J. D. Smith 6346*, *Hinton 8189*, *King 1726*, *1755*, *1892*, *MacDaniels 452*, *McVaugh 19805*, *25314*, *Molina R. 4065*, *Nelson 2824*, *Purpus 6014*, *Standley 11474*, *11648*, *78852*, *78871*, *Stevens 1296*, *1406*, and *Valerio R. 3473*. Many of the fruits of *McVaugh 25314* had conspicuous scars on the outside and the developing seeds were being eaten by weevil larvae. A number of these fruits were brought back to the United States (by me) and after several months the adults emerged. Dr. Daniel H. Janzen has identified the weevil as belonging to the genus *Rhyssomatus*. I also collected similar weevils from *Sarcostemma pannosum* (*McVaugh 24282*) and *Marsdenia coulteri*? (*McVaugh 25285*). This weevil is apparently also a seed

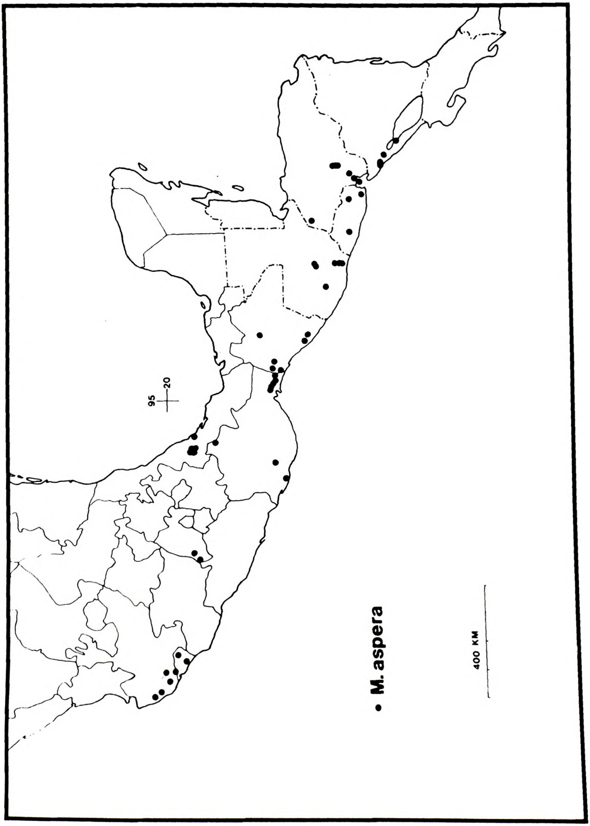


Figure 35. Distribution of Matelea aspera.

predator of Asclepias in Michigan (Janzen, pers. comm.).

No pollination activity has been observed but many pollinia were missing from the flowers I examined and this species appears to produce relatively more fruits than most of the other species considered.

COMMON NAMES AND LOCAL USES. The name atuz has been recorded from the state of México (Hinton 8189). From Honduras the names champerra (Standley 27100), chanchito (Standley 27181), and siempreviva (West 3537) have been noted. No local uses are known.

DISCUSSION. Matelea aspera has the greatest geographic range of the species treated here and is the most variable in appearance. Most of the variation, however, is in the size and coloration of the corolla. There is nearly a three-fold difference in the range of corolla sizes; the largest-flowered specimens are found in the Pacific coastal lowlands of the Isthmus of Tehuantepec, and the plants from the mountains of Chiapas southeastward are rather uniformly small-flowered. Corolla color varies considerably, even within populations, but the palest corollas with faint or no reticulations are all found on Mexican plants and again the plants from the mountains of Chiapas southeastward are rather uniformly dark-colored. The northwestern part of the range tends also to have more substantially woody plants while to the southeast the plants tend to perennate from near ground level. Most of the other characters of the species have less well-marked regional variation and the corona, in particular, appears to be remarkably uniform throughout the range.

The type of Cynanchum asperum is apparently from a specimen cultivated by Miller from seeds sent from Veracruz by Houstoun in about 1730. I have seen only photographs of the holotype, but Dr. Garrett E.

Crow compared the specimen, at BM, with samples of my material and confirmed its identity.

Through an apparent printer's error, the protologue of *Pachystelma cordatum* gives the type collection as *Purpus 8008*, but the UC accession number given corresponds to the marked type specimen, *Purpus 8508*. Unfortunately, *Purpus 8508* is a mixed collection. The majority of the sheet is *Matelea aspera*, but there is a sterile shoot and an isolated leaf of a second species of *Matelea*. The sterile specimen apparently did not influence the type description and I have therefore chosen the fertile element as the lectotype. It is interesting to note that even the fertile element has only very immature flower buds; this might explain why Brandegee failed to recognize that his new genus and species were the same as *Vincetoxicum megacarphum*, which he had described seven years earlier from another Purpus collection from near the same locality. Brandegee (1922) augmented his type description of *Pachystelma cordatum* by describing the fruit of a specimen from the type locality; he did not cite the collection number and I have seen no specimen of this species, other than the holotype, from the type locality.

In the case of the mixed collection of *Dictyanthus brachistanthus*, it appears that Standley based the vegetative aspects of the description on the sterile, probably apocynaceous, vine and based the description of the inflorescence and flowers on the element representing *Matelea aspera*. The name could probably be rejected on the basis of Article 70 of the International Code of Botanical Nomenclature (Stafleu et al., 1972), but on the basis of Standley's apparent intent, I have chosen to follow Article 9 and designate the fertile element as the lectotype.

This is the type species of Woodson's (1941) Matelea subgenus Pachystelma. The previous two species, Matelea sepicola and M. altatensis, could be loosely allied with M. aspera, but the other two species Woodson included in the subgenus appear to be more distantly related. I am reluctant to add Matelea sepicola and M. altatensis to subgenus Pachystelma primarily because all these species have clear affinities with subgenus Matelea section "Reticulatae" and the subgenus Heliostemma. An adequate assessment of the subgenera of Matelea must await careful studies of more of the constituent species.

SPECIMENS EXAMINED. MEXICO. JALISCO: steep ravines in gorge of Río Cihuatlán, below bridge 13 mi N of Santiago, Colima, 175-200 m, 3 July 1957 (fl), McVaugh 15941 (MICH, 2 specimens); mountains 3 mi above (S of) La Huerta, rd to Barra de Navidad, 500-550 m, 3 Oct 1960 (fl & fr), McVaugh 19805 (MICH, 2 specimens); near new rd ca 25 km NW of Río San Nicolás and 20 km SE of Tomatlán, 90-150 m, 11-12 Dec 1970 (fr), McVaugh 25314 (MICH, MSC); ca 7 km S of Tomatlán toward Manzanillo-Puerto Vallarta rd, 30-50 m, 15 Feb 1975 (fr), McVaugh 26304 (MICH); 0.5 mi N of La Resolana, 22 mi SSW of Autlán, ca 1000 ft, 11 Aug 1949 (fl), Wilbur & Wilbur 2253 (MICH). COLIMA: Paso del Río, Nov 1906 (fr), Emrick 224 (F); Colima, Aug 1897 (fl), Palmer 164 (MICH, US). MEXICO: Dist. Temascaltepec, Bejucos, 610 m, 26 Aug 1932 (fl), Hinton 1476 (GH, US); Dist. Temascaltepec, Chorrera, 7 Mar 1934 (fr), Hinton 5741 (K), 19 Aug 1935 (fl), 8189 (K, US). VERACRUZ: "dunes de Vera Cruz," June-Oct 1840 (fl), Galeotti 1545, type of Gonolobus littoralis (F, fragment of G specimen, G, photo from F neg. 26924 of G specimen at MO, P); "E. Vera Cruz," 1730 (fl), Houstoun s.n., type of Cynanchum asperum (BM, not seen, photos from BH neg. 5251 at MICH & US); vicinity

of Palmar, ca 3200 ft, 3 Sep 1935 (fl), *MacDaniels 452* (F); Baños del Carrizal, Aug 1912 (fl), *Purpus 6014*, type of *Vincetoxicum megacarphum* (F, G, 2 specimens, 1 a fragment of F specimen, GH, MO, 3 specimens, 2 are fragments, probably of UC specimen, NY, P, UC); Acaxónica, Aug 1919 (fl), *Purpus 8508*, lectotype of *Pachystelma cordatum* (UC, mixed with sterile *Matelea* sp.); ca 4.5 mi W of Palmilla along hwy through Huatusco, 10 Aug 1971 (fl), *Stevens 1406* (MSC). OAXACA: on Hwy 190, 1.5 mi SE of Niltepec, ca 50 m, 11 July 1972 (fl), *Denton 1776* (MICH, MSC, WTU); 9 mi W of Zanatepe [Zanatepec], 17 Aug 1971 (fl), *Dwyer et al. 755* (MO); 5 mi E of Temascal (10 mi W of Veracruz border), ca 45 ft, 25 Oct 1963 (fr), *Janzen s.n.* (MICH); along Hwy 190, 2 km S of Niltepec, 50 m or less, 17 July 1959 (fl), *King 1726* (TEX), *1752* (TEX), *1755* (MICH, NY, TEX, US); along Hwy 190, 2 km E of Zanatepec, 50 m or less, 21 July 1959 (fl), *King 1892* (MICH, NY, TEX, UC, US); Santa Efigenia, 500 ft, 18 July 1895 (fl), *Nelson 2824* (GH); 70 km (by rd) SE of Pinotepa Nacional on rd to Puerto Escondido, ca 150 m, 23 July 1965 (fl), *Roe et al. 521* (WIS); near bridge ca 4.0 mi SE of Zanatepec on Hwy 190, 21 July 1971 (fl), *Stevens 1296* (MSC); along Hwy 131 ca 3.6 mi N of river bridge near Juchatenango, 27 July 1971 (fl), *Stevens 1363* (MSC). CHIAPAS: slopes on bank of Río Lagas 4 mi SW of Soyala [?Soyaló] along rd to Pan American Hwy, 3400 ft, 26 July 1964 (fl), *Breedlove 6557* (DS, F, MICH, US); slopes S of Tapanatepec, near Oaxaca-Chiapas state line, 200 ft, 25 Aug 1967 (fl), *Clarke 462* (DS); Miramar, 11 Aug 1937 (fl), *Matuda 1624* (MEXU, MICH, 2 specimens, MO, NY); Aguas Calientes, Escuintla, 21 June 1947 (fl), *Matuda 16628* (F, MO); Jalapa, Triunfo, Escuintla, 900 m, 10 July 1948 (fl & fr), *Matuda 18103* (F); Playa Cintalapa, Escuintla, 2 June 1949 (fl), *Matuda 18657* (F); Valley of

Jiquipilas, 2200-2800 ft, 16-18 Aug 1895 (fl), *Nelson 2937* (US, mixed with *Matelea quirosii*); plains near Monserrate, July 1925 (fl), *Purpus 10232* (US); rocky plains, Monserrate, June [?1930] (fl), *Purpus 10615* (UC); Monserrate, June [?1930] (fl), *Purpus 10638 p.p.* (US); rocky plains, Monserrate, June-July [?1930] (fl), *Purpus 10638 p.p.* (UC). STATE UNKNOWN: without locality and date (fl), *Sessé, Mociño, et al. 1300* (F, fragment, MA, not seen, photo from F neg. 41465 at MSC), *8568* (MA, not seen, photo from F neg. 41466 at MSC). *GUATEMALA*. EL PROGRESO: along rd between San Gerónimo and Morazán, near Baja Verapaz line, 1000 m, 9 Oct 1942 (fl), *Steyermark 52133* (F, MO). GUATEMALA: 10 km NE of Motúfar, rdside, 15 July 1970 (fl), *Harmon & Dwyer 3066* (UMO). QUICHE: without precise locality, 1942 (fl), *Ignacio A. 1363* (F). SANTA ROSA: plains of Llano Entero, SE of Chiquimulilla, ca 150 m, 30 Nov 1940 (fr), *Standley 78852* (F); region of La Morenita, NE of Chiquimulilla, ca 400 m, 1 Dec 1940 (fl), *Standley 78871* (F); along Avellana rd, S of Guazacapán, ca 150 m, 6 Dec 1940 (fr), *Standley 79422* (F). SOLOLA: Atitlán, 600 m, Feb 1894 (fl), *Heyde & Lux ex J. D. Smith 6346*, lectotype of *Dictyanthus brachistanthus* (F, mixed with a sterile, probably apocynaceous, vine, photo from F neg. 51447 of F specimen at F, G, GH, mixed collection, MO, NY, US, 2 specimens, 1 a mixed collection). *EL SALVADOR*. MORAZAN: along ditch to reservoir, Monte Cristo, 9 Dec 1941 (fl), *Tucker 497* (UC). SAN MIGUEL: NW of Hacienda Potrero Santo, ca 0.1-0.8 km, S side of Lake Olomega, 13°17'N, 88°04'W, ca 60 m, 2 Feb 1942 (fr), *Tucker 881* (UC). SAN SALVADOR: San Salvador, 1922 (fl), *Calderón 781* (US). DEPARTMENT UNKNOWN: between San Sabastián and Aculhuaca, 1922 (fl), *Calderón 1182* (US). *HONDURAS*. CHOLUTECA: vicinity of Pespire, 160-200 m, 18-27 Oct 1950 (fl),

Standley 27100 (F), 18-27 Oct 1950 (fr), *27181* (F). COPAN: along Copán river between Sta. Rita and Jaral, 700 m, 21 Aug 1971 (fl), *Molina R. 26209* (F, US). EL PARAISO: drainage of Río Yeguare (ca 87°W, 14°N), entre Mata Indio y Lizapa, 950 m, 25 July 1951 (fl), *Molina R. 4065* (F, GH, US). MORAZAN: drainage of Río Yeguare (ca 87°W, 14°N), Yeguare River, 2600 ft, 16 July 1948 (fl), *Glassman 1919* (F, ILL, MIN, NY); drainage of Río Yeguare (ca 87°W, 14°N), along Jicarito Creek, near Jicarito, 950 m, 13 Aug 1947 (fl), *Molina R. 481* (F); vicinity of El Zamorano, 780-900 m, 3-17 Aug 1947 (fl), *Standley 11593* (F), *11648* (F), *11726* (F); above El Zamorano, rd from Jicarito toward El Pedregal, ca 875 m, 14 Aug 1947 (fl), *Standley 12236* (F); vicinity of El Zamorano, ca 800 m, 6 Oct 1948 (fl), *Standley 12878* (F); near Santa Clara, valley of Río Yeguare, E of El Zamorano, ca 850 m, 19 Oct 1948 (fl), *Standley 13187* (F); trail from La Quince, El Zamorano, to El Jicarito, 800-900 m, 15 July 1949 (fl), *Standley 21286* (F); near El Jicarito, along rd toward El Pedregal, ca 900 m, 24 July 1949 (fl), *Standley 21637* (F); vicinity of El Zamorano, 800-850 m, 26 July 1949 (fl), *Standley 21736* (F); region of Río de Orilla, SE of El Zamorano, 900-950 m, 11 Aug 1949 (fl), *Standley 22446* (F, GH); along Quebrada El Gallo above El Jicarito, 900-1000 m, 12 Aug 1949 (fl), *Standley 22517* (F); vicinity of El Zamorano, 800-850 m, 16 Aug 1949 (fl), *Standley 22686* (F); along rd from El Zamorano toward Chagüite, ca 800 m, 5 Aug 1950 (fl), *Standley 26279* (F, GH, US); mountains above El Jicarito, 950 m, 21 Aug 1951 (fl), *Standley 28638* (US); Camino Sn. Antonio, 850 m, 21 Oct 1943 (fl), *Valerio R. 1345* (F, MO); vicinity of El Zamorano, along rd to Chagüite, ca 2200 ft, 23 July 1962 (fl & fr), *Webster et al. 12523* (MO); drainage of Río Yeguare (ca 87°W, 14°N), ca 3 km E of

Chagüite, 850 m, 25 Sep 1949 (fl), Williams 16873 (F, GH). VALLE: Salamar Beach, 2 km E of San Lorenzo, Fonseca Gulf, 0 m, 3 Oct 1968 (fl), Molina R. & Molina 22762 (DS, F, G, 2 specimens, MO, NY); San Lorenzo, 20 m, 13 Sep 1945 (fl), Valerio R. 3473 (F, 2 specimens, GH, MO); lower slopes of El Tigre volcano, above Ampala [Isla El Tigre], 50 m, 16 Sep 1935 (fl), West 3537 (GH). NICARAGUA. GRANADA: "Grenade de Nicaragua," Autumno 1869 (fl), Lévy 1071 (P). LEON: Volcán Santa Clara near Hwy 26 [?Volcán Rota], 600 m, 19 July 1970 (fl), Davidse & Pohl 2407 (MSC). CHINANDEGA: Ameya, near sea level, 19-21 June 1923 (fl), Maxon 7159 (US); vicinity of Chichigalpa, ca 90 m, 12-18 July 1947 (fl), Standley 11217 (F), 11395 (F), 11474 (F), 11526 (F). DEPARTMENT UNKNOWN: "Leoncia 2.," 16 Oct 1927 (fl), Chaves [Chávez] 325 (US).

Cited collections

Alvarez, C., ex L. C. Smith 470 (8).

Anderson, W. R. & C. Anderson 4856 (8); 5146 (4).

Anderson, W. R. & C. W. Laskowski 3659 (4); 3692 (2).

Ansène, G. 4799 (6); s.n. (1).

Bárcena, M. de la 536 (4).

Barkley, F. A., J. B. Paxon, & C. M. Rowell Jr. 7499 (2).

Bell, C. R. & J. A. Duke 16649 (4).

Botteri, M. s.n. (6).

Brandegee, T. S. s.n. (11), s.n. (11).

Breedlove, D. E. 6475 (1); 6557 (13); 7639 (1).

Burch, D. 5270 (4).

Calderón, S. 781 (13); 824 (7); 1017 (1); 1182 (13).

Chaves, D. see Chávez, D.

Chávez, D. 315 (7); 325 (13).

Chávez, Z. 16 (8).

Clarke, O. F. 107 (1); 462 (13).

Collins, G. N. & J. H. Kempton 33 (4).

Conzatti, C. 2168 (8); 3760 (6); 4628 (4).

Conzatti, C. & V. Gonzales 219 (8).

Coville, F. V. 1627 (11).

Cruden, R. W. 2153 (4).

Davidse, G. & R. W. Pohl 2407 (13).

Denton, M. F. 1776 (13).

Detling, L. E. 8455 (4).

Diguet, L. s.n. (4, 5); s.n. (2); s.n. (4).

Diquet, L. see Diguet, L.

Dressler, R. L. & Q. Jones 252 (1).

Dunn, D. B., C. Dziekanowski, & -. Bolingbroke 20451, 20508 (8).

Dwyer, J. D. Spellman, J. Vaughan, & R. Wunderlin 755 (13).

Elias, T., et al. 800 (7).

Emrick, G. M. 224 (13).

Faberge, A. C. s.n. (5).

Feddema, C. 378, 782 (4).

Ferris, R. S. 5506 (12).

Flores, R. S. 1 (9).

Flores Crespo, J. 12 (4).

Galeotti, M. 1394 (4); 1545 (13); 1563 (6); 1567 (8).

Gaumer, G. F. 933 (10); 1173 (9, 10); 1544, 1968 (10).

Gaumer, G. F., J. D. Gaumer, & G. J. Gaumer 803 (10).

Gentry, H. S. 6554 (2); 7065, 7086 (11).

Gentry, H. S. & W. B. Fox 12017 (4).

Ghiesbreght, A. B. 220 (4); 663 (1); s.n. (4); s.n. (1); s.n. (4); s.n. (4, 8).

Ghiesbreght, A. B. ex J. D. P. 37 (4, 8); 38 (4).

Glassman, S. F. 1902 (7); 1919 (13).

Graham, W. L. 1231 (8).

Harmon, W. E. & J. D. Dwyer 3066 (13); 3230 (7); 4208 (1).

Hayes, S. s.n. (7).

Heyde, E. T. & E. Lux ex J. D. Smith 3999 (7); 6346 (13).

Hinton, G. B. 1476 (13); 1498 (4); 1690, 4328, 4471 (1); 4590 (4); 5741 (13); 8008 (1); 8014 (4); 8189 (13); 8201, 10592, 13275, 14481, 15061 (4).

Houstoun, W. s.n. (13).

Ignacio Aguilar, J. 1363 (13).

Iltis, H. H., R. Koeppen, & F. Iltis 1198, 1204 (8).

Janzen, D. H. s.n. (13).

Jurgensen, C. 692 (8).

Keck, -. 5 (6).

Kerber, E. 35 (6).

King, R. M. 1726, 1752, 1755, 1892 (13).

Kruse, H. 523 (4).

Lagos, J. A. 810 (7).

Langlassé, E. 257 (3).

Leavenworth, W. C. & -. Leavenworth 917 (4).

Lévy, P. 1071 (13).

Liebmann, F. M. 12053 (6).

Lundell, C. L. & A. A. Lundell 7885 (10); 8012 (9).

Lyonnet, E. 1033 (4).

MacDaniels, L. H. 452 (13).

Martínez, M. 15116 (4).

Martínez-Calderón, G. 111 (6).

Mason, C. T., Jr. 2895 (11).

Matuda, E. 1624 (13); 1778 (7); 16628, 18103, 18657 (13).

Matuda, E., et al. 26961 (4); 28802 (8); 31345 (4).

Maxon, W. R. 7159 (13).

McVaugh, R. 13278 (2); 15826 (4); 15941 (13); 16349 (4); 16393, 16393A (2); 17340 (4); 19805 (13); 19834 (2); 24934 (5); 25314, 26304 (13).

Mexia, Y. 589 (4); 1060 (12).

Molina R., A. 481 (13); 1084, 4053 (7); 4065 (13); 4121, 18618, 22511 (7); 26209 (13).

Molina R., A. & A. R. Molina 22762 (13).

Molseed, E. & H. Rice 220 (5).

Morales Ruano, J. 1293 (7).

Müller, F. 1108 (8).

Nagel, I. 8038 (4).

Nelson, E. W. 1247, 1296 (8); 2824, 2937 (13).

Oliver, R. L., D. F. Austin, & B. MacBryde 865 (1).

Palmer, E. 113 (4); 164 (13); 251 (2).

Paray, L. 2114 (4).

Pennell, F. W. 19544 (2); 19842 (4); 20207 (11).

Pfeifer, H. W. 1633 (7).

Pringle, C. G. 2994 (4); 3568 (2); 4468 (4); 4482 (2); 4768 (8); 5431 (5); 5439 (12); 6376 (1); 7364 (4); 8629 (5); 11020 (4); 11627, 13112 (1); s.n. (4); s.n. (1).

Purpus, C. A. 206 (1); 2620, 2620A (8); 6014 (13); 8411 (1); 8508 (13); 9075, 9077 (1); 10232, 10615 (13); 10631 (1); 10638 (13); s.n. (1).

Reko, B. P. s.n. (4).

Roe, K., E. Roe, & S. Mori 521 (13).

Rose, J. N. 1645, 1699 (4); 2009 (2); 3122 (12); 3222 (4); 3468, 3473 (2); 4615 (8); 6858 (4); 8586 (8); 10229 (4); 11065 (8); 12863 (2).

Rzedowski, J. 20823 (1); 21370, 22677 (8); 26243 (4).

Santos, J. V. 2318 (6).

Sessé, M., J. M. Mociño, J. del Castillo, & J. Maldonado 835 (4); 837 (1); 838 (4); 1253 (6); 1300 (13); 1301, 3570 (11); 3580, 3581 (4, 6); 3584 (2); 8568 (13); s.n. (4).

Smith, L. C. 595 (6).

Standley, P. C. 11217 (13); 11388 (7); 11395, 11474, 11526, 11593, 11648, 11726, 12236 (13); 12709 (7); 12878, 13187 (13); 13671 (7); 21286, 21637, 21736 (13); 22152, 22377 (7); 22446, 22517 (13); 22683 (7); 22686, 26279 (13); 26902 (7); 27100, 27181, 28638 (13); 75105, 75729, 76325, 76662, 76678 (7); 78852, 78871, 79422 (13).

Standley, P. C., L. O. Williams, & P. H. Allen 547 (7).

Steere, W. C. 1294, 1548, 1621, 2082, 2120, 2208 (10); 3005 (9).

Stevens, W. D. 1145 (9); 1168 (10); 1203 (8); 1245 (7); 1296 (13); 1311, 1343, 1344, 1346 (8); 1362 (4); 1363 (13); 1375 (4); 1392 (6); 1399 (1); 1406 (13); 1427, 1435 (4); 1436 (12); 1453 (4); 1458, 1473 (2); 1895, 2038 (12); 2062 (11); C-158-3 (10).

Steyermark, J. A. 31786 (7); 32972, 50732, 51624 (1); 52133 (13).

Tays, E. A. H. s.n. (11).

Ton, A. S. 4033 (1).

Tucker, J. M. 497, 881 (13).

Valerio Rodriguez, J. 63, 413, 874, 985, 1082 (7); 1345 (13); 3140 (7); 3473 (13).

Villarreal de Puga, L. M. 853 (2); 1651 (4).

Waterfall, U. T. 16368 (2).

Webster, G. L., K. Miller, & L. Miller 12523 (13).

West, J. 3537 (13).

White, S. S. 5243 (7).

Wiggins, I. L. & R. C. Rollins 140, 259 (11).

Wilbur, R. L. & C. R. Wilbur 2079, 2155 (4); 2253 (13).

Williams, L. O. 16873 (13).

Williams, L. O. & A. Molina R. 10569, 11068 (7).

Collector unknown (4, 4, 6).

Cited scientific names

Cynanchum asperum Miller = Matelea aspera

Dictyanthus aeneus Woodson = Matelea aenea

D. brachistanthus Standley = Matelea aspera

D. campanulatus Reichenbach = Matelea pavonii

D. ceratopetalus J. D. Smith = Matelea ceratopetala

D. parviflorus Hemsley = Matelea hemsleyana

D. pavonii Decaisne in de Candolle = Matelea pavonii

D. prostratus Brandegee = Matelea hemsleyana

D. reticulatus (Turczaninow) Bentham & Hooker f. ex Hemsley = Matelea dictyantha

D. stapeliiflorus Reichenbach = Matelea pavonii

D. tigrinus Conzatti & Standley in Standley = Matelea standleyana

D. tuberosus Robinson = Matelea tuberosa

Dictyanthus yucatanensis Standley = Matelea yucatanensis

Gonolobus altatensis Brandegee = Matelea altatensis

G. littoralis Decaisne *in* de Candolle = Matelea aspera

Matelea aenea (Woodson) W. D. Stevens, *ined*. = No. 9

M. altatensis (Brandegee) Woodson = No. 11

M. aspera (Miller) W. D. Stevens = No. 13

M. ceratopetala (J. D. Smith) Woodson = No. 7

M. dictyantha Woodson = No. 8

M. diffusa Woodson = Matelea hemsleyana

M. hamata W. D. Stevens, *ined*. = No. 3

M. hemsleyana Woodson = No. 1

M. macvaughiana W. D. Stevens, *ined*. = No. 5

M. megacarpha (Brandegee) Woodson = Matelea aspera

M. pavonii (Decaisne *in* de Candolle) Woodson = No. 4

M. sepicola W. D. Stevens = No. 12

M. standleyana Woodson = No. 6

M. stapeliiflora (Reichenbach) Woodson = Matelea pavonii

M. tuberosa (Robinson) Woodson = No. 2

M. yucatanensis (Standley) Woodson = No. 10

Pachystelma cordatum Brandegee = Matelea aspera

Rytidoloma reticulatum Turczaninow = Matelea dictyantha

Stapelia campanulata Pavón *ex* Decaisne *in* de Candolle = Matelea pavonii

S. campanulata Sessé & Mociño = Matelea pavonii

Tympananthe suberosa Hasskarl = Matelea pavonii

Vincetoxicum littorale (Decaisne *in* de Candolle) Standley = Matelea pavonii

V. megacarphum Brandegee = Matelea aspera

Cited common names

Atuz = Matelea aspera and Matelea pavonii

Boneta de diablo = Matelea pavonii

Bonete = Matelea tuberosa

Boochin = Matelea yucatanensis

Cabeza de cocodrilo = Matelea aenea

Cochita = Matelea ceratopetala

Cochitos = Matelea ceratopetala

Corazon de loro = Matelea ceratopetala

Cuchampel = Matelea ceratopetala

Champerra = Matelea aspera

Chanchito = Matelea aspera

Chanchitos = Matelea ceratopetala

Chinuna = Matelea hemsleyana

Chununa = Matelea ceratopetala

Hiedra del monte = Matelea pavonii

Maguey = Matelea altatensis

Mata chivo = Matelea aenea

Pegapega = Matelea hemsleyana

Siempreviva = Matelea aspera

Sombreritos = Matelea ceratopetala

Sombreros = Matelea ceratopetala

Taquarinde = Matelea sepicola

Xbockin = Matelea aenea

Yulpate = Matelea hemsleyana

APPENDIX

APPENDIX (TAXONOMIC DATA-MATRIX)

A large part of the data gathered in preparing this revision of Matelea subgenus Dictyanthus has been translated into a Morse taxonomic data-matrix[1]. A listing of this matrix, DICT1M, is shown in Figure 37 and a user-version of the character list is shown in Figure 36. The matrix is in the "general" format and contains data on 19 dichotomous, 14 multistate, and 29 quantitative characters. Although the design and uses of the taxonomic data-matrix have become relatively sophisticated, my use of them is still experimental; DICT1M is an early experiment and should not be used with the same confidence as the acompanying revision. Considerably more effort is needed to most appropriately code the characters useful for asclepiads into data-matrix form. One of the possible uses of a data-matrix is for specimen identification. Using Morse's IDENT4 program on MSU's timesharing system, several sample identifications were made; a few of these are shown in Figure 38. The identifications proceeded easily and directly and were accurate in each case. Although the taxonomic data-matrix definitely warrants further experimental use, it will probably not be of much practical taxonomic value until it can practically be put to more of its potential uses.

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[1] For an explanation of this type of taxonomic data-matrix and its potential uses consult: L. E. Morse, "Computer programs for specimen identification, key construction and description printing using taxonomic data matrices," Publ. Mus. Michigan State Univ., Biol. Ser. 5: 1-128, 1974.

11 Plant with a woody or fleshy caudex
13 Plant without a caudex

21 Long trichomes of internodes mostly straight
23 Long trichomes of internodes mostly uncinate

31 Leaf surface smooth
33 Leaf surface pusticulate

41 Small veins of leaf distinctly raised below
43 Small veins of leaf not distinctly raised below

51 Apex of largest leaf acute
53 Apex of largest leaf acuminate to attenuate

61 Leaf margin somewhat thickened and revolute
63 Leaf margin not thickened and revolute

71 Glandular trichomes of petiole sparse
73 Glandular trichomes of petiole dense

81 Long trichomes of petiole sparse
83 Long trichomes of petiole dense

91 Glandular trichomes of peduncle and petiole sparse
93 Glandular trichomes of peduncle and petiole dense

101 Long trichomes of peduncle and pedicel sparse
103 Long trichomes of peduncle and pedicel dense

111 Long trichomes of peduncle and pedicel straight
113 Long trichomes of peduncle and pedicel uncinate

121 Inflorescence bracts with glandular trichomes
123 Inflorescence bracts without glandular trichomes

131 Calyx lobe apex acute or acuminate
133 Calyx lobe apex attenuate

141 Calyx lobes with a mixed indumentum
143 Calyx lobes with long trichomes only

151 Corolla limb and lobes with revolute margins
153 Corolla limb and lobes without revolute margins

161 Corolla lobes plane or reflexed
163 Corolla lobes ascending

171 Corolla limb and lobes with short trichomes inside
173 Corolla limb and lobes glabrous inside

181 Inside of corolla tube with short trichomes around and/or above corona lobes
183 Inside of corolla tube glabrous

191 Follicles with glandular trichomes
193 Follicles without glandular trichomes

Figure 36. Character list for DICT1M (revised 14 Dec 1975).

2001	Stems erect
2002	Stems trailing
2004	Stems twining
2101	Largest leaf narrow-ovate
2102	Largest leaf ovate
2104	Largest leaf wide-ovate
2108	Largest leaf very-wide-ovate
2201	Lobes of largest leaf overlapping
2202	Lobes of largest leaf convergent
2204	Lobes of largest leaf descending
2208	Lobes of largest leaf divergent
2216	Lobes of largest leaf widely divergent
2301	Inflorescence bracts linear or lorate
2302	Inflorescence bracts lanceolate
2304	Inflorescence bracts narrow-ovate or ovate
2308	Inflorescence bracts very-narrow-elliptic, narrow-elliptic, or elliptic
2316	Inflorescence bracts narrow-oblong
2401	Calyx lobes lanceolate
2402	Calyx lobes narrow-ovate
2404	Calyx lobes ovate
2408	Calyx lobes elliptic
2501	Corolla shallowly campanulate (nearly rotate)
2502	Corolla campanulate
2504	Corolla deeply campanulate (nearly tubular)
2601	Corolla lobe apex acute
2602	Corolla lobe apex obtuse
2604	Corolla lobe rounded
2701	Corolla tube with vertical lines within
2702	Corolla tube with circular lines within
2704	Corolla tube with a distinct reticulate pattern within
2708	Corolla tube with no distinct pattern inside
2801	Corona lobes subulate
2802	Corona lobes short-sagittate
2804	Corona lobes short-spathulate with acute tip
2808	Corona lobes linear or linear-spathulate, tip not specialized
2816	Corona lobes linear-spathulate, tip deeply rugose, dark purple, glistening
2901	Corona lobe without teeth
2902	Corona lobe with two lateral teeth
2904	Corona lobe with one tooth on upper margin
2908	Corona lobe with two teeth on upper margin

Figure 36 (continued)

3001	Style apex basically concave
3002	Style apex convex
3004	Style apex apiculate
3101	Flowering in June
3102	Flowering in July
3104	Flowering in August
3108	Flowering in September
3116	Flowering in October
3132	Flowering in November
3201	Plants of Sonora
3202	Plants of Sinaloa-Nayarit
3204	Plants of Durango
3208	Plants of Guanajuato-Jalisco-Colima
3216	Plants of México-Morelos
3232	Plants of Puebla
3301	Plants of Michoacán
3302	Plants of Veracruz
3304	Plants of Oaxaca
3308	Plants of Guerrero
3316	Plants of Chiapas-Guatemala-El Salvador-Honduras-Nicaragua
3332	Plants of Yucatán
34000	Erect or trailing stem length in cm
35000	Maximum length of long trichomes of stems in 0.1 mm
36000	Largest leaf (midrib) length in mm
37000	Largest leaf width in mm
38000	Acropetiolar gland number
39000	Length of petiole of largest leaf in mm
40000	Peduncle length in 0.1 mm (absent = 0)
41000	Length of largest inflorescence bract in 0.1 mm
42000	Pedicel length in 0.1 mm
43000	Calyx lobe length in 0.1 mm
44000	Calyx lobe width in 0.1 mm
45000	Corolla base-sinus length in mm
46000	Corolla lobe length to width (sinus-sinus) ratio X 100
47000	Corolla lobe length in 0.1 mm
48000	Corona lobe length in 0.1 mm
49000	Gynostegium height in 0.1 mm
50000	Gynostegium width at apex in 0.1 mm

Figure 36 (continued)

51000	Corpusculum length in 0.01 mm
52000	Corpusculum width in 0.01 mm
53000	Pollen sac length in 0.01 mm
54000	Pollen sac width in 0.01 mm
55000	Follicle length in mm
56000	Follicle width in mm
57000	Follicle projection number
58000	Seed length in 0.1 mm
59000	Seed width in 0.1 mm
60000	Coma length in mm
61000	Elevation of collection in 10 m
62000	Maximum length of follicle projections in mm

Figure 36 (continued)

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4000 010,062,020,034,DICT1M,14DEC75
5010 001,32,MATELEA HEMSLEYANA WOODSON                  ,11,00,NOFILE,-99999
5020 002,21,MATELEA TUBEROSA (ROBINSON) WOODSON        ,06,00,NOFILE,-99999
5030 003,01,MATELEA HAMATA STEVENS                     ,00,00,NOFILE,-99999
5020 004,71,MATELEA PAVONII (DECAISNE IN DC) WOODSON,16,00,NOFILE,-99999
5050 005,06,MATELEA MACVAUGHIANA STEVENS               ,04,00,NOFILE,-99999
5060 006,15,MATELEA STANDLEYANA WOODSON                ,03,00,NOFILE,-99999
5070 007,40,MATELEA CERATOPETALA (J.D.SMITH) WOODSON,07,00,NOFILE,-99999
5080 008,32,MATELEA DICTYANTHA WOODSON                 ,07,00,NOFILE,-99999
5090 009,05,MATELEA AENEA (WOODSON) STEVENS            ,01,00,NOFILE,-99999
5100 010,14,MATELEA YUCATANENSIS (STANDLEY) WOODSON ,02,00,NOFILE,-99999
5400 -99,00,END TAXON LIST                             ,00,00,NOFILE,-99999
6000 001,11113,23232,12222,11224
6010 002,11113,21212,23231,11314
6020 003,01232,22122,13130,03304
6030 004,32223,22222,23331,11134
6040 005,11113,22222,11311,11314
6050 006,31133,32121,13311,11134
6060 007,31122,23222,21231,11114
6070 008,21112,23232,31211,11114
6080 009,33132,33333,32213,31304
6090 010,33133,33333,31211,11314
6100 -99,55444,44444,44446,68840
6500 001,03,14,15,03,03,01,05,04,04,01,02,15,16,19
6510 002,03,12,06,03,11,04,01,01,02,01,01,30,15,00
6520 003,04,03,14,08,08,02,06,12,01,01,01,02,00,08
6530 004,04,06,28,31,03,02,07,01,08,13,04,14,26,05
6540 005,07,06,28,03,03,02,07,01,08,02,06,06,08,01
6550 006,04,14,06,03,07,06,01,02,08,01,02,04,00,06
6560 007,07,14,02,03,03,02,01,04,08,04,04,30,00,16
6570 008,07,12,06,03,07,02,05,04,08,01,01,15,48,12
6580 009,04,14,30,03,03,02,05,08,16,01,01,07,00,32
6590 010,04,14,06,03,03,02,01,04,16,01,01,03,00,32
6600 -99,05,05,05,04,05,06,08,06,06,05,04,04,04,04
7000 001,020.060,000.030,013.034,013.036,002.006,007.018,010.040,020.040
7010 002,010.070,000.020,017.045,017.040,003.006,007.031,005.090,020.080
7020 003,000.000,000.015,074.084,049.073,004.009,034.040,200.530,070.100
7030 004,000.000,000.015,060.128,029.100,001.006,022.065,090.600,040.130
7040 005,020.085,000.030,030.095,021.072,002.006,009.037,000.160,040.070
7050 006,000.000,000.015,048.104,036.102,001.007,035.112,050.180,020.060
7060 007,025.055,000.020,025.063,015.055,001.004,013.060,010.150,030.050
7070 008,015.070,000.030,026.062,024.052,001.006,014.034,000.100,025.070
7080 009,000.000,000.030,035.098,026.070,004.011,021.062,040.110,030.040
7090 010,000.000,000.025,045.095,024.081,004.010,042.057,020.090,030.050
7100 -99,005.000,005.000,006.000,006.000,006.000,006.000,006.000,005.000
7500 001,030.050,040.060,015.025,003.006,-99.999,040.060,010.015,013.015
7510 002,040.050,050.090,015.035,006.010,-99.999,025.060,015.025,018.022
7520 003,230.260,110.140,045.065,013.015,-99.999,090.110,005.015,028.032
7530 004,100.250,090.180,030.060,013.025,-99.999,110.250,070.130,030.060
7540 005,080.200,080.120,030.045,009.012,-99.999,090.170,070.090,030.040
7550 006,070.160,120.180,040.065,017.031,-99.999,170.280,090.130,040.050
7560 007,030.120,090.130,035.060,012.020,-99.999,110.180,080.110,035.055
7570 008,050.120,060.110,025.060,009.016,-99.999,080.140,060.080,030.040
7580 009,035.045,060.090,020.045,008.012,067.078,050.090,060.080,028.032
7590 010,030.050,070.100,025.035,013.011,083.120,070.120,050.070,030.035
7600 -99,006.000,006.000,006.000,006.000,008.000,006.000,005.000,005.000
8000 001,015.020,019.022,008.010,058.091,026.034,048.070,010.018,028.054
8010 002,018.022,014.022,008.013,063.086,029.037,055.065,011.019,050.110
8020 003,028.032,022.024,017.019,143.155,040.044,-99.999,-99.999,-99.999
8030 004,030.045,031.038,012.018,145.162,042.048,069.074,019.025,029.044
8040 005,040.050,023.026,012.015,146.148,043.049,080.085,017.022,118.144
8050 006,030.045,048.055,023.028,154.188,045.063,080.090,025.030,045.055
8060 007,030.045,041.046,018.022,152.163,040.049,075.090,020.027,048.060
8070 008,030.035,023.035,009.017,117.145,029.038,055.070,010.022,050.110
8080 009,023.027,021.028,012.015,108.118,035.037,-99.999,-99.999,-99.999
8090 010,025.030,024.026,012.015,111.126,028.035,090.100,013.017,050.060
8100 -99,005.000,005.000,005.000,005.000,005.000,005.000,005.000,005.000
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Figure 37. DICT1M, a general format taxonomic data-matrix for *Matelea* subgenus *Dictyanthus*.

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8500 001,038.042,028.032,023.027,100.150,000.002
8510 002,055.060,045.050,023.027,050.160,000.002
8520 003,-99.999,-99.999,-99.999,000.005,-99.999
8530 004,-99.999,-99.999,-99.999,090.200,000.004
8540 005,055.060,043.047,025.030,150.170,000.003
8550 006,-99.999,-99.999,-99.999,070.090,000.007
8560 007,043.047,025.033,020.030,090.100,000.007
8570 008,053.057,040.045,025.030,150.250,000.003
8580 009,-99.999,-99.999,-99.999,000.005,-99.999
8590 010,043.047,033.037,033.037,000.015,000.004
8600 -99,004.000,004.000,004.000,005.000,005.000
9000 FILE=DICT1M,CHARLIST=DICT1D,GEOG=*NONE*,REF=*NONE*
9005 REV=14DEC75,REL=0,DP=000,TAXA=010,CHARS=062,M1=020,Q1=034,FLAG=WDS
9010        MATELEA SUBGENUS DICTYANTHUS
9015         BY WARREN DOUGLAS STEVENS
9020 WDS
9025 THESE SAMPLE DATA ARE DERIVED FROM A REVISION OF MATELEA SUBGENUS
9030 DICTYANTHUS, BUT HAVE BEEN ALTERED TO CONFORM TO THE DATA MATRIX
9035 FORMAT AND PURPOSE AND ARE NOT INTENDED TO BE DEFINITIVE EVEN IN
9043 THE SENSE OF THE ORIGINAL REVISION.
9045 WDS
9050 ≠SHORT≠ AND ≠GLANDULAR≠ TRICHOMES ARE THOSE SHORTER THAN 0.1 MM.
9055 ≠LONG≠ TRICHOMES ARE THOSE LONGER THAN 0.1 MM.
9060 THE COROLLA IS DIVIDED INTO A TUBE, A LIMB, AND LOBES.
9065 SHAPE TERMINOLOGY IS ACCORDING TO HICKEY, AMER.J.BOT.60:17-33,1973.
9070 FOR OTHER USAGES OF TERMINOLOGY, CONSULT THE ORIGINAL REVISION.
9075 WDS
9080 THE FREQUENCY VALUES ARE THE NUMBERS OF COLLECTIONS EXAMINED IN THE
9085 PREPARATION OF THE ORIGINAL REVISION.  THE NUMBERS OF SPECIMENS
9090 (SHEETS) EXAMINED HAVE BEEN DIVIDED BY 10.
9095 WDS
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Figure 37 (continued)

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*****  M S U  TAXONOMIC DATA MATRIX PROGRAMS  *****

PROGRAM IDENT4

DATA MATRIXDICT4M
FILE <DICT1M> REVISED 14DEC75, RELIABILITY 0


MORE DOCUMENTATION--YES

           MATELEA SUBGENUS DICTYANTHUS
            BY WARREN DOUGLAS STEVENS
MORE DOCUMENTATION--NO


IDENTIFICATION PROGRAM:  1=INSTRUCTIONS  2=START --2


***** NEW SPECIMEN:  COLLECTOR AND NUMBER -- GAUMER ET AL. 1173
VARIABILITY LIMIT --1
CHARACTERS2816,3332,23
THE FOLLOWING  2 OF  10 TAXA REMAIN:
          MATELEA AENEA
          MATELEA YUCATANENSIS
NEXT- 0
USEFUL CHARACTERS:     46    26    15    16    27    37    40    42
NEXT- 1
CHARACTERS153,163,2708
SUGGESTED IDENTIFICATION OF SPECIMEN  GAUMER ET AL. 1173
          MATELEA AENEA
    UNUSUAL CHARACTERS:        163     2708     2816     3332 50023027
    CHARACTERS YOU USED:       23    153     163   2708    2816   3332

NEXT- 4


***** NEW SPECIMEN:  COLLECTOR AND NUMBER -- CONZATTI 3760
VARIABILITY LIMIT --1
CHARACTERS36077,36056,31,2004,2502,2702
   4 OF  10 TAXA REMAIN POSSIBLE.
NEXT- 1
CHARACTERS45018,47240
SUGGESTED IDENTIFICATION OF SPECIMEN  CONZATTI 3760
          MATELEA STANDLEYANA
    UNUSUAL CHARACTERS:      2702 51048055 52023028      3002       3200
    CHARACTERS YOU USED:      31    2004    2502    2702   36056  45018
      47240
NEXT- 4


***** NEW SPECIMEN:  COLLECTOR AND NUMBER -- MOLSEED & RICE 220
VARIABILITY LIMIT --2
CHARACTERS36052,37030,2001,3208
   8 OF  10 TAXA REMAIN POSSIBLE.
NEXT- 1
CHARACTERS2208,40050,42170,2701
SUGGESTED IDENTIFICATION OF SPECIMEN  MOLSEED & RICE 220
          MATELEA MACVAUGHIANA
    UNUSUAL CHARACTERS:      2902 57118144 51023026 55080085 53146148
    CHARACTERS YOU USED:    2001    2208    2701    3208   36052  37030
      40050  42170
NEXT- 4
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Figure 38. Samples of interactive specimen identification using IDENT4 and DICT1M.

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***** NEW SPECIMEN:  COLLECTOR AND NUMBER -- STEYERMARK 51624
VARIABILITY LIMIT --2
CHARACTERS36022,37025,39013,2001,2108
   5 OF  10 TAXA REMAIN POSSIBLE.
NEXT- 1
CHARACTERS42050,43050
THE FOLLOWING  3 OF  10 TAXA REMAIN:
         MATELEA HEMSLEYANA
         MATELEA TUBEROSA
      -2 MATELEA CERATOPETALA
NEXT- 1
CHARACTERS2501,45004,2704
SUGGESTED IDENTIFICATION OF SPECIMEN  STEYERMARK 51624
         MATELEA HEMSLEYANA
    UNUSUAL CHARACTERS:     2501      2804 49013015      3002 45003006
    CHARACTERS YOU USED:   2001    2108    2501    2704   36022   37025
      39013  42050  43050  45004
NEXT- 4


***** NEW SPECIMEN:  COLLECTOR AND NUMBER -- PRINGLE 4482
VARIABILITY LIMIT --2
CHARACTERS36032,37026,39013,11,2001,2504
   5 OF  10 TAXA REMAIN POSSIBLE.
NEXT- 1
CHARACTERS3208,2701,41
THE FOLLOWING  2 OF  10 TAXA REMAIN:
         MATELEA TUBEROSA
      -1 MATELEA MACVAUGHIANA
NEXT- 0
USEFUL CHARACTERS:     26     28     42     47     29     48     49     50
NEXT- 1
CHARACTERS2802,42050
SUGGESTED IDENTIFICATION OF SPECIMEN  PRINGLE 4482
         MATELEA TUBEROSA
    UNUSUAL CHARACTERS:     2802      3300 49018022      2504 50018022
    CHARACTERS YOU USED:     11      41    2001    2504    2701    2802
      3208   36032  37026  39013  42050
NEXT- 4


***** NEW SPECIMEN:  COLLECTOR AND NUMBER -- PENNELL 19842
VARIABILITY LIMIT --2
CHARACTERS39045,40180,36080,37060
   6 OF  10 TAXA REMAIN POSSIBLE.
NEXT- 1
CHARACTERS181,2701,45020,2502
THE FOLLOWING  2 OF  10 TAXA REMAIN:
         MATELEA PAVONII
      -1 MATELEA STANDLEYANA
NEXT- 1
CHARACTERS42102,43120,44040,2604
NO PROGRESS
NEXT- 0
USEFUL CHARACTERS:     51     52     55     57     47     38     14     30
NEXT- 1
CHARACTERS47150
SUGGESTED IDENTIFICATION OF SPECIMEN  PENNELL 19842
         MATELEA PAVONII
    UNUSUAL CHARACTERS:     2701 51031038 34000000 57029044      3004
    CHARACTERS YOU USED:    181    2502    2604    2701   36080   37060
      39045  40180  42102  43120  44040  45020  47150

NEXT- 7

 STOP
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Figure 38 (continued)

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LITERATURE CITED

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