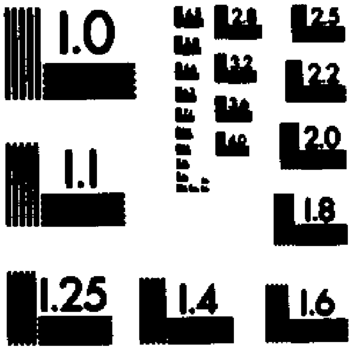
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A SYSTEMATIC REVISION OF THE GENUS CYBIANTHUS SUBGENUS GRAMMADENIA (MYRSINACEAE)

by

JOHN JAMES PIPOLY III

A dissertation submitted to the Graduate
Faculty in Biology in partial fulfillment
of the requirements for the degree of Doctor
of Philosophy, The City University of New York

1986

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ABSTRACT

A SYSTEMATIC REVISION OF THE GENUS CYBIANTHUS SUBGENUS GRAMMADENIA (MYRSINACEAE)

by

John J. Pipoly III

Advisor: Dr. Scott A. Mori

The relationships of species in *Grammadenia* Bentham and the relationship of *Grammadenia* to the genus *Cybianthus* were investigated. A phylogenetic (cladistic) analysis revealed that the genus *Cybianthus* is most closely related to the genus *Embelia*. Using *Embelia* for outgroup comparison, the character states of *Cybianthus* were polarized, and nine of the ten subgenera of Agostini (1980) were supported by the fully resolved cladogram. *Cybianthus* subg. *Iteoides* is relegated to synonymy under subg. *Microconomorpha*. Cladistic analysis of these subgenera revealed that *Grammadenia* belonged to a clade with subgenera *Cybianthus* and *Cybianthopsis*, and the new combination, *Cybianthus* subg. *Grammadenia* (Bentham) Pipoly, is made. Because subgenera *Cybianthus* and *Cybianthopsis* are more closely related to each other than either one is to *Grammadenia*, both were used as a functional outgroup to polarize the character states within

Grammadenia. The number of species within *Grammadenia* is reduced from 24 to 7. Four subspecies are proposed for *C. costaricanus*, and two for *C. magnus*. One new species, *C. piresii*, is described. Each species has autapomorphies and the species cladogram is fully resolved.

Morphological, anatomical and ecological studies of subgenus *Grammadenia* are presented along with descriptions, illustrations and distribution maps. Architectural studies revealed that all taxa exhibit Rauh's Model, and that much taxonomic overdescription was attributable to reiteration, affecting leaf morphology, branching and sexuality. Primary stem anatomy showed all species of subg. *Grammadenia* have a heretofore unknown type of nodal anatomy and vasculature. Primary stem and leaf histological differences were useful at both the subgeneric and specific levels. Inflorescence, floral and wood anatomy were not found taxonomically useful at the specific level. However, preliminary data suggest that their taxonomic utility at the subgeneric level merits further investigation.

The genus *Cybianthus*, now considered to have 150 species in ten subgenera, is cladistically defined by the unique glandular-granules at corolla lobe and tube junction. For practical purposes of identification, the combination of axillary racemes or racemose panicles, and filaments which are shorter than the corolla, connate at least one-fourth

their length, and adnate to the corolla at least one-third its length allows for easy recognition.

RESUMEN

Relaciones "infragenéricas" de *Grammadenia* e intergenéricas entre *Grammadenia* y *Cybianthus* fueron investigadas. Un análisis filogenético (cladístico) reveló que el género *Cybianthus* es estrechamente relacionado al género *Embelia*. Los estadíos de los caracteres de *Cybianthus* fueron polarizados, usando *Embelia* como grupo externo. Como resultado nueve de los diez subgéneros de Agostini (1980) fueron soportados por un cladograma completamente resuelto. *Cybianthus* subg. *Iteoides* es relegado a sinonimia bajo subg. *Microconomorpha*. Análisis cladístico de los subgéneros susodichos reveló que *Grammadenia* pertenece al grupo monofilético comprendiendo subgéneros *Cybianthus* y *Cybianthopsis*; y de allí la nueva combinación, *Cybianthus* subg. *Grammadenia* (Bentham) Pipoly, es propuesta. Dado que *Cybianthus* y *Cybianthopsis* son más estrechamente relacionados entre sí que cualquiera de ellos lo es a *Grammadenia*, ambos son usados como grupo externo funcional de tal subgénero. Se reduce el número de especies en *Grammadenia* de 24 a 7. Cuatro subespecies son consideradas bajo *C. costaricanus* y dos bajo *C. magnus*. *C. piresii* es descrita como nueva especie.

Datos sobre morfología, anatomía, y ecología de *Grammadenia* son acompañados por descripciones, ilustraciones y distribuciones. Arquitectura arbórea reveló que *Grammadenia* exhibe el Modelo de Rauh. Reiteración en este modelo afecta

la morfología foliar (forma y dimensiones), ramificación y sexualidad. Variaciones en estos caracteres fueron interpretadas a nivel específico, causando sobredescripción taxonómica. La anatomía de tallo primario mostró que en Grammadenia los simpódios del sistema cortical son autónomos, que representa un tipo de anatomía nodal previamente desconocido. Diferencias en la anatomía de tallo primario e histología foliar fueron útiles a nivel subgenérico y específico. Datos preliminares sobre la anatomía de inflorescencias, flores y madera surgieren ser de valor a nivel subgenérico. El género Cybianthus se considera compuesto de 10 subgéneros y aproximadamente 150 especies. El género es cladísticamente definido por sus gránulos-glandulares en la unión del tubo y lóbulos corolinos. Sin embargo, y para fines de identificación, el género se puede reconocer por la siguiente combinación de caracteres: racímos ó panículas racemosas axilares, filamentos más cortos que la corola, connatos un cuarto de su longitúd y adnatos a la corola por un tercio de su longitúd ó más.

DISCLAIMER

This material is based upon research supported by the National Science Foundation Grant BSR-8309628. The Foundation provides grants for research and education in the sciences. The awardees are wholly responsible for the conduct of such research and preparation of the results for the publication. The Foundation, therefore, does not assume responsibility for such findings or their interpretation.

Any opinions, conclusions or recommendations expressed in this publication are those of the author and do not necessarily reflect the views of the National Science Foundation.

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Additional field studies of the genus *Cybianthus* and other Myrsinaceae were made possible by joining others in the field, including Dr. James Luteyn in Ecuador, Venezuela and Colombia, Dr. Scott Mori in French Guiana, Dr. Otto Huber in Venezuela and Dr. Ghillean Prance in Brazil. Without these supplementary field trips, the analysis of the subgenera of *Cybianthus* would not have been possible.

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This treatment is dedicated to the memory of my mother, Virginia Mary (Kelly) Pipoly.

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INTRODUCTION

The neotropical genus Cybianthus Martius, as it is here interpreted, contains approximately 150 species in 10 subgenera. Agostini (1980) published a synopsis of the genus in which he formally reduced Comomyrsine, Conomorpha, Cybianthopsis, Microconomorpha, and Weigeltia to synonymy under Cybianthus, but his revision at the species level was only completed for Cybianthus subg. Conomorpha (Agostini, 1971). During the course of my work on the genus (Pipoly, 1981, 1983a, 1983b; Pipoly & Lundell, 1982) for FLORA NEOTROPICA, it became apparent that variation in sexuality and floral merosity, important in the classification of the Myrsinaceae since the monograph of Alphonse de Candolle (1834), precluded their use in separating the genus Cybianthus from the genus Grammadenia Bentham, the latter a poorly known group of 25 taxa, known from a total of approximately 300 collection numbers. This left only the sessile, apically mucronate leaves and "epiphytic" habit of Grammadenia to separate it from Cybianthus. Therefore, a revision of Grammadenia, and an analysis of its relationship to Cybianthus was essential to complete the FLORA NEOTROPICA project.

There were four purposes to the present investigation. First, it was necessary to find the sister genus of Cybian-

thus and with that accomplished, to conduct a phylogenetic analysis of its subgenera. Second, to determine generic limits, the phylogenetic relationships of *Grammadenia* had to be analyzed. Third, once the latter information was known, a phylogenetic analysis of the relationships of the species in *Grammadenia* was performed. Finally, because no group of Myrsinaceae has been studied in the field by a monographer, the integrity of character states historically used in the classification of the family was investigated, based on extensive field, laboratory and herbarium studies. An important goal of the latter investigation was not only to find which character states were variable, but more importantly, to find the bases of variation observed, and how this variation might be predicted in other groups of the family.

Extensive fieldwork through most of the range of *Grammaenia* yielded architectural data which partially explained the causes of sexual variation, along with a much better appreciation of vegetative variation attributable to inherent growth dynamics of Rauh's Model (see Habit and Architecture). Population studies revealed that suspected hybridization between *C. ptariensis* and *C. lineatus* was explained by the fact that at the scrub forest/savanna interface, each species quantitatively varies such that it resembles the other, depending on the location of the individual plant. Thus, the status of *G. ptariensis* subsp. *auyantepuiensis* was resolved, as it was found to be nothing more than a morphological form frequent when plants of *C. ptariensis* are in a savanna, albeit only a few feet from the scrub forest.

Data from primary stem anatomy provided character states useful for specific delimitation, concomitant with data verifying the monophyletic nature of the subgenus. The nodal anatomy and vasculature is new to science, and consists of five autonomous cortical sympodia independent of the stele. Leaf architecture and histology revealed systematically important character states useful at subgeneric and specific levels. Floral and wood anatomy, although not useful in specific delimitation, are constant in subg. *Grammadenia*, and preliminary data for several other subgenera of *Cybianthus* suggested both merit further investigation.

The phylogenetic hypothesis postulated for the genus *Cybianthus* is the first such hypothesis formulated for any myrsinaceous group. Herbarium specimens representing eleven of the twelve sections recognized by Mez (1902) in *Embelia* yielded character states which established its sister group relationship with *Cybianthus*. In this monograph, *Cybianthus* is a genus cladistically defined by the presence of glandular-granules at the junction of the corolla tube and lobes. For practical purposes of identification, the combination of simple axillary racemes, or racemose panicles, with filaments shorter than the corolla, united at least one-fourth their length, and adnate to the corolla tube for at least one-third its length readily marks the genus.

TAXONOMIC HISTORY

Grammadenia was described as a genus by Bentham (1846) in his *Plantae Hartwegianae*. He clearly based (and thus typipified) the genus on *G. marginata*, described from a collection by Hartweg (*1200*) from Popayán, Colombia, and also included *G. lineata*, based on a collection (*Schomburgk 617/992*) from Cerro Roraima, on the border of Guyana and Venezuela.

Bentham correctly noted the close relationship of *Grammadenia* to the genus *Cybianthus* Martius, but distinguished *Grammadenia* by its 5(-6)- (not 4)-merous flowers, quincuncial (not valvate) corolla lobes, subglobose, birimose apically dehiscent (not ovate, longitudinally dehischent) anthers, sessile (not petiolate) leaves, and the short, few-flowered (not long, many-flowered) inflorescences. The name *Grammadenia* comes from the Greek "gramma" (line) and "aden" (gland), referring to the ubiquitous punctate-lineations of the leaves and perianth.

Subsequently, Grisebach (1861) treated the genus for the British West Indies and transferred *Ardisia parasitica* Swartz (1788, 1797) into *Grammadenia*. Later treatments by Hooker (1876) and Pax (1889) were essentially the same, except for the nomen nudum, G. epiphytica Pax, which he mistakenly attributed to Grisebach, undoubtedly representing a lapsus mentis for G. parasitica (Swartz) Grisebach.

In his treatment of Grammadenia for Urban's Symbolae Antillanae, Mez (1901) proposed a new subgenus, Cybianthopsis, to accomodate Ardisia sintenisii Urban (1899). Subgenus Cybianthopsis was characterized by its petiolate (not sessile) leaves, and "subumbellate" (not racemose) inflorescences. Mez then transferred Cybianthus costaricanus Hemsley (1882) into subg. Eugrammadenia, which contained G. lineata, G. marginata, and G. parasitica.

In the following year, Mez (1902) presented the same treatment for Grammadenia in his comprehensive monograph of the Myrsinaceae for Engler's Das Pflanzenreich. By describing five new species, G. alpina, G. lehmannii, G. magna, G. nitida, and G. pastensis, he brought the total number of Grammadenia species to ten. The same conceptual framework was maintained by Mez in his Additamenta Monographica series of papers, in which he added two new species, G. asymmetrica (Mez, 1905) and G. weberbaueri (Mez, 1920).

From that time to the present, taxonomic work on Grammadenia has consisted of local floristic treatments (Standley 1938; Macbride, 1959; Lundell, 1971) and descriptions of new taxa (Pittier, 1931; Cuatrecasas, 1951; Steyermark, 1953; Lundell, 1968, 1976).

Agostini's (1980) reclassification of the complex genus

Cybianthus was of monumental importance in the history of taxonomic work on Myrsinaceae. Albeit far from complete, it demonstrated the tremendous variation present in one monophyletic group, and provided a practical and to a large extent, accurate appraisal of infrageneric groups. Unfortunately, his study and that of his dissertation (1971) were based solely on herbarium material. Because detailed studies of sexual variation patterns were not conducted, he isolated both Cybianthus and Wallenia within the neotropical members of the family because of their dioecy. This character state was later shown untenable by Pipoly (1983b).

MORPHOLOGY

Habit and Architecture

All species of Cybianthus subgenus Grammadenia, with the exception of C. lineatus, have been described as epiphytic or epipetric shrubs (Lundell, 1968, 1976; Mez, 1902; Steyermark, 1953). Apparent contradictions to this exist, such as the many individuals of C. magnus and C. marginatus which grow on detritis between rocks in Andean cloud and elfin forests and páramos, populations of C. costaricanus subsp. costaricanus found on Sphagnum in "bog" (turbera) areas atop the Cordillera de Talamanca, Costa Rica, and C. lineatus , which is shallowly rooted in sand above sandstone in savannas atop tepuis. However, these apparent exceptions do not change the fact that all species of the subgenus share the same morphological feature, a root system which grows parallel to the soil (diageotropic, Fig. 1a), a feature which occurs in the family otherwise only in Vegaea Urban, an epiphyte endemic to the Dominican Republic. Therefore, the terms epiphytic or epipetric may be replaced, and these plants more accurately and functionally characterized by their diageotropic roots, as opposed to the positively geotropic root system of the other subgenera containing "free-standing" taxa.

The diageotropic root system of Grammadenia has not imposed severe size limitations on the plants, based on data accumulated to date. The largest individual, not only of subg. Grammadenia, but of the entire genus Cybianthus known to date, a specimen of C. marginatus, was six meters tall, with a trunk nearly 35 cm DBH, and a canopy eight meters in diameter (Fig. 1b). This individual (Pipoly et al. 6538), had a readily distinguishable diageotropic root system which was entangled around and under massive boulders, thereby supporting the weight of its canopy.

The aspect of the canopies among several species, such as C. lineatus, C. marginatus, C. magnus, and C. costaricanus may each appear distinct at first sight. However, given the plethora of adaptive geometries possible from one morphogenetic program, the only effective way to compare the branching dynamics and habit of different taxa is by analysis of their respective architectures. The architecture of a plant is defined by Hallé et al. (1978) as "the visible, morphological expression of the genetic blueprint of a tree at any one time". The architectural model, therefore, describes the destinies of meristems which are governed by the genetic blueprint. Therefore, it describes the dynamics of architectural changes associated with branching and inflorescence production.

This study revealed that all species of subg. Grammadenia exhibit Rauh's Model (Hallé et al., 1978). Rauh's Model is characterized by a monopodial, rhythmically growing, readily distinguishable trunk, which develops tiers of branches morphogenetically identical to itself (Fig. 1c). All branches are orthotropic and monopodial, with lateral inflorescences which do not affect shoot development. As in most tropical trees exhibiting Rauh's Model, branching in subg. *Grammadenia* is exclusively sylleptic. These sylleptic branches (Fig. 1d) are easily recognized by the absence of basal bud-scales and the elongate hypopodium (Hallé et al., 1978).

Architectural variations resulting in apparent canopy and branching differences aided in the proliferation of taxonomic synonyms. These variations were found to be the result of reiteration, defined by Oldeman (1974) and Hallé et al. (1978) as "any modification of the tree's architecture not inherent in the definition of its model and which is occasioned by damage, environmental stress or supraoptimal conditions". This variation in branching, concomitant with leaf and sexual variation, caused the description of *Grammadenia aurantiaca*, *G. linearifolia*, *G. minor*, and *Cybianthus talamacensis* by Lundell (1968, 1976, 1985), all of which are synonymous with *Cybianthus costaricanus* Hemsley subsp. *costaricanus*. Reiteration is a frequent phenomenon where plants are susceptible to injury by wind (Pipoly, unpubl.), or damages caused by growing next to paths (Hamilton, 1985), or where they are subject to stress by the weight of their canopies (Oldeman, 1972).

Canopy dwellers, such as the segregates *G. aurantiaca*,

G. linearifolia, develop large, pendent branches attributable to gravitational effects. These branches display epitrophous or "river-bank" reiteration, as originally described by Oldeman (1972). In the first stages of the model, some leaf dimorphism occurs, associated with the production of the first tier of branches, coupled with what may be thought of as "precocious" inflorescences, as the new branch, although topographically in the tree canopy, is morphogenetically equivalent to a sapling axis and is therefore, juvenile. My field studies in Panama and Costa Rica showed that these "precocious" inflorescences bore unisexual (mostly staminate) flowers, a character used by Lundell (1968, 1976) for specific delimitation.

In the case of the segregates Grammadenia minor Lundell, and Cybianthus talamacensis Lundell, a series of specimens, Davidse et al. 28824, 28827 and 29084 (CR, MO, NY), demonstrate two other types of reiteration phenomena. In Davidse et al. 28824, the thin, sparsely branched stems with extremely long internodes are suggestive of sucker-shoot reiteration. The leaf morphology is essentially linear, and the inflorescences are extremely short, bearing only a few bisexual flowers, the rest being staminate. On the other hand, the other two Davidse et al. collections demonstrate reiteration after fasciation, evidenced by abnormally thick, somewhat flattened stems with abbreviated internodes and suborbicular leaves. Branches from these internodes repeat the initial branching sequence for the entire plant, as if they were trunks.

Reiteration from breaking of branches, the bayonet effect (Hallé et al., 1978) is seen in Fig. 1e, a specimen of *C. costaricanus* subsp. *acuminatus* , from the slopes of Volcán Barba in Costa Rica. Study of populations in that area revealed that reiterative shoots caused by damage to the branches by wind and those stressed by an open environment outside the canopy of a tree as the result of removal of other surrounding trees, always bore unisexual flowers, occasionally pistillate, but most often staminate. However, those which were from undisturbed plants on large trees (*Pipoly et al. 7082*), bore bisexual flowers. Unfortunately, there were not sufficient numbers of individuals present on the site to determine if any patterns of sexual variation correlated with reiteration due to broken branches versus that due to stress caused by increased exposure.

Another example of reiteration was observed in populations of *Cybianthus magnus* subsp. *magnus* from the Serranía de Turumiquire, Venezuela. Reiterated shoot suckers, such as in *Pipoly 6454* and *6457* had malformed canopies, with non-rythmic branching at first, precocious flowering, and smaller, nearly narrowly oblanceolate leaves, instead of the obovate, larger leaves typical of the subspecies. In the Chocó of Colombia, populations of *C. magnus* subsp. *asymmetricus* exhibited much reiteration from a combination of damage, stress, and riverine effects due to its steeply-sloped montane habitat. There, some specimens, (Luteyn, Pipoly et al. 10414, 10419, Fig. 26c-e) bore unisexual flowers on different branches, were totally bisexual, or totally unisexual. Whether a simple androdioecious breeding system was complicated by reiteration phenomena was not clear, as the entanglement caused by prostrate stems over steep slopes was impossible to sort out during a short stay in the area. It is hoped that future studies on equally perplexing taxa such as C. (§ Microconomorpha) pastensis (Pipoly, 1983b) will aid in understanding this variation.

In summary, this study shows that an understanding of the architectural model or "the growth program which determines the successive architectural phases" (Hallé et al., 1978) of a taxon yielded much information useful in understanding the systematic biology of Cybianthus subg. Grammadenia. Aside from explaining the developmental bases for variation in branching, sexual variation and leaf morphology (see Leaves), the most important feature of the architectural model for the systematist is its value in predicting certain types of variation. This variation, whether intrinsic to the dynamics of the model, or produced as a result of reiteration phenomena, allows more accurate assessments of homologies and integrities of character states. It is also significant to note that all members of the genus Cybianthus display models based on rhythmic, monopodial, sylleptic branching, despite the several specialized habitats occupied by members of the genus. Hallé et al. (1978) reported that one collection of a tentatively identified *Cybianthus*, (*Hallé 2299*), from French Guiana, displayed Aubréville's Model. After conducting an extensive search through the herbarium of ORSTOM (CAY), I have not been able to find the voucher, and would assume it is based on a misidentification. After having seen at least representative species for all the subgenera of *Cybianthus* in the field save one (*Cybianthopsis*), it is highly unlikely that Aubréville's Model would occur in the genus. However, that model is found in the Neotropics in the monotypic genus *Vegaea*.

Trunk and Branchlets

The formation of a pachycaulous trunk by *Cybianthus lineatus* (Fig. 1f), produced by an extremely active cork cambium, is a unique feature within the genus and undoubtedly an adaptation to its xeric savanna habitat. All other species of subg. *Grammadenia* have leptocaulous trunks, and occur in mesic or wet environments (see ECOLOGY).

In this monograph, the term branchlets refers to the upper ten centimeters of any branch. They may be smooth (Fig. 2a) or verrucose-papillate (Fig. 2b, 2c), but always bear at least a few, scattered lenticels. They may also be terete or ridged and may vary in diameter from 2.5 mm to one centimeter. The glandular-papillate branchlets of *C. lineatus* (Fig. 2c,d) are unique within the subgenus.

Leaves

The basally auriculate, sessile leaves of subg. *Grammadenia* are unique within the Myrsinaceae. Although sessile leaves are also found in *Vegaea*, its basal margins are truncate. The scarious margins and obtuse mucronate apices of all subg. *Grammadenia* species are also unique. All leaves are glabrous except for small, glandular-papillae along the adaxial costa.

A most interesting functional aspect of the sessile, auriculate leaves was noted at first by accident, during fieldwork conducted in the states of Mérida and Táchira, Venezuela. While seeking shelter under a large *Cybianthus marginatus* during a rainstorm, I discovered that the majority of water striking the canopy was flowing directly down the stems and trunks, while the area under the canopy *per se* was fairly dry. After distributing newspapers centrifugally about the trunk, it became clear that the majority of water was funneled directly to the diageotropic roots *via* the branches and trunk, and that the leaf bases were acting as funnels to channel water in that manner. I then repeated this experiment under canopies of large specimens of *Cybianthus iteoides*, *C. laurifolius* and *C. nevadensis* , where they co-occur with C. marginatus in the Páramo de Tamá and in the La Grita area, (both of Táchira). These species have drip-tipped, petiolate leaves, which distributed the percolation of water more or less evenly throughout the area below the canopy, and therefore to the positively geotropic root system below. It may be no coincidence that Vegaea, the only other myrsinaceous taxon with sessile leaves, is also epiphytic and has exposed roots (Zanoni, pers. comm.), although their orientation with respect to gravity has not been noted. Another significant feature of the leaf morphology in Grammadenia is that the leaves are v-shaped, approximately 120°, in transverse section, while those of all other subgenera,(except for an adaxial costal depression) are practically flat. This shape helps funnel water down the stem.

As discussed above, the architecture found in subg. Grammadenia has a profound effect on quantitative leaf variation. Above the hypopodium, the two prophylls develop, followed by abruptly distinct leaves which are, in turn, smaller and much narrower than the leaves produced further up the stem. This phenomenon is not a function of syllepsis, but may be attributable to the rhythmic branching characteristic of Rauh's Model. This variation, along with some subtle floral variation was responsible for Mez' segregation of Grammadenia alpina, G. nitida, and G. pastensis from what is now regarded as a single species, Cybianthus marginatus. Thus, variation in quantitative features of the leaves precludes the taxonomic use of this character.

On the other hand, this study has shown that leaf shape, within certain limits, is still useful in specific delimitation. Leaf shape is normally obovate or oblanceolate, except for *C. marginatus*, which has elliptic, oblong, or ovate leaves. That species is also atypical in having symmetric leaves, as all others in the subgenus are at least slightly asymmetric. Leaf texture is commonly chartaceous or coriaceous, except for *C. parasiticus*, the only species with membranaceous leaves.

Leaf punctation and punctate-lineation have historically been heavily relied upon for specific delimitation throughout the Myrsinaceae, particularly by Mez (1901, 1902, 1905, 1920) and Lundell (1966, 1968, 1971, 1976, 1985). Punctations, here defined as rounded, liso-schizogenously formed cavities, are distinguished from punctate-lineations, which are homologous, linear cavities in the leaves. Furthermore, undue emphasis has been placed on gland color, which may be pellucid (translucent), orange, red or black.

In order to test the integrity of punctation color, I preserved herbarium specimens in a variety of solvents (formalin: propionic acid: 70% ethanol, 1: 1: 18 v/v; formalin: glacial acetic acid: 70% ethanol, 1: 1: 18 v/v; glacial acetic acid: absolute ethanol 1: 3 v/v; 30% isopropyl alcohol; 50% ethanol; 50% methanol), and without solvents before drying, which yielded the following results.

Those leaf glands which appear pellucid-punctate in fresh material will dry orange punctate unless they are subjected to extreme heat, which results in a brown color ("castaña" of Agostini, 1980). Glands which are pink to red in fresh material will dry dark red if no solvent is used, or black if dried after preservation with any one of the solvents listed above. However, the most important fact of the experiment was that all young, unexpanded leaves have orange glands, responding as mentioned above, even if the mature leaves have red or black glands. This may indicate that differences in punctation color are correlated with quantitative differences in secondary metabolite accumulations. Unfortunately, the contents of the glands are, at this point, uncertain. It may be significant to note that the use of leaves for fish poison (Pipoly, 1983a) and for toothache may suggest that saponins, known to be ubiquitous in the family (Hegnauer, 1969) might be accumulated in these structures. In any case, punctation color can certainly not be used with any confidence for specific delimitation. The other punctation character states, "conspicuous" versus "inconspicuous" actually reflect the diameter of punctations in transverse section, and "prominent" versus "not prominent" refers to the blister-like projecting cavities common on the rachises of inflorescences and perianth parts.

Inflorescence and Flowers

All species within the subgenus have simple, indeterminate, axillary racemes. The rachis of the raceme is always glandular-papillate and glabrescent, and may be flexuous-reduced (Fig. 3a), flexuous (Fig. 3b), or straight (Fig. 3c). Anatomical investigations based on serial sections revealed that the curvature of the rachis is secondary rather than primary, and does not indicate sympodial growth by substitution.

The flowers are always on pedicels which are terete or clavellate, from 0.8-2.5 mm long in flower, then accrescent to 5 mm long in fruit. The perianth bears glands which may be not prominent (Fig. 3d) or prominent (Fig. 3e). They are normally conspicuous, except in _C._ _costaricanus_ subsp. _morii_.

The calyx lobes are basally connate to form a cotyliform calyx with a tube ca. 0.1 mm long. The lobes are erect and ovate, ovate-triangular, or deltate, with entire, erose or fimbriate margins. The margin vestiture may be glandular-ciliate, ciliolate, or glabrous.

The corolla is rotate, the tube equalling the adnate staminal tube in length. The corolla lobes may be imbricate, quincuncial, or rarely, dextrorsely contorted in bud, the latter malformed and with margins not overlapping in a uniform manner. The lobes are reflexed in anthesis, but not recurved. The margins may be irregular or regular in outline, and are either entire, crenate or erose. The adaxial surface of the corolla always bears glandular-granules (actually papillate trichomes, see Floral Anatomy) at the junction of the corolla tube and lobe, between the anthers. The only taxon with granules covering the entire adaxial surface of the corolla lobe is _C. costaricanus_ subsp. _morii_. The lobes may be chartaceous or coriaceous, and smooth or rugose medially within.

The stamens and staminodes are practically identical, at times differing only in size, but otherwise distinguishable only by the lack of pollen production, or production of non-viable pollen grains. The growths found between the anthers at the apex of the staminal tube are referred to as lobes in this treatment, to avoid confusion. The staminal tube is thus termed lobate (Fig. 3f) or subtruncate (Fig. 3g). As is mentioned under the Floral Anatomy section, the lobes are not vascularized. The staminal or staminodial tube formed by the connate filaments is adnate to the corolla tube for its entire length, and may be carnose or membranous. The anthers may be sessile, or on distally free portions of filaments to 0.3 mm long. The anthers are cuadrate or ovate, apically rounded or emarginate, basally truncate, and always dehiscent by apical, birimose pores. In fresh and liquid-preserved material, the anthers lean inward and cover the pistil, save the upper portions of the style and stigma.

The pistillode and pistil are morphologically identical, unlike the situation in *Cybianthus* subg. *Laxiflorus* (Pipoly, 1983a). They are usually obnapiform (Fig. 3k), but may be ellipsoid (Fig. 3l), or umbonate (Fig. 3j). The ovary may be terete, lobed (Fig. 3h), or costate (Fig. 3i), and may be glandular-lepidote (see Floral Anatomy), or not. The basal placenta is umbonate, and bears one to five campylotropous ovules which are imbedded ca. one-half their length. The ovules, when more than two, may be uniseriate, or biseriate.

Pollen

Pollen morphology is not taxonomically useful, as all species, not only of subg. *Grammadenia*, but of the entire genus *Cybianthus*, possess, psilate, tricolporate pollen (Fig. 2e).

Fruit

Like all members of the genus *Cybianthus*, subg. *Grammadenia* produces drupaceous fruits. Fruit shape may be ellipsoid (Fig. 3m), obovoid (Fig. 3n), or depressed-globose (Fig. 3o). Fruit shape has traditionally been used as a diagnostic character at the species level (Cuatrecasas, 1951; Lundell, 1976; Mez, 1902, 1905) but this character has been found to be only of limited use (see *C. costaricanus*, SYSTEMATIC TREATMENT).

ANATOMY

Materials and Methods

A survey of the primary stem, wood, leaf, and to a lesser extent, floral anatomy was conducted. Voucher specimens are listed in Table 1. For studies of the primary stem, leaf, and floral anatomy, branchlets were preserved in 70% EtOH, FAA or FPA (1: 1: 18 v/v), depending upon reagent availability. Four samples from each of these collections were dehyrated in a TBA series, embedded in Paraplast Plus (melting point 56-57°C), and serially sectioned on a rotary microtome at 7 to 10 microns. Following deceration, one-half of the slides were treated with Sockwell's Bleach (Schmid, 1977) to remove excess tannins and enhance stain differentiation. Staining was effected using Johansen's (1940) Safranin-Fast Green, Safranin-Fast Green-Orange G, or Safranin-Chlorazol Black E (Stevenson, 1980). Longitudinal sections of shoot apices were stained using the zinc chloride-Safranin-Orange G-tannic acid-ferric ammonium sulphate series described by Sharman (1943) to better discern meristematically active areas.

In addition to paraffin sections, freehand sections were made and stained with Phloroglucinol-HCL. For those taxa known only from herbarium specimens, material was removed from the sheets, gently heated to the boiling point in deionized water, soaked in 10% Multiterge (a wetting agent with properties similar to those of Contrad 70- see Schmid & Turner, 1977) solution, washed in deionized water for one hour, dehydrated, and freehand sectioned. Where possible, a duplicate preparation was made and embedded as described above.

All leaves cleared for venation architectural studies were taken from dried herbarium specimens. Leaves were placed in a 10% solution of Multiterge for two weeks, then washed in deionized water for two hours. They were then left in a 5% NaOH solution on a slide warming tray at 70° C until almost clear. The leaves were then transferred to a 50% sodium hypochlorite solution and left for 10-30 minutes. After an ethanol dehydration series, staining was effected using 1% Safranin in absolute ethanol.

Wood samples were collected from trunks with a diameter of 4 to 10 cm DBH. The smaller diameter samples were from _C. lineatus_ and _C. ptariensis_, whose trunks rarely exceed 4 cm in diameter. The samples were air-dried and later prepared for sectioning by alternate baths of boiling and ice water, followed by soaking in equal parts of 60% ethanol and glycerin for two months. Blocks $(2\ \text{cm})^3$ were cut at 18 to 25 microns on a sliding microtome, stained regressively in a 0.5 % aqueous Iron Hematoxylin (Camp, 1930) series, and counterstained with a 1% phenolic Bismark Brown

Y series. Macerations were prepared using Jeffrey's solution and sonication as described by Schmid (1982). Quantitative data for all wood characteristics is based on 25 measurements per sample, four sample blocks per voucher specimen.

TABLE 1

VOUCHER SPECIMENS FOR ANATOMICAL STUDIES

ss= stem section, lc= leaf clearing, ls= leaf section, ws= wood section, m= maceration, is= inflorescence section, fs= flower section

TAXON	COLLECTION	ss	lc	ls	ws	m	is	fs
_C._ costaricanus	Pipoly 7077	x	x	x				x
subsp. acuminat.	Pipoly 7082	x	x	x				
	Burger & Stolze 5962		x	x				
C. costaricanus	Pipoly 7118	x		x				
subsp. costaric.	Pipoly 7099	x	x	x	x	x	x	x

TABLE 1 (cont'd.)

	Pipoly 7098		x					
	Pipoly 7097		x					
	Pipoly 7083	x	x	x	x	x	x	x
	Pipoly 7068	x	x	x				x
C. costaricanus subsp. morii	Pipoly 7017	x	x	x	x	x	x	x
	Pipoly 7019	x	x	x				x
	Pipoly 7021	x	x	x				x
C. costaricanus subsp. panamensis	Pipoly 7062	x	x	x				
	Pipoly 7056	x	x	x				x
C. lineatus	Pipoly 7272	x	x	x	x			x
	Pipoly 7270	x	x	x				x
	Steyermark 126265	x	x	x	x	x	x	x
C. magnus subsp. magnus	Pipoly 6453	x	x	x	x	x	x	x
	Pipoly 6437	x	x	x				
C. magnus subsp. asymmetricus	Luteyn 10561	x	x	x		x	x	x
	Foster 9013	x	x					
	Luteyn 10414	x	x	x			x	x
	Luteyn 10415	x	x	x				x
	Camp 1206	x	x					

TABLE 1 (cont'd.)

C. marginatus	Luteyn 6647		x	x				
	Luteyn 10189	x	x	x				
	Pipoly 6546	x	x	x	x	x	x	x
	Pipoly 6607		x	x				
	Pipoly 6608		x	x				
	Pipoly 6609		x					
	Pipoly 6961	x	x	x				
	Pipoly 6973	x	x	x				
C. parasiticus	Howard 19414	x	x	x				
	Wilbur 7935	x	x	x				
C. piresii	Maguire 60476	x	x	x				
	Thomas 3043	x	x	x				
C. ptariensis	Huber 8630	x	x	x				
	Pipoly 7133	x	x	x	x	x	x	x
	Pipoly 7135	x	x	x				
	Pipoly 7273	x	x	x				
	Pipoly 7279	x	x	x				
	Pipoly 7281	x	x	x				

Primary Stem Anatomy

Histology

In stems of all species of subg. Grammadenia five histological zones are readily apparent. Proceeding centripetally they are: the epidermis, the outer cortex, the inner cortex (including the cortical bundles), the stelar/pericyclic region, and the pith (Fig. 4a). Because of changes associated with secondary growth, all descriptions presented were taken from areas within one node or at the time of periderm formation.

The epidermis is one cell thick and has no outstanding features, save the papillate projections found in C. lineatus and C. marginatus (see MORPHOLOGY). Periderm formation is slightly precocious in relation to secondary vascular growth only insofar as the interfascicular cambium is not fully activated in all areas before the first initial periderm formation takes place. The cork cambium originates in the epidermis (Figs. 5a, 5b) for all species, and after eight to ten radial rows of cork cells are produced, brachysclereids are usually found in the region centripetal to the phellogen.

The outer cortex is here defined as the zone lying between the epidermis (or periderm) up to, but not including, the cortical bundle "ring" (Fig. 4a). In all species, trihydric cluster crystals, here termed druses, are ubiquitous

TABLE 2

Primary Stem Anatomical Features of Cybianthus subgenus Grammadenia
Key: + = present; - = absent

TAXON	CANALS	OUTER CORTEX SCLEREIDS	TISSUE	CORTICAL BUNDLES PERIVASCULAR FIBERS	PITH CANALS
C. ptariensis	+	+	Parenchyma	Well-developed	+
C. lineatus	+	+	Parenchyma	-	+
C. magnus subsp. magnus	+	-	Angular Collenchyma	-	+
C. magnus subsp. aymmetricus	+	-	Angular Collencyma	-	+
C. piresii	+	-	Parenchyma	-	+
C. marginatus	Few	-	Parenchyma	-	-
C. costaricanus subsp. costaricanus	-	-	Parenchyma	Well-developed	-
C. costaricanus subsp. acuminatus	-	-	Parenchyma	Well-developed	+
C. costaricanus subsp. panamensis	-	+	Parenchyma	Well-developed	-
C. costaricanus subsp. morii	Few	-	Parenchyma	Well-developed	-
C. parasiticus	-	-	Parenchyma	Well-developed	-

TABLE 2 (Cont'd)

Primary Stem Anatomical Features of Cybianthus subgenus Grammadenia

TAXON	INNER CORTEX TISSUE	CANALS	STELAR REGION PERICYCLIC FIBERS	PITH TISSUE
C. ptariensis	Poor Aerenchyma	+	Forming a ring	Parenchyma
C. lineatus	Parenchyma	+	Associated w/ traces	Parenchyma
C. magnus subsp. magnus	Aerenchyma	+	Associated w/ traces	Angular Collenchyma
C. magnus subsp. asymmetricus	Aerenchyma	+	None	Tangential Collenchyma
C. piresii	Aerenchyma	+	Associated w/ traces	Parenchyma
C. marginatus	Aerenchyma	+	None	Parenchyma
C. costaricanus subsp. costaricanus	Aerenchyma	+	Forming a ring	Parenchyma
C. costaricanus subsp. acuminatus	Aerenchyma	+	Forming a ring	Parenchyma
C. costaricanus subsp. panamensis	Poor Aerenchyma	+	Forming a ring	Parenchyma
C. costaricanus subsp. morii	Poor Aerenchyma	+	Forming a ring	Parenchyma
C. parasiticus	Aerenchyma	+	Forming a ring	Parenchyma

and appear to be composed of calcium oxalate because of their insolubility in ethanol and complete solubility in sulphuric acid (Fig. 4b). The tissue of the outer cortex is made up of parenchyma cells in all species except C. magnus (Table 2, Figs. 4c, 4d), which is characterized, and cladistically defined (see PHYLOGENY) by centripetal, angular collenchyma. Ecological aspects of this feature are discussed in the ECOLOGICAL ANATOMY section. Resin canals, liso-schizogenous in origin, are numerous in the outer cortex of all non-obligate epiphytes (Table 2, Fig. 4e). Howard (1974) suggested that the study of nodal serial sections may aid in understanding the continuity of resin duct systems between the cortex and leaf, largely because of results obtained by Artschweger (1943). After examining long series (up to 15 nodes) of serial sections from several species, no stable pattern or relation between numbers of traces and canals was evident. Perhaps the fact that canals such as those in Asteraceae, Clusiaceae, etc. may not be developmentally homologous with those found here provides the reason for lack of correlation. It should also be noted that all resin canals in the stem are not continuous throughout; many of them are less than one node long, while some of them extend for more than eight nodes, but initiate and terminate several times. Reasons for the lack or poor development of outer cortical resin canals in obligately epiphytic taxa may be attributable to the concomitant loss in stem tensile strength that would result from the presence of numerous canals. In epiphytes, whose branches are constantly subject to forces from wind and gravitational effects, any design weakening branch tensile strength would presumably be selectively disadvantageous. Unfortunately, no ecological anatomy studies have been conducted to refute or corroborate this idea.

Brachysclereids are present in the outer cortex in *C. costaricanus* subsp. *panamensis*, *C. ptariensis* and *C. lineatus*. In *C. costaricanus* subsp. *panamensis*, the brachysclereids are numerous and arranged in groups (Fig. 4f), while in *C. lineatus* and *C. ptariensis* they are few and solitary. Their formation with respect to that of the periderm is of only limited taxonomic use.

The inner cortex is defined as the region centripetal to the outer cortex, and centrifugal to the stelar/pericylic region. In all species of subg. *Grammadenia*, there are five cortical bundles, except in the lower sections of branches corresponding to the hypopodium (see NODAL ANATOMY AND VASCULATURE). All cortical bundles are amphicribal or hemiamphicribal (Figs. 5c, 5d) except for those from areas immediately above the insertion of a leaf, or departure of a branch trace. Perivascular fibers accompanying the cortical bundles are well-developed in *C. costaricanus*, *C. parasiticus* and *C. ptariensis* (Table 2). It is interesting to note that these fibers are found only immediately below the insertion of leaf or below the departure of branch cortical traces, suggesting their morphogenesis may be tension-related. It might not be coincidental that the obligate epiphytes, whose branches undergo much stress, are the taxa in which they are best developed. Resin canals are ubiquitous in all species (Table 2), and frequently anastomose to form large cavities.

The most significant feature of the inner cortex is the presence of aerenchyma (Fig. 5e) in all species except _C. lineatus_ (Table 2, Fig. 5f). As is hypothesized in the cladistic analysis (see PHYLOGENY), the parenchyma present in the inner cortex of _C. lineatus_ may originate secondarily, given the necessity of invoking a large number of parallelisms to otherwise explain its presence. In addition, the shape of the parenchyma cells in the inner cortex of _C. lineatus_ is much more rounded in transverse section than that of most parenchyma and may indicate that the plant has the capability of producing it. Unfortunately, transplant studies were not possible owing to the remoteness of the populations from greenhouse or garden facilities. The primary stem aerenchyma of subg. _Grammadenia_ is unique within the Myrsinaceae. Within the family, aerenchyma is known otherwise only in the roots of _Aegiceras_ (Metcalfe & Chalk, 1950) a mangrove species of the Paleotropics.

The stelar/pericyclic region includes the vascular "cylinder" _per se_ and the row of parenchyma cells here interpreted as the pericycle. All species possess a stele which is composed of adjacent collateral bundles which touch each other but do not anastomose (see NODAL ANATOMY AND VASCULATURE). Thus, the stele appears as a solid cylinder, when it is not, prior to the initiation of interfascicular cambial activity. Although a region of small parenchyma cells centrifugal to the phloem surrounds the stele, no casparian strips were discernible, eliminating the possibility of the presence of an endodermis. Pericyclic fibers (probably from the primary phloem) are a common feature of the family (Metcalfe & Chalk, 1950). They are well-developed and form a ring around the stele at or just prior to the onset of secondary growth in *C. costaricanus*, *C. parasiticus* and *C. ptariensis* (Fig. 6a). In *C. lineatus*, *C. magnus* subsp. *magnus* and *C. piresii*, pericyclic fibers are found only in association with branch traces. The only taxa without pericyclic fibers are *C. magnus* subsp. *asymmetricus* and *C. marginatus*.

The pith of all species contains druses identical to those found in the outer cortical region (Figs. 6b, 6c). In all species except *C. magnus*, the pith is composed of parenchyma cells (Table 2). A most interesting feature of *C. magnus* is that in subsp. *magnus*, the collenchyma is angular (Figs. 6d, 6e), while in subsp. *asymmetricus* (Fig. 6f), it is mostly tangential. Although many walls are uniformly thickened in the latter, they stain a light pink in Safranin-

Fast Green in some preparations, while in others a very dark green. It is possible that they may represent a parenchyma-collenchyma transitional type, discussed by Esau (1965). Resin canals are present in all South American taxa except _C. marginatus_ (Table 2), and absent in all other taxa except _C. costaricanus_ subsp. _acuminatus_, in which one, poorly-formed canal was found.

Nodal Anatomy and Vasculature

One of the most interesting features of the primary stem anatomy in subg. _Grammadenia_ is its nodal anatomy, or leaf-node continuum (a modified term in the spirit of Howard, 1974). The node is here described, first with reference to leaf traces, then to branches, for the sake of clarity. The nodes with reference to leaf traces are described basipetally, while those of the branches, acropetally, to coincide with their respective development.

Immediately below the shoot apex, the stelar procambium is discernible, appearing as a continuous ring, with no discrete protoxylem elements discernible until approximately after P4. Each leaf contributes one midrib trace to the stele, and two lateral traces to the cortical system. As the leaf joins the stem, the crescentic midrib forms an oval trace which connects directly to the stele, without anastomosing with any other trace, while each cortical trace joins a separate cortical sympodium (Figs. 7a, 7b, 7c, 7d). In all stems examined, the lateral traces do not join their respective cortical sympodia simultaneously, the "cathodic" trace normally joining its sympodium approximately 140 to 150 microns above the "anodic" (It is important to note that the terms "anodic" and "cathodic" were created to indicate the first and second lateral trace to depart from the stem to the leaf when a sequence is viewed acropetally). In addition, midrib traces do not fuse with neighboring sympodia but, rather, barely touch them on either radial face. The vascular reconstruction (Fig. 8) shows the relationship of the cortical sympodia to the stelar, along with the 2/5 phyllotactic pattern (2 + 3 contact parastichies). The same sequence is repeated in Figures 9a through 9c, where longitudinal sections through the shoot apical region reveal the insertion of the cathodic trace (Fig. 9a) on its independent cortical sympodium, followed by that of the midrib trace (Fig. 9b) on the stele, and finally, the anodic (Fig. 9c) on its respective cortical sympodium. Another important feature revealed by the reconstruction (Fig. 8) is the autonomy of each cortical sympodium.

Thus, the leaf-node continuum of subg. <u>Grammadenia</u> may be described as unilacunar-one trace, with two additional traces from the cortical system (Fig. 9d), according to the classification proposed by Howard (1974, 1979). This system is unique, not only within the Myrsinaceae, but in the Magnoliophyta. It is most similar to that reported by Balfour and Philipson (1962) for *Chimonanthus fragrans* (Calycanthaceae). One principal difference between the two systems is that in *Grammadenia*, the cortical system is established immediately below the shoot apex, such that the procambial areas for each cortical sympodium differentiate synchronously with the stelar procambium. However, in *Chimonanthus*, the cortical system does not appear until well below the shoot apex. In addition, Balfour and Philipson indicated that, although the cortical system of *Chimonanthus* is independent of the stele, each sympodium is laterally connected to the other, while in subg. *Grammadenia*, each is autonomous. Reasons for these differences in construction are not readily apparent, but the fact that the phyllotaxis of *Chimonanthus* is decussate, while that of *Grammadenia* is spiral, may be significant. Consequences of this unique leaf-node continuum in classifying leaf venation architecture are discussed in that section.

Branching in subg. *Grammadenia* is exclusively sylleptic (see MORPHOLOGY- Habit and Architecture). Although sylleptic branching was studied in *Myrsine floridana* A. DC. by Wheat (1980) and is implicit in the data of Ogura (1937) for *Ardisia* subg. *Bladhia*, the vascularization of the shoot in subg. *Grammadenia* is distinct from any type known thus far in the family. As Figure 10a shows, the branch stelar trace leaves one gap in the stem's stele almost simultaneously with the formation of a branch in the cathodic cortical sympodium. Then, the anodic sympodium branches twice, forming two bundles (Fig. 10b), one of which divides again. Concomitantly, the cathodic trace branches twice, the latter product anastomosing with the first-formed one. Subsequently, the earliest-formed bundle of the anodic trace enters the hypopodium as the second anodic trace divides again, the product of which later anastomoses with it (Fig. 10d). Then, the second and third products of the anodic cortical trace anastomose and enter the branch base simultaneously with the cathodic cortical trace (Fig. 10e). Thus, the hypopodium base has three cortical bundles, two of which are products of the anodic cortical sympodium, and one of which is a product of the cathodic one (Fig. 10f). Later, that cortical sympodium which originates from the first-produced anodic trace branches once more, as does the sympodium whose origin was from the cathodic trace, to form a cortical system of five sympodia typical of the stem. It is important to note that the other two bundles are formed concomitantly with the development of the prophylls.

The fact that the cortical branch sympodia are continuous with their axillant leaf and at no time anastomose with the stelar trace is yet another nodal feature absolutely unique to subg. _Grammadenia_, based on data accumulated to date. In both _Ardisia_ subg. _Bladhia_ (Ogura, 1937) and _Myrsine_ *floridana* (Wheat, 1980), the cortical sympodia anastomose with the stelar trace by what Wheat termed "bridge bundles". In addition, the most important feature of Wheat's results is that the cortical bundles of *Myrsine floridana* are nothing more than late-fusing (when viewed basipetally) or precocious (when viewed acropetally) leaf traces, thus making the node trilacunar, three-trace for all practical purposes. The same is true for the situation described by Ogura (1937) for *Ardisia sieboldii*, *A*. *lentiginosa* and *A*. *conrnudentata*. The lack of a cortical system in the other taxa of subg. *Blahdia* studied by Ogura may be correlated with their prostrate, weakly woody habit.

The relationship of the vascular system of subg. *Grammadenia* to the rest of *Cybianthus* is not fully resolved at present, owing to lack of material. It appears that the rest of the genus *Cybianthus* may have the same system, or one in which the stelar bundles anastomose with each other. However, it does appear that, at least in subgenera *Microconomorpha*, *Laxiflorus*, and *Weigeltia*, the stelar and cortical systems are independent. This will be an important avenue of research, along with that of the situation in the genus *Embelia* Burman, as monographic work in *Cybianthus* continues.

Leaf Anatomy

Leaf Architecture

All species of subg. Grammadenia have perfect, basal, acrodromous (sensu Hickey, 1979)leaf venation Fig. 11). Although the two marginal veins are about one-half the diameter of the midrib, they are morphogenetically primary because of their direct link to the cortical sympodia of the stem (see Primary Stem, Nodal Anatomy and Vasculature). The marginal veins have numerous free-ending secondary branches, forming an irregular, incomplete margin, (Fig. 12a) giving the leaf a semicraspedodromous aspect. Secondary, pinnate venation unites the marginal and midrib veins, each vein appearing to give rise to several tertiaries (Fig. 12b). The tertiary venation is variable, from composite intersecondary, to weakly precurrent. Each tertiary vein has a dilatated terminus which is not associated with any idioblastic structure (Fig. 12c). Many pseudotertiaries, formed by branching of the marginal primary vein, form quadrangular aereoles, while those tertiaries formed by the secondary veins of the main laminar body anastomose to form pentagonal aereoles. No relation appears to exist with regard to position of liso-schizogenous cavities, hydropotes, and tertiary vein endings (Fig. 12a). The scarious margin and apical mucro are not vascularized.

Within the Myrsinaceae, acrodromous venation is found only in subgenus *Grammadenia* and in the monotypic genus *Vegaea* Urban, coincidentally the only other epiphyte in the family. *Vegaea* is also the only other member of the family with truly sessile leaves and mucronate leaf apices. These features notwithstanding, it has been shown that *Vegaea* is not related to *Cybianthus* in the PHYLOGENY section.

The remainder of the genus *Cybianthus* has eucamptodromous venation, within which brochidodromous is the most frequent type. Mez (1902, 1905, 1920) and Lundell (1968, 1976) have used the presence or absence of a prominent marginal nerve to distinguish species groups within subg. *Grammadenia*. I have found that this character varies with drying technique, and in fact, many of the taxa with allegedly inconspicuous marginal nerves actually have more protoxylem strands than those with allegedly conspicuous ones.

Leaf Histology

In subg. *Grammadenia*, systematically useful leaf histological features are found in the epidermis, palisade, and to a lesser extent, the mesophyll. All species have hypostomatic leaves with paracytic stomata (Figs. 12d, 12e), a feature known otherwise in the family only for *Wallenia yunquensis* (Howard, 1969). A preliminary survey (Pipoly, unpub.) and the work of Agostini (1971) indicate that anomocytic and anisocytic stomata are the most common types within the genus *Cybianthus*. The guard cells are slightly sunken (Fig. 12f) but are not in crypts. The subsidiary and all other epidermal cells (save the subsidiary cells of hydropotes) have thick cuticular wax deposited above the walls.

On the abaxial surface of all species (and on both surfaces of *C. magnus* subsp. *asymmetricus*), numerous hydropotes ("water drinkers", after Mayr, 1915) are found. Hydropotes, described by Mayr (1915) and Grüss (1927a, 1927b) have been reported for numerous submerged aquatics. The hydropote of *Grammadenia* (Figs. 13a, 13b, 13c) is composed of five to seven subsidiary cells, a central foot cell, a basal cell, a stalk cell, and up to twelve cap cells. In early ontogeny, a mucilaginous substance accumulates around the basal cell (Figs. 13d, 13e). Later, the cap breaks off, leaving a mucilaginous ring around the broken basal cell (Fig. 13f). The function of hydropotes is discussed under ECOLOGICAL ANATOMY. Within the Myrsinaceae, hydropotes are unique to subg. *Grammadenia*, based on data accumulated to date.

Table 3 reveals that the internal leaf histology is of little diagnostic use for specific delimitation, as only three characters have unique states within a given species. All species have druses in the uppermost (adaxial) layer of the mesophyll (Fig. 14a). The occurrence of abaxial palisade parenchyma in *C. lineatus* (Fig. 14b, 14c), the only savanna species of the subgenus, is unique. Likewise, the homogeneous adaxial epidermis of C. piresii (Fig. 14d) and the occurrence of bulliform hypodermal idioblasts inside the abaxial epidermis of C. marginatus (Fig. 14e) are also useful features in delimiting these taxa. The presence of phloem in islands (Fig. 14b) and the presence or absence of perivascular fibers (Fig. 14 f, 14g), do not appear to have significant systematic or ecological correlation. The two characters which are of obvious ecological significance, cutical thickness and mesophyll packing (Table 3), show that the Guayana Highland taxa all have cuticles greater than 12 microns in thickness, while all others have thinner ones. In addition, the only obligately epiphytic canopy taxon, C. costaricanus, has a diffuse rather than a compact mesophyll.

Figure 15 shows the unusual lenticular cells of the epidermis, associated with what are here termed hypodermal idioblasts. The idioblasts, reported by Grosse (1908), and thought to store water by Esau, (1965) are somewhat bulliform in shape, and may have a function similar to those found in many monocots. I observed many plants of C. costaricanus subsp. costaricanus with leaves which appeared to be longitudinally folded at mid-day in those plants exposed to full sunlight. Later, after sunset, the leaves were once again open, as well as in the early morning hours. The cells here termed hypodermal idioblasts appear homologous with those reported by Grosse (1908) for the genus Monoporus, whose cells, like these, actually have their origin in the

TABLE 3

Leaf Anatomical Features of Cybianthus subgenus Grammadenia

Key: + = present; - = absent

Taxon	Cuticle Thickness (microns)	Palisade Symmetry	Epidermal Cell Composition	Mesophyll Packing
C. ptariensis	12-14	Dorsiventral	Heterogeneous	Compact
C. lineatus	12-14	Bifacial	Heterogeneous	Compact
C. magnus subsp. magnus	3.6-7.2	Dorsiventral	Heterogeneous	Compact
C. magnus subsp. asymmetricus	7.2-9.6	Dorsiventral	Heterogeneous	Compact
C. piresii	12-14	Dorsiventral	Homogeneous	Compact
C. marginatus	4.8-7.2	Dorsiventral	Heterogeneous	Compact
C. costaricanus subsp. costaricanus	2.4-4.8	Dorsiventral	Heterogeneous	Diffuse
C. costaricanus subsp. acuminatus	7.2-9.6	Dorsiventral	Heterogeneous	Diffuse
C. costaricanus subsp. panamensis	2.4-4.8	Dorsiventral	Heterogeneous	Diffuse
C. costaricanus subsp. morii	6.0-8.4	Dorsiventral	Heterogeneous	Diffuse
C. parasiticus	3.6.-6.0	Dorsiventral	Heterogeneous	Compact

TABLE 3 (Cont'd)

Leaf Anatomical Features of Cybianthus subgenus Grammadenia

Taxon	Canal Distribution	Perivascular Fibers	Bulliform Cells Lower Epidermis	Phloem in Islands
C. ptariensis	Linear	Well-developed	-	+
C. lineatus	Linear	Well-developed	-	+
C. magnus subsp. magnus	Forming ring & above midrib	Well-developed	-	-
C. magnus subsp. asymmetricus	Forming ring & above midrib	Well-developed	-	-
C. piresii	Linear	Well-developed	-	-
C. marginatus	Forming ring	Well-developed	+	+
C. costaricanus subsp. costaricanus	Forming ring	Poorly developed	-	+
C. costaricanus subsp. acuminatus	Linear	Well-developed	-	-
C. costaricanus subsp. panamensis	Linear	Well-developed	-	+
C. costaricanus subsp. morii	Linear	Poorly developed	-	-
C. parasiticus	Linear	Well-developed	-	-

epidermis. These cells occur in every species of subg. *Grammadenia*, but differ between the species in terms of abundance. Only *C. piresii* has an epidermis entirely composed of lenticular cells superposed over the idioblasts (Fig. 14d). Figures 15a and 15c show the distribution of these cell complements in *C. ptariensis* and *C. lineatus*, respectively. Figures 15b and 15d show transverse and longitudinal sections through leaves of *C. costaricanus* subsp. *costaricanus*, which indicate that these cells are not sectioning artifacts.

Inflorescence and Floral Anatomy

Although apparent differences exist between the three types of inflorescences, flexuous-reduced, flexuous, and straight (see MORPHOLOGY), I have found that all are simple, monopodial racemes. The inflorescence rachis and pedicel have steles without accompanying cortical traces. The glandular-papillae of the inflorescence rachis and calyx tube are distinct from those found on the branches (Fig. 16d).

All flowers of subg. *Grammadenia* have simple vasculature and reveal no significant differences at the species level. One trace supplies each calyx lobe, corolla lobe, and stamen. Although the ovary is unilocular, there are five well-devloped dorsal carpel traces, and ten ventral ones, such that two ventral traces are associated with each dorsal one. This indicates that there are five carpels. The glandular-granules are actually papillate trichomes, composed of a foot cell, stalk cell and four to eight apical cells (Figs. 16a, 16b). The term glandular-granule, coined by Agostini (1971) is used in order to avoid confusion with the numerous other types of papillae present in the family (Grosse, 1908). Aestivation, used by Mez (1902) as a principal diagnostic character for species groups within the subgenus was found to be variable within the same inflorescence. As Lundell (1976) reported, both dextrorsely and sinistrorsely imbricate corollas are frequently present in _C_. _costaricanus_ subsp. _costaricanus_. I have found this in all species, and have also found that the contorted corollas described by Mez (1902) for several species, are actually aberrantly imbricate. This was easily discerned, as the amount of overlap of each perianth member is unequal. The glandular-lepidote scales of the ovary (Fig. 15c) are identical to those described by Agostini (1971) for _Cybianthus_ subg. _Conomorpha_.

Floral anatomy may be taxonomically useful when more liquid-preserved flowers of representative subgenera have been collected and can be studied. The vascularized staminal tube lobes reported by Agostini (1971) for subg. _Conomorpha_ have not been found in subg. _Grammadenia_. It may be possible that there is some correlation with lobe vascularization and corolla shape, or anther posture, as the clade including subg. *Conomorpha* has cupuliform corollas with distally recurved anthers, while the clade including *Grammadenia* has rotate corollas with erect anthers.

Wood Anatomy

Before the present investigation, the wood of *Grammadenia* was known only from scattered reports by Dodswell and Record (1936), Record (1936a, 1936b) and Williams (1928, 1936). Metcalfe and Chalk (1957) report on the general features of the Myrsinaceae, and indicated that the wood of *Grammadenia* contains rays with crystals and schizogenous idioblasts, which were not found in the present study. Given the high frequency of generic misdeterminations among herbarium specimens of the family, the reports for *Grammadenia*, *Cybianthus* and other genera in Metcalfe and Chalk (1950) cannot be relied upon. This is to be expected in a family with a currently chaotic situation with regard to generic limits.

As indicated in Table 1, a total of four species, representing all habitat types found in the genus, were studied. All qualitative features among species were identical, and the only significant quantitative difference was that *C. costaricanus* subsp. *costaricanus* had a slightly higher percentage of solitary pores per square millimeter. Therefore, only a subgeneric description is provided below. Terminology follows that of the International Association of Wood Anatomists (1967).

Wood diffuse-porous, the growth rings faint (Fig. 17a) or absent (Fig. 17b); vessels mostly in radial multiples of 2-4(-12) (Fig. 17b, 17c, 17d); solitary pores less than 40% per sq. mm (except in C. costaricanus subsp. costaricanus, 65-81%), 8-13 per sq. mm, rarely in contact with the rays; vessels mostly hexagonal, tangential diameter 88-125 microns; vessel member length 340-400 microns. Perforations simple (Figs. 17c, 17d), the end walls oblique (Fig. 18c), at times almost transverse (Fig. 17d); intervascular pits alternate, transitional (Figs. 18b, 18c, 19a-19b), 8-11 microns diam. Vessel-ray and vessel-axial parenchyma pits oval to rounded, fully bordered (Figs. 18d, 17c). Tyloses not present. Fiber-tracheids non-septate (Figs. 17a, 18d) simple, with circular-bordered pits on radial walls, non-gelatinous, 500-800 microns in length. Rays multiseriate, heterocellular type II (Figs. 20a-20c), mostly less than 2 per sq. mm, composed mostly of square cells (Fig. 19a), with weakly procumbent cells and upright cells (20a, 20b), always with sheath cells (Fig. 19d), (2-)3-5(-7) cells wide, up to 1400 microns high, all cells frequently with storage products. Axial parenchyma scanty paratracheal, the pitting circular-bordered, the strands to 10 cells long. Crystals and resin canals not present.

Preliminary data available for the genus Cybianthus as a whole indicates that wood features may be taxonomically useful at the subgeneric level (Pipoly, 1983a). For example, an as yet undescribed species of subg. Comomyrsine (Ollgaard 19401) contained septate fibers, and starch in the rays, axial parenchyma and fibers. I have reported that subg. Conomorpha has short uniseriate and biseriate rays (Pipoly, 1983a), while subg. Laxiflorus has only multiseriate rays which are up to 12 cells wide, and so long that their ends are not included in a typical section. It is hoped that further fieldwork will allow the collection of well-vouchered wood to explore the taxonomic usefulness of these features as the subgeneric cladogram in the present work is tested.

Ecological Anatomy/Morphology

As was discussed in the Primary Stem and Leaf Histology sections, several features of subg. Grammadenia are unique to it, and are correlated with its epipytic growth habit, including the diageotropic root, sessile, auriculate leaves, usually aerenchymatous inner cortex, and hydropotes on the leaf surface. In addition, the parenchymatous inner cortex of C. lineatus is of secondary origin, along with the densely glandular-papillate branchlet apices, the thick cuticle and pachycaulous trunk are adaptations to its savanna habitat.

Within the primary stem, the unique presence of collenchyma in *C. magnus* is most interesting because of the difference in pith collenchyma types between subspecies. In subsp. *magnus*, both the outer cortical and pith collenchyma are extremely well-developed and are angular. However, in subsp. *asymmetricus*, the outer cortical type is angular, while the pith collenchyma may be termed tangential (Carlquist, 1962), or lamellar (Esau, 1965). Why this difference occurs is unknown, and no studies comparing relative strengths of collenchymatic types have been carried out. It is interesting to note that collenchyma wall thickness has been shown to increase with motion induced by wind (Walker, 1960). In general, collenchyma is thought to provide great tensile strength concomitant with flexibility and plasticity (Esau, 1936, 1965).

The principle difference between the subspecies' habitats is that subsp. *magnus* occurs on mountains with altitudinally large zones of cloud forest, a less windy and more equable environment when compare to that of subsp. *asymmetricus*, which occurs in very wet, but windy, open environments on low mountains.

The parenchymatous inner cortex of *C. lineatus* is composed of cells which are, in transverse section, somewhat more rounded than typical parenchyma cells. The remainder of species in the subgenus have aerenchymatous inner cortices (Table 2). Aerenchyma, most frequently encountered in submerged aquatics (Esau, 1965; Sifton, 1945, 1957) is thought to improve gas exchange, and to provide strength with the least possible weight per cubic volume (Williams & Barber, 1961). The latter asset would certainly be selectively advantageous for an epiphyte. It is interesting to note that taxa which are not obligately epipetric or epiphytic, such as *C. ptariensis*, *C. piresii*, and *C. lineatus*, lack, or have poorly developed aerenchyma.

The presence of hydropotes is likewise an unusual feature of the subgenus normally associated with submerged aquatics (Fahn, 1979). Although even the savanna species, *C. lineatus*, has numerous hydropotes, their mineral absorptive function may be the critical factor responsible for their occurrence in subg. *Grammadenia*. Elegant studies by Lüttge (1964) and Lüttge and Krapf (1972) have demonstrated the ultrastructural and chemical dynamics of mineral absorption by hydropotes. Not a single species of subg. *Grammadenia* grows in what might be considered a nutrient-rich environment.

DISTRIBUTION

Members of subg. *Grammadenia* are locally common in montane regions from the Cordillera de Tilarán, Costa Rica south (through Panama) to Colombia, in the Andes from the state of Lara, Venezuela to the department of Cuzco, Peru, across the contiguous Guayana Highland (sensu Maguire, 1979) and in the

Lesser Antilles. Of the seven species recognized in this treatment, two species, *C. piresii* and *C. ptariensis*, are narrow endemics. The former species is restricted to granitic outcrops on Cerro de la Neblina, while the latter is endemic to the Auyán-tepuí-Chimantá Floristic Complex of Maguire (1979). While the large floristic province Pantepuí (Mayr & Phelps, 1967; Huber, pers. comm.) harbors three endemic species, the greatest morphological diversity among populations is seen in Colombia, from which nine (here treated as two) species were described. With only preliminary data available for the entire genus *Cybianthus* (Agostini, 1971; Pipoly, 1981, 1983a, 1983b), no biogeographic analysis of subg. *Grammadenia* with respect to the remainder of the genus is possible at this time. It is significant to note, however, that seven of the ten subgenera here recognized (see PHYLOGENY) have been found in the area of Cerro de la Neblina. Three of these subgenera (*Microconomorpha*, *Comomyrsine*, *Weigeltia*), containing at least two new species, have been found only as a result of recent exploration efforts directed by Dr. James L. Luteyn (NY). The three subgenera of *Cybianthus* not found in the Neblina area include the monotypic *Cybianthopsis*, endemic to the Sierra de Luquillo, Puerto Rico, subg. *Triadophora*, which contains two species from the northern Andes and adjacent Panama, and one species from the Matto Grosso of Brazil, and finally, subg. *Stapfia*, known from the Zulian Floristic District

(Huber, unpubl.) and Volcán Barú of Panama (Pipoly, 1983b).

There are no species in subg. *Grammadenia* which cross the floristic provinces described by Hueck and Seibert (1972) or Huber (unpub.). Mesoamerica (excluding the Darién of Panama), contains only *C. costaricanus*. *C. magnus* occurs in the Northern Andean Province (including the Venezuelan Costal Cordillera District of Huber, unpubl.), and the mon-montane regions of the Chocó of Colombia and adjacent Darién of Panama. *C. marginatus* is restricted to the High Elevation Andean Montane Region of Hueck and Seibert (1972). Having already discussed the taxa of Pantepuí, the remaining species of the subgenus, *C. parasiticus*, is endemic to the Lesser Antilles.

ECOLOGY

With the sole exception of *C. lineatus*, all members of subg. *Grammadenia* inhabit forested areas. There are four habitat types in which species of the subgenus occur, including: cloud and elfin forests (*C. costaricanus*, *C. magnus*, *C. parasiticus*), páramo thickets (*C. marginatus*), scrub forests (*C. ptariensis*, *C. piresii*) and savannas (*C. lineatus*).

The cloud and elfin forest taxa are all epiphytic and occur in areas with broad altitudinal zones of forest. They generally occur in natural ecotones at the limit of the cloud forest zone, such that one may find them in the cloud forestsubpåramo thicket transition (*C. magnus* subsp. *magnus*), the upper montane forest-cloud forest transition (*C. magnus* subsp. *asymmetricus*, *C. parasiticus*, *C. costaricanus* subspp. *acuminatus*, *morii*, and *panamensis*) or at the cloud-elfin forest transistion, where both are well-developed (*C. costaricanus* subsp. *costaricanus*). One form of the latter subspecies is restricted to the *Lomaria-Sphagnum* associations on the summits of several peaks in the Cordillera de Talamanca, Costa Rica. This variant, described by Lundell (1968) as *Grammadenia minor* occurs in a habitat very much resembling the paramos of the Andes. All cloud forest taxa are characterized by frequent reiteration from wind and exposure stress, and from riverine effects (see HABIT AND ARCHITECTURE). The highest incidence of unisexual flowers occurs in this group.

The sole påramo species, *C. marginatus*, occupies an extremely narrow habitat, occurring only in small thicket areas on or between rock walls above lagoons in high påramos. Although it forms large populations in this narrow habitat, populations are normally distant from each other, and hence, these many isolated populations have allowed fixation of local variations, resulting in taxonomic overdescription. A most interesting morphological feature of *C. marginatus* is the variation in verrucose papillae of the branchlets. Populations from the Cuzco area of Peru, have the best developed, papillae, followed by those plants from the Laguna del Coromoto in Mérida, Venezuela. The remainder of the populations all bear these papillae, but their numbers on the stem are greatly reduced, and they are often restricted to the area aligned with leaf orthostichies. Although their function is unknown, it appears that populations which grow in areas more exposed to wind form larger papillae.

The scrub forest taxa are endemic to Pantepuí. The scrub formations present in this area are unusual because their general physiognomy resembles that of a cloud forest, but they are notably poor in epiphytic mosses and liverworts, and lack lianas altogether. These taxa are loosely rooted in the litter, normally near small surface water streams or at the edge of bog-like areas (*turberas*).

C. lineatus, the only savanna species, has several features (see MORPHOLOGY, Primary Stem Anatomy, Leaf Anatomy) which are correlated with its xeric habitat. Although it occurs sympatrically with *C. ptariensis* throughout the latter's range, the two are found growing together only where a scrub forest-savanna interface occurs. I had originally suspected hybridization, based on a number of apparently intermediate forms found on Chimantá-tepui, an intensive population study revealed that the variation was only quantitative.

On the Macizo del Chimantá, in the wide valley between Chimantá- and Torono-tepuís, a scrub forest-savanna interface contained 47 individuals of *C. ptariensis* and more than 160 of *C. lineatus* present, growing together. Of these, only four plants, *Pipoly et al. 7268, 7270, 7273*, and *7276* (Fig. 28b) appeared quantitatively intermediate. However, when each was examined for qualitative features, they were readily separable. Thus, the individuals of *C. ptariensis*, (*Pipoly et al. 7268, 7273, 7276*), although they had somewhat more acute leaf apices, atypically thick trunk bases and shorter (but straight) inflorescences; the aerenchymatous stems, lobate ovaries, and membranous staminal tubes affirmed their proper identities. The collection of *C. lineatus* (*Pipoly et al. 7270*) despite the longer (but flexuous) inflorescence with obtuse leaf apices and longer leaves was otherwise identical to typical *C. lineatus* by the absence of aerenchyma in the stem, glandular-papillate branchlets, and ellipsoid pistil. It is most probable that *C. ptariensis* subsp. *auyantepuiensis*, described by Agostini (1967) is nothing more than a variant from such an interface (see SYSTEMATIC TREATMENT).

In summary, subg. *Grammadenia* is montane and its species inhabit very narrowly defined habitats. Particulary noteworthy is the fact that these plants are extremely sensitive to disturbance, and thus, are indicators of virginity. Approximately one-half of the localities visited in Colombia, and all those in Ecuador, from which collections had been made before or during 1980 contained not a single plant. Were it not for long treks away from secondary roads, and national parks, recollection and observation of populations would not have been possible.

PHYLOGENY

Methods

In order to develop the present classification of *Cybianthus* subgenus *Grammadenia*, a cladistic analysis (Eldredge & Cracraft, 1980; Nelson & Platnick, 1981; Wiley, 1981) was employed to construct hypotheses of phylogenetic relationship. A detailed discussion of the merits of the cladistic method will not be presented here, but one of its basic tenets is that the phylogeny of a particular group is best expressed by a cladogram, defined by Wiley (1981) as "A branching diagram of entities where the branching is based on the inferred historical connections between the entities as evidenced by synapomorphies. That is, a cladogram is a phylogenetic or historical dendrogram." To produce a cladogram, the synapomorphies (shared, derived character states) can be determined only after the character states have been polarized. Among the several methods available for the polarization of characters, the out-group comparison method (Stevens, 1980; Whatrous & Wheeler, 1981; Maddison et al., 1984; Brooks & Wiley, 1985; Kluge, 1985), based on simple parsimony was employed. Although Crisci and Steussy (1981) and Steussy and Crisci (1984) criticize this method, detailed rebuttals explaining its advantanges are enumerated in Stevens (1981) and Wheeler (1981). In this method, any character state occurring in both the ingroup and the outgroup is assummed plesiomorphic (ancestral), while the character state occurring only in the in-group is considered apomorphic (derived).

The polarization of character states requires not only the use of an out-group but also that contrasting character states be homologous (Kaplan, 1984; Stevens, 1984). In the present analysis, all structures considered non-homologous are so designated as the result of developmental studies .

The present cladistic analysis was conducted in three steps. First, the genus *Embelia* Burman was chosen as the sister group (taxonomic out-group) of the genus *Cybianthus*. Second, the relationships of the ten subgenera of *Cybianthus* were analyzed using *Embelia* as the out-group and the systematic position of *Grammadenia* was determined. Finally, the relationships of the species of *Cybianthus* subg. *Grammadenia* were analyzed, using the clade containing subgenera *Cybianthus* and *Cybianthopsis* as the functional out-group.

Selection of *Embelia* as the sister group of *Cybianthus*

One of the most critical processes involved in conducting a cladistic analysis is the selection of a sister group which will serve as the outgroup for character polarization. In a family such as the Myrsinaceae, the only existing comprehensive tribal and generic classification (Mez, 1902) is based on several characters which have been shown to vary within species, such as ovule position (Lundell, 1966a; see morphology), floral sex (Pipoly, 1983b, see morphology), and floral merosity (Agostini, 1971; see morphology). Therefore, to find an appropriate sister group for the genus *Cybianthus*, it was necessary to survey the family to determine which characters and character states had limited distribution and ideally, to determine which states ocurred only in *Cybianthus* and one other group.

An extensive survey of the family resulted in the discovery of a single character state, the "glandular-granules" (cf. Agostini, 1971, 1980), which are actually papillate trichomes (see Floral Anatomy), found on the adaxial corolla surface, unique to *Cybianthus* (Fig. 21b, c) and *Embelia* (Fig. 21d, e). Thus, even with a single character state, its uniqueness enables the postulation of a common ancestry bebetween the two genera, and thus, that they form a monophyletic group. SEM studies have confirmed that these granules are not homologous to the "glandular-granules" of *Vegaea* Urban (Fig. 21a). Another possible synapomorphy is the reticulate pattern of epicuticular wax on the adaxial corolla surface (Figs 21b, c).

From there, the autapomorphic lianous habit, distichous phyllotaxy and apomorphic free petals define *Embelia*, while the ring of glandular-granules at the corolla tube apex defines *Cybianthus*.

Analysis of the subgenera of *Cybianthus*

The cladogram (Fig. 22), based on 36 characters (Tab.4,5) shows that two principal phylogenetic lines are discernible. The line on the left side of the cladogram (*Microconomorpha* through *Conomorpha*), defined by distally curved anthers (character 32), includes what Mez (1902) recognized as the genus *Conomorpha* A. DC. The clade on the right (*Comomyrsine* through *Grammadenia*), defined by anthers as wide or wider than long (26) and poricidal anther dehiscence (33), includes those groups formerly recognized as the genera *Weigeltia* A. DC., *Cybianthus* Martius, and *Grammadenia* Bentham (Mez, 1902).

Although the cladogram generally supports the infrageneric treatments of Agostini (1971, 1980) and Pipoly (1983a, 1983b), it is significant that subgenera *Iteoides* Agostini and *Microconomorpha* (Mez) Agostini contain no apomorphies by which they may be separated. Agostini (1980) and Pipoly (1983b) used pseudoverticillate phyllotaxy and 3:1 ratio of filament to anther length to separate *Microconomorpha* from *Iteoides*. However, data obtained from herbarium study and regional monographs and floristic works (Perrier, 1953; Coode, 1983; Lundell, 1966a, 1966b, 1971; Pitard, 1930; Ridley, 1923; Smith, 1973; Stearn, 1969; Taton, 1980; Walker, 1940) demonstrate the sporadic occurrence of pseudoverticillate phyllotaxy for several species scattered in major genera (*Ardisia*, *Badula*, *Tapeinosperma*, *Discocalyx*, *Oncostemon*,

TABLE 4

Polarized character states for analysis of the subgenera of *Cybianthus*

CHARACTER	PLESIOMORPHIC STATE	APOMORPHIC STATE
1. Axis number	polyaxial	monoaxial
2. Plant sex	strictly dioecious	monoecious or bisexual
3. Root tropism	positively geotropic	diageotropic
4. Branchlets w/ dendroid & stellate trichomes	absent	present
5. Branchlets w/ malphigiaceous hairs	absent	present
6. Branchlets w/ stalked lepi-		

TABLE 4 (cont'd.)

dote scales	absent	present
7. Branchlets w/ sessile furfuaceous scales	absent	present
8. Pistillode	well-developed	vestigial
9. Inner cortex	parenchymatous	aerenchymatous
10. Petioles	present	absent
11. Petiole base shape	tapering	abruptly pulvinate
12. Leaf venation	camptodromous	acrodromous
13. Leaf subepidermal fibers	absent	present
14. Leaf margin texture	turgid	scarious
15. Leaf apex	without mucro	mucronate

TABLE 4 (cont'd.)

16. Leaf margin base shape	cuneate	auriculate
17. Adaxial leaf midrib vestiture	not papillate	glandular-papilate
18. Inflorescence position	solitary, terminal or axillary	pseudoverticillate
19. Inflorescene bract	small, leaflike, caducous	large, leaflike persistent
20. Inflorescence type	raceme or panicle	indeterminate umbel
21. Floral merosity	4- or 5-merous	3-merous
22. Abaxial calyx surface	not lepidote	lepidote

TABLE 4 (cont'd.)

23. Calyx lobe x-section outline	medially flat	medially thick
24. Corolla tube apex vestiture	glabrous	glandular-granulose
25. Calyx aestivation	non-valvate	valvate
26. Corolla shape	cupuliform or campanulate	subrotate to rotate
27. Corolla lobe aestivation	non-valvate	valvate
28. Abaxial corolla near margin	glabrous	glandular-granulose
29. Staminal tube to corolla	merely adnate	complete fusion stamens appear epipetalous
30. Anther position	erect	versatile

TABLE 4 (cont'd.)

31. Anther/filament attachment	dorsifixed	basifixed
32. Anther habit	straight	curved distally
33. Anther symmetry	longer than wide	as wide or wider than long
34. Anther dehiscence	longitudinal	poricidal
35. Longitudinal anther dehis.	slits wide	slits narrow
36. Pistillode shape	not lageniform	lageniform

TABLE 5

DATA MATRIX FOR SUBGENERA OF CYBIANTHUS

TAXON	CHARACTER (0= plesiomorphic; 1= apomorphic)																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Iteoides	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Microconomorpha	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Conomorpha	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Stapfia	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Laxiflorus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Comomyrsine	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
Triadophora	1	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0
Weigeltia	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
Cybianthopsis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cybianthus	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Grammadenia	0	1	1	0	0	0	0	0	1	1	0	1	0	1	1	1	1	0	0
Embelia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

TABLE 5 (Cont'd)

TAXON	CHARACTER (0= plesiomorphic; 1= apomorphic)																
	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Iteoides	0	0	0	1	1	1	0	1	0	0	0	0	1	0	0	1	0
Microconomorpha	0	0	0	1	1	1	0	1	0	0	0	0	1	0	0	1	0
Conomorpha	0	0	1	0	1	1	0	1	0	0	0	0	1	0	0	0	0
Stapfia	0	0	0	1	1	0	0	0	1	0	0	0	1	0	0	0	0
Laxiflorus	0	0	0	1	1	1	0	1	1	0	0	0	1	0	0	0	1
Comomyrsine	0	0	0	0	1	1	1	1	0	0	0	0	0	1	0	0	0
Triadophora	0	1	0	0	1	1	1	1	0	0	0	0	0	1	0	0	0
Weigeltia	0	0	0	0	1	1	1	0	0	0	1	0	0	1	0	0	0
Cybianthopsis	1	0	0	0	1	0	1	0	0	1	0	1	0	1	1	0	0
Cybianthus	0	0	0	0	1	0	1	0	0	1	0	1	0	1	1	0	0
Grammadenia	0	0	0	0	1	0	1	0	0	0	0	1	0	1	1	0	0
Embelia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Hymenandra), thus making polarization of this character impossible at the present time. In addition, during recent fieldwork I conducted in Venezuela and Colombia, it was shown that in several disturbed populations of *Cybianthus* (§ *Iteoides*) *iteoides* (Bentham) Agostini, pseudoverticillate leaves were produced at nodes where a pseudowhorl of branches (typical of all trees showing Rauh's Model- see architecture) had not occurred, thus implying that the state may be more plastic than was originally estimated.

The character state of a 3:1 ratio of filament to anther length also occurs sporadically in some species of *Cybianthus* subg. *Weigeltia*, and likewise in some species of the genus *Embelia* in subgenera *Choripetalum*, *Embeliopsis*, *Heterembelia*, *Micrembelia*, and *Pattara*, thus precluding its polarization. Therefore, it is here proposed that all species in the *Microconomorpha*-*Iteoides* clade be included in one subgenus, for which the earliest name would be *Microconomorpha*. Other character states thought to be useful in defining this clade (Agostini, 1980; Pipoly, 1981, 1983b) such as glabrous or glandular-granulose branchlets, presence or absence of glandular cilia on the calyx lobe margins, and raised perianth glands were not polarizable because they were found to vary between species within other subgenera.

Another striking feature of the cladogram is the occurrence of parallelism for three characters: calyx (25) and corolla (27) lobe aestivation, and plant sex (2). Despite the fact that valvate aestivation is the only type which is constant within a species (Pipoly, unpubl. data), its parallel occurrence precludes its use in defining infrageneric taxa. The data available when Agostini (1980) published his infrageneric classification indicated that the entire genus *Cybianthus* was dioecious. Now that Pipoly (1983b, and here) has found bisexual and monoecious plants in subgenera *Microconomorpha*, *Stapfia*, and *Grammadenia*, the distribution of non-dioecious taxa may be an artifact of information currently available rather than a biological reality. Therefore, the occurrence of non-dioecious plants in parallel groups is meaningless until a complete survey of the genus in the field, especially of species in subgenera *Comomyrsine*, *Triadophora* and *Weigeltia*, is completed.

The systematic position of *Grammadenia*

The cladogram (Fig. 22) of hypothesized relationships among the subgenera of *Cybianthus* clearly illustrates the synapomorphies which require the placement of *Grammadenia* as a monophyletic unit within the genus *Cybianthus*.

Since its circumscription, (Bentham, 1846) *Grammadenia* has traditionally been considered a close relative of *Cybianthus*, but was always considered a distinct genus because of its sessile leaves and alleged five-merous flowers and bisexual flowers (Agostini, 1980; Hooker, 1876;

Lundell, 1971; Macbride, 1959; Miquel, 1856; Pax, 1897; Mez, 1901, 1902). The present study reveals not only that floral merosity and sexuality are variable characters at the generic and specific levels, but that the much-emphasized sessile leaves, an apomorphic state within the genus *Cybianthus*, occurs convergently in the monotypic genus *Vegaea* Urban, the only other epiphytic member of the Myrsinaceae. The occurrence of sessile leaves in *Vegaea* thus eliminates the possibility of using this character state to define *Grammadenia* as a genus.

Unlike the cladistic system presented here, which is based on shared, derived, characters, previous systems, including that of Agostini (1980) were constructed on principles of overall similarity (the sum of primitive and derived characters) and on the unique combination of characters, with weight added to certain ones. These previous systems ignored the evolutionary significance of the ring of glandular-granules at the junction of the corolla tube and lobe, which defines *Cybianthus*. They also ignored not only the apomorphic anther symmetry (33) and corolla shape (26) which *Grammadenia* shares with the *Comomyrsine* through *Grammadenia* clade, but also the apomorphic anther attachment (31) and dehiscence (34), which define the *Cybianthopsis*-*Cybianthus*/*Grammadenia* clade.

In summary, the taxonomy presented here is the result of a specific set of eight falsifiable hypotheses which may be tested as future monographic work continues. The hypotheses upon which the polarization of character states are based are a result of outgroup comparison (Stevens, 1980; Whatrous & Wheeler, 1981; Brooks & Wiley, 1985) for which the homology of contrasting character states was discerned through developmental studies. These hypotheses are as follows. First, the presence of homologous glandular-granules on the corollas of Embelia and Cybianthus, a unique character state within the family, implies a common ancestry between them, and is probably not the result of parallel or convergent evolution. If they share a common ancestry, they form a monophyletic group. Second, within the monophyletic group Cybianthus, all taxa share the unique features of a ring of glandular-granules at the junction of the corolla tube and lobes, which may be used to define the genus. Third, the fact that Grammadenia possesses the aforementioned characters suggests its common ancestry with the rest of Cybianthus and therefore, indicates it is a member of the genus. Fourth, within the monophyletic genus Cybianthus, the apomorphic rotate to subrotate corollas and anthers as wide or wider than long define a monophyletic group containing Comomyrsine Triadophora, Weigeltia, Cybianthopsis, Cybianthus and Grammadenia. Fifth, within that clade, the synapomorphic basifixed and poricidally dehiscent anthers each independently define the monophyletic group Cybianthus/ Cybianthopsis/Grammadenia. Sixth, the complete developmental fusion of the staminal tube to the adaxial corolla tube in *Cybianthopsis* and *Cybianthus* indicates that those two subgenera are more closely related to each other than either one is to *Grammadenia*. Seventh, subgenus *Cybianthopsis* is defined by its unique indeterminate umbel, and subgenus *Cybianthus* by its unique vestigial pistillode. Finally, subgenus *Grammadenia* is defined by each of its autapomorphs, including diageotropic roots, aerenchymatous inner cortex sessile leaves, acrodromous leaf venation, scarious leaf margins, mucronate leaf apex, auriculate leaf base, and glandular-papillate adaxial leaf midrib. Each of these hypotheses will be rigorously tested as I proceed with the revision of the genus for FLORA NEOTROPICA.

The species of *Cybianthus* subgenus *Grammadenia*

Using the cladogram illustrating the relationships of infrageneric groups in the genus *Cybianthus*, the character states present in subgenus *Grammadenia* were polarized using the *Cybianthopsis*-*Cybianthus* clade as the outgroup. After an extensive survey of characters within subgenus *Grammadenia*, 37 of these (Tables 6, 7) were found useful in reconstructing a phylogenetic hypothesis for the species of the subgenus.

The cladogram (Fig. 23) is well corroborated and suggests that several major phyletic lines are present within *Gramma-*

TABLE 6

Polarized character states for analysis of the species of *Cybianthus* subgenus *Grammadenia*

CHARACTER	PLESIOMORPHIC STATE	APOMORPHIC STATE
1. Branchlet surface	smooth	verrucose
2. Branchlet vestiture	glabrous	glandular-papillate
3. Trunk shape	leptocaulous	pachycaulous
4. Inner cortex tissue type	parenchymatous	aerenchymatous
5. Pith tissue type	parenchymatous	collenchymatous

TABLE 6 (cont'd.)

6. Outer cortex tissue type	parenchymatous	collenchymatous
7. Leaf spongy mesophyll distribution	diffuse	compact
8. Leaf texture	non-membranaceous	membranaceous
9. Leaf symmetry	symmetrical	asymmetrical
10. Leaf margin outline	entire	minutely crenulate to denticulate
11. Leaf shape	oblanceolate to obovate	oblong, elliptic to ovate
12. Leaf palisade distribution	only adaxial	adaxial & abaxial
13. Inflorescence rachis posture	erect, straight	flexuous

TABLE 6 (cont'd.)

14. Calyx lobe margin outline	erose	entire to crenulate
15. Calyx lobe margin vestiture	glandular-ciliate	glabrous
16. Corolla texture	coriaceous	chartaceous
17. Corolla lobe adaxial vestiture	glandular-granulose	glabrous
18. Medial adaxial corolla lobe surface	smooth	rugose
19. Corolla lobe margin outline	entire or erose	crenulate
20. Corolla lobe symmetry	regular	irregular
21. Staminal tube texture	membranous	carnose

TABLE 6 (cont'd.)

22. Staminal tube apex	truncate	lobate
23. Staminal tube lobe punctation	epunctate	punctate
24. Ventral connective punctation	epunctate	punctate
25. Dorsal connective punctation	prominent	not prominent
26. Pistil shape	obnapiform	not obnapiform
27. Ovary when not obnapiform	ellipsoid	umbonate
28. Ovary x-section shape	terete	non-terete
29. Ovary inter-lobular region shape	costate	sulcate
30. Ovule position	uniseriate	biseriate

TABLE 6 (cont'd.)

31. Distribuion	non-Mesoamerica	Mesoamerica
32. Root tropism	positively geotropic	diageotropic
33. Petioles	present	absent
34. Leaf venation	camptodromous	acrodromous
35. Leaf apex	without mucro	mucronate
36. Leaf margin text.	turgid	scarious
37. Adaxial leaf midrib vestiture	glabrous	glandular-papillate
38. Leaf margin base shape	cuneate	auriculate
39. Leaf margin posture	flat	subrevolute to revolute
40. Fruit shape	depressed-globose to obovoid	ellipsoid

TABLE 7

DATA MATRIX FOR SPECIES OF CYBIANTHUS SUBGENUS GRAMMADENIA

TAXON CHARACTER (0= plesiomorphic; 1= apomorphic)

TAXON	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
ptariensis	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0
piresii	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	1
lineatus	0	1	1	0	0	0	1	0	0	0	0	1	1	0	0	0	1	0	0	0	1
marginatus	1	0	0	1	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	0	1
parasiticus	0	0	0	1	0	0	1	1	1	0	0	0	0	1	1	1	1	1	0	0	0
magnus	0	0	0	1	1	1	1	0	1	0	0	0	0	0	0	1	1	1	0	1	0
costaricanus	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Cyb/ Cybsis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

TAXON	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
ptariensis	1	0	0	1	0	0	1	1	0	0	1	1	1	1	1	1	1	1	0
piresii	1	1	1	0	0	0	1	1	0	0	1	1	1	1	1	1	1	1	0
lineatus	1	0	0	0	1	0	0	0	1	0	1	1	1	1	1	1	1	1	0
marginatus	1	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1	1	1	1
parasiticus	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0
magnus	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	0	0
costaricanus	1	0	0	0	1	1	0	0	1	1	1	1	1	1	1	1	1	0	0
Cyb/ Cybsis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

denia. The first contains only *C. costaricanus* and is defined by each of the following apomorphies: crenulate corolla lobe margins (19), umbonate pistil (27), and Mesoamerican distribution (31). The second contains the other six species of the subgenus and is defined by compact leaf mesphyll (7) and glabrous adaxial corolla lobes (17).

Despite the fact that all species and clades have non-homoplasic apomorphies defining them, the occurrence of parallelism in characters 18, 26 and 30, and of postulated reversals for characters 4, 20 and 21, merits further discussion. Four of the characters which occur in parallel, rugose medial portion of the adaxial corolla lobe surface (18), non-obnapiform pistil shape (26) and biseriate ovules (30), occur in *C. costaricanus*. Placement of *C. costaricanus* in the *C. parasiticus-magnus* clade to eliminate parallelism for character 18, but necessitate postulation of reversals for characters 8, 14 and 15, along with those which define the major break in the cladogram, characters 7 and 17. Likewise, placement of *C. costaricanus* in the *C. lineatus-marginatus* clade to eliminate paralellism for character 30 would require an additional two reversals for characters 21 and 39. To eliminate parallelism for character 20, by placing *C. costaricanus* in the *C. ptariensis-piresii* clade, would require four reversals and would not eliminate two other parallelisms. Finally, replacement of *C. costaricanus* to resolve the paralellism for character 26 by moving it to the

C. lineatus-marginatus clade would result in the postulation of five reversals. All of these alternatives are less parsimonius than the present hypothesis.

Reversals in characters 20 (irregular corolla lobe symmetry), 21 (staminal tube texture), 22 (lobate staminal tube) and 4 (inner cortex tissue type) are found in *C. ptariensis* and *C. lineatus*, respectively. To eliminate the postulation of a reversal for character 20 and 21 would require the placement of *C. ptariensis* on the *C. parasiticus-magnus* clade, thereby creating paralellisms for two characters, 28 (ovary shape), and 40 (leaf margin posture), a less parsimonius alternative. Likewise, to eliminate a reversal for character 22, parallelisms would have to postulated for all other taxa. The rationale of a postulated reversal for character 4 may be explained in terms of function. Although the subgenus is defined by an aerenchymatous inner cortex, *C. lineatus*, the only savanna species, has a parenchymatous inner cortex. It is here postulated that the inner cortex of *C. lineatus* is secondarily parenchymatous, as an adaptation to the xeric savanna habitat. This hypothesis is supported by data presented in this monograph (see ANATOMY) which indicate that this character, as well as the others which define *C. lineatus*, are xeromorphic adaptations, such as the glandular-papillate branchlet vestiture (2), pachycaulous trunk morphology (3), and abaxial palisade distribution (12). To hypothesize a major phylogenetic clade consisting of _C_. _lineatus_ apart from the remainder of subgenus _Grammadenia_ would require the postulation of no less than 13 parallelisms, a hypothesis which is here rejected.

The present classification of species within _Grammadenia_ is radically different from that of Mez (1901, 1902, 1905) and does not support the recognition of a single species described by Cuatrecasas (1951), Pittier (1931) or Lundell (1968, 1971, 1976, 1985). The use of such characters as the presence or absence of a "conspicuous" marginal nerve (Lundell, 1976; Mez, 1902), floral merosity (Pittier, 1931), apiculae on fruits (Cuatrecasas, 1951), color and aggregation of punctations (Cuatrecasas, 1951; Lundell, 1968, 1976, 1985), diminutive size (Lundell, 1968), and ample distinctiveness (Lundell, 1968) are now known to be unstable (see morphology) or unpolarizable character states useless for specific delimitation. Instead of selecting and preferrentially weighting particular character states, the cladistic analysis shown here, as well as the subgeneric analysis, is based on the premise that the possession of shared unique character states implies descent from a common ancestor. This enables the hypotheses regarding phylogenetic relationships to be falsifiable when tested with new data.

In summary, the cladogram postulating the relationships of the species in _Cybianthus_ subgenus _Grammadenia_ presented here is the result of seven hypotheses. First, the unique crenulate corolla lobe margin, umbonate pistil and Mesoamerican distribution of C. costaricanus indicate that it has diverged form the rest of the subgenus. Second, the unique compact leaf mesophyll and glabrous adaxial corolla lobes defines a monophyletic group containing all species of the subgenus save C. costaricanus. Third, apomorphic asymmetrical leaves and chartaceous corollas indicate that C. parasiticus and C. magnus shared a common ancestor. Fourth, the unique possession of collenchyma in the pith, and in the outer cortex defines C. magnus while apomorphic membranaceous leaves; glabrous calyx margins, with an entire to crenulate outline, define C. parasiticus. Fifth, a carnose staminal tube , and subrevolute to revolute leaf margin posture imply that the clade including C. ptariensis through C. marginatus share a common ancestry. Sixth, within that clade, the apomorphic zig-zag inflorescence rachis defines the C. lineatus-marginatus clade, while the non-terete ovaries of C. ptariensis and C. piresii define that monophyletic group. Finally, each species is defined by unique feature,including: the apomorphic branchlet surface, leaf shape, and fruit shape of C. marginatus; branchlet vestiture, trunk morphology and palisade distribution of C. lineatus; the leaf margin, punctation of the staminal tube lobes, and punctation of the ventral connective surface of C. piresii; and finally, the posture of the dorsal connective punctation and morphology of the interlobular region of the ovary of C. ptariensis, define each one as a separate entity, here recongnized as a species.

TAXONOMIC CONCEPTS AND NOTES ON KEYS

Phylogenetic concepts outlined in the preceeding section have been directly translated into a systematic treatment. My species concept follows that of Wiley (1978, 1981), who defines a species as follows: "An evolutionary species is a single lineage of ancestor-descendant populations which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate." Thus, terminal taxa on the cladogram for subg. Grammadenia are defined by unique apomorphies (autapomorphies), while monophyletic species groups (clades) are defined by shared apomorphies (synapomorphies). These character states may be morphological, anatomical, or otherwise. It should be emphasized that, although a taxon may have only anatomical autapomorphies to define it (e.g., C. magnus), it may still be separated from other species by unique combinations of plesiomorphic character states for the practical purposes of identification.

The rank of subspecies used here is defined as groups of populations within a single lineage of ancestor-descendant populations that show variation by unique combinations of plesiomorphies, or homoplasic apomorphies, correlated with biogeography and/or ecology. This rank is primarily used to convey information regarding variation in the life histories of these populations and character state differences hypothesized to be result of this variation. The subspecific rank in no way attempts to predict speciation events.

The keys are artificial and designed to expedite identification of herbarium specimens. The numbers appearing before the taxa refer to their phylogenetic position as indicated by the cladogram (see PHYLOGENY). Both quantitative and qualitative data presented in keys and descriptions for floral parts and bracts were taken from organs rehydrated from herbarium specimens by boiling in water. This results in measurements ranging from 8 to 15 % greater when compared to measurements taken directly from dried material. Data regarding stem diameters, inflorescence rachises, pedicels, leaf and fruit shape and size were taken directly from dried herbarium specimens. Leaf, calyx and corolla lobe, and floral bract measurements are given as length times width.

The distribution map of Cybianthus costaricanus was adapted from the Esso Service Station map for Central America, and the symbols representing populations were mapped at one per 15 km^2. All other distribution maps were plotted by the degree-square method on Flora Neotropica Base Map No. 1, prepared by Henry Rypkema, University of Utrecht.

Photographs of cited type specimens include the herbarium acronym and negative number. All specimens cited were seen by me unless otherwise indicated. Herbarium acronyms follow Holmgren et al. (1981).

SYSTEMATIC TREATMENT

Cybianthus Martius, Nov. Gen. sp. pl. 3: 87. 1831 (nom. cons.); Agostini, Acta Bot. Venez. 10(2): 141. 1980. Type species: C. penduliflorus Martius.

Terrestrial or epiphytic, monoaxial or polyaxial shrubs or trees to 15 m tall. Roots positively geotropic or diageotropic. Branchlets glabrous, glandular-granulose, dendroid- and stellate-tomentose, furfuraceous- or ferrugineous stipitate-lepidote. Leaves sessile or petiolate, alternate, subopposite, or pseudoverticillate, the venation camptodromous or acrodromous, the petioles canaliculate or pulvinate. Inflorescence axillary, a simple raceme, a panicle of racemose branches, or an indeterminate umbel, appearing racemose. Flowers functionally unisexual or bisexual, 3-6(-7)-merous. Staminate flowers with a conic, lageniform, turbinate or irregularly shaped vestigial pistillode, the pistillode hollow or bearing a sterile placenta. Pistillate flowers with staminodes morphologically similar to the stamens but greatly reduced in size, at times producing abortive pollen. Calyx cotyliform or cupuliform, the lobes imbricate, valvate or aberrantly contorted, basally connate 1/5-2/3 their length, abaxially glabrous, glandular-granulose or stipitate-lepidote, adaxially glabrous, glandular-granulose or translucent glandular-lepidote. Stamens adnate to corolla tube at least 2/3 their length, the filaments variously connate to form a tube, the staminal tube adnate to the corolla tube or at times developmentally fused with it, bearing fleshy lobes alternate with the anthers or not, the anthers ovate, widely ovate or triangular, basifixed or dorsifixed, apically acute, rounded, emarginate or minutely apiculate, basally cordate, dehiscent by confluent apical pores or by wide to narrow longitudinal slits; pollen tricolporate, psilate; pistil obnapiform, umbonate or turbinate, the ovary sparsely to densely translucent glandular-lepidote, the style glabrous, the stigma capitate, capitate-lobate, or punctiform, the placenta free-central, carnose, umbonate, the ovules campylotropous, (1-)2-5(-7) , uni- or biseriate. Fruit drupaceous, 1(-2)-seeded, the endosperm translucent, non-starchy, the embryo small, linear, flexuous, erect or curved, longitudinal or transverse, the cotyledons not well-developed.

A Neotropical genus of approximately 150 species, _Cybianthus_ inhabits mesic or humid sites in pāramos, subpāramo thickets, elfin, cloud, montane and lowland moist or wet forests. Members of the genus are primarily found in natural ecotones and in riparian areas and are restricted to primary habitats. Therefore, their occurrence in a given locality is a direct indication of low levels of disturbance.

As here interpreted, _Cybianthus_ includes those taxa formerly placed in Comomyrsine, Hooker f., Conomorpha A. DC., Correlliana D'Arcy, Cybianthopsis (Mez) Lundell, Grammadenia Bentham, Microconomorpha (Mez) Lundell, and Weigeltia A. DC. Agostini (1980) presented an infrageneric classification which closely parallels that of the present treatment, but which did not include Grammadenia because of its bisexual flowers and sessile leaves. Further discussion of the differences in subgeneric delimitation is presented in the PHYLOGENY section.

A formal treatment of Cybianthus subg. Grammadenia (Bentham) Pipoly is presented below. A complete list of generic synonymy for the genus Cybianthus will be presented in the treatment to appear in FLORA NEOTROPICA.

KEY TO SUBGENERA OF CYBIANTHUS

1. Corolla cupuliform to camplanulate. Anthers longer than wide, distally recurved, apically acute or minutely apiculate.
    2. Branchlets and calyx glabrous or glandular-granulose. Anthers dehiscent by narrow longitudinal slits. Microconomorpha.
    2. Branchlets and calyx ferrugineous tomentose or stipitate-lepidote. Anthers dehiscent by wide longitudinal slits.

3. Branchlets and calyx stipitate-lepidote. Abaxial corolla surface marginally glabrous. Conomorpha.

3. Branchlets and calyx tomentose. Abaxial corolla surface marginally glandular-granulose.

 4. Fruit depressed-globose, wider than long. Inflorescences pseudoverticels of racemes, subtended by foliaceous bracts. Stapfia.

 4. Fruit globose, as wide as long. Inflorescences simple axillary racemes, the bracts minute, not foliaceous. Laxiflorus.

1. Corolla rotate to subrotate. Anthers wider than long, erect, apically rounded or emarginate.

 5. Petioles abruptly pulvinate. Anthers dorsifixed, longitudinally dehiscent.

 6. Plants monoaxial. Anthers erect, not versatile.

 7. Inflorescence bract large, foliaceous, persistent. Flowers 4- or 5-merous, the adaxial corolla lobes and branchlets glandular-granulose. Leaves without subepidermal fibers. Comomyrsine.

 7. Inflorescence bract small, not foliaceous, early caducous. Flowers 3-merous, the adaxial corolla lobes glabrous; branchlets bearing malphigiaceous hairs. Leaves with numerous subepidermal fibers. Triadophora.

 6. Plants polyaxial. Anthers versatile. Weigeltia.

5. Petioles canaliculate or absent. Anthers basifixed, poricidally dehiscent.
    8. Leaves apically mucronate, the petioles absent, the margins scarious, the venation acrodromous, the bases auriculate. Staminal tube merely nate to corolla tube. Grammadenia.
    8. Leaves apically not mucronate, the petioles present, the margins opaque, the venation camptodromous, the bases attenuate, acute or cuneate. Staminal tube developmentally fused to corolla tube, the stamens thus appearing epipetalous.
        9. Inflorescence an indeterminate umbel, the flowers bisexual. Cybianthopsis.
        9. Inflorescence a simple, elongate raceme, the flowers functionally unisexual. Cybianthus.

Cybianthus Martius subgenus Grammadenia (Bentham) Pipoly comb. et stat. nov.

Grammadenia Bentham, Pl. hartw. 218. 1846; Miquel in Martius, Fl. bras. 10: 306. 1856; Grisebach, Fl. Brit. West-Ind. Isl. 393. 1861; Hooker f. in Bentham & Hooker, Gen. Pl. 2: 644. 1876; Hemsley, Biol. Centr.-amer., Bot. 2: 290. 1882 (as Cybianthus); Pax in Engler & Prantl, Nat. Pflanzenfam. IV. 1: 92. 1897; Mez in Urban, Symbolae Antillanae 2: 245. 1901; Mez in Engler, Pflanzenr. IV. 236: 228-232. 1902; Standley, Flora of Costa Rica, Publ. Field Mus. Nat. Hist. Bot. Ser. 18: 895. 1938; Lasser in Pittier et al., Catàlago de la Flora Venezolana 277. 1947; Steyermark, Contr. Flora of Venezuela, Fieldiana, Bot. 28(3): 476-477, Fig. 107. 1953; Macbride, Flora of Peru, Publ. Field Mus. Nat. Hist. Bot. Ser. 13, (V, no. 1): 175-176. 1959; Lundell, Flora of Panama, Ann. Missouri Bot. Gard. 58(3): 292-293, Fig. 3. 1971; Fournet, Flore Ilustr. des Phanèrog. de Guadeloupe et Martinique 1051. 1978; Agostini, Acta Biol. Venez. 10(2): 140. 1980. *Grammadenia* subgenus *Eugrammadenia* Mez in Urban, Symbolae Antillanae 2: 425. 1901. Type species. *Cybianthus marginatus* (Bentham) Pipoly. *Grammadenia* , from the Greek, gramma (γραμμη)- "line" and aden (αδην)-"gland", referring to the punctate-lineations of the leaves and perianth.

Erect or pendent, evergreen, epiphytic or epipetric shrubs or small trees to 7 m tall. Roots diageotropic, Bark mostly smooth, gray or sometimes brown, cracking transversely on older parts. Trunk distinguishable, normally more or less terete, rarely pachycaulous basally, branching rythmic, mostly in pseudoverticels of 3, the branches orthotropic, morphogenetically equivalent, sylleptic. Branchlets thin to moderately thick, terete or ridged, smooth or verruculose to verrucose, glabrous or rarely glandular-papillate apically, glandular-papillate at first in the leaf axils then glabrescent, without lenticels. Leaves alternate, supervolute, exstipulate, sessile, acrodromous, apically obtuse-mucronate, basally auriculate, subamplexicaul, minutely glandular-papillate along costa above, glabrescent, glabrous below, hydropotes few or absent above, numerous below, the margins hyaline, membranous, prominently punctate, entire or minutely crenulate to denticulate. Inflorescence a simple, axillary raceme, at times reduced to appear dichasial; inflorescence bract ovate to deltate, to 2.0 x 2.0 mm, acute, prominently punctate, the margins entire or erose, early caducous; rachis terete, straight or flexuous, minutely glandular-papillate, glabrescent; floral bracts solitary, at pedicel base, ovate to lanceolate, persistent; pedicels terete or clavate, minutely glandular-papillate, glabrescent, accrescent in fruit. Flowers unisexual or bisexual, the plants dioecious, bisexual, or monoecious, (4-)5-6(-7)- merous; calyx cotyliform, the lobes imbricate or quincuncial or rarely and aberrantly dextrorsely contorted, erect, at times reflexed in fruit; corolla rotate, the tube bearing a ring of glandular-granules apically, the lobes imbricate, quincuncial, or rarely and aberrantly dextrorsely contorted, glabrous without, glabrous or rarely glandular-granulose and smooth or rugose within, apically obtuse or emarginate, the margins irregular or regular, entire or minutely crenulate; stamens and staminodes similar, connate to form a conspicuous, membranous or carnose tube adnate to the corolla tube, the anthers basifixed, sessile or on minute apically free filaments, cuadrate or ovate, apically emarginate or rounded, basally truncate, dehiscent by apical birimose pores, usually dorsally or rarely ventrally punctate; pistil and pistillode similar, obnapiform, ellipsoid or umbonate, the ovary terete, lobed or costate, sparsely to densely translucent-lepidote, the placenta umbonate, (1-)2-3(-5) ovulate, the ovules half-immersed in the basal placenta, uniseriate or biseriate, the style short, truncate, the stigma punctiform. Fruit drupaceous, depressed-globose, obovoid or ellipsoid, the exocarp sometimes fleshy, the mesocarp and endocarp stony, prominently punctate-lineate, white, lavender or purple-black at maturity, one-seeded, the testa corrugate, the embryo cylindrical, transverse.

A subgenus of seven species, in the Lesser Antilles, from northern Costa Rica through Panama to the Andes of Venezuela to southern Peru, east through the Guayana Highland and to the Serranía de Turumiquire, Anzoátegui, Venezuela.

KEY TO SPECIES OF CYBIANTHUS SUBGENUS GRAMMADENIA

1. Corolla lobes glandular-granulose within, the margins crenulate; pistil umbonate. Mesoamerica.

   1. *C. costaricanus*.

1. Corolla lobes glabrous within, the margins entire or erose; pistil obnapiform or ellipsoid. Darién, Panama, South America and the Lesser Antilles.

   2. Branchlets glandular-papillate apically. Pistil ellipsoid. Trunk thickened basally (pachycaulous). plants of open Guayana Highland savannas.

      5. *C. lineatus*.

   2. Branchlets glabrous apically. Pistil obnapiform. Trunk not thickened basally. Plants of cloud and elfin forest, scrub thickets and páramos, Andes and Guayana Highland.

      3. Leaves chartaceous or membranaceous, conspicuously asymmetrical, abruptly or long-acuminate apically. Corolla chartaceous, rugose medially. Fruit obovoid at maturity.

         4. Leaves membranaceous. Calyx lobes entire, glabrous; staminal tube subtruncate between anthers; anthers on free filaments to 0.3 mm long. Lesser Antilles.

            3. *C. parasiticus*.

         4. Leaves chartaceous. Calyx lobes erose to

fimbriate, densely glandular-ciliate; staminal tube bearing lobes between the anthers; anthers sessile. Andes and Serranía de Turimiquire. 2. C. magnus.

3. Leaves coriaceous, symmetrical to slightly asymmetrical, obtuse to acute apically. Corolla coriaceous, smooth medially. Fruit depressed-globose or ellipsoid at maturity.

  5. Leaves oblanceolate. Branchlets smooth, terete. Corolla lobe margins irregular. Fruit depressed-globose at maturity. Guayana Highland.

    9. Leaf margins minutely crenulate to denticulate. Ovary costate; staminal tube carnose, lobate, the lobes punctate, connectives prominently black punctate ventrally and dorsally. Inflorescence prominently black punctate-lineate. Endemic to Cerro de la Neblina.6. C. piresii.

    9. Leaf margins entire. Ovary lobate; staminal tube membranous, subtruncate, epunctate; connectives epunctate ventrally, pellucid-punctate dorsally. Inflorescence rachis pellucid-punctate. endemic to the Auyán-tepuí/Chimantá floristic complex. 7. C. ptariensis

5. Leaves oblong, elliptic or lanceolate. Branchlets verruculose to verrucose, prominently ridged. Corolla lobe margins regular. Fruit ellipsoid at maturity. Andean páramos. 4. *C. marginatus*

1. Cybianthus costaricanus Hemsley, Biol. Centr.-amer., Bot. 2: 290. 1882. (Figs. 1a, 24).

Epiphytic shrub or tree to 3 m tall. Branchlets terete or ridged, (2.0-)2.5-5.0 mm thick, glabrous, smooth. Leaves chartaceous or coriaceous, asymmetrical, linear- to wide-oblanceolate, (2.0-)2.5-9.0(-12.0) x (0.4-)0.7-2.5(-2.9) cm, obtuse, acute or abruptly acuminate, inconspicuously pellucid to orange punctate or conspicuously black punctate and punctate-lineate below, the margins entire, flat or slightly revolute basally. Inflorescence lax, straight, 1.0-10.2 cm long, the rachis inconspicuously pellucid to orange punctate or conspicuously black punctate and punctate-lineate; floral bracts ovate to lanceolate, 1.2-3.2 x 0.6-1.4 mm, acute to acuminate, inconspicuously pellucid to orange punctate or conspicuously and prominently black punctate and punctate-lineate, the margins erose or merely irregular, glabrous or glandular-ciliate; pedicels terete or clavate, to 2.5 mm long at anthesis, accrescent to 3.5-5.0 mm long in fruit, epunctate or prominently black punctate-lineate, glandular-papillate, glabrescent. Flowers coriaceous, (4-)5(-6)-merous;

calyx lobes ovate to wide ovate, 0.6-1.4 x 0.7-1.2 mm, obtuse or acute to acuminate, inconspicuously pellucid or prominently black punctate and punctate-lineate, the margins entire or erose, glabrous or densely glandular-ciliate; corolla 1.6-2.5 mm long, the lobes ovate to wide ovate, 0.9-1.4 (-1.9) x 1.2-1.5(-2.0) mm, obtuse to emarginate, obscurely pellucid or prominently orange or prominently black punctate-lineate, the margins crenulate, regular; staminal tube carnose, 0.4-0.8(-1.0) mm long, lobate, the lobes 0.1-0.2(-0.3) mm long, epunctate, the anthers sessile or on short free filaments to 0.1 mm long, ovate or quadrate, (0.2-)0.3-0.6 x (0.2-)0.3-0.7 mm, rounded or obtuse to emarginate apically, the connectives epunctate ventrally, prominently pellucid to orange or black punctate dorsally; pistil umbonate, 0.8-1.4 mm long and 0.8-2.0 mm diam., the ovary 0.5-0.9 mm long, densely glandular-translucent-lepidote, the ovules 2(-3), uniseriate, the style (0.2-)0.4-0.7 mm long, epunctate, the stigma punctiform. Fruit obovoid, white to pink, orange or black punctate-lineate or depressed-globose, purple-black, orange punctate-lineate at maturity, 2.0-4.0 mm long and 2.0-4.0(-5.0) mm diam. when dried.

Distribution. _C. costaricanus_ occurs in cloud and elfin forests in Mesoamerican Costa Rica and Panama from (800-) 1000-2600(-2850) m.

KEY TO SUBSPECIES OF CYBIANTHUS COSTARICANUS

1. Fruit depressed-globose, purple-black at maturity, the exocarp carnose. Calyx lobes acute to acuminate. Branchlets ridged.
    2. Leaves inconspicuously pellucid to orange punctate below, obtuse to subacuminate, never abruptly acuminate apically. Inflorescence rachis and perianth inconspicuously pellucid to orange punctate. Perianth prominently orange punctate, the corolla lobe margin opaque. Cordilleras of Tilarán and Talamanca, Costa Rica and adjacent Cordillera Central of Chiriquí, Panama. 1a. subsp. _costaricanus_.
    2. Leaves conspicuously black punctate and punctate-lineate at least proximally below, abruptly acuminate apically. Inflorescence rachis and perianth conspicuously and prominently black punctate and punctate-lineate, the corolla lobe margin hyaline. Endemic to the Cordillera Central of Costa Rica. 1b. subsp. _acuminatus_.
1. Fruit obovoid, white to pink at maturity, the exocarp thin. Calyx lobes obtuse to rounded. Branchlets terete.
    3. Leaves chartaceous, abruptly acuminate apically, conspicuously black punctate-lineate below. Corolla lobes rugose, glandular-granulose medially within, the punctations black, prominently raised; anthers

ovate, rounded apically; connectives black punctate dorsally. Cerro Campana and Continental Divide east of Chiriquí, Panama. 1c. subsp. <u>panamensis</u>.

3. Leaves coriaceous, obtuse to acute apically, inconspicuously pellucid to orange punctate below. Corolla lobes smooth, glandular-granulose throughout within, the punctations pellucid, flat, not prominently raised; anthers quadrate, obtuse to emarginate apically; connectives orange punctate dorsally. Endemic to Cerro Jefe, Panama.

1d. subsp. <u>morii</u>.

1a. Cybianthus costaricanus Hemsley subsp. costaricanus (Figs. 1a, 24, 25a)

<u>Cybianthus</u> <u>costaricanus</u> Hemsley, Biol. Centr.-amer., Bot. 2: 290. 1882; <u>Grammadenia</u> <u>costaricana</u> (Hemsley) Mez in Urban, Symbollae Antillanae 2: 245. 1901. Type. Costa Rica. Without locality, Aug 1875 (fl), <u>Endres</u> <u>146</u> (holotype, K, photo LL Neg. 71-152; isotypes, BM, W, photo F Neg. 32001).

<u>Grammadenia</u> <u>linearifolia</u> Lundell, Wrightia 4(2): 70. 1968. Type. Panama. Bocas del Toro: N slopes of Cerro Horqueta, 1818-2121 m, 6 Aug 1947 (fl), <u>Allen</u> <u>4803</u> (holotype, MO, photo LL Neg. 71-173; isotypes, G, U).

<u>Grammadenia</u> <u>minor</u> Lundell, Wrightia 4(2): 71. 1968.

Type. Costa Rica. San José: Cordillera de Talamanca, the bog elfin cloud forest area N of Cerro de la Muerte, 2600 m, 1 Feb 1963 (fr), L.O. Williams et al. 24167 (holotype, F, photo LL Neg. 71-135; isotypes, CR, NY).

Grammadenia aurantiaca Lundell, Wrightia 5(8): 292. 1976. Type. Panama. Chiriquí: Cerro Pando, on continental divide and Panama-Costa Rica border, ca. 16 km NW of El Hato del Volcán, 2000-2482 m, 20 Jul 1975 (fl), Mori & Bolten 7296 (holotype, LL; isotype, PMA).

Cybianthus talamacensis Lundell, Phytologia 57(5): 368. 1985. Type. Costa Rica. Limón: Cordillera de Talamanca, Cerro Kámuk massif, between Cerro Dudu and Cerro Apri, 2900-3100 m, 23 & 26 Apr 1984 (fl), Davidse et al. 25920 (holotype, LL-n.v.; isotypes, CR-n.v., MO).

Branchlets prominently ridged. Leaves chartaceous, acute to acuminate apically, inconspicuously pellucid to orange punctate below. Inflorescence rachis inconspicuously pellucid to orange punctate-lineate. Flowers with calyx lobes acute to acuminate, erose and densely glandular-ciliate marginally, prominently orange punctate; corolla lobes rugose and glandular-granulose medially within, prominently orange punctate; anthers ovate, rounded apically, the connectives orange-punctate dorsally. Fruit depressed-globose, (2.0-) 4.0-5.0 mm long and (2.0-)4.0-5.0 mm diam. when dried, purple-black at maturity, the punctations orange, inconspicuous.

Distribution. Subspecies _costaricanus_ grows as an epiphytic shrub in exposed areas of upper cloud and elfin forest formations from 1500-2500 m, or as a scandent shrub in _Lomaria_-_Sphagnum_ associations in pāramo-like formations from 2600-3100 m. It is known from peaks of the Cordilleras of Tilarān and Talamanca in Costa Rica and the contiguous Cordillera Central of Panama to northeastern Chiriquí, Panama.

Specimens examined. COSTA RICA. Alajuela: Cordillera de Tilarān, Monteverde Cloud Forest Reserve, Cerro del Roble, off Chomogo Trail, 1515 m, 26 Feb 1981 (st), _Almeda & Nakai 4600_ (CAS), 1610-1690 m, 13 Jul 1984 (fr), _Pipoly 7083_, _7084_, _7088_ (CR, NY), 13 Jul 1984 (st seedling), _Pipoly_, _7087_, _7089_, _7091_, _7092_ (CR, NY), S of road, 1520-1580 m, 16 Jun 1976 (fl, fr), _Dryer 200_ (CR, F), 29 Jul 1976 (fr), _Dryer 476_ (CR, F), El Brillante Trail, 1500-1580 m, 14 Dec 1976 (fl, fr), _Dryer 1100_ (CR, F), El Brillante and Nuboso Trails, 1550-1600 m, 14 Jul 1984 (st), _Pipoly 7093_, _7100_ (CR, NY), 14 Jul 1984 (fr), _Pipoly 7095_, _7098_ (CR, NY), 14 Jul 1984 (fl), _Pipoly_

7099 (CR, NY); San Carlos, Hacienda Sta. Elena, 1450 m, 18 Jan 1939 (fl, fr), *Austin Smith* *1512* (A, CR, NY); Quebrada Azul, 14 km NW of San Ramón, 1020 m, 18 Jun 1972 (fr), *Lent* *2611* (CR, F, NY); Cataratas de San Ramón, 17-20 Apr 1935 (fl), *Quirós* *130* (CR, F); Balsa de San Ramón, 900 m, 29 Dec 1974 (fl), *Taylor* *17764* (NY); La Palma de San Ramón, 13 Mar 1929 (fl, fr), *Brenes* *6740* (CR, F), 30 Mar 1929 (fl, fr), *Brenes* *6761* (CR, CU, F, NY), 22 Jan 1934 (fl, fr), *Brenes* *19002* (CR, F, NY); Los Angeles de San Ramón, 1500 m, 20 Jul 1984 (st), *Pipoly* *7112*, *7114*, *7115*, *7117* (CR, NY), 20 Jul 1984 (fl), *Pipoly* *7116* (CR, NY), 20 Jul 1984 (fl, fr), *Pipoly* *7118* (CR, NY); Cerros de la Balsa, Los Angeles de San Ramón, 16 Mar 1928 (fl), *Brenes* *6052* (CR, F), *6078* (CR, F, NY); Reserva Forestál San Ramón, nr. Colonia Palmareña, 1000 m, 20 Jul 1984 (st), *Pipoly* *7119*, *7120* (CR, NY); San Rafael de San Ramón, 1250 m, Nov 1921 (fl), *Brenes* *3569* (CR, F, NY); Alto de Villegas, Dtto. Volío de San Ramón, 1250 m, Jan 1922 (fl), *Brenes* *3601* (CR, F, NY); Zarcero, Caribbean Slope, 1364 m, 3 Feb 1938 (fl), *Austin Smith* *H273* (CR, F, MO); La Peña de Zarcero, Pacific Slope, 1364 m, 13 Dec 1937 (fl, fr), *Austin Smith* *A695* (CR, MICH, MO); La Peña Alfaro Ruíz, 1400 m, 24 Dec 1939 (fl), *Austin Smith* *P2163* (A, CR). Limón: Cordillera de Talamanca, Atlantic Slope, Cerros Tararia (locally known as Tres Picos), 2400-2600 m, 10 Sep 1984 (fl, fr), *Davidse et al.* *28791* (CR, MO), 10 Sep 1984 (fl), *Davidse et al.* *28824* (CR, MO, NY), 10 Sep 1984 (fr), *Davidse et al.*

28827 (CR, MO, NY); N base of unnamed cordillera between Río Terbi and Río Siní, 2000-2500 m, 14 Sep 1984 (fr), *Davidse & Herrera* *29084* (CR, LL, MO, NY). Puntarenas: Cordillera de Talamanca, Cerro Urán, 1 Feb 1981 (fl, fr), *Weston* *12305A* (CR, UC); Peñas Blancas Trail, 3.5 km NE of Monteverde, 1500 m, 3 Jan 1972 (fr), *Wilbur et al.* *15793* (DUKE, LL).

PANAMA. Bocas del Toro: Cordillera de Talamanca Cordillera Central , 2-5 airline km NW of Cerro Echandí on Costa Rican-Panamanian border, 2600-2850 m, 1 & 9 Mar 1984 (fr), *Davidse et al.* *25120* (CR, LL, MO, NY). Chiriquí: Cerro Colorado, on continental divide, 1400 m, 25 Jul 1979 (fr), *T. Antonio* *1410* (LL), 1300-1700 m, 4 May 1975 (fl), *Mori & Kallunki* *5858* (LL, SCZ); Dtto. Boquette: Cerro Horqueta, summit, N and S slopes, 2000-2231 m, 28 Jun 1984 (fl, fr), *Pipoly* *7067*, *7068*, *7070*, *7072*, *7073*, *7074* (NY, PMA), 28 Jun 1984 (st), *Pipoly* *7075* (NY, PMA), 21 Jan 1971 (fl). *Wilbur et al.* *1342* (DUKE); Fortuna Dam site, 1200 m, 5 Feb 1985 (fr), *van der Werff & van Hardeveld* *6529* (MO); Dtto. Bugaba, Cerro Punta, along ridge to watershed to Bocas del Toro, 2200 m, 26 Jan 1985 (fl, fr), *van der Werff & Herrera* *6429* (MO).

1b. Cybianthus costaricanus Hemsley subsp. acuminatus (Lundell) Pipoly, comb. et stat. nov.(Figs. 1e, 24)

Grammadenia *acuminata* Lundell, Wrightia 4(2): 69. 1968. Type. Costa Rica. San José: Nr. Vara

Blanca, on slopes of Volcán Poás, 2121 m, 23 Nov 1949 (fl, fr) Allen 5396 (holotype, US, fragment LL, photo LL Neg. 71-134; isotypes, UC, F-2 sheets, MO, NY).

Branchlets ridged. Leaves chartaceous, abruptly acuminate apically, conspicuously black punctate and punctate-lineate at least proximally below. Inflorescence rachis prominently black punctate and punctate-lineate; calyx lobes acute to acuminate, erose and glandular-ciliate marginally, prominently black punctate and punctate-lineate; corolla lobes rugose and glandular-granulose medially within, prominently black punctate and punctate-lineate; anthers ovate, rounded apically, the connectives black punctate dorsally. Fruit depressed-globose, 2.0-3.0 mm long and 2.0-3.0 mm diam. when dried, purple-black at maturity, the punctations black, prominent.

Distribution. Subspecies acuminatus is restricted to the Cordillera Central of Costa Rica, in the provinces of San José, Cartago and adjacent Heredia, from 1600-2400(-2700) m. It is most often found in disturbed, remnant cloud forests, and in gaps of cloud forests, where it occurs as a trunk epiphyte on lower portions of large trees, ca. 10-15 m above the ground.

Specimens examined. COSTA RICA. Cartago: 5.4 km NW of jct at Trinidad en route to Volcán Turrialba, 10 May 1971 (fl, fr), Almeda et al. 3102 (CAS); nr. El Trinidad & Km 72 (20 km SE of El Empalme), along Interamerican Hwy, 2600 m, 19 Jun 1968 (fl, fr), Burger & Stolze 5962 (CR, F, MO, NY); along rd. to Volcán Turrialba, 2240 m, 9 Jul 1967 (fl, fr), Lent 1090 (COL, CR, F, PMA); Cerro de la Carpintera, 1500-1850 m, Feb 1924 (fr), Standley 34391 (US); Volcán Turrialba, above Pastora or Trinidad, 2000 m, 10 May 1971 (fl, fr), Wilbur 14348 (CR, DUKE, F-2 sheets, MICH); 3 km SE of El Empalme on Interamerican Hwy, 2450 m, 21 May 1972 (fl), Wilbur & Almeda 16757 (DUKE). Heredia: end of Hwy 114 to Volcán Barba, 2700 m, 3 May 1971 (fr), Almeda 582 (DUKE); between Cerro Chompipe and SE flank of Volcán Barba, secondary rd. N of CR 113 connecting with Calle Gallito, 2000-2100 m, 8 Dec 1975 (fl, fr), R. Baker et al. 237 (CR, DUKE, F); E slopes of Volcán Barba between Río Las Vueltas and Río Nuevo (upper Río Patria), 2000 m, 25 Oct 1975 (fr), Burger & Baker 9480 (AAU, CR, F, PMA); Cerros de Zurquí, along Río Para Blanca, 1600-1800 m, 6-7 Feb 1977 (fr), Burger et al. 10272 (AAU, F, MO); 1 km N of San Rafael de Vara Blanca, 1900 m, 3 Mar 1974 (fl), Lent 3828 (CR, F) abandoned rd. N of Cerro Chompipe, S of Camino Gallito, E of Quebrada Grande (headwaters of Río Patria), on SE slopes of Volcán Barba, 2000 m, 5 Jul 1984 (fl), Pipoly et al. 7077, 7082 (CR, NY); nr. Vara Blanca, N slope of Cordillera Central, between Volcán Poás and Volcán

Barba, 1710 m, Apr 1938 (fl), *Skutch* *3766* (A, CR, MO, NY, S); Cerros de Zurquí, NE of San Isidro, 2000-2400 m, 3 Mar 1926 (fr), *Standley & Valerio* *50753* (US); Cerro de las Caricias, N of San Isidro, 2000-2400 m, 11 Mar 1926 (fl), *Standley & Valerio* *52198* (US, LL-fragment), 11 Mar 1926 (st seedling), *Standley & Valerio* *52257* (US); 5 km from Vara Blanca toward Volcán Poás, 16 May 1971 (fl), *Wilbur* *14359* (DUKE) nr. El Copey, 1900 m, 17 Apr 1949 (fl), *L. O. Williams* *16391* (F). San José: Cascajal de Coronado, 1900 m, 6 Aug 1950 (fr), *J. León* *2634* (CR, NA); 12 km NE of San Isidro del Colorado, 700 m, 5 Jul 1977 (fr), *Wilbur et al.* *22034* (DUKE).

1c. Cybianthus costaricanus Hemsley subsp. panamensis (Lundell) Pipoly, comb. et stat. nov. (Fig. 24)

Grammadenia *panamensis* Lundell, Wrightia 5(8): 294. 1976. Type. Panama. Panamá: Along trail to top of Cerro Campana, SW slope from road, 825-1000 m, 12 May 1974 (fl), *Nee & Stockwell* *11602* (holotype, LL), *non* *Conomorpha* (§ *Microconomorpha*) *panamensis* Lundell, = *Cybianthus* *pastensis* (Mez) Agostini, *fide* Pipoly, 1983b.

Branchlets terete. Leaves chartaceous, abruptly acuminate apically, conspicuously black punctate and punctate-lineate below. Inflorescence rachis prominently black punctate and punctate-lineate. Flowers with calyx lobes rounded to obtuse, erose and densely glandular-ciliate marginally, prominently black punctate; corolla lobes rugose and glandular-granulose medially within, prominently black punctate; anthers ovate, rounded apically, the connectives prominently black punctate dorsally. Fruit obovoid, 3.0-4.0 mm long and 2.0-3.0 mm diam. when dried, pink at maturity, the punctations black, prominently raised.

Distribution. Subspecies _panamensis_ occurs as en epiphyte in cloud forests on the summit of Cerro Campana, Panamá province, Panama from 900-1000 m.

Specimens examined. PANAMA. Panamá: Dtto. Capira. Parque Nacional Altos de Campana, Cerro Campana, summit, 900-1000 m, 23-24 Jun 1984 (fl, fr), _Pipoly 7053_, _7054_, _7055_, _7056_, _7057_, _7058_, _7059_, _7060_, _7061_, _7062_ (NY,PMA), 23-23 Jun 1984 (st seedling), _Pipoly 7049_ (NY, PMA).

1d. Cybianthus costaricanus Hemsley subsp. morii (Lundell)
Pipoly, comb. et stat. nov. (Figs. 1c, 24, 25b)

Grammadenia morii Lundell, Wrightia 5(8): 293. 1976. Type. Panama. Panamá: Cerro Jefe, along trail on ridge running NE from summit, 1000 m, 18 Dec 1974 (fl), _Mori et al. 3761_ (holotype, LL; isotypes, PMA, WIS), _non Cybianthus_ (§ _Microconomorpha_) _morii_ Agostini, = _Cybianthus pastensis_ (Mez) Agostini, fide Pipoly, 1983.

Branchlets terete. Leaves coriaceous, obtuse to acute apically, inconspicuously pellucid to orange punctate. Flowers with calyx lobes obtuse to rounded, minutely erose and sparingly glandular-ciliolate marginally, inconspicuously pellucid to orange punctate; corolla lobes smooth and glandular-granulose throughout within, sparsely orange punctate medially, the punctations inconspicuous; anthers quadrate, obtuse to emarginate apically, the connectives prominently orange punctate dorsally. Fruit obovoid, 2.5-4.0 mm long and 1.2-2.2 mm diam. when dried, white to pink at maturity, the punctations orange to pink, not prominent.

Distribution. Endemic to cloud forest on the summit of Cerro Jefe, Panamá province, Panama, 1000 m.

Specimens examined. PANAMA. Panamá: Dtto. Panamá, After Goofy Lake along trail to Cerro Jefe, 14 Jan 1968 (fr), Correa & Dressler 551 (PMA), cloud forest nr. summit, 29 Aug 1975 (fl, fr), Dressler 5137 (MO), summit nr. radio tower, 900 m, 27 June 1984 (fr), D'Arcy et al. 15517 (MO, NY, PMA, SCZ), 22 May 1980 (fl, fr), Folsom et al. 7804 (NY, TEX), 3 Mar 1979 (fl, fr), Hammel 6304 (LL), 30 Aug 1977 (fr), Maas et al. 2711 (MO, U), cloud forest dominated by Clusia spp. and Colpothrinax cookii, 8 Oct 1974 (fr), Mori & Kallunki 2392 (LL, MO), 18 Dec 1974 (fr), Mori & Kallunki 3759 (LL, MO, WIS), 11 May 1975 (stam. fl), Mori & Kallunki 6085 (LL, MO), 5 Jun 1975 (stam. fl), Mori & Kallunki 6494, 6496 (LL, MO), 14 Jul 1975 (fr), Mori & Kallunki 7119 (LL, MO), 18 Jun 1984 (fl, fr), Pipoly 7017, 7020, 7021, 7023, 7024, 7027, 7028, 7029, 7030, 7031 (NY, PMA, dups. to be distr.), 18 Jun 1984 (stam. fl), Pipoly 7019 (NY, PMA, dups. to be distr.), N slope, along trail leading from antenna, 19 Jun 1984 (fl, fr), Pipoly & R. Bethancourt 7032, 7033, 7034, 7035, 7036, 7037, 7041, 7044 (NY, PMA, dups. to be distr.), along trail leading W from summit, 24 Sep 1975 (fr), J. & F.-Witherspoon 8495 (LL, MO), 920 m, 16 Feb 1985 (fl bud), van der Werff & van Herdeveld 6967 (MO), 900 m, 17 Mar 1985 (fl), McPherson 6863 (MO).

Cybianthus costaricanus is a highly variable species with variation second only to that of C. marginatus. Despite homoplasic character states such as asymmetrical leaves, rugose inner surface of the corolla lobes and the staminal tube bearing fleshy lobes alternate with the anthers shared with the vicariant C. magnus and C. parasiticus clade, the autapomorphic crenulate corolla lobe margin and umbonate pistil clearly distinguish C.costaricanus within subg. Grammadenia. The former species occurs from the Darién of Panama through the Chocó to the Andes of Peru, while the latter is endemic to the Lesser Antilles (see DISTRIBUTION).

Despite the historical importance of corolla lobe aestivation (Mez, 1902) and fruit morphology (Lundell, 1976; Mez, 1905), they are not constant and are not correlated with derived character states. With regard to corolla lobe aestivation, Lundell (1968) reported that he found dextrorse, quincuncial and imbricate lobes in the same inflorescence. As for fruit morphology, my field studies have shown that all fruits in the subgenus are obovoid and white to pink in early ontogeny, and their final morphology is correlated with the thickness of the endocarp produced. Those entities which bear globose fruits at maturity have exocarps to 0.5 mm thick, such as those in some populations of subspecies costaricanus (Pipoly 7099). On the other hand, entities with obovoid fruits at maturity rarely have exocarps over 0.2 mm thick. Despite the fact that the obovoid fruit shape is a derived feature unique to the subgenus, the lack of correlative advanced features and its tenuity render it useless for specific delimitation. The segregation of species based on fruit morphology is unwarranted, impractical and ignores that transformation from one state to another may represent a rather simple morphogenetic change.

Although C. costaricanus may at first appear heterogeneous, there is not even a single derived character state which would be useful in segregating species from it. The numerous scattered cloud and elfin forest formations of Costa Rica and Panama provide a biological problem analagous to that of islands in which isolation, founder's effects and differing combinations of ecological parameters may be expected to produce many local variations within a single taxon. These factors, combined with the geological history of the region (see Phylogeny) form a mosaic of possible morphologies.

Subspecies *costaricanus* is the most variable of the infraspecific taxa here recognized. The type of *Grammadenia linearifolia* Lundell represents an extreme in variation typical of plants from the tops of canopies in cloud forest formations supporting trees to ca. 15 m tall. On Cerro Horqueta, Chiriquí Province, Panama, I observed shrubs quantitatively identical to this and the type of *G. aurantiaca* Lundell growing on the periphery of canopies in the largest trees, while those corresponding to the type of *Cybianthus costaricanus* Hemsley occurred within the canopies, in a somewhat more sheltered environment. During my studies at Monteverde Cloud Forest and San Ramón Forest Reserves, I observed the same phenomenon, but plants growing in the very top of the canopy (ca. 20 m above the forest floor) had leaves much narrower than that of *G. linearifolia*, mostly less than 0.7 cm wide, and with small inflorescences barely over one cm long. At the same time, plants observed in the elfin forest at Monteverde were much more robust trunk epiphytes, with leaves to 13 cm long and 2.9 cm wide, inflorescences 9.5 cm long and large, more fleshy fruits to 5 mm in diameter.

Ecophysiological parameters affecting these morphogentic responses are unknown, but would provide useful future research.

Yet another form of subspecies *costaricanus* is represented by the types of *Grammadenia minor* Lundell, and *Cybianthus talamacensis* Lundell. This diminutive growth form, occurring on a *Sphagnum* substrate in páramo-like formations at the highest points along the contiguous Cordillera de Talamanca of Costa Rica and the Cordillera Central of Panama has no qualitative features which distinguish it. The dwarfing of cloud forest and subpáramo taxa is a frequent phenomenon in all Neotropical Myrsinaceae, but continues to be a source of spurious names.

Subspecies *acuminatus* is the only entity within the genus tolerant of disturbed conditions, and it may be no coincidence that it is restricted to the lower slopes of the volcanic Cordillera Central of Costa Rica. The close correlation of its distribution with Quaternary volcanic formations (as opposed to Tertiary volcanic, sedimentary or intrusive) as illustrated by Castillo-Muñoz (1983) is most likely not significant in determining the habitat for the subgenus *per se*, but rather, the physiognomy of the forests and therefore the canopies which these plants inhabit. Subspecies *acuminatus* thrives as an epiphyte in disturbed cloud forest areas and differs from subspecies *costaricanus* by the nature of its punctations, anther shape, hyaline corolla lobe margins, and abruptly acuminate leaves. More unisexual flowers have been found in this subspecies than in any other. Although leaf base margins are variable within all subspecies of *C. costaricanus*, the somewhat more enlarged bases coupled with the more plicate leaf morphology appear more efficient in funnelling water down the stems and trunk to the rather exposed, large root system which is more readily observable in subspecies *acuminatus* than in any other subspecies.

Subspecies *panamensis* is very similar to subspecies *acuminatus*, but has leaves which have many more black punctate-lineations and which have, as in subsp. *morii*, obovoid, white to pink fruits with obtuse to rounded calyx lobes. Although subsp. *panamensis* occurs at a lower elevation than does subsp. *acuminatus*, the cloud forest on Cerro Campana is an extremely dense, closed and wet environment, where subsp. *panamensis* grows as a massive prostrate epiphyte on the lower branches of canopy species.

Subspecies *morii*, the most strikingly variant of the subspecies, is notable for its depauperate punctation , coriaceous leaves, and smooth corolla lobes glandular-granulose throughout within. Despite these differences, its geographical isolation and Cerro Jefe's unique *Colpothrinax-Clusia* dominated cloud forest habitat, there is not a single apomorphic character which separates it from the other subspecies of *C. costaricanus*.

2. Cybianthus magnus (Mez) Pipoly, comb. nov. (Fig. 26a)

Facultative epiphytic shrub or tree to 7 m tall. Branchlets terete, smooth, glabrous. Leaves chartaceous, asymmetrical, narrowly oblanceolate, oblanceolate, or narrowly obovate, (4.5-)5.2-15 x (1.0-)2.1-5.2 cm, apically acute to abruptly acuminate, tapering abruptly or gradually to base, bearing hydropotes above or not, conspicuously black punctate and punctate-lineate or inconspicuously pellucid to orange punctate below, the margins entire, flat or subrevolute. Inflorescence lax, straight, (1.5-)2.0-8.0(-11.5) cm long, slender, densely glandular-granulose and papillate, prominently black punctate-lineate or conspicuously orange punctate-lineate; floral bracts ovate, wide ovate or deltate, (0.7-)1.1-2.2 x (0.6-)1.3-2.0 mm, acute to acuminate, prominently black or orange punctate and punctate-lineate, the margins erose and glandular-ciliate; pedicels 1.0-2.2. mm long in flower, accrescent to 4.0 mm long in fruit. Flowers chartaceous, 5(-6)-merous, whitish-green or pink to maroon; calyx lobes wide ovate to deltate, (0.8-)1.0-1.5 (-2.0) x (0.8-)1.0-2.1 mm, acute to acuminate, prominently black punctate and punctate-lineate or prominently orange to brown punctate, the margins erose to fimbriate and densely glandular-ciliate; corolla (1.7-)2.0-2.6(-3.0) mm long, the lobes wide ovate, 1.1-1.6(-2.2) x (0.9-)1.1-2.6 mm, obtuse to emarginate, rugose medially within, densely and prominently black punctate and punctate-lineate or orange to brown punctate, the margins irregular, entire; staminal tube membranous, (0.4-)0.7-1.0(-1.2) mm long, lobate, the lobes 0.1-0.2 mm long, the anthers sessile, alternate with the lobes, ovate or quadrate, (0.3-)0.4-0.6(-0.7) x 0.4-0.6 mm, rounded or emarginate, the connectives epunctate ventrally, prominently black or orange punctate dorsally; pistil obnapiform, 1.0-1.2 mm long and 0.9-1.5 mm diam., the ovary 0.6-0.9(-1.3) mm long, densely translucent-lepidote, the ovules 2-4(-5), uniseriate, the style 0.3-0.5(-0.7) mm long, glabrous. Fruit obovoid, 2.5-3.5 mm long and 2.0-3.0 mm diam. when dried, pink, then purple-black or white, then lavender at maturity, prominently black punctate-lineate or orange to brown punctate-lineate.

Distribution. A relatively rare but widely distributed species, _Cybianthus magnus_ occurs in the Andes of Venezuela, Colombia, Ecuador and Peru as an epiphyte in the cloud forest zone below subpáramo thickets and as a facultative epiphyte in montane and elfin forests from 1000-3000 m. And in the Serranía de Turumiquire, states of Monagas, Sucre and Anzoátegui, Venezuela from 2000-2400 m.

KEY TO SUBSPECIES OF CYBIANTHUS MAGNUS

1. Leaves not bearing hydropotes above, conspicuously black punctate and punctate-lineate below. Inflorescence rachis

black punctate-lineate. Perianth whitish-green, prominently black punctate and punctate-lineate; anthers ovate, rounded apically; Branchlets 4.0-7.0 mm thick. Fruit purple-black at maturity. Closed cloud forests of the central and eastern Andean cordilleras from Venezuela to Peru and the Serranía de Turumiquire, Venezuela.

2a. subsp. magnus.

1. Leaves bearing hydropotes above, at least proximally, inconspicuously pellucid to orange punctate. Inflorescence rachis orange punctate-lineate. Perianth maroon to purple, rarely white (then pistillate), prominently orange punctate; anthers quadrate, emarginate apically. Branchlets 2.5-3.5(-4.0) mm thick. Fruit white, then lavender at maturity. Open montane forest and elfin forest formations of Darién, Panama, Chocó, Colombia, and eastern Andean slopes of Napo, Ecuador and Cuzco, Peru. 2b. subsp. asymmetricus.

2a. Cybianthus magnus (Mez) Pipoly subsp. magnus

(Figs.25f,26a)

Grammadenia magna Mez, Pflanzenr. IV. 236: 231. 1902. Type. Colombia. Santander del Norte: Ocaña to Pamplona, 2000-2500 m, 4 Mar 1879 (fl), Kalbreyer 1087 (holotype, K).

Grammadenia oxygyna Cuatrecasas, Rev. Acad. Colomb. Ci. Exact. 8: 321. 1951. Type. Colombia.

Valle: Cordillera Occidental, W slope, bank of Río Digua, left side, Piedra de Moler, 900-1100 m, 20 Aug 1943 (fl, fr), Cuatrecasas 14947 (lectotype, F , NY Neg. 12136, isolectotypes, COL-3 sheets, F, U, US.

Facultative epiphytic shrub or tree to 7 m tall and 7-15 (-30) cm diam., the canopy often bowl-shaped. Branchlets (4.0-)5.0-7.0 mm thick. Leaves not bearing hydropotes above, conspicuously black punctate and punctate-lineate below. Inflorescence rachis prominently black punctate and punctate-lineate; perianth whitish-green, prominently black punctate and punctate-lineate; anthers ovate, rounded apically, the connectives prominently black punctate dorsally. Fruit purple-black at maturity, prominently black punctate-lineate when dried.

Distribution. Subspecies magnus occurs as an epiphyte in closed cloud forests below subpáramo thickets in the Andes of Venezuela (Mérida, Trujillo) and Colombia (Santander, Boyacá, Huila, Valle), with one disjunct from below the Nudo de Sabanillas, Napo, Ecuador. It also forms large populations on the coastal Serranía de Turumiquire in the states of Anzoátegui, Monagas and Sucre, where it grows as an epiphyte on detritis between rocks in the scrub forest between the cloud and elfin forest formations.

Specimens examined. COLOMBIA. Boyacá: Buenavista, headwaters of Río Pauto, ridge E of Quebrada Laja, 30 km ESE of Socha, 2700 m, 10 Nov 1944 (fl), *Fosberg* *22247* (NY, US); Cordillera Oriental, NE of Arcabuco, Boyacá-Santander border, 2600 m, 7 May 1972 (fl, fr), *García-Barriga & R. Jaramillo* *20272* (COL); Sierra Nevada del Cocuy, nr. Cobugón, 3000 m, 15 Aug 1957 (fl, fr), *Grubb et al.* *500* (COL, K, MSC); Hacienda El Diamante, 4 km NE of Arcabuco, 2800 m, 12 Oct 1966 (fl, fr), *L. Uribe* *5725* (COL). Huila: El Roble, NE of Santa Ana, 2121-2733 m, 9 Jan 1944 (fl), *Little* *7051* (COL, US). Santander: Vic. Las Vegas, 2600 m, 21-23 Dec 1926 (fl),*Killip & Smith* *15906* (GH, NY, US).

VENEZUELA. Anzoátegui: Dtto. Libertad, Serranía de Turumiquire, ridges of Montañas Negras, along the Sucre and Anzoátegui border, ca. 20 airline km NE of Bergantín, 2000-2350 m, 28 Nov 1981 (fl), *Davidse & González* *19618* (VEN), Dtto. Freites, Cerro Peonía, above Los Pajaritos, N of Mundo Nuevo, 1700 m, 2-3 Dec 1981 (fl, fr), *Davidse & González* *19857* (VEN), 2200-2400 m, 8 Dec 1983 (fl, fr), *Pipoly* *6413*, *6453*, *6455*, *6457*. *6458*, *6459*, 1800-2000 m, 20 Mar 1945 (fl, fr) *Steyermark* *61624* (F, MO, NY, US, VEN). Mérida: Mcpio. Tabay, 30 km ESE of Tabay, between Arangure and San Juan Bautista, 2500 m, 23 Jul 1953 (fl), *Little* *15383* (MER, VEN); Dtto. Sucre, Páramo de los Colorados, 30 km SW of Estanques, 90 km S of Mérida, 2000-2500 m, 20 Dec 1983 (sterile), *Pipoly et al.* *6536*, 2800 m, 4 Nov 1975 (sterile), Quintero et al. 1262 (MER), 2900 m, 29 May 1971 (fl), Ruíz-Terán & López-Palacios 1937 (MERF). Monagas: Cerro Negro, above La Sabana de las Piedras, NW of Caripe, 15 Apr 1945 (fl, fr), Steyermark 62104 (F, NY, VEN). Sucre: Cerro Turumiquire, N-facing slopes above La Trinidad, SW of Cocollar, 2100-2200 m, 5 May 1945 (fl, fr), Steyermark 62520 (F, MO, NY, US, VEN), 1800-2100 m, 1925 (fl, fr) Tate 208, 209 (US). Trujillo: Guirigay, near Peñas Blancas, 3300 m, Aug 1958 (fl, fr), Aristeguieta & Medina 3592 (NY, VEN), Páramo del Guirigay, 3050 m, 18 Oct 1972 (fl, fr), López-Figueiras & H. Rodríguez 8833 (MER, VEN).

ECUADOR. Loja: Between Nudo de Sabanillas and Río Cachiyacu at Tambo Cachiyacu, 3000-3500 m, 17 Oct 1943 (fr), Steyermark 53584 (NY).

2b. Cybianthus magnus (Mez) Pipoly subsp. asymmetricus (Mez) Pipoly, comb. et stat. nov.(Figs. 25a, 26c, d, e)

Grammadenia asymmetrica Mez, Bull. Herb. Boissier ser. 2. 5: 246. 1905. Type. Peru. Loreto: Cerro de Ponasa, 1300 m, Mar 1903 (fr), Ule 6792 (holotype, B-destroyed, photos GH, MICH, MO, NY, F Neg. 4861; lectotype here designated, HBG; isolectotypes F-fragment, G, K, L). The holotype, destroyed at B, was the only specimen annotated by Mez. The fragment at F does not have its origin indicated and contains only a few leaves and fruits. Given that the remaining material was annotated with the Mez determination by Ule, and is identical with what is described in the protologue, I selected the sheet at HBG because it was in the best condition.

Grammadenia macrocarpa Lundell, Wrightia 5(8): 292. 1976. Type. Ecuador. Napo: 17 km W of Lumbaque, 70 73 km W of Lago Agrio, 1130 m, 4 Nov 1974 (fl, fr), *A. Gentry 12419* (holotype, LL; isotypes, MO, S).

Facultative epiphytic shrub to 2 m tall and 7 cm diam., the canopy open, conical. Branchlets 2.5-3.5 (-4.0) mm thick. Leaves bearing hydropotes above at least proximally, inconspicuously pellucid to orange punctate below. Inflorescence rachis conspicuously orange to brown punctate-lineate. Flowers with calyx greenish-pink, the staminate and bisexual with corolla maroon, the pistillate with corolla white, prominently orange punctate and punctate-lineate; anthers quadrate, emarginate, the connectives prominently orange punctate dorsally. Fruit white, then lavender at maturity, prominently orange punctate and punctate-lineate when dried.

Distribution. Subspecies *asymmetricus* occurs as an obligate epiphyte, growing on detritis in open montane forests from the Darién of Panama to Cuzco, Peru, from 1000-2000(-2700) m.

Specimens examined. PANAMA. Darién: Cerro Pirre, on peak S of Pirre, "Cerro Toupee", 10-20 Jul 1977 (fr), Folsom et al. 4538 (LL); Cana and vic., 1650 m, 17 Apr-8 Jun 1908 (fr), R. S. Williams 811 (NY).

COLOMBIA. Chocó: Ansermanuevo-San José del Palmar rd., between Alto de Galápago and San José del Palmar, 2100 m, 28 Jul 1976 (fl, fr), Forero et al. 2251 (COL, MO, NY, VEN), 2070 m, 29 Oct 1976 (fl), Forero et al. 2314 (COL, MO), 2000 m, 19 Feb 1977 (fr), Forero et al. 2968 (COL), ca. 51-53 km W of Ansermanuevo, 1925-2000 m, 13 May 1984 (pist. fl, fr), Luteyn, Pipoly et al. 10414 (COL, JAUM, NY), 13 May 1984 (fl), Luteyn, Pipoly et al. 10415, 10416, 10417, 10420, 10421 (COL, JAUM, NY), ca. 3-5 km E of San José del Palmar, 1341-1450 m, 14 May 1984 (fl), Luteyn, Pipoly et al. 10442 (COL, JAUM, NY), 10 km W of Chocó-Valle border toward San José del Palmar, 2000 m, 15 May 1984 (fl,fr), Luteyn, Pipoly et al. 10525, 10527, 10532, (COL, JAUM, NY), 15 May 1984 (stam. fl), Luteyn, Pipoly et al. 10533 (COL, JAUM, NY), 2050 m, 15 May 1984 (fl), Luteyn, Pipoly et al. 10566, 10567 (COL, JAUM, NY), 15 May 1984 (fr), Luteyn, Pipoly et al. 10562 (COL, JAUM, NY). Valle: Ansermanuevo-San José del Palmar rd., km 60-62, 1870-1950 m, 19 Apr 1979 (fl), Luteyn et al. 7278 (COL, NY).

ECUADOR. Morona-Santiago: Cordillera Cutucú. 1060 m, 17 Nov-5 Dec 1944 (fr), *Camp E-1275* (NY); E slopes of Páramos de Matanga, ca. 30-40 km s of Sigsig rd. toward Gualaquiza, 2800-3100 m, 22 Jun 1985 (fl, fr), *Luteyn & Cotton 11184* (NY, QCA); between Campanas & Arenillas, along Río Tintas, 5 km SE of El Pan, 2195 m, 13 Jul 1943 (fl bud), *Steyermark 53584* (NY).

PERU. Cuzco: La Convención, Cordillera Vilcabamba, ca. 1/2 way between Camps 2 1/2 and 3, 1980 m, 1 Jul 1968 (fl, fr), *Dudley 10668* (F, NA), 1800 m, 24 July 1968 (fl, fr), *Dudley 11324* (NA). Pasco: Oaxapampa, Cordillera Yanachaga, Cerro Pajonal, chacos, 12 km SE of Oaxapampa, 2700-2800 m, 7 Oct 1983 (fl), *Foster 9013* (MO, NY, USM).

Cybianthus magnus is most closely related to *C. parasiticus* by its chartaceous corolla rugose medially within, asymmetrical leaves and obovoid fruits, but is easily separated from it by erose and fimbriate (not entire and glabrous) calyx lobes, lobate (not subtruncate) staminal tube and anthers sessile (not on apically free filaments). *C. magnus* superficially resembles *C. marginatus*; its relation to that taxon is discussed under that species.

The most striking morphological feature of *C. magnus* is its stems, which appear succulent, both in the field and in dried herbarium specimens. The anatomical basis of this apparent succulence is that of well-developed aerenchyma, like that of no other member of the subgenus except C. marginatus. However, the aerenchyma of the inner cortex is also accpompanied by collenchyma in the pith and outer cortex, an autapomorphic character not only within the entire genus Cyclanthus, but in the family as well.

Variation within C. magnus corresponds to its two habitats which, although similar, are distinct in both their light and moisture regimes. Subspecies magnus occurs only in primary cloud forests below subpáramo thickets, while subsp. asymmetricus is restricted to open montane forests. Although the two subspecies are readily identifiable by unique combinations of characters, no single derived character state exists which would allow specific recognition.

Subspecies magnus has a rather unusual distribution, with a large population on the coastal Serranía de Turumiquire, and populations of smaller proportions in the Andes of Venezuela in only two localities, one in the state of Mérida, and the other in the state of Trujillo. Likewise, in Colombia, it is known only from the type locality in Santander del Norte, and from eastern Santander, adjacent Boyacá, Huila and one locality in Valle. Subspecies magnus is largely sympatric with C. marginatus, but has never been found in close proximity to it, but rather in isolated, primary cloud forests. I attempted to recollect subspecies magnus in all of its previously known localities in Andean Venezuela and Colombia, but found only one population intact.

The mountains which once supported it have altitudinally large zones of cloud forest, but increasing agricultural expansion to support crops in need of the same conditions, such as onions, potatoes and carrots, has resulted in the almost complete destruction of these forests and concomitantly the subspecies' restricted habitat. The relation between the flora of Serranía de Turumiquire (Steyermark, 1966, 1979) and the lack of intact cloud forests in the northern Andes may account for the subspecies' apparent rarity.

Within subspecies magnus, variation is encountered in the frequency and type of leaf punctation, which has resulted in overdescription. Populations corresponding to the type of Grammadenia magna Mez are characterized by leaves which are primarily black punctate, with only a few, scattered punctate-lineations on the abaxial surface. On the other hand, the type of Grammadenia oxygyna Cuatrecasas represents populations which have leaves with black punctate-lineations and only a few scattered punctations. While on the Serranía de Turumiquire, I found that within one population the punctations were a function of chance and no pattern, not even within a single plant, was discernible. The apiculate fruits on the type of G. oxygyna was used by Cuatrecasas to distinguish it from other taxa of the group, but my studies clearly indicate that all species of the subgenus have fruits which are apiculate in the early stages of development, thus negating the value of the character.

Subspecies asymmetricus is biogeographically interesting because of its close correlation with Pleistocene refuges postulated by Haffer (1974, 1982) and Prance (1973, 1982). These populations correspond to the Darién, Chocó, Napo and East Peru-Acre refuges, and are located on the foothills of the refuge areas per se. Whether this correlation is coincidence or an artifact of collecting is not known, but more collections from Napo, Morona-Santiago and Zamora-Chinchipe would certainly be illuminating.

Variation within subspecies asymmetricus consists largely of leaf size, frequency of hydropotes on the adaxial surface, and distribution of functionally unisexual and bisexual flowers. Extensive population studies in the large populations near Alto de Galápagos, along the Ansermanuevo-San José del Palmar road in Chocó, Colombia showed that plants may be polygamo-monoecious, strictly dioecious, or andromonoecious within the same population. Aside from the obvious size reduction of non-functional sexual parts, the only variation notable was that of flower color. Functionally pistillate flowers, found on only one of the plants surveyed, had white corollas, while the corollas of bisexual and functionally staminate flowers were maroon. The pistillate flowers were found on an otherwise bisexual plant, but on different shoots, and on extremely short (1.5 cm) inflorescences with aborted terminal buds. Although the color of all fruits of the subspecies are lavender, a unique feature, the fact that they are pink at first, then white, as in many of the subspecies of Cybianthus costaricanus, indicates the lack of utility of fruit color at the species' level. Lundell (1976), in his description of Grammadenia macrocarpa, makes note of its large orange fruits, and small flowers. I have examined one fruit from each of the isotypes and found an insect larva in each one, accounting for the size and peculiar morphology.

3. Cybianthus parasiticus (Swartz) Pipoly, comb. nov.

(Fig. 26b)

Ardisia parasitica Swartz, Prodr. 48. 1788. Anguillaria parasitica (Swartz) Poiret, Encyl. Méth. 7: 687. 1806. Grammadenia parasitica (Swartz) Grisebach, Fl. Brit. West-Ind. Isl. 393. 1861. Type. Dominica. without date (fr), Andersson s.n. (lectotype here designated, BM; fragment, S.)

Grammadenia epiphytica Pax in Engler et Prantl, Nat. Pflanzenfam. IV. 1: 92. 1889. nom. nud. Published as a transfer, the basionym wrongly attributed to Grisebach.

Epiphytic shrub to 3 m tall. Branchlets terete, (2.0-) 2.5-3.0(-3.5) mm thick, smooth, glabrous. Leaves membrana ceous, asymmetrical, oblanceolate, (3.5-)4.0-9.0 x (0.5-)0.9-1.5(1.7) cm, long-acuminate, glabrous, conspicuously black punctate and punctate-lineate below, the margins, entire, flat. Inflorescence lax, the rachis prominently punctate-lineate, glandular-papillate, 2.5-4.0 cm long; floral bracts very narrowly lanceolate, 0.9-1.2 x 0.3-0.5 mm, acute, densely and prominently punctate-lineate, the margins entire, glandular-papillate, glabrescent. Flowers membranous, 4-5-merous; calyx lobes deltate to ovate, (0.8-)1.0-1.2 x 0.9-1.2 mm, acute to acuminate, prominently punctate-lineate, the margins regular, entire, glabrous; corolla (1.4-)1.6-1.8 mm long, the lobes wide ovate, 0.8-1.2 x 0.8-1.4 mm, rugose and prominently punctate-lineate medially, glabrous, the margins regular, entire; staminal tube membranous, 0.6-0.7 mm long, not lobate, subtruncate between the anthers, the anthers subsessile, on apically free filaments 0.1-0.3 mm long, quadrate, (0.3-)0.4 x 0.4(-0.5) mm, emarginate, prominently black punctate dorsally; pistil obnapiform, 1.1-1.3 mm long and (0.7-)1.1-1.2 mm diam., the ovary 0.8-1.0 mm long, densely translucent-lepidote, ovules 2, uniseriate, the style (0.2-)0.3-0.4 mm long, prominently black punctate-lineate. Fruit depressed-globose, 2.0(-3.0) mm long and 2.0(-3.0) mm diam. when dried, black at maturity, the punctations prominent.

Distribution. Cybianthus parasiticus is known only from the islands of Nevis, Guadeloupe, Dominica and St. Vincent, West Indies, in mossy forests from 330-1000 m.

Specimens examined. LEEWARD ISLANDS. Nevis: summit of Nevis Peak, 1090 m, 5 Mar 1959 (fr), Proctor 19317 (US), 900-1095 m, 11 Apr 1956 (fr), A. C. Smith 10547 (A, NY).

WINDWARD ISLANDS. Dominica: Castle Bruce & Trace, 600 m, 19 Apr 1959 (fl, fr), Cowan 1602 (UC- 2 sheets, NY, S); nr. Breakfast River, between Laudat and Boiling Lake, 708 m, 10 Mar 1940 (fl, fr), Hodge & Hodge 1910 (GH); St. Patrick Parish, summit of Morne Nicholls, 970 m, 9 Nov 1964 (fl, fr), Nicholson 1955 (DUKE); Terra Femme, St. David, 400 m, 21 Jan 1966 (fl, fr), Shillingford 476 (DUKE); vic. Fresh Water Lake, nr. Laudat, 450-600 m, 26 Mar 1956 (fl, fr), A.C. Smith 10286 (A, K, NY, S, UC), 727-788 m, 1 Jun 1967 (fl, fr), Wasshausen & Ayensu 337 (B), along path NW of Fresh Water Lake toward Boeri Lake, 818 m, 15 Jul 1964 (fr), Wilbur et al 7495 (DUKE, GH, LL, MO); ca. 1 km SW of Point Casse, without date (fr), Wilbur et al. 7725 (DUKE, MICH); lower slopes of Trois Piton along rd. to Rosalie ca. 1.25 km from Point Casse, 1818 m, 22 Jul 1964 (fl, fr), Wilbur et al. 7818 (DUKE -2 sheets, FLAS); nr. summit of Morne Anglais, 1116 m, 25 Jul 1964 (fl, fr), Wilbur et al. 7935 (DUKE, FLAS, GH, MICH, NY, TEX); without defininite locality, 1000 m, Jan 1882 (fl, fr), Eggers 634 (BR, CAS-2 sheets, G-DEL, GH, GOET, HBG, L, LY-3 sheets, M, P, UC, W, WRSL, Z-2 sheets), 25 Feb 1880 (fl, fr), Eggers s.n. (GH), 1839 (fl, fr), Imray s.n. (GH, GOET, LE, NY). Guadeloupe: Basse Terre, on rd. to Soufriere above St. Claude, 8-11 Jul 1964 (fl, fr), Hespenheide & Wiseman 476

(DUKE, MSC), Massif de la Soufriere, Bains Jaunes, 800-900 m, 10 Aug 1973 (fl), Sastre & Jeremie 1932 (A), 750-1000 m, 17 Jul 1959 (fl), Webster et al. 9009 (DUKE, MICH); Hans Matoula, 240 m, 1893 (fl, fr), Duss 3479 (NY); trail between Riv. Le Gaillon and summit of La Citerne, 17-27 Apr 1979 (fr), Howard & Howard 19414 (NY); without locality, 1944-1946 (fl), Bena s.n. (P), 1894 (fl, fr), Duss 3479 (LY, MO, NY, P, PH, US), 1897 (fl, fr) Duss 3479 (NY, P, US), without date (fl, fr), M. L'Herminier s.n. (G-BOISS, P), without date (fl), S.C.P. s.n. (K). St. Vincent: 303 m, Mar 1890 (fr), H. Smith & G. Smith 1254 (NY).

West Indies, without further locality data. (fl), Forsyth (G-DEL), "St. Domingo", (fl), Herb. Schreber 114 (M).

Cybianthus parasiticus is most closely related to the vicariant C. magnus of the Andes and Serranía de Turumiquire, coastal Venezuela. Synapomorphies include the medially rugose, chartaceous corolla and membranous staminal tube. C. parasiticus is easily separated from C. magnus by the membranaceous (not chartaceous) leaves, entire and glabrous (not erose and glandular-ciliate) sepals, and parenchymatous (not collenchymatous) pith and outer cortex.

The distribution of C. parasiticus and its nearest relative, C. magnus, is most interesting when compared to the work of Malfait and Dinkleman (1972), Rosen (1975) and Coney (1982). These analyses of Caribbean tectonic evolution by vicariance have particular relevance when viewed in light of the subspecific events evident in *C. magnus*.

In analysis of present-day biogeographic distributions it important to note that *C. magnus* subsp. *asymmetricus* has a definite correlation with postulated Pleistocene refuges linked with the Chocó floristic province, whose northern limit is the area of Cerro Pirre, in the Darién of Panama coincidentally the northern limit of the subspecies, and the area of biological South America which was in contact with the Proto-Antilles, *sensu* Rosen (1975). In addition, corresponding sister species exist, such as the case of *Cybianthus perpuncticulosus* (Lundell) Pipoly et Lundell, known from the Chocó and Cerro Tacaracuna, Panama, most closely related to *Cybianthus antillanus* (Mez) Agostini, endemic to the Lesser Antilles as is *C. parasiticus*. It is also interesting to note that the islands north of the parent Aves Ridge (Rosen, 1971) are devoid of any member of the genus *Cybianthus*, with the exception of *C. sintinesii* (Urban) Agostini, which is endemic to the Luquillo Mountains of Puerto Rico, and Nevis, which has *C. parasiticus*. *C. sintenisii* is a member of the monotypic subgenus *Cybianthopsis*, closely related to, and once thought a part of what is now considered subgenus *Grammadenia*.

Given the current dearth of information regarding the flora of Serranía de Turumiquire, it is not possible to fully resolve the problem of biogeography between *C. parasiticus* and C. magnus. It is hoped that more data on the other subgenera, particularly those who have Caribbean members, will aid in resolution of the problem.

4. Cybianthus marginatus (Bentham) Pipoly, comb. nov.

(Fig. 27)

Grammadenia marginata Bentham, Pl. hartw. 218. 1846. Type. Colombia. Cauca: nr. Pitayo, 3636 m, 1843 (fl), Hartweg 1200 (holotype, K; isotypes, BM, E, G-DEL, G-BOISS, LD, OXF, P, W-2 sheets).

Grammadenia lehmannii Mez, Pflanzenr. IV. 236: 231. 1902. Type. Colombia. Tolima: Altos de Otesas, 3300 m, 11 Jan 1883 (fl), Lehmann 2399 (lectotype here designated, G; isolectotypes, LE, US).

Grammadenia alpina Mez, Pflanzenr. IV. 236: 231. 1902. Type. Venezuela. Andes of Trujillo and Mérida: 1212-4390 m, 1842 (fl), Linden 447 (lectotype here designated, P; isolectotypes, BM-2 sheets, BR, F Neg. 32000, G, G-DEL, G-BOISS, K, OXF, S, VEN).

Grammadenia pastensis Mez, Pflanzenr. IV. 236: 232. 1902. Type. Colombia. Nariño: W cordillera of Pasto, 3000-3200 m, 20 Feb 1881 (fl), Lehmann 599 (holotype, G; isotypes, BM, LE).

Grammadenia nitida Mez, Pflanzenr. IV. 236: 232. 1902. Type. Peru. Huanuco: Pozuzo, 2727-2131 m, 1863 (fl, fr), Pearce 250 (holotype, K).

Grammadenia weberbaueri Mez, Rep. Spec. Nov. Regni Veg. 16: 418. 1920. Type. Peru. Cajamarca: Jaén, cordillera E of Huancabamba, E slopes, 2400-2500 m, Apr 1912 (fl), Weberbauer 6121 (holotype, B-destroyed; lectotype here designated, GH; isolectotype, F).

Grammadenia hexamera Pittier, J. Wash. Acad. Sci. 21: 140. 1931. Type. Venezuela. Mérida: Tabay, 2500-3000 m, 18 Sep 1930 (fl), Gehriger 471 (holotype, VEN; isotypes, A, F, G, NY, PH).

Grammadenia andicola Cuatrecasas, Rev. Acad. Colomb. Ci. Exact. 8(31): 321. 1951. Type. Colombia. Valle: Cordillera Occidental, Los Farallones, NW slope, Quebrada Las Nieves, below El Diamante, 2900 m, 30 Jul 1946 (fl, fr), Cuatrecasas 21805 (lectotype, F, NY Neg. 12113; isolectotypes, F, COL-2 sheets, U, US).

Epipetric shrub or small tree to 6 m tall. Branchlets prominently ridged, 3-4.0(-5.0) mm thick, verruculose to verrucose, rugose when dried, glabrous. Leaves coriaceous, symmetrical, oblong, elliptic or lanceolate, (3.0-)3.5-6.0 (-6.5) x (1.1-)1.4-2.0(-2.5) cm, nitid above, the margins entire, revolute. Inflorescence erect, the rachis flexuous, slender, (1.0-)1.3-2.0(-3.2) cm long, densely black punctate-lineate; floral bracts wide ovate to deltate, (0.8-)1.2-1.5 (-1.8) x 0.8-1.4(-1.8) mm; pedicels (1.0-)1.5-2.0 x (1.2-)

1.5(-2.0) mm, prominently and densely punctate and punctate-lineate, apex acute, the margins minutely crenulate, glabrous to minutely ciliolate at first apically; corolla (2.0-)2.2-3.0 mm long, the lobes wide ovate, (1.0-)1.2-2.0 x (1.2-)1.5-2.0(-2.5) mm, obtuse to rounded, glabrous without, glandular-granulose within at base, densely and prominently punctate medially, the margins entire; staminal tube carnose, 0.6-0.8 (-1.0) mm long, the anthers sessile, alternate with fleshy lobes to 0.2 mm long, quadrate, 0.4-0.7 x 0.4-0.7 mm, rounded apically, epunctate ventrally, prominently black punctate dorsally; pistil obnapiform, (0.9-)1.2-1.5 mm long and (0.8-)1.2-1.6 mm diam., the ovary (0.4-)0.6-1.0 mm long, glabrous to sparingly translucent-lepidote, ovules 2(-4), uni-or biseriate, the style 0.3-0.5 mm long, epunctate. Fruit somewhat ovoid, then ellipsoid at maturity, 4.5-5.0 (-6.0) mm long and (2.5-)3.0-4.0 mm diam., white, then purple-black at maturity, the punctations red-black, prominent.

Distribution. Cybianthus marginatus is the most common species of the subgenus, occurring in large populations on rocks above lagunas in páramos and elfin forests throughout the Andes from Venezuela to Peru, to 3400 m.

Specimens examined. COLOMBIA. Antioquia: Cerro Padre Amaya, Boquerón, along rd. to repeating tower, 2975-2985 m, 15 Mar 1979 (fl, fr), *Camargo et al. 7069* (MEDEL), 3050 m, 1 Feb 1977 (fl, fr), *S. Espinal & E. Bautista 4147* (MEDEL-2 sheets); Cordillera Occidental, Páramo de Chaquiro, 2800-3100 m, 24 Feb 1918 (fl, fr), *Pennell 4302* (NY). Boyacá: rd. between Urama and Antesales, Alto El Chaquiro, 3120 m, 5 Apr 1944 (fl, fr), *Core 545* (B, NY, US); El Pino, on ridge 12 km NE of Villa de Leyva, just S of Arcabuco, 2460 m, 19 Jan 1949 (fl), *Mason 13730* (COL, UC, US); between Arcabuco and Villa de Leyva, Quebrada Las Coloradas, 2800 m, 31 Aug 1967 (fl), *Jaramillo et al. 3132* (COL); Santuario de Iguaque, Cañon de Mamarramos, 12 km N of Villa de Leyva, 3400 m, 19 Aug 1980 (fl), *Melampy 1043* (MO), 3350 m, 4 Dec 1980 (fr), *Melampy 1232* (MO), 18 Mar 1981 (fl, fr), *Melampy 1302* (MO), along trail from Cabaña El Carrizal, 2800-3000 m, 22 Apr 1984 (sterile sapling), *Pipoly & Monje 6979*, *6983* (COL, JAUM, NY), 22 Apr 1984 (fl), *Pipoly & Monje 6972*, *6977* (COL, JAUM, NY), 22 Apr 1984 (fl, fr), *Pipoly & Monje 6974*, *6976* (COL, JAUM, NY), 22 Apr 1984 (fr), *Pipoly & Monje 6973*, *6975* (COL, JAUM, NY). Cauca: Macizo Colombiano, Páramo de las Papas, nr. Laguna de Cusiyaco, E end of Laguna, 3530 m, 11 Oct 1958 (fl, fr), *Barclay & Juajiboy 6020* (MO, US); Cerro Plateado, 2700 m, 20-29 Sep 1944 (fl), *Core et al. 1384* (NY); Cordillera Central, W slope, headwaters of Río Palo, creek of Río López, Quebrada del Duende, 3400-3500 m, 6 Dec 1944 (fl, fr), *Cuatrecasas 19143* (A-2 sheets, COL, F, NA, NY, US); Páramo Guanacas, 3000-3500 m, without date, (fl, fr), *Lehmann*

5579 (F); Páramo de las Delicias, nr. Popayán, 3400-3500 m, without date (fl), *Lehmann* *186* (K); ca. 28 km E ot Totoró, 3075 m, 6 May 1984 (fl), *Luteyn, Pipoly, et al.* *10187* (COL, JAUM, NY), 6 May 1984 (fl, fr), *Luteyn, Pipoly et al.* *10173*, *10185*, *10190* (COL, JAUM, NY); Páramo de Puracé, 3450 m, Feb 1938 (fl), *Sneidern* *1881* (S). Cundinamarca: Cordillera Oriental, N side of Quebrada San Roque, Río Blanco Valley, 10 km W of Gutiérrez, 45 km S of Bogotá, 27 Jul 1944 (fl, fr), *Grant* *9722* (NA, NY, US); Sibaté, Vereda El Ramal, 2900-3000 m, 21 Sep 1951 (fl), *Huertas & Camargo* *5208* (COL); 16 km W of Sibaté, 3000-3100 m, 13-15 Oct 1917 (fl), *Pennell* *2488* (NY, US). Huila: Cordillera Oriental, 20 km S of El Gigante, 3121 m, 20 Sep 1944 (fl, fr), *Little* *8683* (COL, NY, US); La Plata, 29 Mar 1939 (fl, fr), *Sneidern* *2520* (S). Huila-Cauca: Páramo de las Papas, 3100-3500 m, Jan 1947 (fl), *Hmo. Antonio* *48* (F); jct. of ridge between drainages of Río Guarapas and Río Guachicas with main divide of Cordillera Oriental, at head of Río Villalobos, SW of Pitalito, 2400 m, 6 Feb 1943 (fl, fr), *Fosberg* *19956* (NY, US); Páramo de las Papas, El Boquerón, S slope, afluent of Río Caquetá, 1 km S of Laguna La Magdalena, 3350-3450 m, 6 Sep 1958 (fl, fr), *Idrobo et al.* *2991* (COL). Nariño: Pasto, 1912 (fl), *Andre* *1357* (K); Páramo de Bordoncillo, 3250 m, 5 Mar 1963 (fl, fr), *S.Espinal* *1005* (COL). Putumayo: headwaters of Río Putumayo, Cordillera Oriental between El Encano and Sibundoy, Páramo de San Antonio de Bordoncillo, 3250 m, 4 Jan 1941 (fl, fr), *Cuatre-*

casas 11702 (COL, F); Santiago, Valle de Sibundoy, 2250 m, Feb 1942 (fl), *Miguel 46* (F), 2800 m, 30 Jun 1953 (fl), *Schultes & Cabrera 20125* (NY). Santander: vic. Las Vegas, 2600-3000 m, 21-23 Dec 1926 (fl), *Killip & A.C. Smith 15891* (A, F, GH, NY, US). Santander del Norte: Cordillera Oriental, Región del Sarare, Alto de Santa Inés, 2150-2250 m, 19-23 Oct 1941 (fr), *Cuatrecasas et al. 12505* (COL, U); Cacotá, Páramo del Cachiri, without date (fl, fr), *Karsten s.n.* (LE, W); Las Jurisdicciones, Cerro Oroque, 41.3 km S of Abrego, along rd. to La María, 2800-3000 m, 16 Apr 1984 (sterile seedling), *Pipoly & Monje 6940*, *6941*, *6942*, *6943*, *6962*, *6963* (COL, JAUM, NY), 16 Apr 1984 (fl, fr), *Pipoly & Monje 6945*, *6957*, *6958* (COL, JAUM, NY), on César-Norte de Santander border, 3440-3750 m, 22-23 May 1969 (fr), *García-Barriga & Jaramillo 19814* (COL); Páramo del Hatico, along Toledo-Pamplona rd., 2900 m, 12-13 Mar 1927 (fl, fr), *Killip & A.C. Smith 20655* (A, BM, GH,NY, S, US).

VENEZUELA. Lara: Dtto. Moran, trail from Humocaro to Buenos Aires, below Páramo de Las Rosas, 3300 m, 25 Jun 1979 (fl), *Liesner et al. 8038* (VEN). Lara-Trujillo: Páramo de los Nepes, above La Peña, 2740 m, 24-25 Dec 1959 (fl), *Barclay & Juajiboy 10304* (US). Mérida: Dtto. Libertador, Parque Nacional Simón Bolívar, Sierra Nevada de Mérida, Laguna La Fría, N slope, 3700 m, 27 Mar 1980 (fl), *Aymard 90* (MER), 3000 m, 2700-3000 m, 21 Dec 1983 (fl, fr), *Pipoly et al. 6537*, *6538*, *6539*, *6544*, *6545* (MER, NY, PORT, VEN), La Aguada, 3000 m, 18 Feb 1971 (fl, fr), López-Figueiras 8689 (MER), 3200 m, without collector & date (fl), (MER), from Las Vegas to 2900 m, without collector & date (fl), (MER), Mcpio. Tabay, La Mucuy, 15 km E of Mérida, Laguna del Coromoto, 3000 m, 9 Sep 1953 (fl, fr), Little & Aymard 15532 (MER), 3400 m, 22 Dec 1983 (sterile sapling), Pipoly & Aymard 6548, 6549 (MER, NY, PORT, VEN), 22 Dec 1983 (fl, fr), Pipoly & Aymard 6546 (MER, NY, PORT, VEN), 3100-3400 m, 19 Jul 1963 (fl, fr), Ruíz-Terán 1648 (MER, MO), 3300-3400 m, 15-18 Feb 1966 (sterile), Schulz et al. 339 (MER, VEN), 3400 m, 13 Jan 1957 (fl), Vareschi & Vareschi 6029 (VEN), trail to Pico Bolívar, 3100-4100 m, 6 Apr 1950 (fl, fr), Velasco & Ramia 675 (MY); Mcpio. San José, Páramo de San José (Páramo de Cupís), nr. Piedra la Pirela, 11.4 km S of San José de Acequias, 3080 m, 19 Nov 1972 (fl, fr), López-Figueiras et al. 8917 (MER, MERF, VEN), 3100 m, 27 Dec 1983 (sterile seedling) Pipoly & Monje 6575 (MER, NY, PORT, VEN), 27 Dec 1983 (fl), Pipoly & Monje 6576 (MER, NY, PORT, VEN), 27 Dec 1983 (fl, fr), Pipoly & Monje 6577, 6581, 6582, 6583, 6584 (MER, NY, PORT, VEN), 3080 m, 19 Nov 1972 (fl), Rodriguez & Wurdack 8917 (VEN); Dtto. Campo Elías, Sierra de la Culata, Páramo de los Conejos, 3200 m, 25 Jun 1955 (fl), Bernardi 692 (MER, NY, VEN), El Canalón, between Manzano Alto & El Campanario, 2800 m, 10 Apr 1972 (fl), Ruíz-Terán 7171 (MERF), W flank of Los Adobes, 3500-3650 m, 25 Mar 1972 (fl, fr), Ruíz-Terán 7043 (MERF), Páramo de la Culata, without date (fl, fr), *Moritz* *1173* (B, BM, F, GH, HBG-2 sheets, K, W); Sierra del Norte, 6-8 Oct 1952 (fl), *Humbert* *26763* (MER); Páramo de Mijará, 3300 m, 19 Mar 1922 (fl, fr), *Jahn* *970* (GH, US, VEN). Táchira: Dtto. Uribante, El Portachuelo, nr. Quemiquea, 2600 m, Sep 1956 (fl), *Aristeguieta* *2560* (F, NY, US, VEN), at jct. of Mérida and La Grita rds., 30 Dec 1983 (sterile seedling), *Pipoly* *6607* (NY, VEN), 30 Dec 1983 (fl), *Pipoly* *6601*, *6602*, *6604*, *6605*, *6609* (NY, VEN); 30 Dec 1983 (fl, fr), *Pipoly* *6603*, *6606*, *6608* (NY, VEN), at entrance to repeating tower, 3000 m, without date (fr), *Quintero & Salcedo* *1426* (MER), 150 m S of El Portachuelo on small rd. toward Páramo del Batallón off Bailadores-La Grita rd., 2700 m, 27 Nov 1983 (fr), *Weitzman & Sobrevilla* *28* (GH, MERF, NY, VEN); Dtto. Jauregui, La Grita, below military school, 1500 m, 24 Jan 1975 (fl), *Ruíz-Terán & López-Figueiras* *11773* (MERF); Dttos. Junín/Córdoba, Parque Nacional El Tamá, in páramo, 3100-3300 m, 1938 (fl), *Cardona* *126* (VEN), headwaters of Río Quinimarí Cerro de las Copas, cliffs on N slope, 2700 m, 29 Dec 1983 (fl), *Pipoly* *6588*, *6590*, *6593*, *6595*, *6598* (NY, VEN), Páramo de Tamá, 4-10 km N of Betania, 2500-2895 m, 15 Jul 1944 (fr), *Steyermark* *57345* (F, VEN), below Páramo, on Colombo-Venezuelan frontier, 2750-2950 m, 20-23 May 1967 (fl, fr), *Steyermark* *et al.* *98546* (LL, MO, NY, VEN-2 sheets); headwaters of Río Quinimarí, narrow ridge above Quebrada de las Copas, below Páramo del Judio, 20 kms S of San Vincente de la Revancha, 35 km S of Alquitrana, SW of Santa Ana, 2600-2630 m, 13 Jan 1968 (fl, fr), *Steyermark et al. 100867* (NY-2 sheets, VEN). Trujillo: Páramo de las Rosas, without date (fl, fr), *Karsten s.n.* (W); Dtto. Boconó, Páramo Guramacal, 12.2 km beyond jct. outside Boconó, 2600 m, 19 Jan 1984 (sterile sapling), *Luteyn & Pipoly 9309* (NY, VEN), 19 Jan 1984 (fl), *Luteyn & Pipoly 9297*, *9302*, *9307*, *9311* (NY, VEN), 19 Jan 1984 (fl, fr), *Luteyn & Pipoly 9301*, *9303*, *9304*, *9305*, *9306* (NY, VEN), 16.2-17.3 km beyond jct. with hwy., NE of Boconó along rd. to TV towers, 2680-2880 m, 13 Mar 1984 (fl, fr), *Luteyn & Cotton 9622* (NY, PH, VEN); Páramo Pumar, los Cedros E of Boconó, 2850 m, 17 Mar 1965 (fl), *Matos 1108* (VEN); along hwy. between Flor de Pátria and Boconó, 64 km from Boconó, between Boconó and Guaramacal, 2800 m, 24 Feb 1971 (fl, fr), *Steyermark 10481* (CAS, LL, NY, VEN), 24 Feb 1971 (fr), *Steyermark 104823* (LL, NY, VEN).

ECUADOR. Azuay: "Oriente" border, Páramo del Castillo, crest of E cordillera on trail between Sevilla de Oro and Méndez, 2727-3333 m, 18 Aug 1945 (fl, fr), *Camp E- 4809* (NY, VEN); Río Collay, Huagarancha, S of El Pan, 2650-3290 m, 6 Jul 1943 (fl), *Steyermark 53354* (NY). Imbabura: Cordillera Oriental, Camp Arelán, E of Volcán Cayambe, 2803 m, 21 Jul 1944 (fl, fr), *Drew E-351* (MSC); ridge just S of Río Clavadero, along trail to Río San Pedro, E of Cayambe, 2893 m, 27 Jul 1944 (fl, fr) *Wiggins 10484* (DS, US). Loja: Zamora-Chinchipe border, crest of Cordillera Oriental, 2840 m, 28 Jan 1985 (fl), *Luteyn & Cotton 11295* (NY, QCA); W slopes of Cordillera del Condor and NW slopes of Nudo de Sabanillas, around Tambo Cachiyacu, ca. 2 km SE of Yangana, 2000-3000 m, 19 Oct 1943 (fl, fr), *Steyermark 54800* (NY, U); S of El Playón de San Francisco, slopes of Cerro Mirador, 3300-3600 m, 29 Dec 1980 (fl, fr), *Holm-Nielsen et al. 29949* (AAU), *Jaramillo et al. 3929* (AAU, QCA).

PERU. Cajamarca: Jaén, SW of Querocotillo, 3150 m, Aug 1915 (fl, fr), *Weberbauer 7168* (F, G, GH). Cuzco: La Convención, 2800 m, 9 Jul 1968 (fl, fr), *Dudley 10910* (NA), 10 Jul 1968 (fl, fr), *Dudley 10922*, *10931B* (F, NA).

Cybianthus marginatus is most closely related to the vicariant *C. lineatus* by virtue of the synapomorphic flexuous inflorescences and biseriate ovules. However, *C. marginatus* is easily distinguished from *C. lineatus* by the glabrous, ridged, verrucose-papillate (not glandular-papillate, terete, smooth) branchlets, oblong, elliptic or ovate (not oblanceolate) leaves, obnapiform (not ellipsoid) pistil and ellipsoid (not obovoid) fruits. The verrucose-papillate branchlets, leaf and fruit shape are autapomorphic within the subgenus.

As might be expected in the most variable taxon of the subgenus, one-third of the names attributed to *Grammadenia* are here placed in synonymy with *C. marginatus*. The species occurs most frequently on cliffs above lagoons in high páramos, but may also be found in elfin forests and in the páramo thicket-páramo transition zone. Variation in leaf size and punctation (Fig.13) and to a lesser extent, some quantitative floral variation have led to much overdescription.

The type of *Grammadenia alpina* Mez represents populations occurring in high, wet pāramos, and is identical to the type of *G. hexamera* Pittier. Pittier (1931) was overly impressed by the hexamerous flowers of this specimen, but not only does the type have a few pentamerous flowers, but in the original circumscription of the genus, Bentham (1846) specifically mentioned the occasional hexamerous flowers of *G. marginata*, the type species of the subgenus.

The type of *G. pastensis* Mez is notable only for its more coriaceous, smaller leaves, and much reduced inflorescence, but it is qualitatively identical to the remainder of the species in every detail.

Ceja ecotypic forms from Cuzco and Pasco, Peru match the type of *Grammadenia nitida* Mez. The most notable morphological feature of these populations is the well-developed verrucose papillae, the upper portion of which breaks off to leave a mammalate verruculum which is waxy to the touch (Fig.2a). Mez (1902) separated this entity from his *G. pastensis* by the vernicose-nitid adaxial leaf surface with poorly developed punctate-lineations, but these quantitative distinctions break down even among the few specimens at hand. A similar habitat, paramoid elfin forest, harbors populations of plants matching the types of *G. andicola* Cuatrecasas and *G. weberbaueri* Mez. These ecotypes are notable only for their diminutive size, not unlike the situation discussed under *C. costaricanus* subsp. *costaricanus*.

Finally, populations corresponding to the type of *G. lehmannii* Mez possess many convergent features with *C. magnus* subsp. *magnus*, which has caused much confusion. The large leaves, long terminal bud, long punctate-lineations and paramo thicket habitat, coupled with poorly developed verruculae make determination of sterile specimens difficult. The coriaceous, elliptic leaves, ridged stems, ellipsoid fruits and parenchymatous pith and outer cortex verify its placement in synonymy with *C. marginatus*.

5. Cybianthus lineatus (Bentham) Pipoly, comb. nov.

(Figs. 1f, 25a, 26d)

Grammadenia lineata Bentham, Pl. hartw. 218, 1846.

Type. Venezuela (erroneously cited Guyana). Bolivar: savannas near Roraima, 1843 (fl, fr), *R. Schomburgk 647/992* (holotype, K; isotypes, B, BM, G-DC, G-DEL, P, U, W-2 sheets).

Terrestrial shrub to 1.5 m tall, the trunk pachycaulous. Branchlets terete, (2.5-)3.0-4.0(-6.0) thick, densely glandular-papillate apically. Leaves coriaceous, symmetrical, oblanceolate, (1.2-)1.6-3.0(-3.9) x (0.4-)0.6-1.0(-1.2) cm, acute, the margins flat. Inflorescences erect, flexuous, at times reduced to an apparent simple dichasium, sparingly glandular-papillate, 0.6-1.0(-2.5) cm long; floral bracts widely ovate, 0.8-1.1 x 1.1-1.4 mm, acute; pedicels (2.2-) 2.5-3.5(-4.0) mm long; flowers chartaceous, 5-7(-7)-merous; calyx lobes wide-triangular to deltate, (0.8-)1.0-1.5 x (0.7-)1.0-1.2(-1.4) mm, acute punctate and punctate-lineate, the margins entire, glandular-ciliolate; corolla (1.8-)2.0-2.5(-3.0) mm long, the lobes wide ovate, (1.0-)1.3-1.6(-2.0) x (1.0-)1.3-1.7(-2.0) mm, obtuse to emarginate, inconspicuously punctate medially, the margins irregular, entire; staminal tube conspicuous, carnose, (0.6-)0.8-1.0 mm long, the anthers sessile, alternate with prominent fleshy lobes, cuadrate, 0.4-0.6 x 0.4-0.6 mm, rounded, prominently punctate dorsally; pistil ellipsoid, (0.9-)1.0-1.2(-1.4) mm long and (0.8-)1.0-1.3 mm diam., the ovary 0.8-1.0 mm long, glabrous to translucent-lepidote apically, ovules 2(-3), when more than two, biseriate, the style (0.1-)0.2(-0.3) mm long, glabrous. Fruit ovovoid, (3.0-)4.0-5.0 mm long and (2.0-)2.5-3.0 mm diam., purple, then black at maturity, the punctations green, prominent.

Distribution. Cybianthus lineatus is endemic to the Guayana Highland, occurring in open savannas of tepuí summits throughout the floristic province Pantepuí (sensu Mayr & Phelps, 1967; Steyermark, 1982).

Specimens examined. VENEZUELA. Amazonas: Cerro Duida, 2100 m, Jan-Feb 1969 (fl), *Fariñas 542* (NY, VEN), summit, 1820-2100 m, 4 Sep 1944 (fr), *Steyermark 58316* (F, NY, VEN), slopes of ridge 25, 1666-1818 m, 26 Nov-16 Dec 1928 (fl), *Tate 416* (NY, US), summit of peak 7, 2121 m, Aug 1928-Apr 1929 (fr), *Tate 612* (NY), *Tate 657* (NY, US), station D 13, NW of "savanna hills camp" of Tate, N of La Esmeralda, 1400 m, 1 Feb 1975 (fl), *Tillett & Talukdar 75-118* (MYF, NY, VEN); Cerro Huachamacari, Río Cunucunuma, 4 Dec 1950 (fl, fr), *Maguire et al. 29808* (NY, PH, VEN), SW escarpment, 1850 m, 17 Dec 1950 (fl), *Maguire et al. 30281* (NY, VEN), *30288* (NY, PH, VEN), *30292* (F, NY-2 sheets, PH, VEN); Cerro Marahuaca-Autana-Shiho, summit, isolated SW portion of mountain, 2450 m, 9-10 Feb 1982 (fl), *Steyermark et al. 126334* (NY, VEN), 9-10 Feb 1982 (fr), *Steyermark et al. 126365* (NY, VEN); Cerro Sipapo (Paraque), summit, Peak 1, 1818-2000 m, 12 Dec 1948 (fl), *Maguire & Politi 27628* (F, NY, VEN), 1830 m, 12 Dec 1948 (fr), *Maguire & Politi 27642* (NY, VEN), 1400 m, 17 Dec 1948 (fl), *Maguire & Politi 27768* (F, NY-2 sheets, US, VEN), E escarpment, central drainage, 2000 m, 14 Jan 1949 (fl, fr), *Maguire & Politi 28341* (F, NY, VEN), N mountain, 1500 m, 25 Jan 1949 (fl), *Maguire & Politi 28587* (NY, VEN), 25 Jan 1949 (fr), *Maguire & Politi 28588* (NY); Cerro Yaví, 2200 m, 1-3 Mar 1947 (fl, fr), *K. Phelps & C. Hitchcock 44* (VEN), 2100 m, Feb 1947 (fl, fr), *K. Phelps 133* (VEN); Serranía Yutajé, Río Manipiare, Caño Yutajé, 1250 m, 12 Feb 1953 (fl, fr), *Maguire et al. 35225* (NY, VEN), 2200 m, 17-19 Feb 1953 (fr), *Maguire 35318* (NY), 21 Feb 1953 (fr), *Maguire 35363* (F, NY, VEN). Bolívar: Auyán-tepuí, central section, above Salto de la Catira, E of Río Churún, 1750 m, 27-28 Dec 1977 (sterile), *Brewer-Carías s.n.* (VEN), summit of NE arm of the W portion of mountain, nr. plane of Jimmy Angel 1800 m, 7 May 1964 (fr), *Steyermark 93498* (B, F, GH, NY, S, U, VEN); Cerro Guaiqunima, 1740 m, Oct 1943 (fr), *Cardona 962* (NY, US, VEN), Alto Río Paragua, 1600 m, 15 Jul 1944 (fr), *Cardona 1109* (US, VEN), 1 km S of cumbre camp, 1800 m, 29 Dec 1951 (fr), *Maguire 32821* (NY), along W escarpment 1 km W of cumbre camp, 1800 m, 30 Dec 1951 (fr), *Maguire 32871* (F, NY, VEN), SE section, 1250 m, 26 May 1978 (fr), *Steyermark et al. 117444* (MO, VEN, U); Macizo del Chimantá, small plateau at S base of large escarpments, Amurí-tepuí (W section of Acopán-tepuí), 1850 m, 2-5 Feb 1983 (fl, fr), *Huber & Steyermark 7087* (MYF, NY, VEN), *Steyermark et al. 128558* (NY, VEN), 2-5 Feb 1983 (fl), *Steyermark et al. 128577* (NY, VEN); Apacará-tepuí, SE section, 2850 m, 6-9 Feb 1984 (fl), *Huber et al. 8861*, *8862* (MYF, NY, VEN), plateau of SE-facing upper shoulder, 2000 m, 19 Jun 1953 (fl, fr), *Steyermark et al. 75747* (F, NY, VEN), Chimantá-tepuí, central-NE section, E headwaters of Caño Chimantá, 2000 m, 26-29 Jan 1983 (fl), *Huber & Steyermark 6882*, *6889* (NY, VEN), 26-29 Jan 1983 (fl, fr), *Steyermark et al. 128138-A*, *128158* (NY, VEN), S-central section, large valley between NE limit of Torono-tepuí and central section of Chimantá-tepuí, 2100 m, 11-15 Feb 1985 (sterile), Pipoly et al. 7215 (MO, NY, VEN), 11-15 Feb 1985 (fl), Pipoly et al. 7230, 7233, 7268, 7270, 7274, 7275, 7277 (MYF, NY, VEN), 1-15 Feb 1985 (fl, fr), Pipoly et al. 7229, 7231, 7236, 7238, 7240, 7242, 7244, 7247, 7249, 7272, 7295 (MYF, NY, VEN); Meseta de Jaua, Cerro Jaua, summit of central W portion, 60 km NW of hygine camp of Río Kanarakuni, 1922-2100 m, 22-27 May 1967 (fl), Steyermark 97916 (F, MO, NY, VEN), summit of SW portion, 2228-2250 m, 27 Feb 1974 (fl), Steyermark et al. 109582, 109592 (VEN); Cerro Roraima (mistakenly reported as Guyana), 1742 m, 8 Dec 1884 (fl), Jenman 108 (US), without date (fr), Schomburgk s.n. (U), mistakenly reported from Brazil, Dec 1909 (fl), Ule 8645 (G-DEL, L); Uaipan-tepuí, 1800 m, 26 Nov 1946 (sterile), Cardona 2027 (US).

Cybianthus lineatus is most closely related to the vicariant C. marginatus by virtue of its flexuous inflorescence and biseriate ovules. However, C. lineatus is easily distinguished from C. marginatus by the pachycaulous (not leptocaulous) trunk, densely glandular- (not verrucose-) papillate branchlet apices, ellipsoid (not obnapiform) pistil and obovoid (not ellipsoid) fruit. Of these aforementioned characters, only the obovoid fruit is not autapomorphic for the subgenus. Anatomically, C. lineatus is unique within subg. Grammadenia by having a parenchymatous inner cortex, and abaxial palisade parenchyma, both of which are adaptive features to xeric environments (Carlquist, 1962; Esau, 1965).

C. lineatus grows in fully exposed, dry savannas in shallow sand over sandstone throughout Pantepuí. Its conspicuous absence from the flora of Cerro de la Neblina may be attributable to the lack of well-developed savannas on that mountain. In the eastern parts of its range (Fig. 26), it is wholly sympatric with C. ptariensis, and at the scrub forest/savanna interface, populations may come in very close contact. Although apparent intermediates exist, they are only quantitative variants, and qualitative features defining the species maintain their integrity. Studies conducted on the Macizo del Chimantá indicate that no hybridization is involved, but that each species displays many of the quantitative variation of the other for those taxa out of their own habitat. The study I conducted on the Macizo is further discussed under C. ptariensis and ECOLOGY.

7. Cybianthus piresii Pipoly, sp. nov. Type. Brazil. Amazonas: Serra da Neblina, Rio Negro, Rio Cauaburí, along open slopes to base of cliffs, 2576-2727 m, 2 Dec 1965 (fl), Maguire, Pires, et al. 69476 (holotype, INPA; isotypes, F, NY, VEN). (Fig. 26b)

Ob folia coriacea, aequilatera vel aliquantum inaequilatera, corollam coriaceam secus mediam laevem, corollae tubumque carnosum, species haec cum Andino C. marginato primo intuitu confusa est, sed ab hac foliis oblanceolatis (nec oblongis vel lanceolatis), ramulis teretibus laevibusque (nec costatis verrucosisque), corollae lobis margine irregularibus (nec regularibus), fructu depresso-globoso (nec ellipsoideo) praeclare differt. Quoad characteres prius enumeratos, *C. ptariensi* arcte species haec affinis est, sed foliis margine minute crenulatis vel denticulatis (nec integerrimis), staminum tubo carnoso lobato atro-punctato (nec membranaceo subtruncato epunctato), ovario costato (nec lobato), inflorescentiarum rhachidi atro-punctato-lineata (nec pellucido-punctata), necnon antherarum connectivo dorso ventroque atro-punctato statim distinguitur.

Shrub, to 2 m tall. Branchlets 4.0-7.0 mm thick, terete, smooth, glabrous. Leaves coriaceous, oblanceolate, 3.8-6.9 x (1.2-) 1.4-1.9 cm, acute, conspicuously black-punctate and punctate-lineate below, the hyaline margins minutely crenulate or denticulate apically. Inflorescence erect, straight, (1.5-)2.2-3.0 cm long, the rachis conspicuously black punctate-lineate. Flowers coriaceous, 5-merous; floral bracts ovate to delatate, 1.6-1.8 x 1.6-1.8 mm, acute, prominently black punctate and punctate-lineate, the margins erose and glandular-ciliate; corolla 2.5-2.7 mm long the lobes wide ovate, 1.6-1.8 x 1.8-2.0 mm, obtuse to emarginate, prominently black punctate and punctate-lineate, the margins irregular, entire, glabrous;

staminal tube coriaceous, 0.8-1.0 mm long, the anthers sessile, alternate with punctate lobes to 0.2 mm long, cuadrate, the connectives prominently black punctate ventrally and dorsally; pistil obnapiform, 1.5-1.6 mm long and 1.3-1.5 mm diam., the ovary prominently costate, 0.8-1.1 mm long, translucent-lepidote, the ovules 1 (-2), the style 0.4-0.6 mm long, punctate. Fruit depressed-globose, 5 mm long and 5 mm diam., black at maturity, the punctations black, proment when dried.

Distribution. Known only from diabasic (granitic) outcrops above 1200 m on Cerro de la Neblina, Amazonas, on the Venezuelan-Brazilian frontier.

Paratypes. VENEZUELA. Amazonas. Cerro de la Neblina, Venezuelan-Brazilian frontier, 1800-2200 m, 25 April 1964 (fr), Ewel 164 (VEN), 1900-2100 m, 17 Apr 1984 (fl), Gentry & Stein 46725 (MO, NY, US, VEN) erroneously labeled Brazil , Camp 3, Cerro de la Neblina and Massif, NW plateau 13.5 km ENE of Cerro de la Nebina base camp, 1750-1850 m, 16-18 Feb 1984 (fl), Liesner 16091 (MO, NY, VEN), NW escarpment, 1-8 km N of cumbre camp, 1700-2000 m, 10 Jan 1954 (fl, fr), Maguire et al. 37197 (NY), summit, cumbre camp, 1200-2200 m, 15 Nov 1957 (fr), Maguire et al. 42112 (NY-2 sheets, US, VEN), plateau on summit of NW arm, N of base camp along Río Mawarinuma, afluent of Río Baria, 1880 m, 7-8 Feb 1984 (fr), Steyermark & Luteyn 129791 (MO, NY, VEN), vic. Camp 6, ridge on Venezuelan-Brazilian border, 3.5 km W of Pico Zuloaga, on N-facing slope, 2000 m, 13-15 Apr 1984 (fl, fr), Thomas & Plowman 3043 (F, MO, NY, VEN).

Brazil. Amazonas. Serra da Neblina, Rio Negro, Rio Cauraburí, along E trail escarpment, 2424 m, 3 Dec 1965 (fl, fr), Maguire et al. 60526 (NY).

Cybianthus piresii is most closely related to the vicariant C. ptariensis by its synapomorphic non-terete pistil and irregular corolla lobe margins. However, its autapomorphic minutely crenulate or dentate leaf margins, costate ovary, and ventrally black punctate anther connectives clearly distinguish C. piresii from all other species of the subgenus. Anatomically, C. piresii is unique in the subgenus by its homogeneous adaxial epidermis (Fig. 14d).

Drs. Murça Pires and Wayt Thomas (pers. comm.) indicated that the habitat of C. piresii was much like that of an Andean páramo, hence the convergence in overall aspect with C. marginatus is not unexpected. It is with much pleasure that I dedicate the species to Dr. Murça Pires, currently of the EMBRAPA, and formerly of the Museo Goeldi, Belém, Pará, Brazil, who has been one of the pillars of Brazilian Botany.

7. Cybianthus ptariensis (Steyermark) Pipoly, comb. nov.

(Figs. 1d, 26b, 28a, c)

Grammadenia ptariensis Steyermark, Fieldiana, Bot. 28(3): 476. 1953. Type. Venezuela. Bolívar: Ptari-tepuí, S slope, on "cave rock", 1810 m, 29 Oct 1944 (fl), Steyermark 59497 (holotype, F; isotypes, K, NY, US, VEN).

Grammadenia ptariensis Steyermark subsp. auyantepuiensis Agostini, Acta Bot. Venez. 2(5-8): 283. 1967. Type. Venezuela. Bolívar: Gran Sabana, summit of Uaipan-tepuí, 1900 m, Jan 1948 (fl), K. Phelps & C. Hitchcock 378 (holotype, VEN; isotypes, NY, VEN)

Terrestrial shrub or small tree to 2(-3) m tall, the trunk leptocaulous. Branchlets terete, (5.0-)6.0-8.0(-10) mm thick, smooth, glabrous. Leaves coriaceous, symmetrical to slightly asymmetrical, oblanceolate to oblanceolate-spathulate, 4.5-7.0(-10) x (1.1-)1.3-2.0(-2.4) cm, obtuse to acute, the margins revolute. Inflorescence erect, straight, sparingly glandular-papillate, (2.0-)2.5-5.0 cm long, the rachis pellucid to orange punctate-lineate; floral bracts wide ovate, 1.2-1.5 x 1.4-1.8 mm, pellucid to orange punctate, the margins irregular, glandular-ciliate; pedicels 1.3-2.5 mm long in flower, accrescent to 3.5(-4.0) mm long in fruit. Flowers coriaceous, 4-6(-7)-merous; calyx lobes wide ovate, (0.9-)1.2-1.4(-1.6) x (1.3-)1.5-1.8 mm, obtuse to rounded, inconspicuously pellucid to orange-punctate, the margins entire, glandular-ciliate; corolla (1.9-) 2.2-2.5(-3.0) mm long, the lobes wide ovate, (0.8-)1.1-1.6 x 1.5-1.8(-2.0) mm obtuse to emarginate, inconspicuously punctate medially, the margins irregular; staminal tube membranous, (0.8-)0.9-1.0 mm long, the anthers sessile, alternate with minute fleshy lobes, cuadrate, (0.4-)0.5-0.6 x 0.5-0.7 mm, obtuse to emarginate apically, the connective epunctate ventrally, inconspicuously pellucid punctate dorsally; pistil obnapiform, (1.0-)1.2-1.5 mm long and 1.1-1.6 mm diam., the ovary lobate, 0.8-1.1 mm long, translucent-lepidote, ovules (2-)3, uniseriate, the style (0.2-)0.3-0.4 mm long, glabrous, punctate. Fruit depressed-globose, 2.0-3.0 mm long and 2.0-3.0 mm diam., purple at maturity, the punctations pellucid, not prominent.

Distribution. Endemic to the northeastern section of Pantepuí (sensu Mayr & Phelps, 1967),in the Auyán-tepuí-Chimantá Complex of the Guyana Pakaraima-Venezuelan Gran Sabana Subprovince of Maguire (1979). *C. ptariensis* is known only from the Ilú-, Auyán-, Uaipan-, and Ptari-tepuis, and the Macizo del Chimantá from 1600-2450 m.

Specimens examined. VENEZUELA. Bolívar: Auyán-tepuí, summit, 1900 m, Apr 1956 (sterile), *Foldats 2617* (VEN).

without date (fl), *Pannier & Schwabe s.n.* (VEN); Ilú-tepuí, saddle between N peak and central plateau, 15 Mar 1952 (fl), *Maguire 33424* (NY); Uaipan-tepuí, 1800 m, 26 Nov 1946 (fl), *Cardona 2027* (VEN), without date, (sterile), *Cardona s.n.* (VEN), 1640 m, Feb 1948 (fl), *Cardona 2404* (VEN); Ptarí-tepuí, N of Mission of Santa Teresita de Kavanayén, summit, 2360-2420 m, 23 Feb 1978 (fl, fr), *Steyermark & Carreño 115656* (MO, VEN); Macizo del Chimantá, S plateau of Abacapá-tepuí, SW section of Macizo, central-N section of plateau, 2200 m, 31 Jan-2 Feb 1984 (fr), *Huber & Dezzeo 8629* (MYF, NY, VEN), NW part of summit of Abacapá-tepuí, 2125-2300 m, 13 Apr 1953 (fl), *Steyermark 74860* (F, MO, NY, VEN, WIS), SE sector of Macizo, Churí-tepuí, central-SE section, 2250 m, 10-12 Feb 1984 (fl), *Huber & Colella 8993* (MYF, NY, VEN), 6-8 Feb 1985 (fl), *Pipoly et al. 7129*, *7135*, *7137*, *7138*, *7149*, *7153* (MYF, NY, VEN), 6-8 Feb 1985 (fl, fr), *Pipoly et al. 7133* (MYF, NY, VEN), upper cumbre and deep canyons of upper cumbre, Churí-tepuí, NW cumbre, (Murú-tepuí), 2250-2300 m, 26 Jan 1953 (fl), *Wurdack 34229* (NY, VEN), Torono-tepuí, 9 Feb 1955 (fl), *Steyermark & Wurdack 659* (F, NY, VEN), N-facing slopes on summit above valley of Caño Mojado, 2030-2150 m, 21 Feb 1955 (fl, fr), *Steyermark & Wurdack 1030* (F-2 sheets, MO, NY, VEN-2 sheets, WIS), wide valley between NE border of Torono-tepuí and central secion of Chimantá-tepuí, draining toward S, 2100 m, 11-15 Feb 1985 (fl), *Pipoly et al. 7267*, *7279* (MYF, NY, VEN), 11-15 Feb 1985 (pistillate fl), *Pipoly et al. 7269* (MYF, NY, VEN), 11-15 Feb 1985 (fl, fr), *Pipoly et al. 7266*, *7271*, *7273*, *7276*, *7281*, *7282* (MYF, NY, VEN), 11-15 Feb 1985 9fr), *Pipoly et al. 7280* (MYF, NY, VEN), central-NE section of Chimantá-tepuí, E headwaters of Caño Chimantá, 2000 m, 26-29 Jan 1983 (fr), *Steyermark et al. 128138* (NY, VEN), E section of Chimantá-tepuí, headwaters of Río Tírica, Caño del Grillo, 2450 m, 7-9 Feb 1983 (fl, fr), *Steyermark et al. 129007* (NY, VEN), 2150-2200 m, 12 Feb 1955 (fl, fr), *Steyermark & Wurdack 807* (F, MO, NY, VEN), SW summit Amurí-tepuí, W section of Acopán-tepuí, 2170 m, 6 Feb 1983 (fl, fr), *Steyermark et al. 128776* (NY, MO, VEN), Apacará-tepuí, 2100 m, 15 Jul 1946 (fl), *Cardona 1533* (VEN), plateau at S base of upper cliffs, Apacará-tepuí, N section of Macizo, 2150 m, 30 Jan-1 Feb 1983 (fl, fr), *Huber & Steyermark 6992* (NY, VEN), *Steyermark et al. 128334* (NY, VEN), wide valley, SE section of Apacará-tepuí, 2150 m, 6-9 Feb 1983 (fl), *Huber et al. 8837* (NY, VEN), N section of Apacará-tepuí, N extension of Macizo, 2350 m, 3-5 Feb 1984 (fl), *Huber & Colella 8706*, *8752* (NY, VEN), 3-5 Feb 1984 (fr), *Huber & Colella 8756* (NY, VEN), summit, E-central section of Apacará-tepuí, 2450-2500 m, 21-22 Jun 1953 (fl, fr), *Steyermark 75914* (F-2 sheets, MO, NY, VEN).

The synapomorphic irregular corolla lobe margins and non-terete pistil clearly indicate that *C. ptariensis* is most closely related to the allopatric *C. piresii*. However, *C. ptariensis* is easily distinguished from *C. piresii* by its entire (not minutely crenulate to denticulate) scarious leaf margins, membranous (not carnose) staminal tube, the inconspicuous (not conspicuous and prominent) dorsal connective punctation, the epunctate (not prominently punctate) ventral connective punctation, and the lobate (not costate) ovary shape.

C. ptariensis grows sympatrically with *C. lineatus* (see *C. lineatus*) and on the Macizo del Chimantá populations studies (see ECOLOGY, Fig. 26b) have shown that the apparent intermediates between the two taxa are so only quantitatively, and are qualitatively separable for all differential character states. Agostini (1967) recognized two subspecies, based on collections from Auyán- and Uaipan-tepuis, which had smaller leaves, and abbreviated, few-flowered inflorescences when compared with the type of *C. ptariensis*. However, given the variation encountered in just one population at the scrub forest/savanna interface on the Macizo del Chimantá, this variation may be considered insignificant. It is most likely that the same situation as that of the Macizo occurs on Auyán- and Uaipan-tepuis, where both taxa are known to occur.

Excluded Taxa

Grammadenia sintenisii (Urban) Mez, in Urban, Symbolae antillanae 2: 425. 1901; Mez in Engler, Pflanzenr. IV. 236: 228. 1902.

Ardisia sintenisii Urban, Symbolae Antillanae 1(2): 1(2): 381. 1899. Cybianthopsis sintenisii Lundell, Wrightia 4(2): 68. 1968. Cybianthus sintenisii (Urban) Agostini, Acta Bot. Venez. 10(2): 166. 1980. Type. PUERTO RICO. Sierra de Luquillo, on rd. to Cerro Yunque, 14 Jul 1885 (fl), Sintenis 1366 (holotype, B-destroyed; lectotype here designated, LD; isolectotypes, C, GOET.

C. sintenisii, the only member of Cybianthus subg. Cybianthopsis (Mez) Agostini (1980), is endemic to the Sierra de Luquillo. For discussion of its phylogenetic position within the genus Cybianthus, see Phylogeny.

APPENDIX I

Numerical List of Taxa

1. C. costaricanus Hemsley
    1a. subsp. costaricanus
    1b. subsp. acuminatus (Lundell) Pipoly
    1c. subsp. panamensis (Lundell) Pipoly
    1d. subsp. morii (Lundell) Pipoly
2. C. magnus (Mez) Pipoly
3. C. parasiticus (Swartz) Pipoly
    3a. subsp. magnus
    3b. subsp. asymmetricus (Mez) Pipoly
4. C. marginatus (Bentham) Pipoly
5. C. lineatus (Bentham) Pipoly
6. C. piresii Pipoly
7. C. ptariensis (Steyermark) Pipoly

List of Exsiccatae

Allen, P., 4803 (1a); 5396 (1b).

Almeda, F., 582 (1b); 702 (1b).

Almeda, F. & K. Nakai, 4600 (1a).

Almeda, F. et al., 3102 (1b).

André, E., 1357 (4).

Antonio, H., 48 (4).

Antonio, T., 1410 (1a).

Aristeguieta, L., 2560 (4).

Aristeguieta, L. & E. Medina, 3592 (2a).

Aymard, G., 90 (4).

Baker, R. et al., 237 (1b).

Barclay, H. & P. Juajibioy, 6020 (4); 10304 (4).

Bena, P., s.n. (2).

Bernardi, L., 692 (4).

Brenes, A., 3569 (1a); 3601 (1a); 6052 (1a); 6078 (1a); 6740 (1a); 6761 (1a); 19002 (1a).

Brewer-Carías, C., s.n. (5).

Burger, W. & R. Baker, 9480 (1b).

Burger, W. & R. Stolze, 5962 (1b).

Burger, W. et al., 10272 (1b).

Camargo, L. et al., 7069 (4).

Camp, W., 1206 (2b); 1275 (2b); 4809 (4).

Cardona, F., 126 (4); 962 (5); 1109 (5); 1533 (7); 2027 (7); 2404 (7); s.n. (7).

Core, E., 545 (4); 1384 (4).

Correa, M. & R. Dressler, 551 (1d).

Cowan, R., 1602 (3).

Croat, T., 37176 (1d).

Cuatrecasas, J., 11702 (4); 14647 (4); 14947 (2a); 19143 4); 21805 (4).

Cuatrecasas, J. et al., 12505 (4).

D'Arcy, W. et al., 15517 (2d).

Davidse, G. & A. González, 19618 (2a); 19857 (2a).

Davidse, G. et al., 25120 (1a); 25920 (1a); 28791 (1a); 28824 (1a); 28827 (1a); 29804 (1a).

Dressler, R., 5137 (1d).

Drew, W., 351 (4).

Dryer, V., 200 (1a); 476 (1a); 1070 (1a); 1100 (1a); 1237 (1a).

Dudley, T., 10668 (2b); 10910 (4); 10922 (4); 10931B 4); 11324 (2b).

Duss, P., "3479" (coll. 1893) (3), (coll. 1894) (3), (coll. 1897) (3).

Eggers, H. von, 634 (3); s.n. (coll. 1880) (3).

Endres, M., 146 (1a).

Espinal, S., 1005 (4); 4147 (4).

Ewel, J., 164 (6).

Fariñas, M. et al., 542 (5).

Foldats, E., 2617 (7).

Folsom, J. et al., 4538 (3b); 7804 (1d).

Forero, E. & R. Jaramillo, 2251 (2b).

Forero, E. et al., 2314 (2b); 2968 (2b).

Forsyth, _, s.n. (3).

Fosberg, F. R., 19956 (4); 22247 (2a).

Foster, R., 7641 (2b); 9013 (2b).

García-Barriga, H. & R. Jaramillo, 19814 (4); 20272 (2a).

Gehriger, W., 471 (4).

Gentry, A., 12419 (2b); 46725 (6).

Grant, M., 9722 (4).

Grubb, P. et al., 500 (2a).

Hammel, B., 6304 (1d).

Hartweg, C., 1200 (4).

Hespenheide, H. & D. Wiseman, 476 (3).

Hodge, W. & B. Hodge, 1910 (3).

Holm-Nielsen, L., 29949 (4).

Howard, R. & E. Howard, 19414 (3).

Huber, O. & M. Colella, 8706 (7); 8752 (7); 8756 (7); 8993 (7).

Huber, O. & N. Dezzeo, 8629 (7); 8630 (7).

Huber, O. & J. Steyermark, 6882 (5); 6899 (5); 6992 (7); 7087 (5).

Huber, O. et al., 8837 (7); 8867 (5); 8862 (5).

Huertas, G. & L. Camargo, 5208 (4).

Humbert, H., 26763 (4).

Imray, J., s.n. (coll. 1839) (3).

Idrobo, J. et al., 2991 (4).

Jahn, A., 970 (4).

Jaramillo, J. & F. Coello, 3929 (4).

Jaramillo, R. et al., 3132 (4).

Jenman, E., 108 (5).

Kalbreyer, W., 1087 (2a).

Karsten, B., s.n. (4).

Killip, E. & A.C. Smith, 15891 (4); 15906 (2a); 20655 (4).

L'Herminier, M., s.n. (3).

Lehmann, F., 186 (4); 599 (4); 2399 (4); 5579 (4).

Lent, R., 1090 (1b); 2611 (1a); 3828 (1b).

León, J., 2634 (1b).

Liesner, R., 16091 (6).

Liesner, R. et al., 8038 (4).

Linden, M.J., 447 (4).

Little, E., Jr., 7051 (2a); 8683 (4); 15383 (2a); 15532 (4).

López-Figueiras, M., 8689 (4).

López-Figueiras, M. et H. Rodríguez C., 8833 (2a).

López-Figueiras, M. et al., 8917 (4).

Luteyn, J. & E. Cotton, 9622 (4); 11184 (3b); 11295 (4).

Luteyn, J. & J. Pipoly, 9301 (4); 9302 (4); 9303 (4); 9304 (4); 9305 (4); 9306 (4); 9307 (4); 9309 (4); 9311 (4); 9297 (4).

Luteyn, J., J. Pipoly, et al., 10173 (4); 10175 (4); 10185 (4); 10187 (4); 10189 (4); 10190 (4); 10414 (2b); 10415 (2b); 10416 (2b); 10417 (2b); 10420 (2b); 10421 (2b); 10442 (2b); 10525 (2b); 10526 (2b); 10527 (2b); 10528 (2b); 10529 (2b); 10530 (2b); 10531 (2b); 10532 (2b); 10533 (2b); 10534 (2b); 10535 (2b); 10536 (2b); 10561 (2b); 10562 (2b); 10565 (2b); 10566 (2b); 10567 (2b).

Luteyn, J. et al., 6647 (4); 7278 (2b).

Maas, P. et al., 2711 (1d).

Maguire, B., 32821 (5); 32835 (5); 32871 (5).

Maguire, B. & C. Maguire, 35225 (5); 35318 (5); 35363 (5).

Maguire, B. & L. Politi, 27628 (5); 27642 (5); 27768 (5);

28341 (5); 28587 (5); 28588 (5).

Maguire, B. et al., 29808 (5); 30281 (5); 30288 (5); 30292 (5); 37197 (6); 42112 (6); 60476 (6); 60526 (6).

Mason, H., 13730 (4).

Matos, G., 1108 (4).

McPherson, G., 6863 (1d).

Melampy, M., 1043 (4); 1232 (4); 1302 (4).

Miguel, P., 46 (4);

Mori, S., 7119 (1d).

Mori, S. & A. Bolten, 7296 (1a).

Mori, S. & J. Kallunki, 2392 (1d); 3759 (1d); 3761 (1d); 5858 (1a); 6085 (1d); 6494 (1d); 6496 (1d).

Moritz, K., 1173 (4).

Nee, M. & H. Stockwell, 11602 (1c).

Nicolson, D., 1955 (3).

Pannier & Schwabe, s.n. (7).

Pearce, R., 250 (4).

Pennell, F., 2488 (4); 4302 (4).

Phelps, K., 133 (5).

Phelps, K. & C. B. Hitchcock, 44 (5); 378 (7).

Pipoly, J., 6413 (2a); 6437 (2a); 6453 (2a); 6454 (2a); 6455 (2a); 6456 (2a); 6457 (2a); 6458 (2a); 6459 (2a); 6588 (4); 6590 (4); 6593 (4); 6595 (4); 6598 (4); 6601 (4); 6602 (4); 6603 (4); 6604 (4); 6605 (4); 6606 (4); 6608 (4); 6607 (4); 6609 (4); 7017 (1d); 7019 (1d); 7021 (1d); 7023 (1d); 7024 (1d); 7027 (1d); 7028 (1d); 7029 (1d);

7030 (1d); 7030 (1d); 7049 (1c); 7053 (1c); 7054 (1c); 7055 (1c); 7056 (1c); 7057 (1c); 7058 (1c); 7059 (1c); 7060 (1c); 7061 (1c); 7062 (1c); 7067 (1a); 7068 (1a); 7070 (1a); 7072 (1a); 7073 (1a); 7074 (1a); 7075 (1a); 7083 (1a); 7084 (1a); 7087 (1a); 7088 (1a); 7089 (1a); 7091 (1a); 7092 (1a); 7093 (1a); 7095 (1a); 7097 (1a); 7098 (1a); 7099 (1a); 7100 (1a); 7112 (1a); 7114 (1a); 7115 (1a); 7116 (1a); 7117 (1a); 7118 (1a); 7119 (1a); 7120 (1a).

Pipoly, J. & G. Aymard, 6548 (4); 6549 (4).

Pipoly, J. & R. Bethancourt, 7032 (1d); 7033 (1d); 7034 (1d); 7035 (1d); 7036 (1d); 7037 (1d); 7041 (1d); 7044 (1d).

Pipoly, J. & F. Monje S., 6575 (4); 6576 (4); 6581 (4); 6577 (4); 6581 (4); 6582 (4); 6583 (4); 6584 (4); 6940 (4); 6941 (4); 6942 (4); 6943 (4); 6945 (4); 6947 (4); 6953 (4); 6954 (4); 6957 (4); 6958 (4); 6960 (4); 6961 (4); 6962 (4); 6963 (4); 6972 (4); 6973 (4); 6974 (4); 6975 (4); 6976 (4); 6977 (4); 6979 (4); 6983 (4).

Pipoly, J. et al., 6536 (2a); 6537 (4); 6538 (4); 6539 (4); 6544 (4); 6545 (4); 6546 (4); 7077 (1b); 7082 (1b); 7129 (7); 7133 (7); 7135 (7); 7137 (7); 7138 (7); 7149 (7); 7150 (7); 7153 (7); 7213 (5); 7215 (5); 7229 (5); 7230 (5); 7231 (5); 7233 (5); 7236 (5); 7238 (5); 7240 (5); 7242 (5); 7244 (5); 7247 (5); 7249 (5); 7266 (7); 7267 (7); 7269 (7); 7271 (7); 7272 (5); 7274 (5); 7275 (5); 7277 (5); 7279 (7); 7280 (7); 7281 (7); 7282 (7); 7295

Steyermark, J. & V. Carreño, 115656 (7).

Steyermark, J. & J. Luteyn, 129791 (6).

Steyermark, J. & J. Wurdack, 395 (5); 659 (7); 807 (7); 1030 (7).

Steyermark, J. et al., 98546 (4); 100867 (4); 109582 (5); 109592 (5); 117444 (5); 126334 (5); 126365 (5); 128138 (7); 128138A (5); 128334 (7); 128558 (5); 128577 (5); 128776 (7).

Swartz, O., herb., sine collector et dies (3).

Tate, G., 208 (2a); 209 (2a); 416 (5); 612 (5); 657 (5).

Taylor, J., 17764 (1a).

Thomas, W. & T. Plowman, 3043 (6).

Tillett, S. & S. Talukdar, 752-118 (5).

Ule, E., 6792 (3b); 8645 (5).

Uribe U., L., 5725 (2a).

Vareschi, V. & L. Vareschi, 6029 (4).

Velasco, R. & M. Ramia, 675 (4).

Wasshausen, D. & E. Ayensu, 337 (3).

Weberbauer, A., 6121 (4); 7168 (4).

Webster, G. et al., 9009 (3).

Weitzman, A. & C. Sobrevilla, 28 (4).

Werff, H. van der, 6429 (1a); 6529 (1a); 6967 (1d).

Weston, A., 12305A, (1a).

Wiggins, I., 10484 (4).

Wilbur, R., 14348 (1b); 14539 (1b).

Wilbur, R. & F. Almeda, 16757 (1b).

APPENDIX II

FIGURES FOR TEXT

FIGURE 1. Architectural features of subg. *Grammadenia*.

A. *C. costaricanus* subsp. *costaricanus* (*Pipoly 7068*), habit showing diageotropic root. B. *C. marginatus* (*Pipoly et al. 6538*), trunk. C. *C. costaricanus* subsp. *morii* (*Pipoly 7017*), showing rythmic branching. D. *C. ptariensis* (*Pipoly et al. 7133*), sylleptic branch. E. *C. costaricanus* subsp. *acuminatus* (*Pipoly et al. 7077*), showing reiterative shoots. F. *C. lineatus* (*Pipoly et al. 7229*), showing habit, note pachycaulous trunk.

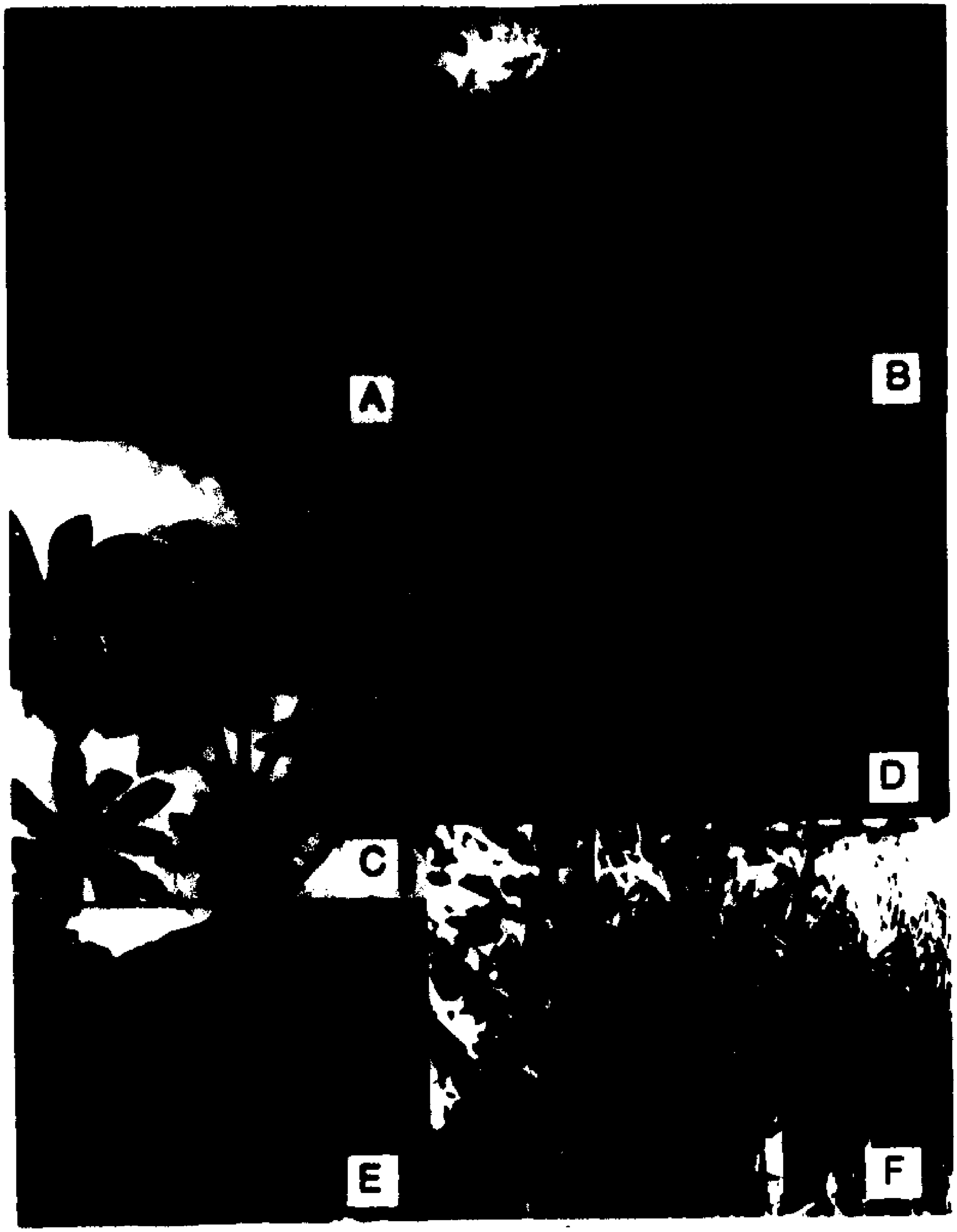
A
B
C
D
E
F

FIGURE 2. SEM photos of morphological
features in subg. _Grammadenia_.

A. _C_. _marginatus_ (_Pipoly_ _et_ _al_. _6546_), verrucose papillae. B. Same, (_Dudley_ _10922_), close-up. C-D. _C_. _lineatus_ (_Pipoly_ _et_ _al_. _7229_), C, stem surface; D, glandular-papillae. E. _C_. _costaricanus_ _subsp_. _morii_ (_Pipoly_ _7017_), pollen, equatorial and polar views. (Bars of figures equal: A. 50 um, B. 22.2 um, C & D. 48 um, E. 12.3 um).

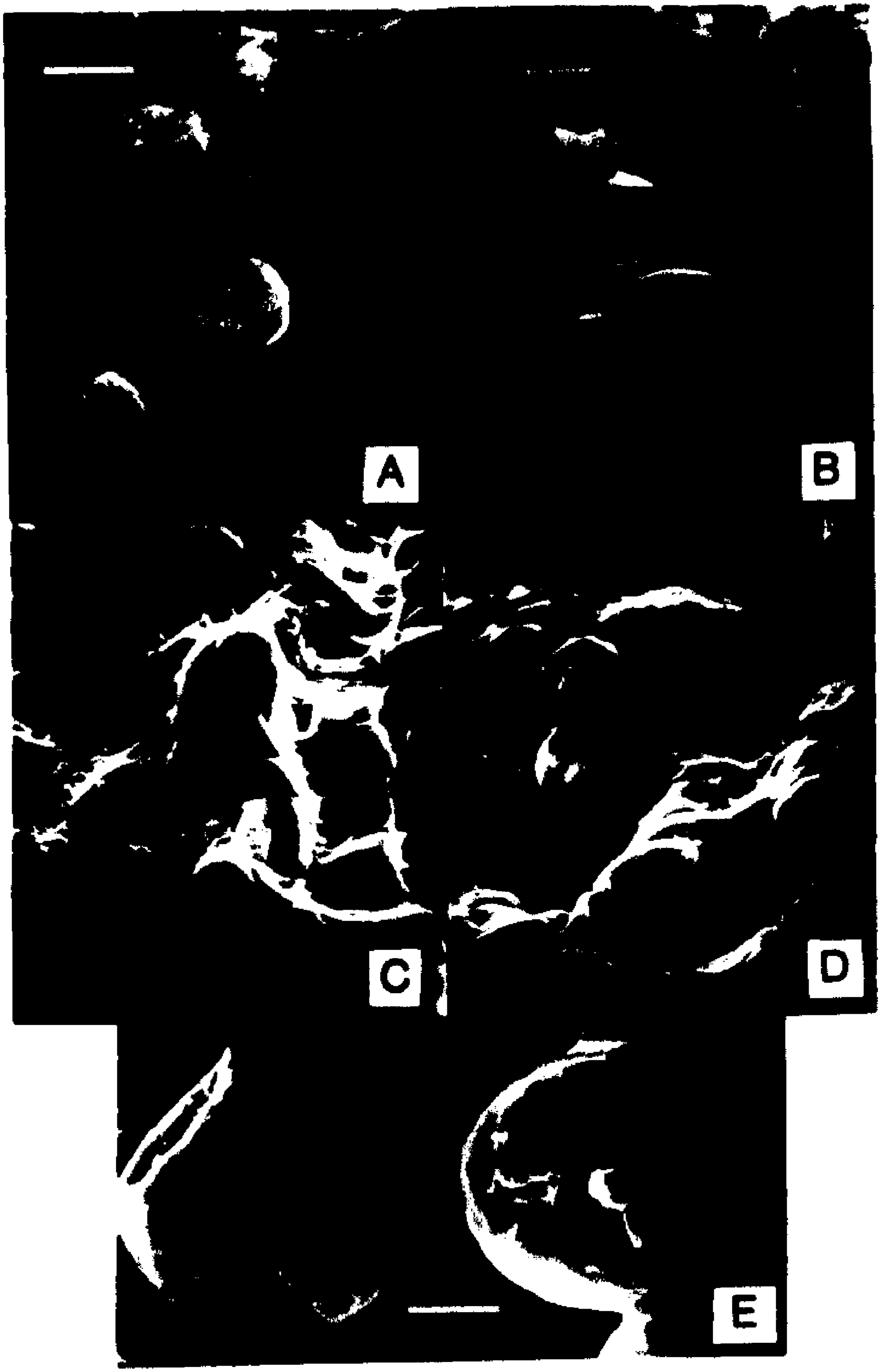
A
B
C
D
E

FIGURE 3. Morphology of reproductive organs
in subg. *Grammadenia*.

A, E, F, & L. *C. lineatus* (*Pipoly et al. 7249*). B, D, & M. *C. marginatus* (*Pipoly & Monje 6953*). C, J, & N. *C. costaricanus* subsp. *panamensis* (*Pipoly 7061*). G, I,& O. *C. ptariensis* (*Pipoly et al. 7133*). H. *C. piresii* (*Maguire et al. 60476*). K. *C. magnus subsp. magnus* (*Pipoly 6458*).

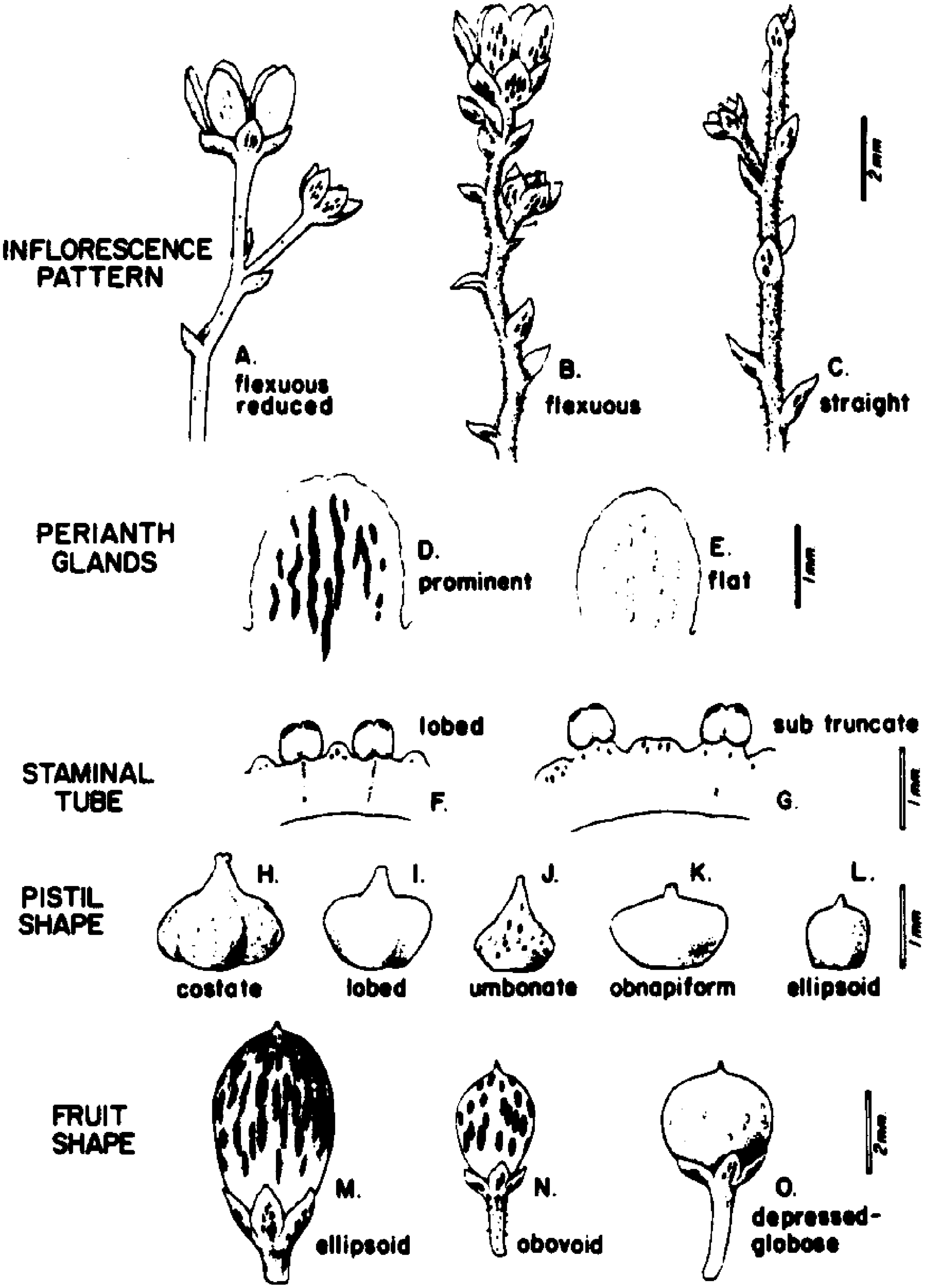
INFLORESCENCE PATTERN
A. flexuous reduced
B. flexuous
C. straight
2 mm
PERIANTH GLANDS
D. prominent
E. flat
1 mm
STAMINAL TUBE
lobed
F.
sub truncate
G.
1 mm
PISTIL SHAPE
H.
I.
J.
K.
L.
costate
lobed
umbonate
obnapiform
ellipsoid
1 mm
FRUIT SHAPE
M. ellipsoid
N. obovoid
O. depressed-globose
2 mm

FIGURE 4. Primary stem histological features in subg. *Grammadenia*.

A. *C. marginatus* (*Pipoly et al. 6546*), transverse section, showing outer cortex (oc), inner cortex (ic), pith (pi), cortical bundles (cb), midrib trace (mt). B. *C. costaricanus* subsp. *costaricanus* (*Pipoly 7068*), transverse section, showing druses of outer cortex. C & D. *C. magnus* subsp. *magnus* (*Pipoly 6453*), transverse sections, showing collenchyma (co) and aerenchyma (ae). E. *C. magnus* subsp. *asymmetricus* (*Luteyn, Pipoly et al. 10414*), transverse section showing resin canals (arrows). F. *C. costaricanus* subsp. *panamensis* (*Pipoly 7056*), transverse section showing brachysclereids (bs). (Bars in figures A-F equal: A. 350 um, B. 50 um, C. 120 um, D. 50 um, E. 200 um, F. 160 um.)

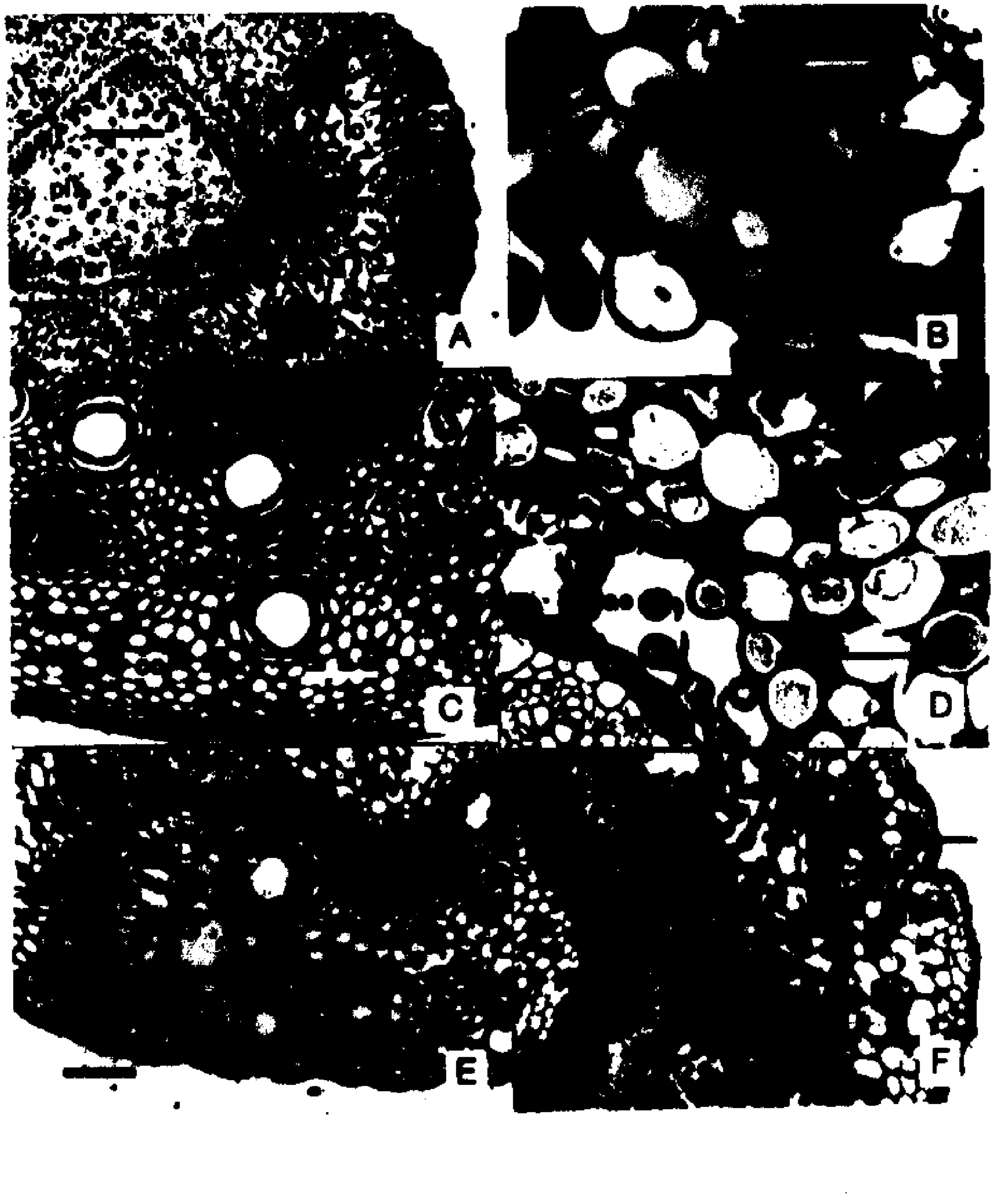
pl
A
B
C
D
E
F

FIGURE 5. Primary stem histological features in subg. _Grammadenia_

A-B. _C. ptariensis_ (_Pipoly et al. 7133_), periderm formation, showing epidermal cork. C. _C. marginatus_ (_Pipoly 6546_), amphicribal cortical bundle without perivascular fibers. D. _C. ptariensis_ (_Pipoly et al. 7133_) , hemiamphicribal bundle with perivascular fibers (pf). E. _C. lineatus_ (_Pipoly 7229_), section showing parenchymatous inner cortex. F. _C. marginatus_ (_Pipoly 6546_), section showing aerenchymatous inner cortex. (Bars in Figures A-F equal to: A. 30 um, B. 120 um, C. 48 um, D. 60 um, E. 465 um, F. 120 um.


B
D
E
F

FIGURE 6. Primary stem histological features of subg. _Grammadenia_.

A. _C_. _costaricanus_ subsp. _morii_ (_Pipoly 7017_), showing pericyclic fibers (arrow). B. _C_. _costaricanus_ subsp. _costaricanus_ (_Pipoly 7068_), showing druses in pith. C. _C_. _costaricanus_ subsp. _panamensis_ (_Pipoly 7056_), showing druses in pith, with polarized light. D-E. _C_. _magnus_ subsp. _magnus_ (_Pipoly 6453_), showing angular pith collenchyma. F. _C_. _magnus_ subsp. _asymmetricus_ (_Luteyn_, _Pipoly et al_. _10415_), showing transitional tangential pith collenchyma. (Bars for figures A-F equal to: A. 195 um, B. 45 um, C. 48 um, D. 230 um, E. 74 um, F. 60 um.)

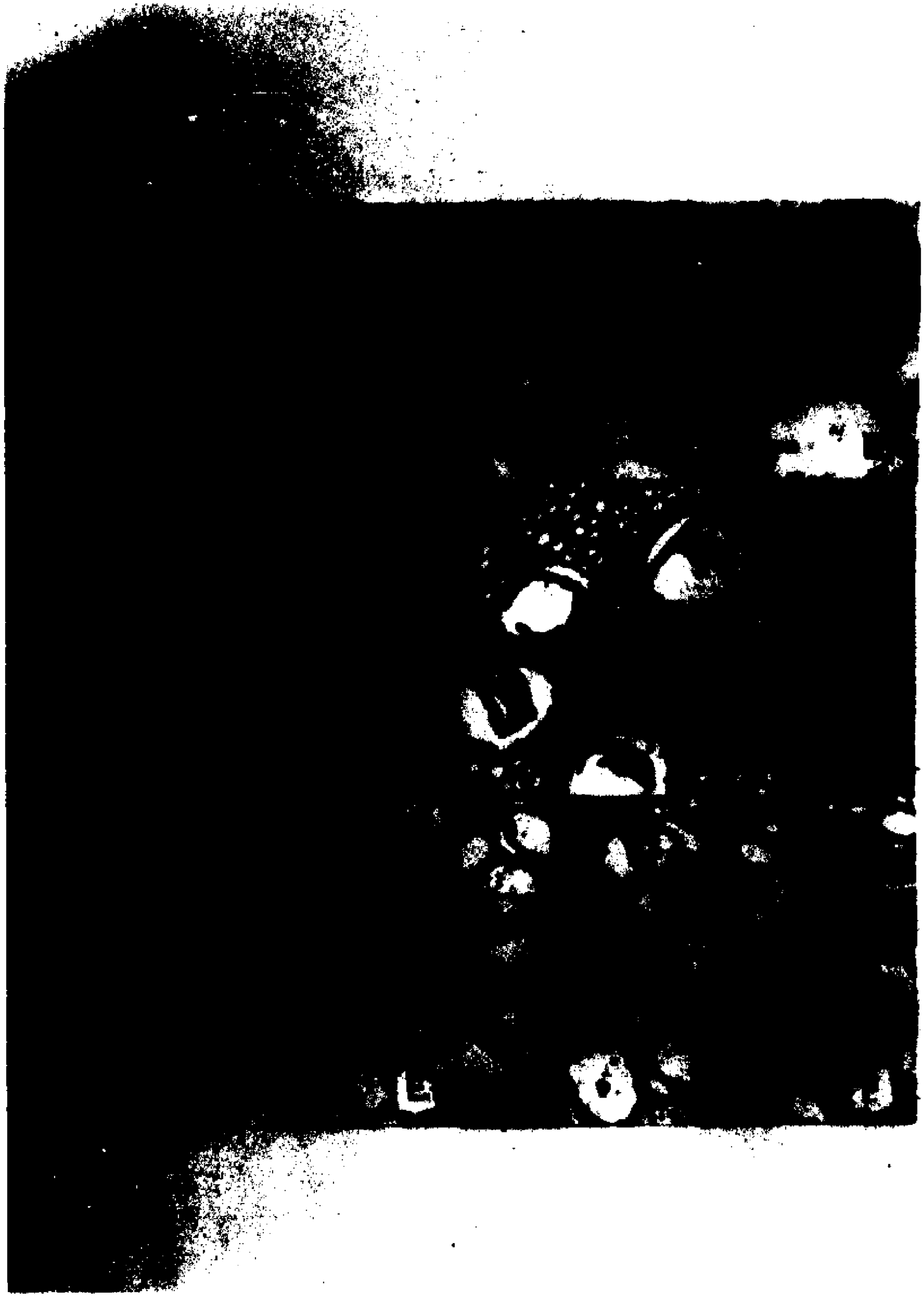

FIGURE 7. Nodal vasculature of subg. *Grammadenia*:
Basipetal series showing leaf trace insertion

A-D. *C. ptariensis* (*Pipoly et al. 7135*), explanation in text. (Distances between sections : A to B. 30 um, B to C. 50 um, C to D. 170 um.)

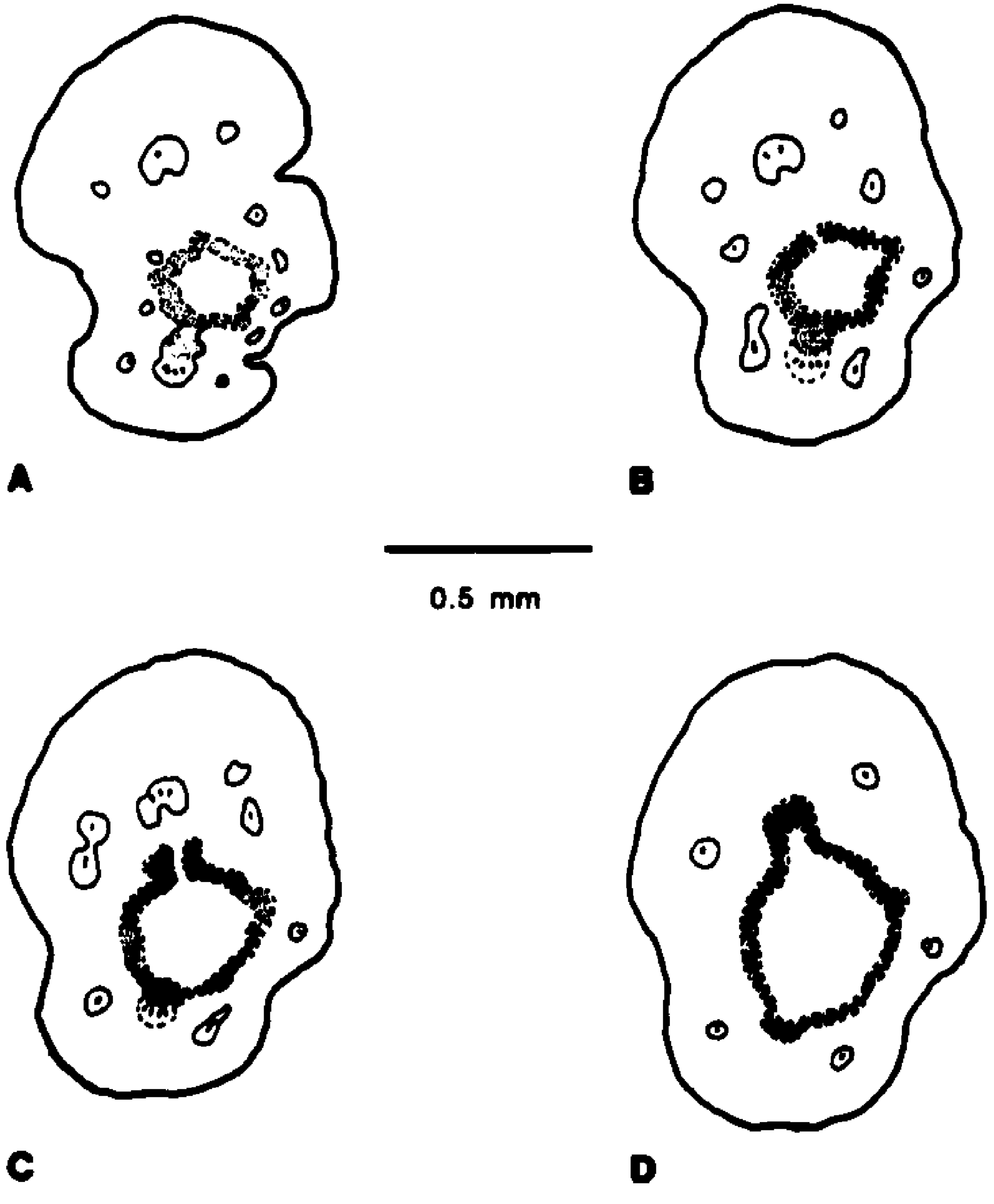
A
B
0.5 mm
C
D

FIGURE 8. Vascular reconstruction of primary stem in subg. *Grammadenia*.

C. lineatus (*Steyermark 126365*), numbered tubes represent midrib traces, unnumbered tubes represent cortical traces.

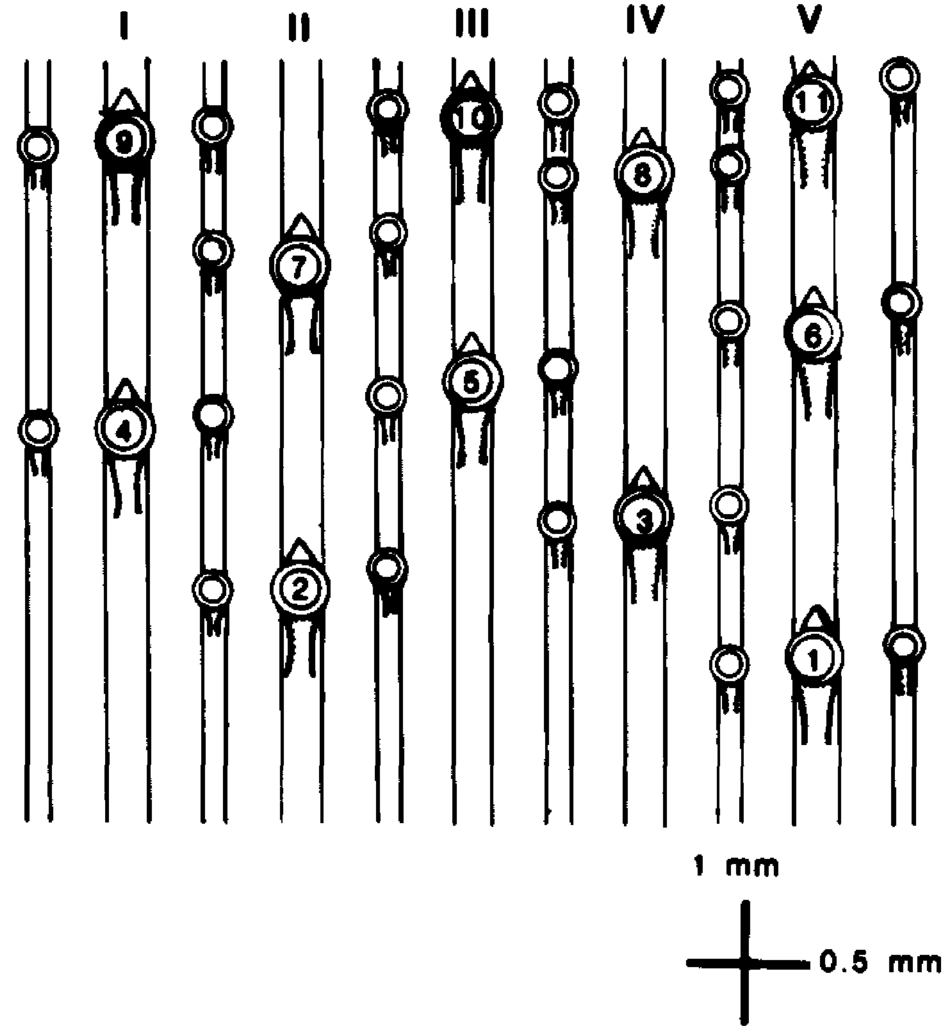
I
II
III
IV
V
9
4
7
2
10
5
8
3
11
6
1
1 mm
0.5 mm

FIGURE 9. Nodal vasculature of subg. *Grammadenia*:
Sections including apex showing
leaf trace insertion

A-C. *C. ptariensis* (*Pipoly et al. 7135*), longitudinal sections showing insertion of leaf traces. A. Insertion of cathodic lateral trace (ct), independent of stelar procambium (sp), and showing branch stelar trace (bt); B. Midrib traces (mt), connecting to stelar procambium (sp); C. Anodic lateral trace (at), connecting to cortical sympodium, not stelar procambium (sp). D. *C. magnus* subsp. *magnus* (*Pipoly 6453*), transverse section showing midrib trace (mt) approaching one gap in stele, anodic (at) and cathodic (ct) traces, and cortical bundles (cb). (Bars in figures A-D equal: A-C. 900 um, D. 420 um.)


B
D

FIGURE 10. Branch vasculature in subg. _Grammadenia_: Representative sections from acropetal series.

A-F. _C._ _lineatus_ (_Steyermark_ _126365_). (Distances between sections: A to B. 210 um, B to C. 110 um, C to D. 440 um, D to E. 110 um, E to F. 46 um.

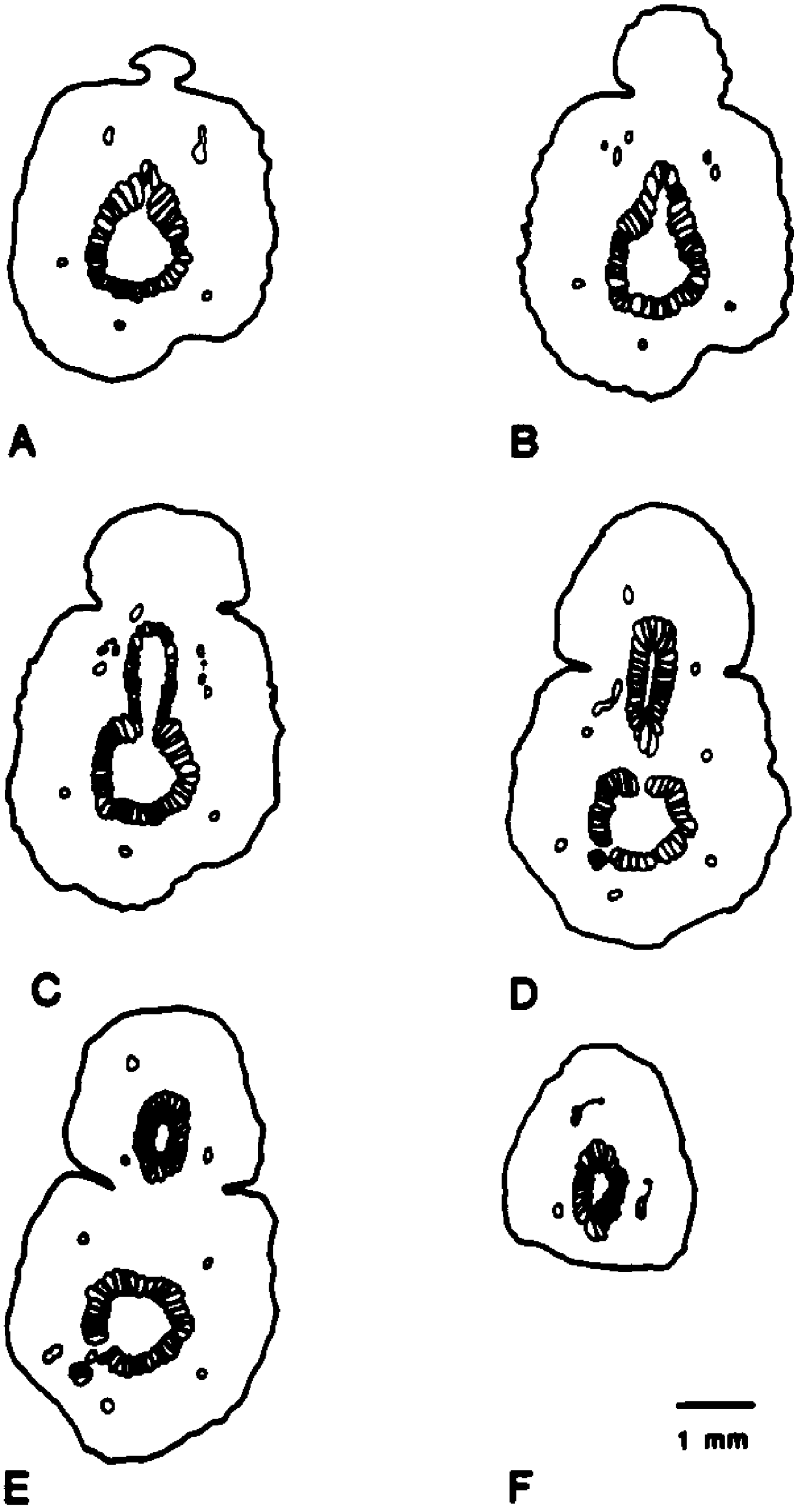
A
B
C
D
E
F
1 mm

FIGURE 11. Leaf architecture of subg. *Grammadenia*.

C. *costaricanus* subsp. *morii* (*Pipoly 7017*).

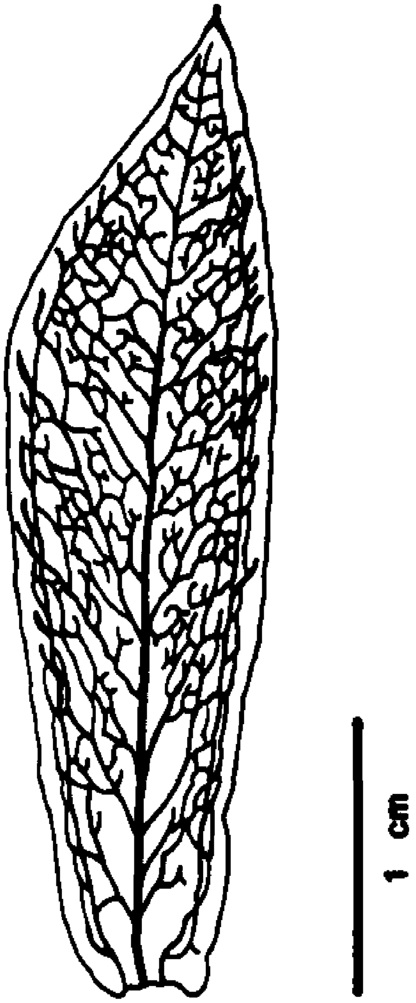
1 cm

FIGURE 12. Leaf architecture and epidermal features of subg. Grammadenia

A-C. C. costaricanus subsp. costaricanus (Pipoly 7099), leaf clearings; A-B. Showing lateral primary (lp), lateral secondary (ls), lateral tertiary (lt), and midrib secondary veins (ms); hydropote (hp); liso-schizogenous gland (lg); C. Showing midrib tertiary veins with dilatated terminae. D-F. C. costaricanus subsp. costaricanus (Pipoly 7068). D. Leaf clearing, showing paracytic stomata and hydropote (hp); E. SEM photo showing cuticular ridges on stomata and subsidiary cells; F. Anatomy of stomatal apparatus and hydropotes, showing guard cells (gs), subsidiary cells (sc), foot cell (fs), basal cell (bc), stalk cell (st), cap cell (ca). (Bars in figures A-F equal to: A. 0.5 mm, B. 1.5 mm, C. 0.32 mm, D. 60 um, E. 20 um, F. 36 um.)

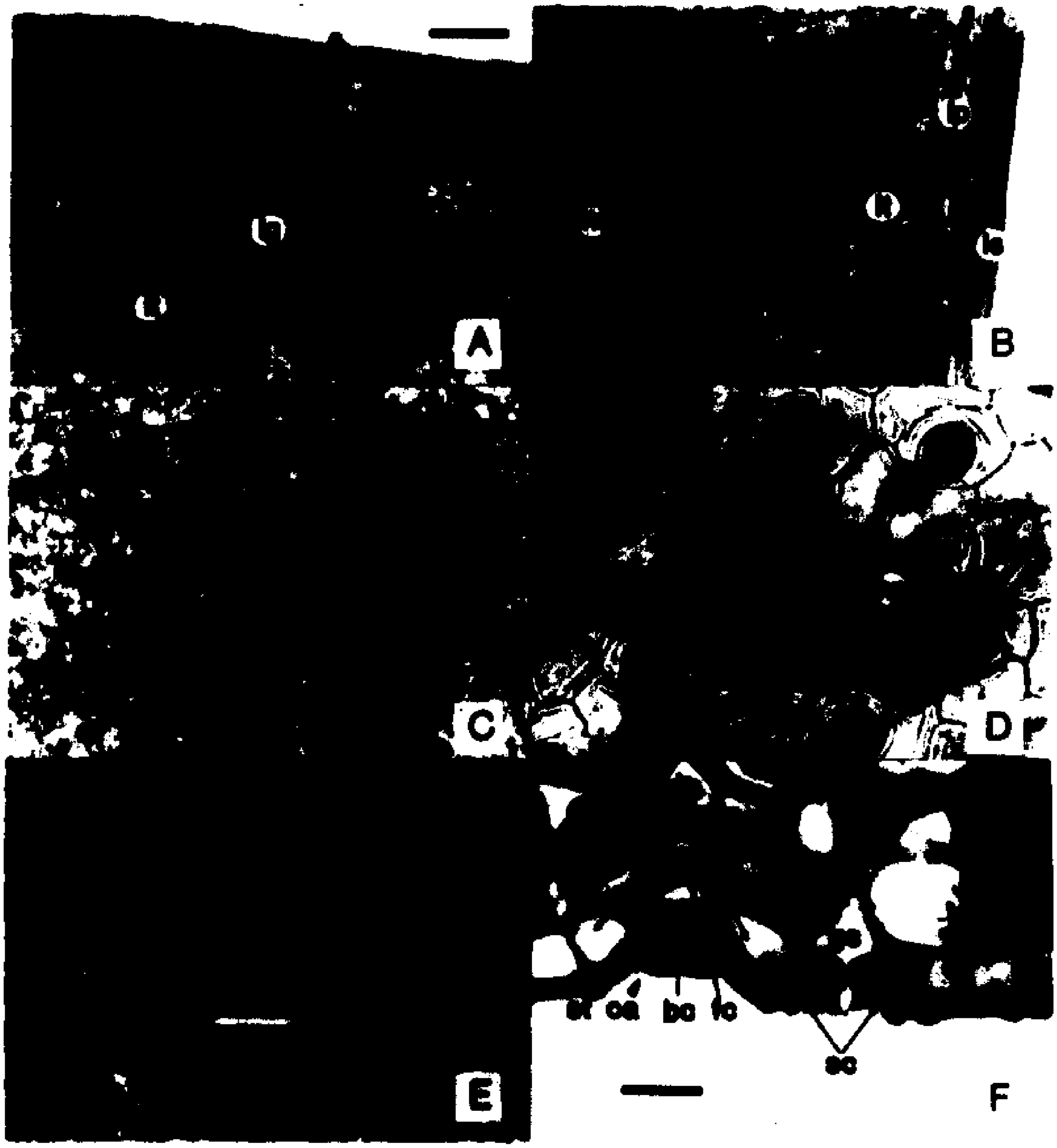
A
B
C
D
E
st
oa
bo
fo
sc
F

FIGURE 13. Ontogeny of hydropotes in subg. _Grammadenia_.

A-B & D. _C_. _costaricanus_ subsp. _costaricanus_ (_Pipoly 7068_), SEM photos; A. Mature hydropote, cap with at least 8 cells, and with 5 subsidiary cells. B. Younger hydropote, cap with 4 cells, but with 6 subsidiary cells. C. _C_. _costaricanus_ subsp. _morii_ (_Pipoly 7017_), longisection of young hydropote, showing subsidiary cells (sc), foot cell (fc), stalk cell (st), cap cell (ca), basal cell not discernible. D. Young hydropote, with 2-celled cap, showing mucilaginous substance (ms). E-F. _C_. _costaricanus_ subsp. _panamensis_ (_Pipoly 7056_), paradermal sections. E. Showing mature hydropote, with 12-celled cap. F. Showing hydropote after cap has broken off. (Bars of figures A-F equal : A & C. 28 um, B. 20 um, D. 10 um, E. 36 um, F. 53 um.)

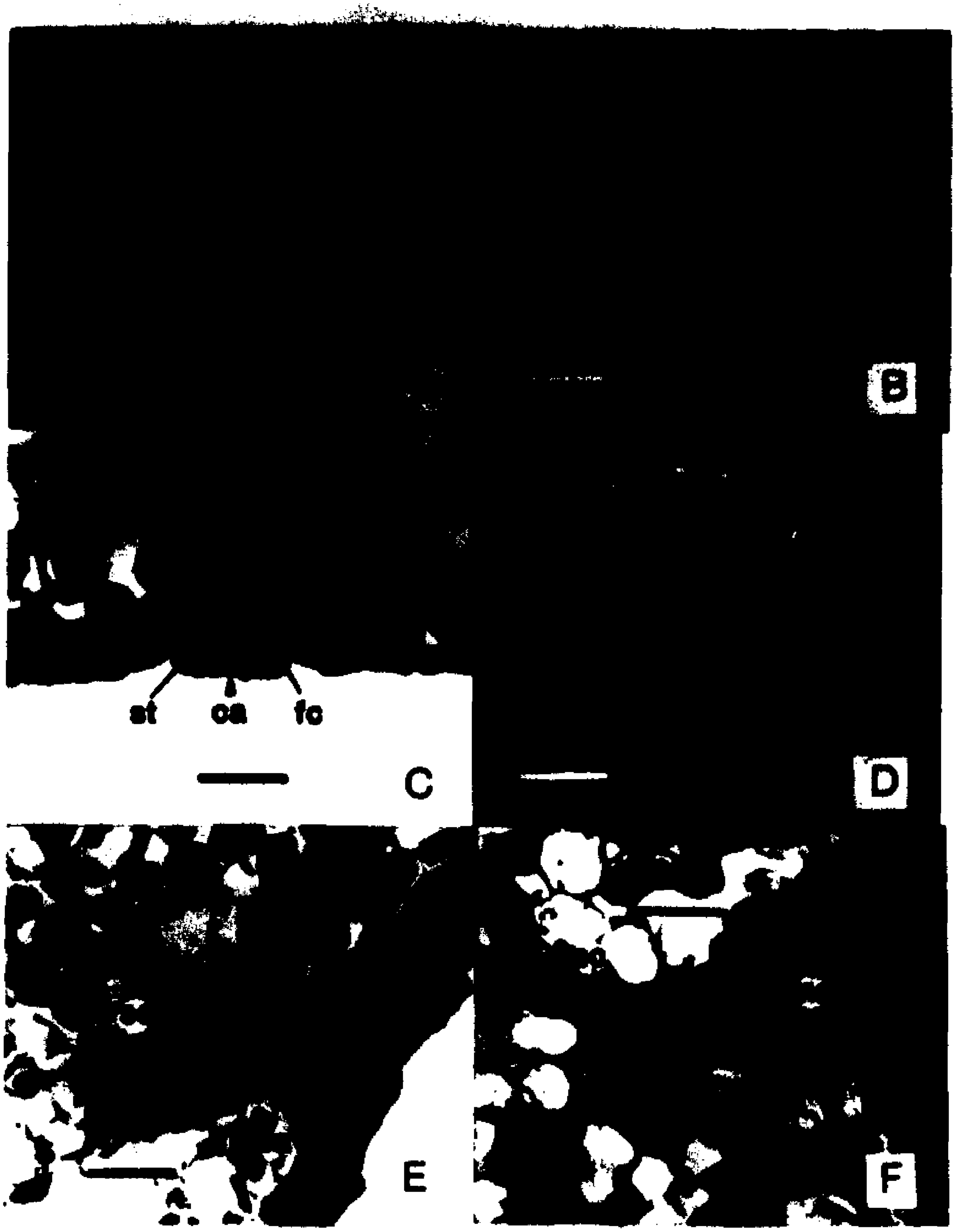
B
st
ca
fc
C
D
E
F

FIGURE 14. Leaf histological features of subg. *Grammadenia*.

A. *C. costaricanus* subsp. *panamensis* (*Pipoly 7056*), showing druses in uppermost layer of mesophyll. B-C. *C. lineatus* (*Pipoly et al. 7272*), showing distribution of palisade parenchyma (pp). D. *C. piresii* (*Maguire et al. 64760*), showing homogeneous epidermis, with hypodermal idioblasts (hi). E. *C. marginatus* (*Luteyn, Pipoly et al. 10189*), showing abaxial and adaxial hypodermal idioblasts (hi). F. *C. costaricanus* subsp. *panamensis* (*Pipoly 7056*), showing phloem islands (pi), and xylem (xy). G. *C. costaricanus* subsp. *morii* (*Pipoly 7017*), showing midrib bundle, xylem (xy), phloem (ph); note lack of bundle sheath. (Bars for figures A-G equal to: A. 60 um, B. 176 um, C. 50 um, D. 240 um, E. 150 um, F. 95 um, G. 120 um.)

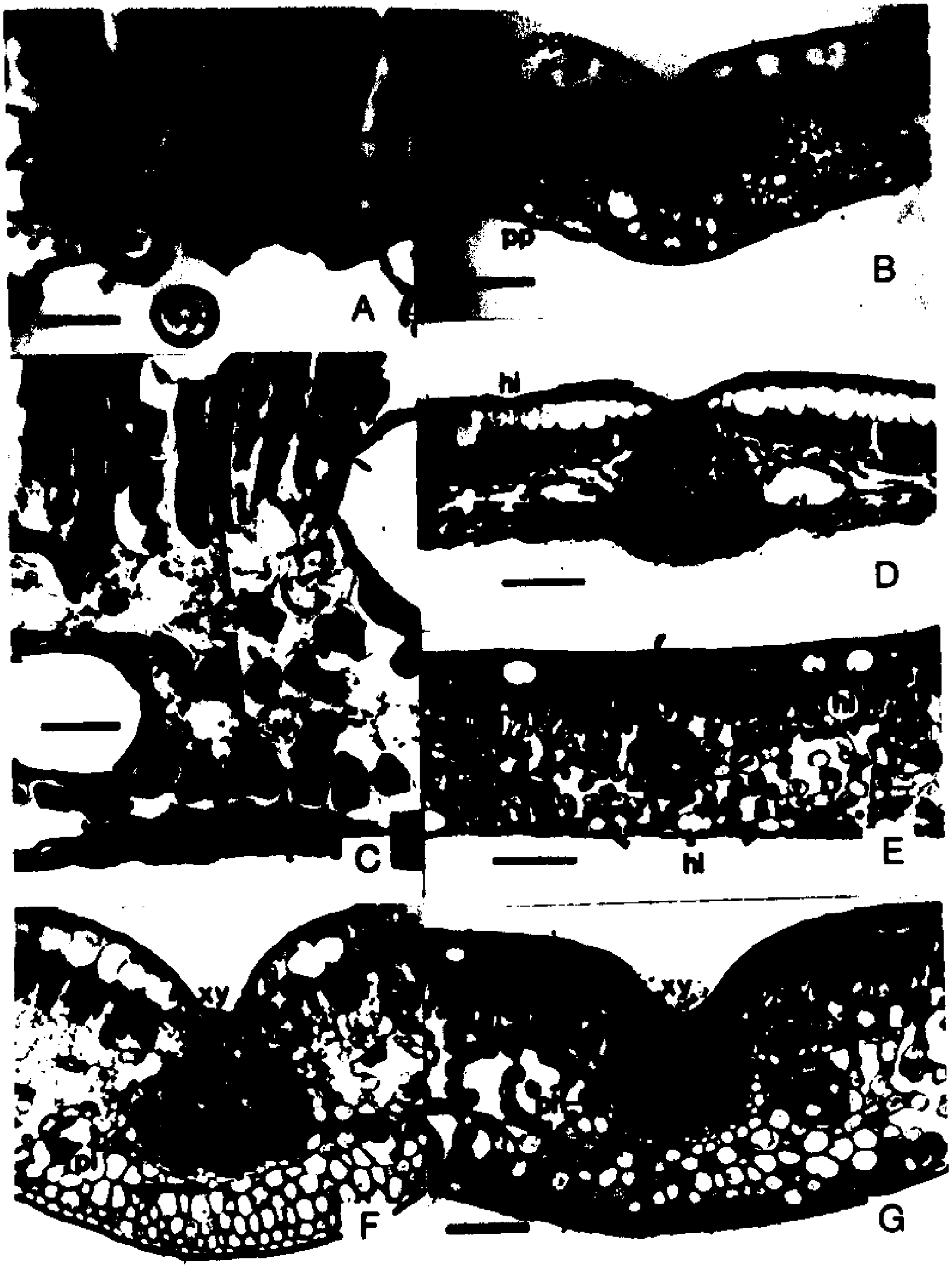
pp
B
A
hl
D
C
E
hl
xy
xy
pl
F
G

FIGURE 15. Leaf lenticular epidermal cells and hypodermal idoblasts in subg. *Grammadenia*.

A. *C. ptariensis* (*Pipoly et al. 7133*), transverse section, showing lenticular cells (arrows). B. *C. costaricanus* subsp. *costaricanus* (*Pipoly 7099*), Transverse section. C. *C. lineatus* (*Pipoly 7272*), showing lenticular cells (arrows). D. *C. costaricanus* subsp. *costaricanus* (*Pipoly 7099*), longisection.(Bars for figures A-D equal to: A. 60 um, B. 26 um, C. 240 um, D. 44 um.


A
B
C
D

FIGURE 16. Floral features of subg. _Grammadenia_.

A-D. _C._ _costaricanus_ subsp. _morii_(_Pipoly_ _7017_).
A. SEM photo of glanduar-granule. B. Longisection of same, showing foot cell (fc), stalk cell (st), cap cell (ca). C. Glandular-lepidote scale of ovary. D. Glandular-papilla of calyx. (Bars for figures A-D equal to: A & B. 20 um, C. 180 um, D. 35.2 um.)


B
D

FIGURE 17. Wood of subg. *Grammadenia*.

A-B. Transverse sections. A. *C. costaricanus* subsp. *costaricanus* (*Pipoly 7068*). B. *C. magnus* subsp. *magnus* (*Pipoly 6453*). C-D. *C. costaricanus* subsp. *costaricanus* (*Pipoly 7068*), macerations showing vessels and fiber-tracheids. Note simple perforation plates of vessels. (Bars in figures A-D equal: A. 420 um, B. 730 um, C. 130 um, D. 46 um.

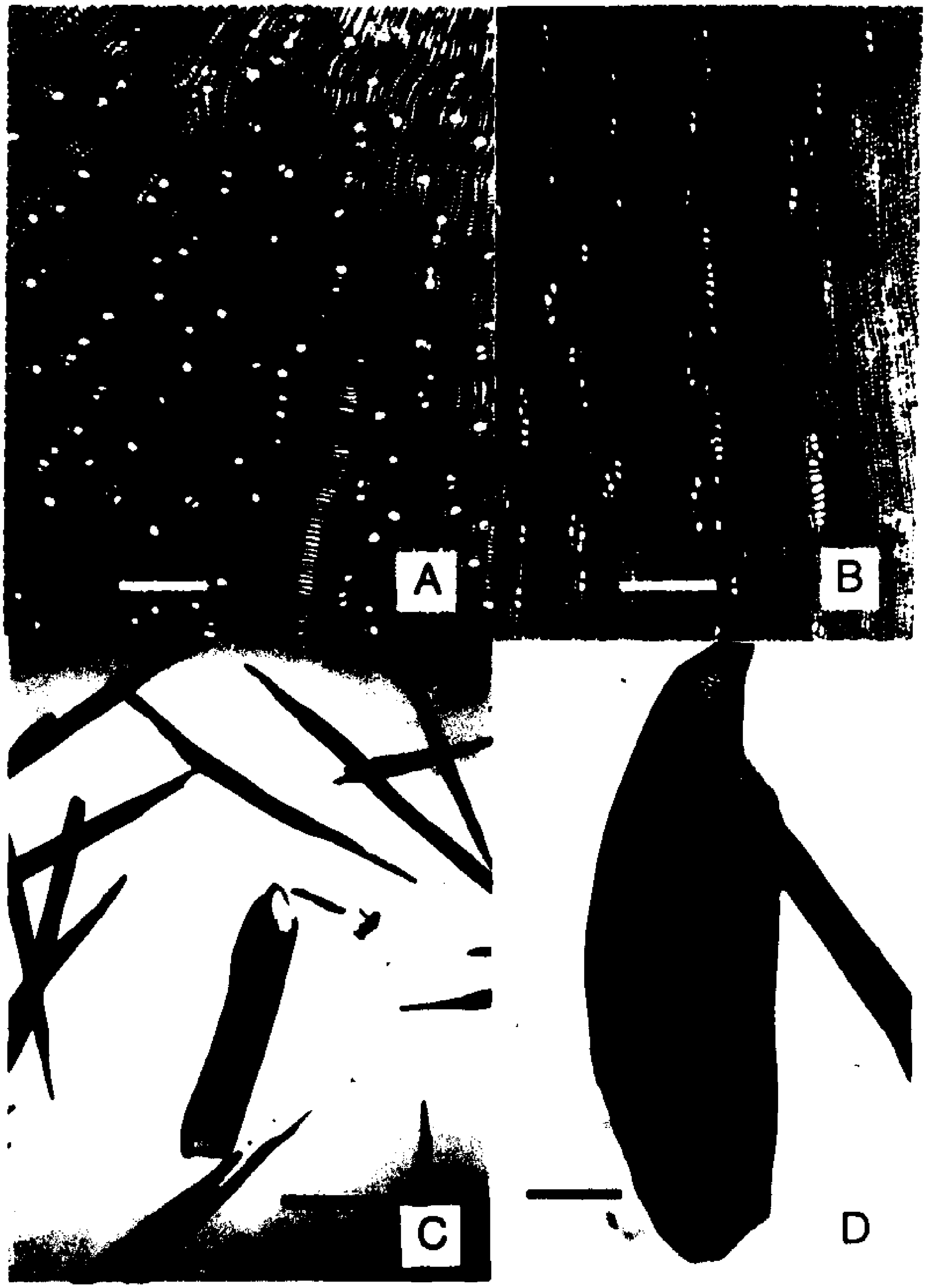
A
B
C
D

FIGURE 18. Wood of subg. *Grammadenia*

A. *C. ptariensis* (*Pipoly 7133*), tangential section of vessel showing simple perforation plate and transitional pitting of tail. B. *C. costaricanus* subsp. *costaricanus* (*Pipoly 7083*), tangential section of vessel (right) showing transitional intervascular pitting; fiber (left) showing circular-bordered pits. C. *C. lineatus* (*Steyermark 126365*), radial section showing intervascular pitting (right) and circular-bordered vessel/parenchyma pitting (left). D. *C. magnus* subsp. *magnus* (*Pipoly 6453*), maceration showing fiber-tracheid with circular-bordered pits. (Bars in figures A-D equal : A. 360 um, B. 300 um, C. 300 um, D. 30 um.)


A
B
C
D

FIGURE 19. Wood of subg. *Grammadenia*

A-D. Tangential sections. A. *C. costaricanus* subsp. *costaricanus* (*Pipoly 7083*). B-D. *C. lineatus* (*Steyermark 126365*). B & C. Showing variation in ray length. D. Showing well-developed sheath cells on both sides of ray. (Bars in figures A-D equal: A. 300 um, B & C. 300 um, D. 30 um.)

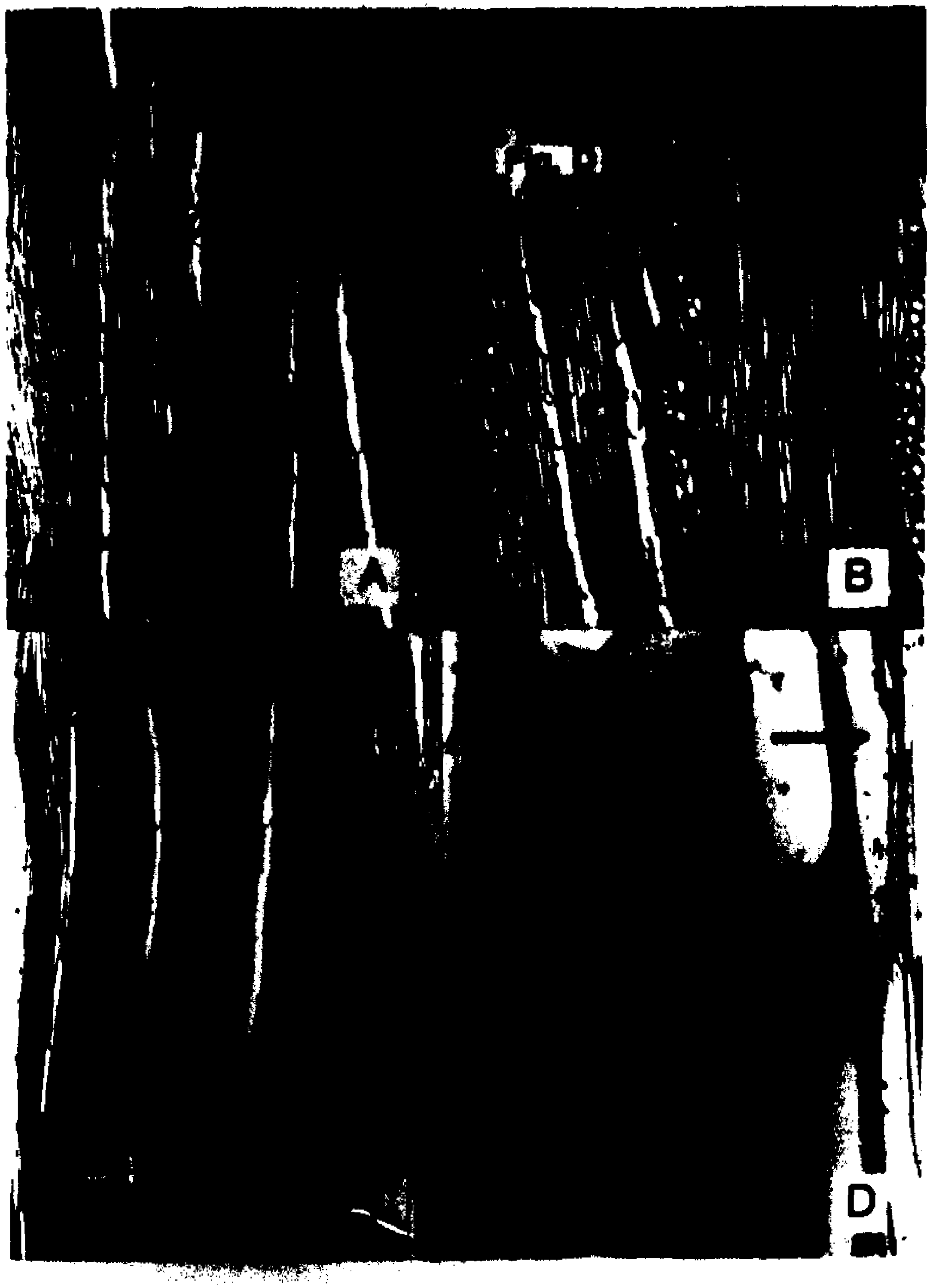
A
B
D

FIGURE 20. Wood of subg. *Grammadenia*.

A. *C. lineatus* (*Steyermark 126365*), radial section showing weakly procumbent cells (pc). B. *C. costaricanus* subsp. *costaricanus* (*Pipoly 7083*), radial section showing procumbent cells (pc). C. *C. marginatus* (*Pipoly 6608*), transverse section showing vasicentric axial parenchyma (ap). D. *C. lineatus* (*Steyermark 126365*), showing scanty axial parenchyma (ap). (Bars for figures A-D equal: A. 360 um, B. 200 um, C. 80 um, D. 100 um.)

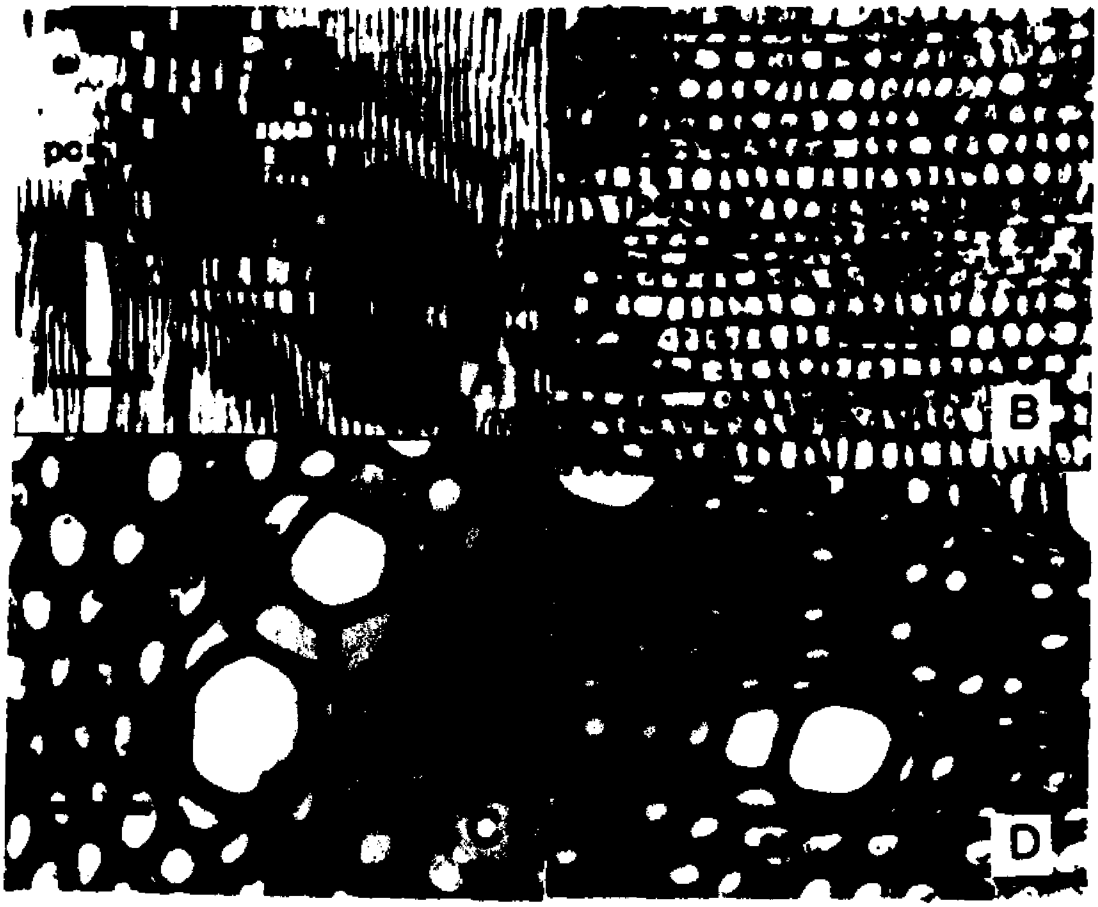
pc
B
D

FIGURE 21. Groups of Myrsinaceae used in cladistic analyses.

A. Vegaea pungens (Liogier 16100), SEM photo showing papillae of adaxial corolla surface. B. C. costaricanus subsp. morii (Pipoly 7017), SEM photo showing glandular-granules of adaxial corolla surface. C. C. (subg. Cybianthus) aff. nitidus (Mori & Pipoly 15496), habit. D-E. Embelia ribes. D. (Liang 64061), SEM photo showing glandular-granules of adaxial corolla surface. E. Habit, (photo courtesy of B. C. Stone). F. C. (subg. Cybianthopsis) sintenisii (Acevedo 721), habit. (Bars of figures A, B, & D equal: A. 13 um, B. 20 um, D. 27.2 um.)

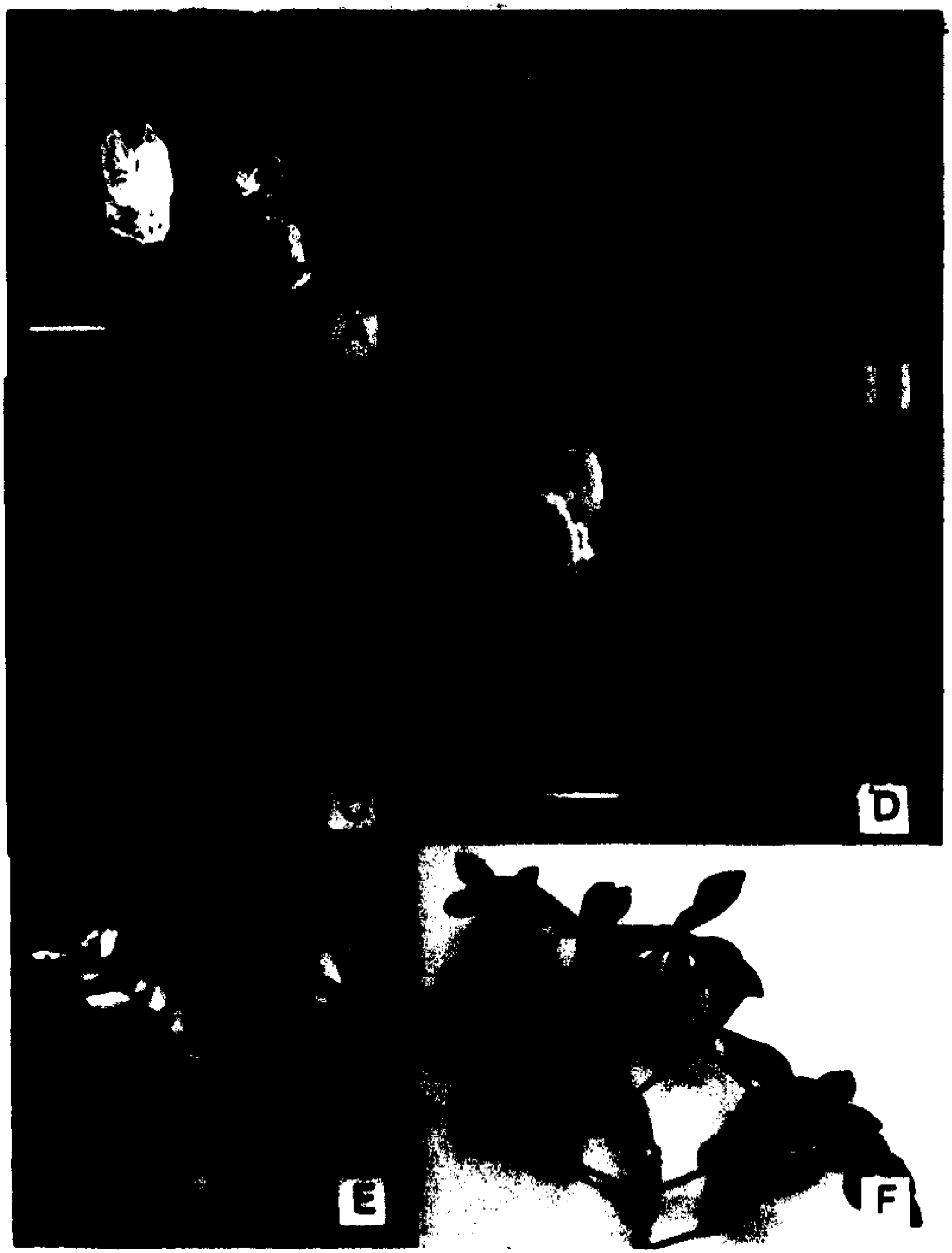
D
E
F

FIGURE 22. Phylogenetic relationships of subgenera of *Cybianthus*

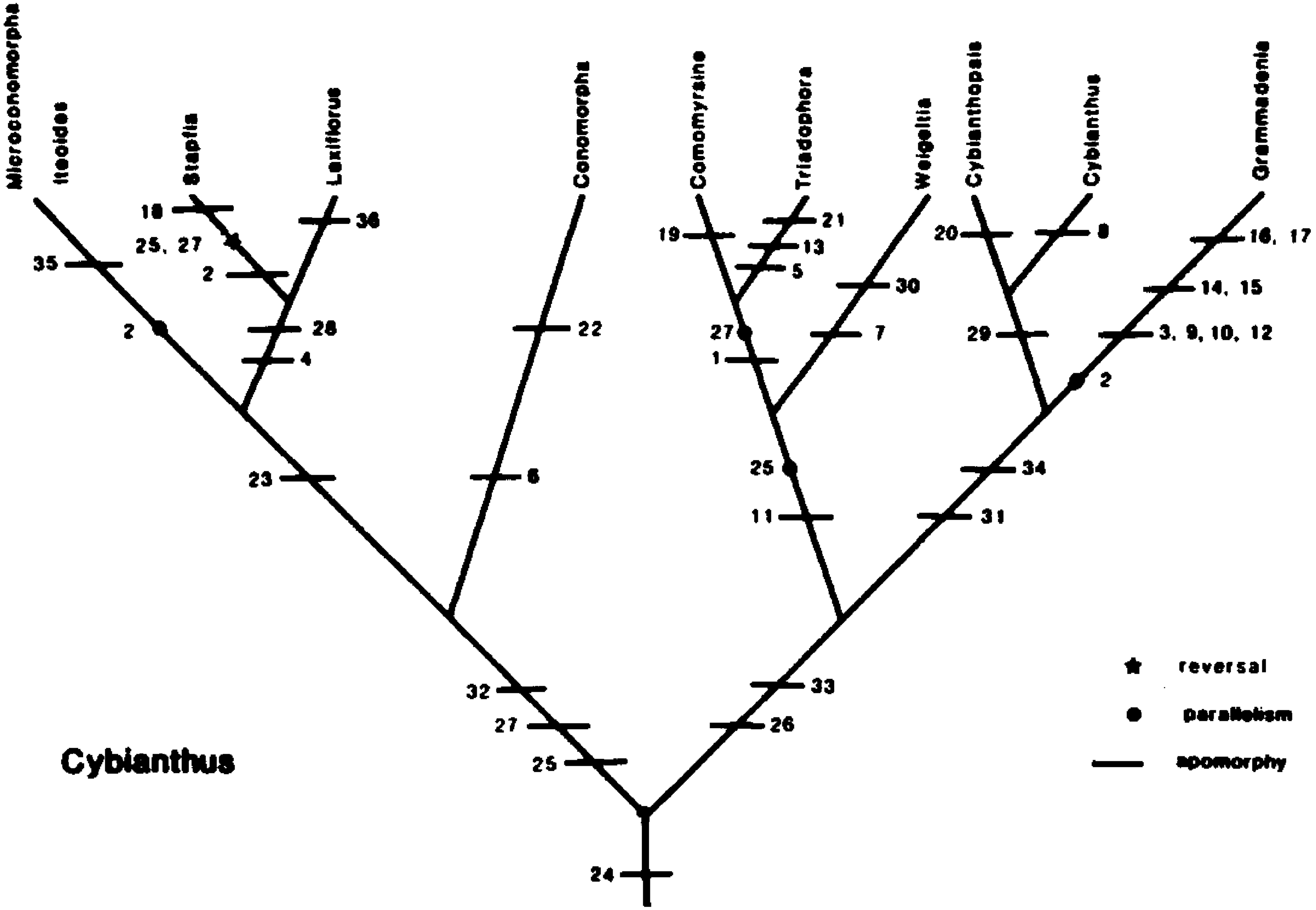
Micropconomorpha
Iteoides
Stapfia
Laxiflorus
Conomorpha
Comomyrsine
Triadophora
Weigeltia
Cybianthopsis
Cybianthus
Grammadenia
35
2
18
25, 27
2
28
4
36
23
22
6
19
21
13
5
27
1
30
7
25
11
20
8
29
16, 17
14, 15
3, 9, 10, 12
2
34
31
32
27
25
33
26
24
Cybianthus
reversal
parallelism
apomorphy

FIGURE 23. Phylogenetic relationships of species of subgenus *Grammadenia*

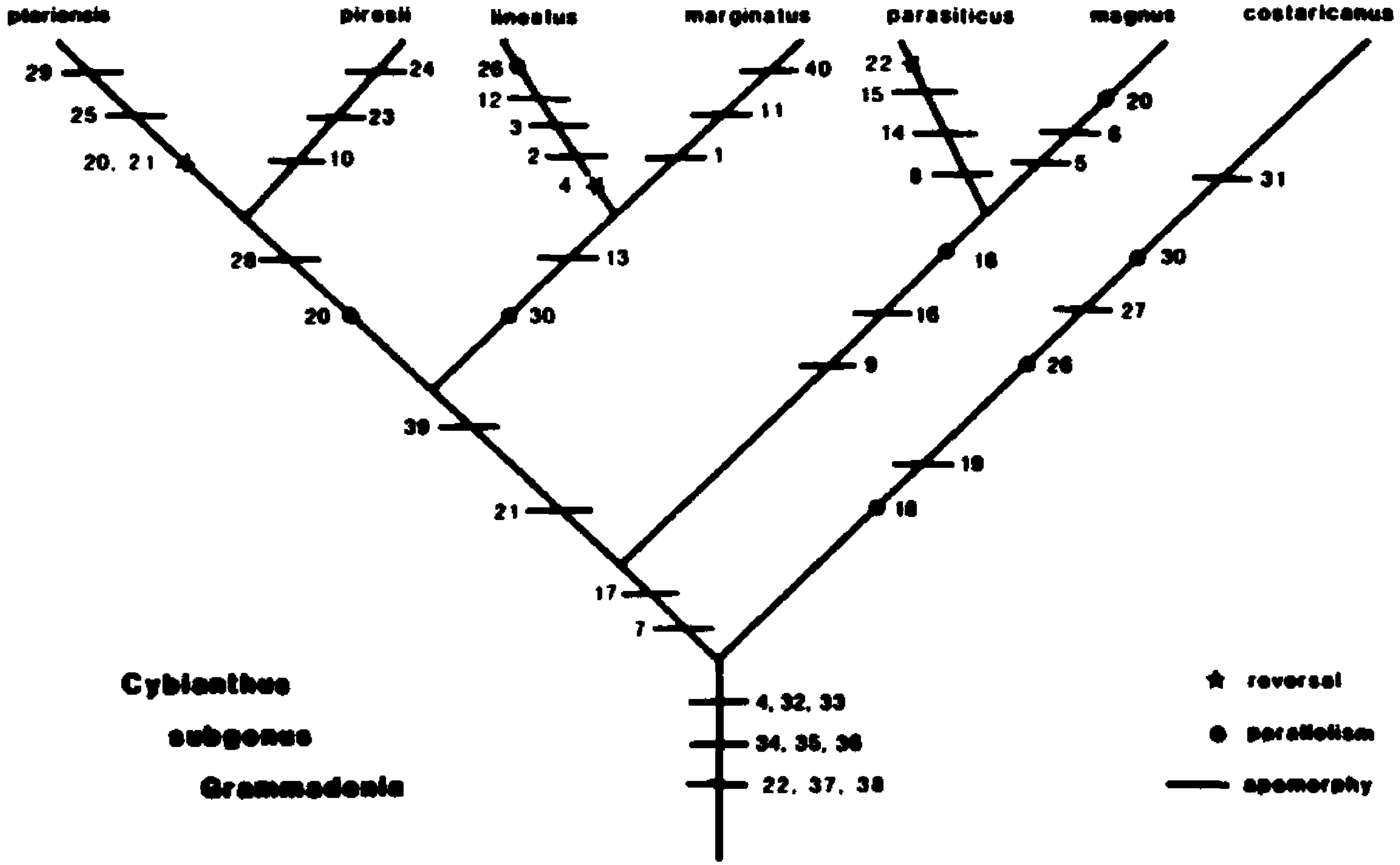
ptariensis
piresii
lineatus
marginatus
parasiticus
magnus
costaricanus
29
25
20, 21
24
23
10
28
20
26
12
3
2
4
40
11
1
13
30
39
21
17
7
22
15
14
8
20
6
5
18
16
9
31
30
27
26
19
18
4, 32, 33
34, 35, 36
22, 37, 38
Cybianthus
subgenus
Grammadenia
reversal
parallelism
apomorphy

FIGURE 24. Distribution of *C. costaricanus*.

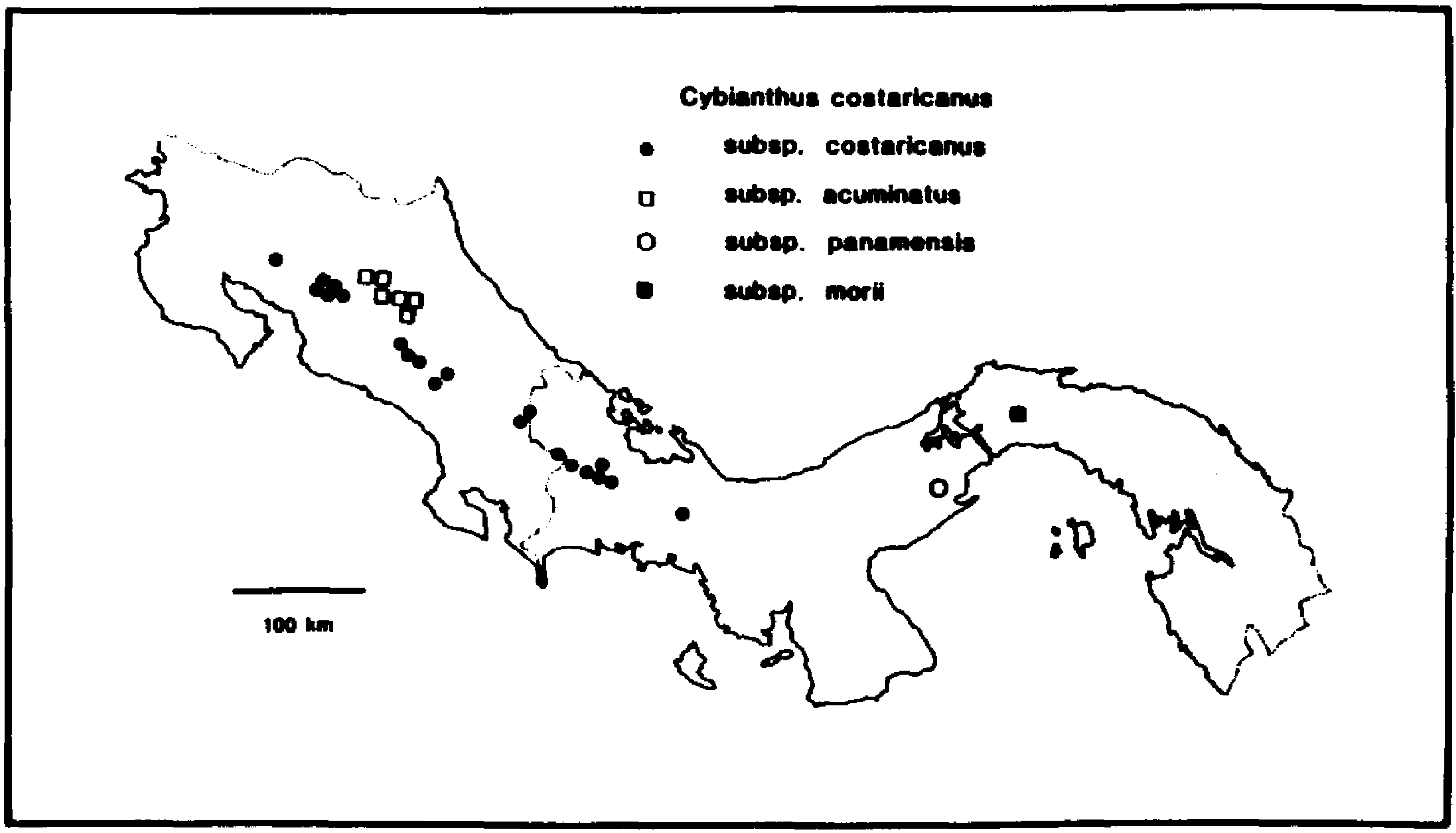
Cybianthus costaricanus
● subsp. costaricanus
□ subsp. acuminatus
○ subsp. panamensis
■ subsp. morii
100 km

FIGURE 25. Species of subg. *Grammadenia*

A. *C. costaricanus* subsp. *costaricanus* (*Pipoly 7073*), habit. B. *C. costaricanus* subsp. *morii* (*Pipoly* & *Bethancourt 7034*), habit. C-E. *C. magnus* subsp. *asymmetricus*. C. *Luteyn*, *Pipoly et al*. *10525*, bisexual plant in fruit. D. *Luteyn*, *Pipoly et al*. *10414*, pistillate inflorescence. E. *Luteyn*, *Pipoly et al*. *10533*, staminate inflorescence. F. *C. magnus* subsp. *magnus* (*Pipoly 6453*), habit, tree of 4 m height.

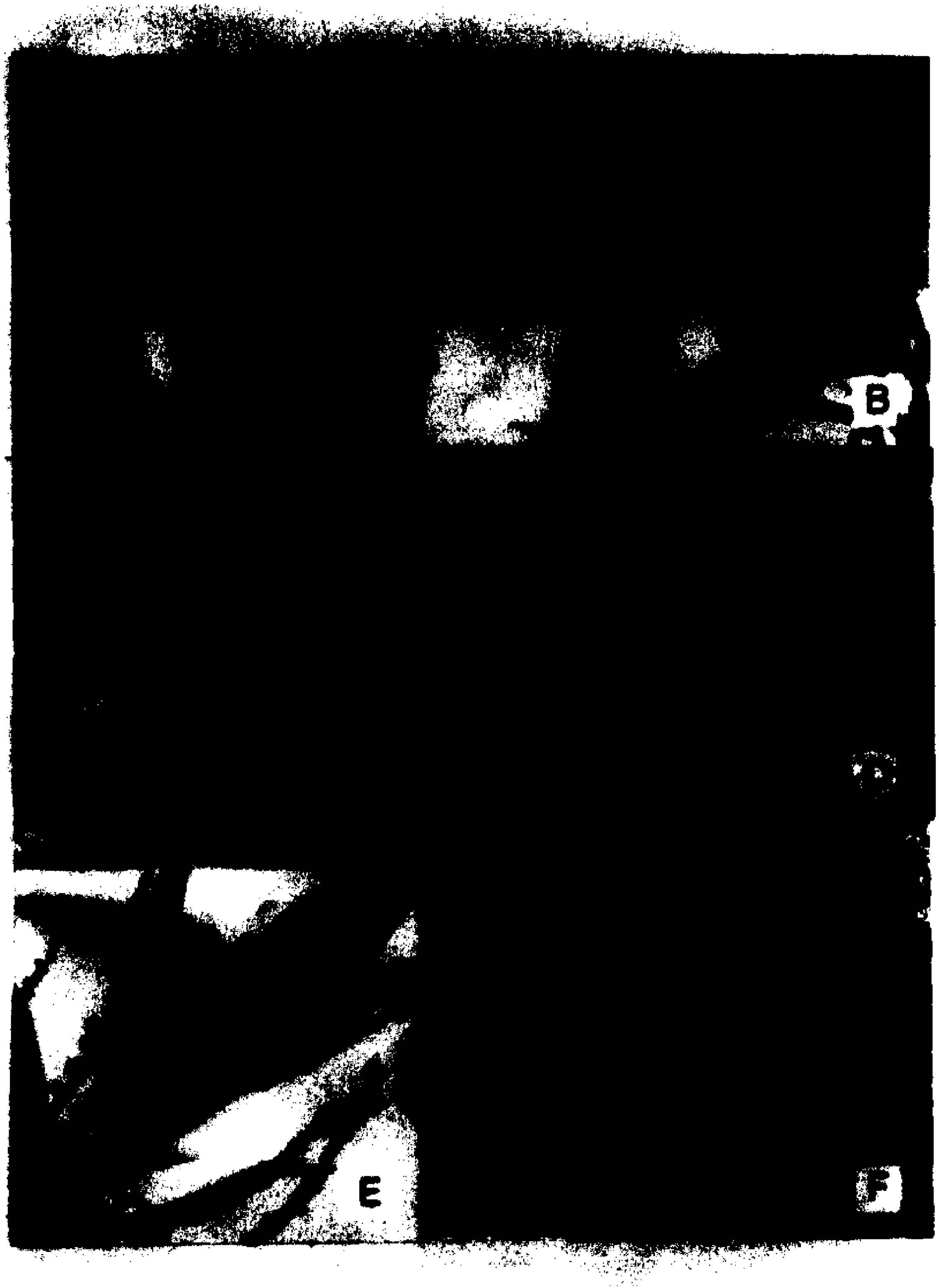
B
E
F

FIGURE 26. Distribution of species in subg. *Grammadenia*

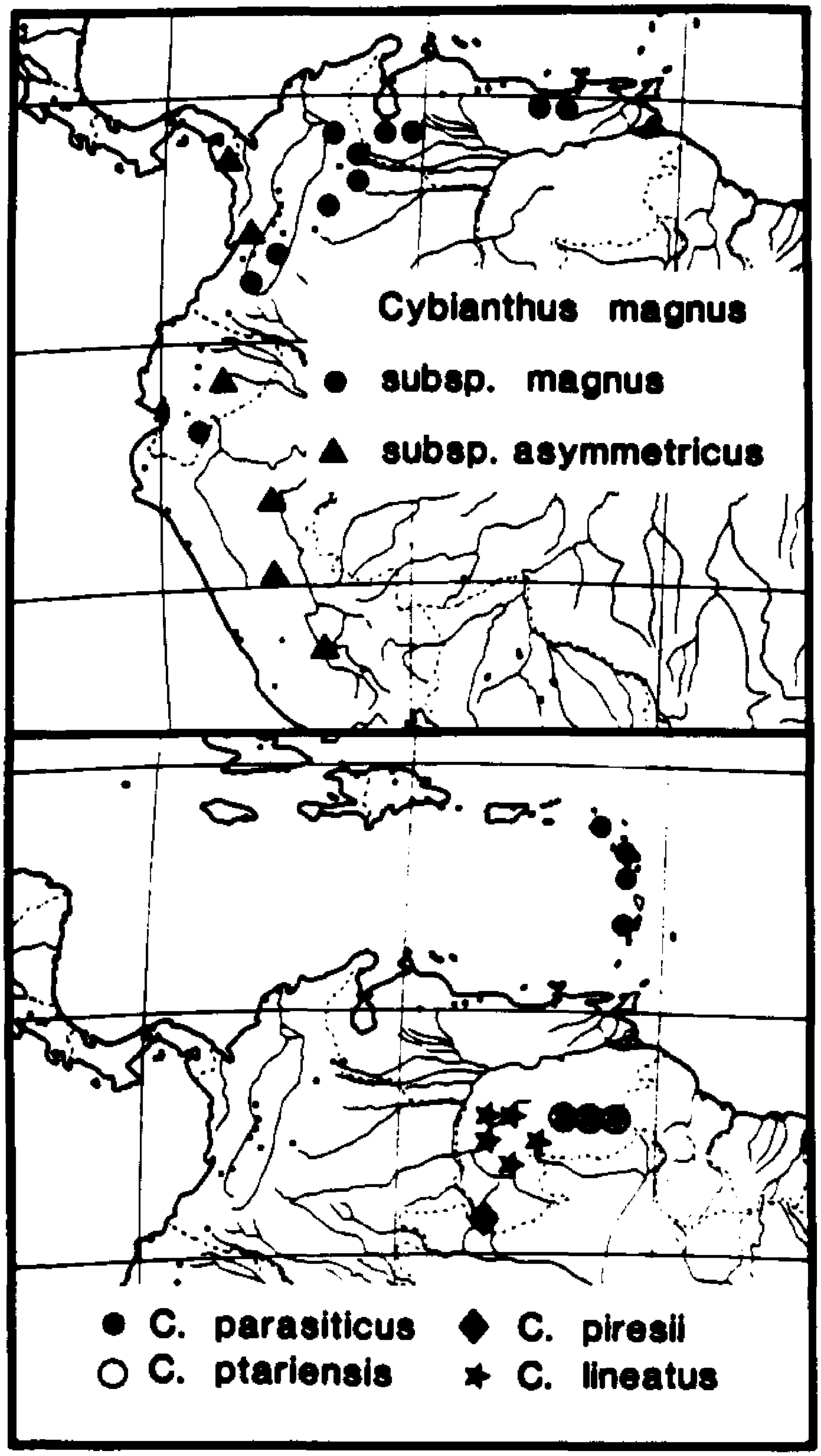
Cybianthus magnus
● subsp. magnus
▲ subsp. asymmetricus
● C. parasiticus
○ C. ptariensis
◆ C. piresii
✶ C. lineatus

FIGURE 27. Pictorialized distribution of C. marginatus.

Figs. A-K. Variation in leaf shape, marginal venation and punctation. Figs. drawn from: A. Cuatrecasas 21805, B. Pipoly 6954, C. Pipoly 6539, D. Liesner 8038, E. Luteyn 9302, F. Steyermark 100867, G. Mason 13730, H. Pipoly 6975, I. Pearce 250, J. Lehmann 599, K. Luteyn 10175.

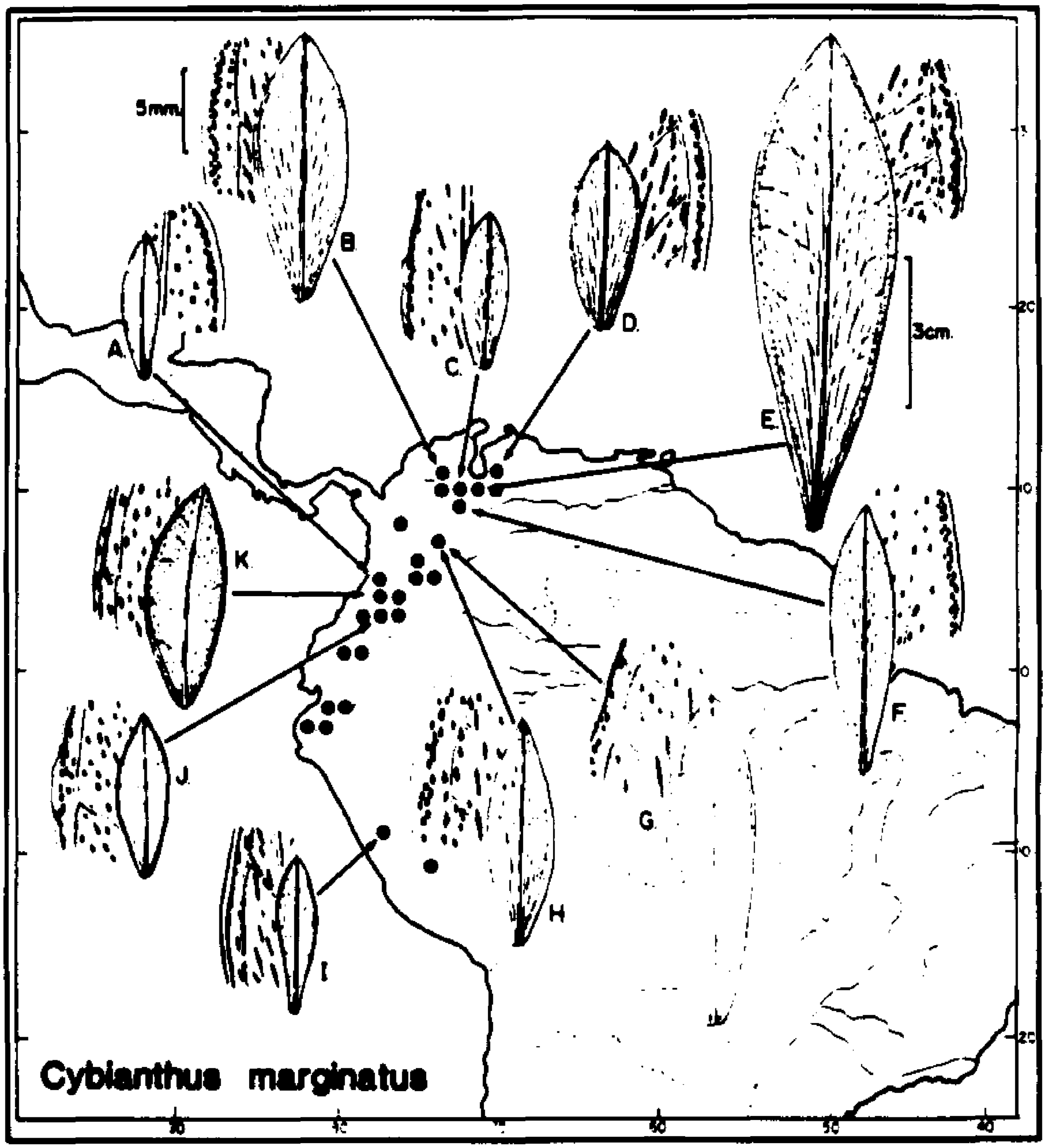
5mm
A
B
C
D
E
F
G
H
I
J
K
3cm
20
10
0
10
20
90
80
70
60
50
40
Cybianthus marginatus

FIGURE 28. Species of subg. *Grammadenia*

A. *C. ptariensis* (*Pipoly et al. 7279*), inflorescence. B. *C. ptariensis* (*Pipoly et al. 7273*, right side), growing with *C. lineatus* (*Pipoly et al. 7272*, left side). C. *C. ptariensis* (*Pipoly et al. 7133*), infructescence. D. *C. lineatus* (*Pipoly et al. 7274*), inflorescence.


B
D

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