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TAXONOMIC STUDIES IN THE
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(MELASTOMATACEAE)
IV. GENERIC REALIGNMENTS AMONG
TERMINAL-FLOWERED TAXA

Walter S. Judd and James D. Skee, Jr.

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TAXONOMIC STUDIES IN THE MICONIEAE (MELASTOMATACEAE). IV. GENERIC REALIGNMENTS AMONG TERMINAL-FLOWERED TAXA

Walter S. Judd¹ and James D. Skee, Jr.²

ABSTRACT

Rapid diversification and high levels of homoplasy have combined in *Miconia* and relatives to make generic delimitation extremely difficult. Historically, the morphologically divergent members of particular clades have been recognized as segregate genera, leaving a diverse and paraphyletic remnant within *Miconia*. Here the monophyly and cladistic relationships of the commonly recognized terminal-flowered genera of Miconieae are investigated, and a provisional generic classification is constructed. Recognized genera include: *Anaectocalyx*, *Calycogonium* (including *Mommsenia*, and a few species of *Clidemia* and *Ossaea*), *Clidemia* (including *Heterotrichum*, *Miconia* sect. *Octomeris* p.p., *Myrmidone*, and a few species of *Tococa*), *Conostegia*, *Leandra* (including *Platycentrum*, *Pleiochiton*, and several species of *Ossaea* and *Clidemia*), *Pachyanthus* (including *Miconia lundelliana*), *Tetrazygia* (including *Tetrazygiopsis* and several species of *Miconia*), *Tococa* (including *Microphysca*), and *Miconia* (including *Charianthus*, *Ossaea* sect. *Octopleura*, *Icaria*, and a few species of *Clidemia*). It is hypothesized that all of the above, except *Miconia*, represent monophyletic groups. Most species of *Miconia* likely are members of a single clade, but a few primitive members of this genus may belong to isolated clades, or clades whose derived species are placed in other genera, making *Miconia* paraphyletic. It may eventually be possible to realign and/or segregate some of these basal lineages within *Miconia*. However, at this time high homoplasy levels and lack of clear morphological gaps between basal members of the various lineages combine to make phylogenetic decisions very difficult. Although not fully phylogenetic, the proposed generic classification is considered an improvement of the present system, basically that of Cogniaux, in that the artificial and polyphyletic genera *Clidemia* sensu lato, *Calycogonium* sensu lato, *Ossaea*, and *Charianthus* are abandoned. The traditional maintenance of these genera has resulted from selected weighting of variable features such as petal shape, apex, and color, along with the confusion of terminal with axillary inflorescences. Nomenclatural changes have been avoided with the exception of *Calycogonium apleurum*, *C. lomensis*, *C. reticulatum*, *C. tetragonolobum*, *Clidemia angustilamina*, *Leandra alloeotricha*, *L. glomerata*, *L. hirsuta*, *L. inaequidens*, *L. krugiana*, *L. krugii*, *L. lima*, *L. limoides*, *L. pratensis*, *Miconia coccinea*, *M. corymbosa*, *M. leblondii*, *M. purpureus*, *M. fadyenii*, *M. neomicrantha*, and *Pachyanthus lundellianus*.

RESUMEN

Una diversificación rápida y altos niveles de homoplásia se han combinado en *Miconia* y sus relativos para hacer extremadamente difíciles las delimitaciones genéricas. Históricamente,

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los miembros de clades particulares morfológicamente divergentes han sido reconocidos como géneros segregados, dejando un remanente diverso y parafilético dentro de *Miconia*. En este trabajo se investigan la monofilía y relaciones cladísticas de los géneros de Miconieae con inflorescencia terminal comunmente reconocidos, y se construye una clasificación genérica provisional. Los generos reconocidos incluyen: *Anaectocalyx*, *Calycogonium* (incluyendo *Mommsenia*, y algunas especies de *Clidemia* y *Ossaea*), *Clidemia* (incluyendo *Heterotrichum*, *Miconia* sect. *Octomeris* p.p., *Myrmidone*, y algunas especies de *Tococa*), *Conostegia*, *Leandra* (incluyendo *Platycentrum*, *Pleiochiton*, y varias especies de *Ossaea* y *Clidemia*), *Pachyanthus* (incluyendo *Miconia lundelliana*), *Tetrazygia* (incluyendo *Tetrazygiopsis* y varias especies de *Miconia*), *Tococa* (incluyendo *Microphysca*), y *Miconia* (incluyendo *Charianthus*, *Ossaea* sect. *Octopleura*, *Icaria*, y algunas especies de *Clidemia*). Se hipotetiza que todos los géneros mencionados, excepto *Miconia*, representan grupos monofiléticos. La mayoría de las especies de *Miconia* son posiblemente miembros de un mismo clade, pero unos pocos miembros primitivos de este género pueden pertenecer a clades aislados, o a clades cuyas especies derivadas son colocadas en otros géneros, haciendo de *Miconia* un grupo parafilético. Eventualmente sería posible re-alinear y/o segregar algunos de éstos linajes basales dentro de *Miconia*. Sin embargo, al presente, los altos niveles de homoplástia así como la falta de diferencias morfológicas claras entre miembros basales de los varios linajes se combinan para hacer muy difíciles las decisiones filogenética, la clasificación genérica propuesta es considerada un mejoramiento del sistema actual, básicamente el de Cogniaux, en que los generos artificiales y polifiléticos *Clidemia* sensu lato, *Calycogonium* sensu lato, *Ossaea*, y *Charianthus* son abandonados. El mantenimiento tradicional de estos géneros ha resultado del sopesamiento selectivo de características variables como la forma, apéx y color del pétalo, junto a la confusión sobre inflorescencias terminales con axilares. Los cambios de nomenclatura han sido evitados con la excepción de *Calycogonium apleurum*, *C. lomensis*, *C. reticulatum*, *C. tetragonolobum*, *Clidemia angustilamina*, *Leandra alloeotricha*, *L. glomerata*, *L. hirsuta*, *L. inaequidens*, *L. krugiana*, *L. krugii*, *L. lima*, *L. limoides*, *L. pratensis*, *Miconia coccinea*, *M. corymbosa*, *M. leblondii*, *M. purpureus*, *M. fadyenii*, *M. neomicrantha*, y *Pachyanthus lundellianus*.

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INTRODUCTION

The Miconieae are a diverse group here considered to represent 20 neotropical genera, including ca 1800 species, of which ca 1000 are members of *Miconia* Ruiz Lopez and Pavón. The genera within the Miconieae are poorly characterized (Gleason 1932), are often difficult to discern, and are defined quite arbitrarily (Cogniaux 1891; Macbride 1941; Gleason 1958; Wurdack 1962, 1972; Judd 1986a, 1989). Intermediate species or species-groups are frequent, and many characters show reversals or parallelisms (Macbride 1941; Wurdack 1972, 1980; Judd 1986a, 1989). Most botanists working on this group have agreed with Cogniaux (1891) who stated that within the Miconieae "the delimitation of genera is rather arbitrary; one could easily distinguish more of them; at the same time one could justify the union of many of those which are generally recognized today" (p. 4, translated from the French). Macbride (1941: 250) echoed this view, stating that there is often nothing to be contributed by generic realignments within the tribe "because the lines of demarcation are arbitrary." The confusion regarding generic limits is easily seen in the complex keys to the genera of Miconieae in various tropical floras, e.g., León and Alain (1957), Standley and Williams (1963), and Wurdack (1973, 1980). This confusion has hindered both practical identification of these plants and an understanding of their evolutionary relationships.

The arbitrariness of some of the presently recognized genera of Miconieae is obvious (see Judd 1986a, 1986b, 1989) and it is not clear that the present system is often convenient, as claimed by Macbride (1941). Thus, a preliminary study of generic relationships within this complex group was conducted. The cladistic relationships among the axillary-flowered taxa were outlined in Judd (1989), where nine genera were recognized: *Henriettea* DC. (incl. *Henriettea* Naudin and *Llewelynina* Pittier), *Huilaea* Wurd., *Killipia* Gleason, *Kirkbridea* Wurd., *Loreya* DC. (incl. *Bellucia* Raf. and *Myriaspora* DC.), *Maieta* Aublet, *Mecranium* Hook. f. (incl. *Ekmaniocharis* Urban), *Pentossaea* Judd, and *Sagraea* DC. (incl. *Necranium* Britton). *Chalybea* Naudin is also axillary flowered, and is closely related to *Huilaea* (see discussion under *Pachyanthus*). The results of an investigation of cladistic relationships among the terminal-flowered taxa are presented below. Although preliminary, these results are considered to be an improvement of the present largely artificial generic circumscriptions, and it is hoped that the paper will generate further interest in the evolutionary relationships of these taxa.

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METHODS, CHARACTERS, OUTGROUP CONSIDERATIONS, AND POLARITIES

The cladistic analyses presented by Judd (1989) suggest that the terminal-flowered genera of Miconieae are either basal in the tribe (with the above listed axillary-flowered genera forming a monophyletic group) or form a monophyletic group along with *Killipia*, *Maieta*, *Mecranium*, *Pentossaea*, and *Sagraea*, with *Huillaea* being cladistically basal. The first hypothesis supports the use of the Merianieae as a generalized outgroup as was done in the analyses in Judd (1989), while the second possibility supports the use of *Huillaea* as an outgroup. The use of either outgroup (following the approach of Cantino 1982) would suggest that an ancestral species should possess cymose inflorescences of moderate-sized, pedicellate, \pm 5-merous flowers (borne on leafy shoots), having a nonribbed and \pm nonconstricted hypanthium, short and persistent external calyx teeth, \pm short internal calyx lobes not forming a stout conical cap, glabrous petals with \pm blunt apices, stamens twice the number of petals with ovoid/elongated and at least slightly curved anthers that open by one minute apical pore, glabrous styles, and baccate fruits (the last a synapomorphy of the tribe Miconieae) with nonappendaged seeds. It is likely that the anthers would be unappendaged or nearly so, because *Huillaea* essentially lacks anther appendages, and the appendages common in the Merianieae, which typically form a sharp projection at the anther-filament junction, are likely not homologous with those of the Miconieae, which are different in form and involve various dorsal and/or basal thickenings of the connective. Ancestral vegetative characters include opposite leaves that lack fornicaria and lack numerous fine tertiary veins.

Species possessing the above suite of characters are found only in certain groups within *Miconia*. It is thus possible that sister-taxa to the various segregate genera, e.g., *Tococa* Aublet, *Leandra* Raddi, *Clidemia* D. Don, *Pachyanthus* A. Rich., *Tetrazygia* Rich. ex DC., etc., may occur among the primitive species of *Miconia*. (It is noteworthy that no synapomorphy could be found that unites all species of *Miconia*, which does not also characterize at least some associated genera. In contrast, the species of the variously

recognized segregate genera contain from few to numerous apomorphic features, making it unlikely that any of these genera contain species that are basal members of clades leading to other genera.) *Miconia* species possessing the ancestral suite of characters listed above are concentrated in sections *Octomeris* Triana, *Laceraria* Naudin, and *Jucunda* (Cham.) Naudin, and include *M. schlimii* Triana, *M. nitidissima* Cogn., *M. reducens* Triana, *M. mexicana* (Humb. and Bonpl.) Naudin, and *M. humilis* Cogn. Thus, an element within *Miconia* is considered to represent the primitive complex within terminal-flowered Miconieae, and is occasionally employed in the determination of character polarity, in addition to *Huilaea* and the Merianieae.

Sixty-seven characters were investigated and assigned plesiomorphic (or ancestral) and apomorphic (or derived) states. Characters were polarized using both the Merianieae and *Huilaea* as outgroups (see Judd 1989, and discussion above). Certain species of *Miconia*, i.e., those possessing the ancestral suite of characters listed above, were also used as a functional outgroup in assessing polarity of some characters. Character states uniformly found (or most commonly represented) in the outgroups were considered plesiomorphic (Stevens 1980; Wiley 1981; Maddison et al. 1984; Frolich 1987). Apomorphic characters are listed below.

1. Plants herbaceous; plesiomorphic condition: plants woody (shrubs, trees, lianas). This character is an autapomorphy of *Catocoryne* Hook. f., a distinctive genus of uncertain taxonomic placement.

2. Plants epiphytic (with coriaceous leaves); plesiomorphic condition: plants terrestrial (with leaves membranous to coriaceous). The liana habit of some species also is considered to be derived.

3. Shoots indeterminate and inflorescences in leaf axils; plesiomorphic condition: shoots determinate and inflorescences terminal.

4. Shoots usually producing only a single node bearing leaves prior to initiation of terminal cyme; plesiomorphic condition: shoots producing several nodes bearing leaves prior to conversion of apical meristem into an inflorescence. Most taxa showing this condition develop pseudolateral inflorescences; however, some obviously terminal-flowered groups, e.g., *Calycogonium* DC., also have this feature.

5. Elongate multicellular hairs absent; plesiomorphic condition: elongate multicellular hairs present. There is some doubt concerning the polarity of this feature because these hairs are lacking in most of the likely cladistically basal species of *Miconia* (as determined above). However, the presence of a densely strigose indumentum is uncommon in the outgroups and may be apomorphic.

6. Multicellular hairs stellate (with short to elongate arms) on the lower leaf surface and stem, or hairs clearly derived from the stellate condition, i.e., peltate scales; plesiomorphic condition: multicellular hairs various, but not as above. There is some doubt concerning this polarity decision, because stellate hairs occur in some cladistically basal *Miconia* species, e.g., *M. schlimii*.

7. Plants densely covered with stiff, elongate, multicellular hairs, i.e., densely strigose; plesiomorphic condition: plants lacking elongate multicellular hairs or only \pm sparsely strigose. Continuous variation in the density of such hairs in some groups makes this feature difficult to apply.

8. Stellate hairs on abaxial leaf surface with elongate, crisped arms, the indumentum thus appearing cob-webby; plesiomorphic condition: indumentum not stellate, or if so, then hairs not as above.

9. Elongate multicellular hairs of stems and leaves with a minutely to strikingly roughened surface (due to projections of individual cells); plesiomorphic condition: elongate multicellular hairs \pm smooth.

10. Peltate scales; plesiomorphic condition: indumentum various but not of peltate scales. Such scales likely evolved through modifications of stellate hairs.

11. Indumentum composed of only minute glandular hairs; plesiomorphic condition: indumentum variable, but not as above.

12. Leaves clearly anisophyllous; plesiomorphic condition: leaves isophyllous or nearly so.

13. Leaves with pouchlike formicaria at base of blade; plesiomorphic condition: leaves lacking formicaria.

14. Leaves with bilobed formicaria at base of petiole; plesiomorphic condition: leaves lacking formicaria.

15. Leaves with conspicuous mite-domatia at junctions of the midvein with the two largest secondary veins, which are formed by a dense tuft of elongate, often connate, multicellular hairs; plesiomorphic condition: mite-domatia lacking or not formed as above.

16. Leaves small, narrowly elliptic to linear, strongly coriaceous, and \pm revolute; plesiomorphic condition: leaves various but without the above combination of characters.

17. Leaves densely white to ferruginous, stellate-pubescent on abaxial surface; plesiomorphic condition: leaves glabrous to densely pubescent, but not as above.

18. Inflorescences pseudolateral; plesiomorphic condition: inflorescences clearly terminal.

19. Inflorescences borne on shoots on which the leaves have already fallen; plesiomorphic condition: inflorescences produced on leafy shoots.

20. Inflorescences reduced to 1 (or very few) flowers; plesiomorphic condition: inflorescences several to many-flowered. Polarity is questionable due to variation in outgroups, but several-flowered cymes are considered ancestral because such inflorescences occur in basal species of *Miconia*.

21. Inflorescences with flattened axes; plesiomorphic condition: inflorescences with terete to ridged axes.

22. Inflorescences spicate; plesiomorphic condition: inflorescences not spicate.

23. Inflorescences fasciculate or capitate; plesiomorphic condition: inflorescences cymose.

24. Inflorescences with unilateral cymose branches; plesiomorphic condition: lateral inflorescence branches not unilateral cymes.

25. Inflorescence bracts expanded and persistent; plesiomorphic condition: inflorescence bracts \pm inconspicuous and often deciduous. Large, but deciduous, bracts are also considered derived.

26. Flowers \pm sessile; plesiomorphic condition: flowers pedicellate.

27. Flowers 4-merous; plesiomorphic condition: flowers 5-merous (or not as above).

28. Flower parts greater than five; plesiomorphic condition: flowers 5-merous (or not as above).

29. Hypanthium strongly ribbed; plesiomorphic condition: hypanthium nonribbed.

30. Hypanthium/calyx clearly constricted above the ovary; plesiomorphic condition: hypanthium \pm not constricted.

31. Hypanthium quadrangular; plesiomorphic condition: hypanthium \pm terete.

32. Hypanthium winged; plesiomorphic condition: hypanthium not winged. Other aspects of hypanthium shape (and length) have not been included in this analysis, although they are quite variable within several genera and may prove useful in discerning species relationships (especially in *Miconia* and *Tetrazygia*).

33. Hypanthium covered with stout, very thick-based, elongate, multicellular hairs (and such hairs often on leaves, inflorescence axes, and stems as well); plesiomorphic condition: hypanthium lacking elongate hairs, or, if present, then not as above.

34. Open calyx dehiscent as a unit by a circumscissile slit; plesiomorphic condition: calyx dehiscent by some other means.

35. External calyx lobes \pm conspicuous and well developed; plesiomorphic condition: external calyx lobes inconspicuous. Variation in this feature is essentially continuous and, thus, is difficult to delimit into nonarbitrary states (see Almeida and Bisby 1984). Hence value of character is quite limited.

36. External calyx lobes absent; plesiomorphic condition: external calyx lobes present.

37. External calyx lobes flattened parallel to the floral radii; plesiomorphic condition: external calyx lobes \pm terete (or not as above).

38. External calyx lobes flattened perpendicular to the floral radii; plesiomorphic condition: external calyx lobes \pm terete (or not as above).

39. Internal calyx lobes very elongate and deciduous; plesiomorphic condition: internal calyx lobes short and persistent.

40. Internal calyx lobes connate into a stout, conical, circumscissily dehiscent cap; plesiomorphic condition: internal calyx lobes free. Several species of *Tetrazygia*, *Miconia*, and *Tococa* have internal calyx lobes fused into

a minute, membranous, dome-shaped cap which ruptures \pm irregularly; this condition is difficult to observe in dried material and may be more widespread in the tribe than is realized; it is not considered to be homologous with the stout, conical cap present in the flowers of *Conostegia* D. Don.

41. Petals narrowly ovate to triangular and acute to acuminate at apex; plesiomorphic condition: petals ovate to obovate with \pm blunt apices. There is some doubt concerning polarity here, because a few outgroup taxa have slightly acuminate petals, in any case, it is likely that narrowly triangular petals with acute apices are apomorphic. The basal species within *Miconia* have petals with blunt apices.

42. Petals red, showy, erect, and connivent; plesiomorphic condition: petals various, but without the above character combination.

43. Petals pubescent; plesiomorphic condition: petals glabrous.

44. Petals with a dorso-apical hair (or cluster of hairs); plesiomorphic condition: petals lacking dorso-apical hair.

45. Androecium actinomorphic, i.e., stamens arranged in a circle around the gynoecium; plesiomorphic condition: androecium zygomorphic, i.e., stamens deflexed to one side of flower. Androecium reduced in staminate flowers (in dioecious species); see Howard (1989).

46. Anthers numerous, i.e., more than twice the number of petals; plesiomorphic condition: stamens twice the number of petals. This feature may be correlated with an increased number of carpels (see *Conostegia*). Anther numbers equalling the number of petals are also considered apomorphic.

47. Anther sacs basally bifurcate, i.e., sagittate; plesiomorphic condition: anther sacs not bifurcate.

48. Anthers short, \pm straight; plesiomorphic condition: anthers elongate, curved.

49. Anthers obovate; plesiomorphic condition: anthers ovate or narrowly ovate.

50. Anthers oblong; plesiomorphic condition: anthers ovate or narrowly ovate.

51. Anthers opening by longitudinal slits; plesiomorphic condition: anthers with a small apical pore.

52. Anthers opening by an expanded apical pore, often with a protruding septum; plesiomorphic condition: anthers opening by a small apical pore. (The condition of the anthers opening by two small pores may also be derived.)

53. Anther with variously developed basal appendage composed of sterile portion of anther sacs and connective tissue; plesiomorphic condition: anthers not appendaged, without sterilization of a portion of anther sacs. Anther appendages likely function as landing platforms for floral visitors in species with zygomorphic flowers (S. Renner, pers. comm.). Anther appendages occur in diverse groups of melastomes and probably evolved several times.

54. Anther with conspicuous dorso-basal appendage or tooth derived from connective; plesiomorphic condition: anther not appendaged.

55. Anther with a \pm prominent dorsally thickened connective; plesiomorphic condition: anther connective not prominently thickened. More or less continuous variation within some groups, e.g., *Leandra*, make application of this character very difficult.

56. Anther bearing gland-headed or globular hairs on connective; plesiomorphic condition: anther glabrous. The filament may be pubescent as well (also considered to be apomorphic).

57. Anthers white; plesiomorphic condition: anthers non-white, especially yellow, pink, or purple. Problems in the scoring of this character occur due to the difficulty of assessing color of living plants in herbarium material.

58. Style strongly curved distally with minute, non-expanded stigma; plesiomorphic condition: style straight to slightly curved and stigma slightly to clearly expanded.

59. Style with multicellular, gland-headed hairs or stellate-branched hairs; plesiomorphic condition: style glabrous. Some taxa have a conspicuous apical fringe of hairs (around the base of style); this is considered to be a separate condition, is likely apomorphic, and occurs sporadically in the tribe.

60. Ovary strongly four-lobed (with the lobes separated by longitudinal grooves); plesiomorphic condition: ovary \pm terete. (The number of ovary locules is quite variable in the tribe, even varying within a species or closely related group of species, and frequently differs from number of petals and calyx lobes. Locule number was not used in generic delimitation, but a survey of its variation would be of interest.)

61. Fruit a berry; plesiomorphic condition: fruit a capsule. This likely is a synapomorphy of the species of the Miconieae (see Cogniaux 1891), although berries are also present in the Blakeeae, Dissochaeteae, and Melastomeae. Capsular fruited taxa have a superior ovary, while in baccate taxa the ovary is usually at least partly inferior.

62. Fruit \pm robust; plesiomorphic condition: fruits small to moderate-sized. Continuously varying characters such as this are difficult to delimit into nonarbitrary states (see Almeida and Bisby 1984). This character is somewhat arbitrarily applied as an autapomorphy of *Pachyanthus*, where it is correlated with the presence of a persistent, coriaceous hypanthium/calyx.

63. Seeds with appendage composed of enlarged cells; plesiomorphic condition: seeds \pm not appendaged. This character (and no. 64) were observed under the light/dissecting microscope; in addition, several seeds were prepared for scanning electron microscope (SEM) observation (see Figs. 8-10). In preparation for examination by SEM, seeds were removed from dried herbarium material, attached to stubs with quick-mounts, plated with gold in a Ladd 8-30800 ion coater for two minutes at 20mA, and examined and photographed using a JEOL JSM-T200 scanning electron microscope.

Ladd 8-30800 ion coater for two minutes at 20mA, and examined and photographed using a JEOL JSM-T200 scanning electron microscope.

64. Seed moderately to strongly papillose; plesiomorphic condition: testa smooth or only slightly roughened/papillose. This feature is difficult to apply due to continuous variation within the tribe; state delimitations are \pm arbitrary (Almeida and Bisby 1984). Testa surface was examined at both the light microscope and SEM levels.

65. Wood with oblong intervacular and vessel-ray pits, and two to three seriate rays; plesiomorphic condition: wood with polygonal to round intervacular pits, uniseriate and multiseriate rays (Welle and Koek-Noorman 1981). Unfortunately, variation within this character (and the following) is difficult to evaluate because very few species within each genus have been surveyed for anatomical variation.

66. Wood with abundant (mainly apotracheal) parenchyma in tangential bands, two to six cells wide; plesiomorphic condition: wood with bands of pseudoparenchyma consisting of fibers and parenchyma strands, or fibers only (Welle and Koek-Noorman 1981).

67. Chromosome number of $n = 25$ or 30 ; plesiomorphic condition: $n = 17$ or multiples thereof (Solt and Wurdack 1980). A few species of *Clidemia* also show $n = 23$; this unusual condition is likely also derived. Polyploidy is frequent in the tribe.

The present taxonomic study is based on a survey of ca 1350 herbarium specimens representing ca 560 species (see Appendix), and supplemented, where possible, by the addition of information from published taxonomic studies. Several species were also studied during the course of field work in the Greater Antilles and southern Florida.

The present knowledge of synapomorphic patterns within this large tribe is considered sufficient to make a preliminary attempt at circumscription of monophyletic genera. However, the cladistic relationships of these genera appear to be obscured by extensive homoplasy, and generic delimitation is difficult due to the lack of clear morphological gaps between basal members of the various recognizable lineages. The large size of the tribe also creates practical difficulties (and the numerous South American species are especially in need of further study). In addition, some quantitative characters present difficulties in state-delimitation. Thus, a detailed cladistic analysis of terminal-flowered Miconieae has not been attempted. Instead, each of the tribe's commonly recognized genera is discussed below, with special attention paid to the question of whether or not the genus can be hypothesized to be monophyletic. *Catocoryne* Hook. f., a very poorly known, monotypic, South American genus of creeping, slender-stemmed herbs with minute leaves (2-5 mm long and wide), terminal, solitary, 5-merous flowers, and berry fruits (Cogniaux 1891; Macbride 1941; Wurdack 1970), is not included in this study. Its taxonomic placement is problematic. The relationships of each genus to various groups within *Miconia* are also considered. It is hoped that the present

RESULTS AND DISCUSSION

Although not fully phylogenetic, the tentative generic classification proposed below is considered to be an improvement over those presently in use because polyphyletic genera such as *Clidemia* sensu lato, *Ossaea* DC., and *Charianthus* D. Don are abandoned, and the paraphyly of *Miconia* is at least reduced by suggesting that several of its species be transferred to various segregate genera. Table 1 presents the apomorphic characters possessed by each of the recognized genera. Species examined as representatives of each recognized genus are listed in the Appendix, as are generic descriptions (for those groups whose circumscription has been significantly altered as a result of this investigation).

A brief discussion of the circumscription and phylogenetic relationships of included species for each terminal-flowered genus of Miconieae is presented below. Genera are listed in alphabetical order, except for the large and complex groups, *Leandra* and *Miconia*, which are discussed last.

Anaectocalyx Triana

This obscure South American genus of three species (Wurdack 1973, fig. 55) is likely monophyletic. Important synapomorphies include: 6-merous flowers with a calyx composed of prominent, individually caducous, narrowly triangular or oblong lobes, which are five to 15 mm long; a lack of external calyx lobes; anthers with thecae and part of the connective bilobed and prolonged ventrally below the insertion of the filament; inflorescences of six to eight conspicuously bracted flowers clustered in a head or paniculate cyme; and a densely strigose indumentum of multicellular elongate hairs (on stems, leaves, and hypanthia). This genus is clearly placed in the Miconieae by its baccate fruits, but its exact position is uncertain. Its anthers have been compared to those of *Maieta* (Wurdack 1973); however, their resemblance is only superficial. The two genera differ in many other features, and *Maieta* possesses axillary inflorescences, indicating its relationship with genera such as *Sagraea*, *Mecranium*, and *Pentossaea* (see Judd 1989). Because the group is phenetically distinctive and monophyletic, and is not clearly linked to species in other recognized genera, its generic status is considered justified.

Calycogonium DC.

This distinctive, and likely monophyletic, genus of ca 30 species (Moscoso 1943; León and Alain 1957; Proctor *in* Adams 1972) is limited to the Greater Antilles and may be circumscribed by its 4-merous flowers and architectural growth pattern, in which shoots produce only a single node (or sometimes two) before forming a terminal inflorescence (Fig. 1C; Fawcett and Rendle 1926, fig. 138). Few-flowered cymes occur in most species. In addition, the group may be united by the presence of stellate hairs, although the polarity of this feature is unclear.

The species of this group may be members of three clades. The largest contains those species with leaves in which \pm conspicuous domatia are located in the axil of the midvein and the two largest secondary veins--a probable synapomorphy (Fig 1 A,B). The domatia are formed by a dense tuft of elongate multicellular hairs, and are likely inhabited by mites. Cladistically basal species in this clade probably include *C. domatiatum* Urban and E. Ekman, *C. turbinatum* Urban and E. Ekman, and *C. impressum* Urban and E. Ekman. More specialized species in the group possess the additional synapomorphies of reduced stellate hairs and domatia in which the hairs tend to be \pm connate, forming a brownish conical structure (Fig. 1 A). Species showing these features include: *C. glabratum* (Sw.) DC., *C. rhamnoides* Naudin, *C. microphyllum* C. Wright in Sauvalle, *C. rhomboideum* Urban and E. Ekman, *C. ekmanii* Urban, and *C. torbecianum* Urban and E. Ekman. Within this complex a shift from terete (plesiomorphic) to four-angled (apomorphic) hypanthia occurs, with *C. lindenianum* Naudin and *C. grisebachii* Triana showing this synapomorphy. The latter species possesses the distinctive apomorphies of abaxially densely stellate-pubescent leaves and the loss of mite-domatia. Some members of this domatia-containing clade have scattered multicellular strigose hairs on their leaves (and sometimes also hypanthia, e.g., *C. domatiatum*); this condition is possibly plesiomorphic. The external calyx lobes of members of this group are terete or flattened perpendicular (occasionally parallel) to the floral radii; elongate external calyx lobes (an apomorphy) have evolved in some species. The inflorescence sometimes is reduced to a solitary flower. Petal shape and apex are quite diverse, varying from rounded to acute/acuminate, and anthers lack any appendages or unusual development of connective tissue.

A second *Calycogonium* clade can be defined on the basis of hypanthia and ovaries with four conspicuous lobes separated by longitudinal grooves, and external calyx lobes that are flattened parallel to the floral radii (Fig 1 G,H). Hypothesized basal members of this clade, traditionally placed in *Clidemia*, have thin, delicate inflorescence axes, e.g., *C. tetragonoloba* Cogn., *C. pterosepala* (Urban) Alain, and *C. wrightii* Griseb. These species have conspicuous stellate hairs and petals with blunt apices. The remaining

members of this clade show very reduced inflorescences in which the flower clusters are sessile or nearly so (a potential synapomorphy). Most members of the group have consistently terminal inflorescences, e.g., *Calycogonium calycopteris* (Rich.) Urban, *C. hispidulum* Cogn., and *C. heterophyllum* Naudin, but a few have both terminal and axillary inflorescences, e.g., *Ossaea lomensis* Urban and *Ossaea reticulata* (Cogn.) E. Ekman ex Urban. Petal apex varies from \pm blunt to acute in the \pm sessile-inflorescenced species. A few species, such as *Calycogonium hispidulum* and *Clidemia tetragonoloba*, possess elongate multicellular hairs, although these are not conspicuous. The anthers may be unappendaged or possess a slight to moderate dorso-basal thickening on the connective; see especially *Clidemia tetragonoloba*.

A third small group may be defined by the presence of distinctive small, coriaceous, \pm revolute leaves that are densely ferruginous and stellate-pubescent on the abaxial surface. In *Calycogonium rosmarinifolium* Griseb. the hairs are stellate, while in *Mommsenia apleura* Urban and E. Ekman (Urban 1926) the hairs are peltate scales (possibly evolved from fusion of radiate arms of a stellate ancestral condition).

All of the above groups were treated by Cogniaux (1891) within *Calycogonium* sect. *Calycogonium*, which is likely monophyletic (as outlined above). However, the affinities of Cogniaux's (1891) remaining sections of this genus actually lie elsewhere. The species of section *Calycogoniopsis* Cogn. probably are related to a group of Caribbean species of *Ossaea* (see discussion under *Ossaea* and *Leandra*; León and Alain 1957; and Judd 1986a) as evidenced by their lack of stellate hairs, hypanthia with dense, stout, elongate, multicellular hairs, acute petals, and lack of either conspicuous mite-domatia or four-lobed ovaries. (Some of these species possess solitary flowers or few-flowered inflorescences.) Section *Krugiophytum* Cogn., i.e., *C. krugii* Cogn., has a very similar indumentum and solitary flowers, and probably is related to these terminal-flowered West Indian species of *Ossaea* with hypanthia and fruits (and often the leaves as well) possessing strikingly thickened, strigose multicellular hairs. Cladistically, these species of *Ossaea* are placed within *Leandra*. *Calycogonium squamulosum* Cogn., placed in section *Calycogonium* by Cogniaux (1891), is actually a species of *Henriettea*, being linked by the following synapomorphies: plants with Rauh's architectural model (i.e., inflorescences axillary), presence of megastyloids in leaf and stem tissues, and petals with an external tooth (see Judd 1986b, 1989). Finally, section *Pseudocalycogonium* Cogn. (Cogniaux 1891), i.e., *C. obliquum* (Griseb.) Cogn., is actually a species of *Miconia* as was noted by Alain (León and Alain 1957), and it is a synonym of *M. obtusa* (Griseb.) Triana (see discussion under *Tetrazygia*).

The affinities of *Calycogonium* are obscure. It is possibly related to *Miconia*, and is separable by the combination of 4-merous flowers, either solitary or few-flowered cymes, often well developed (or at least conspicuous) external calyx lobes, distinctive architecture, and anthers opening by a small

apical pore, usually without any elaboration of the connective tissue (see also Judd 1986a). Its seeds are \pm smooth (see Fig. 8 A).

Charianthus D. Don

This Antillean genus of five species (Howard 1989), as circumscribed by Cogniaux (1891), is composed of two very different sections. Section *Charianthus* has \pm ovate anthers that open by two long slits; 4-loculate ovaries, scattered druse crystals, multicellular peltate scales (having cells in a radiate pattern), strigose hairs (in a few species, e.g., *C. purpureus* D. Don), and a calyx not or only slightly constricted in fruit. In contrast, section *Eccharianthus* Cogn. has \pm oblong anthers opening by a single apical pore and with an appendaged base (due to development of connective), 2-locular ovaries, dense druse crystals, globular-branched multicellular hairs (which may be elongated in mite-domatia), no strigose hairs, and a calyx clearly constricted in fruit. The two sections traditionally are united on the basis of their flowers with showy erect, usually reddish, and connivent petals (Fawcett and Rendle 1926, fig. 135)--clear adaptations for bird pollination (Renner 1989). The flowers are usually disposed in broadly spreading, \pm flat-topped cymes.

The genus is surely polyphyletic, being derived from two different species-groups within *Miconia*. The species of section *Charianthus* likely are linked to some species of *Miconia* section *Chaenantha* Naudin (or section *Chaenopleura* (DC.) Triana) on the basis of anther dehiscence by two longitudinal slits (a synapomorphy). Clearly, a species like *Miconia melanotricha* (Triana) Gleason, which has similar inflorescences, and bright red petals with exposed stamens, yet 5-merous flowers with 3-locular ovaries, is a member of the lineage within *Miconia* that gave rise to *Charianthus* sect. *Charianthus*. This species was placed by Gleason (1958) in section *Chaenopleura* (a group with obovate anthers); however, it may be better placed in section *Chaenantha*, as indicated by its ovate/oblong anthers. (Anthers that open by elongate slits probably have evolved more than once within *Miconia*; see discussion under this genus.) Thus, stamens opening by elongate slits likely evolved first, followed by red and connivent petals, and finally 4-merous flowers with 4-locular ovaries.

Section *Eccharianthus* probably evolved from a species-group within *Miconia* section *Miconia*, since *C. fadyenii* (Hook.) Griseb. possesses \pm oblong anthers, each opening by a terminal pore and having a slight basal appendage derived from connective tissue and sterile bases of the anther sacs (a synapomorphy of many advanced *Miconia* species, see discussion).

The recognition of *Charianthus* at the generic level, thus, cannot be maintained, and these species must be transferred to *Miconia* (see Nomenclatural Changes). The similarities of the two sections of this genus are

very likely parallel developments in response to selection for bird pollination. Similar shifts are seen in other tropical montane genera, e.g., *Psychotria* L. vs. *Cephaelis* Sw. or *Vaccinium* L. vs. *Agapetes* D. Don ex G. Don. Not only is the group polyphyletic, but its recognition makes even the advanced clade(s) within *Miconia* paraphyletic.

Clidemia D. Don

Clidemia sect. *Clidemia* (see Cogniaux 1891), along with *Clidemia* section *Capitellaria* (Naudin) Cogn., *Heterotrichum* DC., and some species of *Miconia* section *Octomeris* Hook. f., are hypothesized to form a single clade with *Miconia* section *Octomeris* p.p., being basal and *Clidemia* section *Clidemia* most divergent. This group of ca 100 species is distributed throughout the neotropics. Possible synapomorphies of the clade include the presence of a \pm dense indumentum of multicellular elongate and strigose hairs and flowers with a numerical plan greater than five (Fig 2 C,F). Both characters show some reversals (Fig. 2 B). *Miconia tuberculata* (Naudin) Triana (= *Heterotrichum rostratum* (Naudin) Gleason), a member of *Miconia* section *Octomeris*, may be representative of the primitive members of this clade, and is phenetically quite similar to other species of *Miconia*, such as *M. schlimii* and *M. meridensis* Triana (both also of section *Octomeris*) and *M. hexamera* Wurd. (of section *Amblyarrhena*). Most members of *Clidemia* (as delimited here) have the additional synapomorphies of elongate external calyx lobes (Fig. 2 A,D-F) and rounded seeds with slightly to conspicuously papillate testae (Fig. 8 C and D). Species showing this level of advancement include *Miconia macrodon* (Naudin) Wurd. (= *Heterotrichum macrodon* (Naudin) Planch. ex Hook. f.), *Miconia laevipilis* (Wurd.) Wurd. (= *H. racemosum* Wurd.), *Clidemia scopulina* (Brandege) L. O. Williams (= *H. scopulinum* Brandege), *C. petiolaris* (Schlecht. and Cham.) Schlecht. ex Triana (= *C. deppeana* Steud.), and *C. fulva* Gleason. These species all possess an indumentum of strigose hairs intermixed with minute glandular hairs. A phenetically similar species-group has strigose hairs intermixed with conspicuous stellate hairs (see Wurdack 1986, fig. 25), and it is possible that a stellate indumentum evolved at this level in the phylogeny of the genus; these species include: *Clidemia octona* (Bonpl.) L. O. Williams (= *Heterotrichum ocotonum* (Bonpl.) DC.), *Heterotrichum angustifolium* DC. (Fig. 2 E,F), *H. cymosum* Urban, *H. umbellatum* (Mill.) Urban (Figs. 2 C,D, 8 C; Fawcett and Rendle 1926, fig. 139), *H. porphyrotrichum* Markgraf (= *Miconia porphyrotricha* (Markgraf) Wurd.), and *H. glandulosum* Cogn. (= *M. araguensis* Wurd.). These stellate-haired species may form either a paraphyletic or monophyletic group; many have ovaries with numerous locules. Note that generic placement of these species is quite variable, with taxa being variously placed in *Miconia*, *Clidemia*,

or *Heterotrichum* by taxonomists (compare Standley and Williams 1963, Wurdack 1972, and Proctor in Adams 1972). The remaining species within the *Clidemia* clade show a more consistent placement in the genus and are united by the additional apomorphy of clearly pseudolateral inflorescences, i.e., the terminal inflorescence is quickly deflexed to a seemingly lateral position by the development of an axillary branch, with the shoot forming a sympodium (Fig. 2 A; Judd 1986a). These derived members of *Clidemia* may also be united by a reversal to mainly five- (or four-) merous flowers. Most species showing these characters have been placed in *Clidemia* section *Clidemia*--a large probably paraphyletic complex as currently circumscribed; the following are representative: *Clidemia erythropogon* DC., *C. urceolata* DC., *C. capitellata* (Bonpl.) D. Don, *C. dentata* D. Don, *C. pilosa* D. Don, *C. laevifolia* Gleason, *C. pustulata* DC., *C. bullosa* DC., *C. biserrata* DC., *C. allardii* Wurd., *C. hirta* (L.) D. Don (Figs. 2 A,B, 8 D; Fawcett and Rendle 1926, fig. 140; Wurdack 1980, fig. 29), *C. strigillosa* (Sw.) DC., and *C. ciliata* D. Don. It is of interest that several species among *Clidemia* section *Clidemia* and the phenetically similar species of *Miconia* or *Heterotrichum* show the apomorphy of a chromosome number of $2n=30$, e.g., *C. erythropogon*, *C. bullata*, and *H. umbellatum*, or $2n=25$, e.g., *C. strigillosa*, *C. urceolata* (Solt and Wurdack 1980). The significance of this chromosomal variation is unclear because counts are known from very few species.

Two small myrmecophilous clades likely are related to this advanced complex characterized by pseudolateral inflorescences (see Gleason 1931). The first includes *Clidemia killipii* Gleason and *Tococa spadiciflora* Triana, which are united by their unusual corrugated formicaria (with enlarged stomata) that are positioned at the base of the leaf blade, and glandular-pubescent styles. In addition this group has \pm spicate cymose inflorescences. The anthers of these species lack the dorso-basal appendage characteristic of *Tococa*, and usually have slender, \pm curved anthers, unlike the stout, \pm straight anthers of *Tococa*. The long terete external calyx lobes of these species are also very comparable to those of *Clidemia*. The second myrmecophilous group includes *Clidemia taurina* Gleason, *C. collina* Gleason, *C. setosa* (Triana) Gleason (see Standley and Williams 1963, fig. 65), *C. heptamera* Wurd., *Tococa carolensis* Gleason, and *Myrmidone macrosperma* (C. Martius) C. Martius (among others). These species are linked by the probable synapomorphies of pouchlike formicaria at the base of the leaf blade and reduced stellate hairs. Additionally, *Myrmidone macrosperma* (see Martius 1829; Cogniaux 1891; Wurdack 1973, fig. 51) may be weakly linked with *Tococa carolensis* by its 6-merous flowers (but differing in ovary locule number) with smooth, conspicuous petals. This may suggest that *Myrmidone* is a specialized clade within *Tococa*, in agreement with Wurdack's statement (1973: 559) that it is "probablemente solamente un segregado académico de *Tococa*." However, both *T. carolensis* and *M. macrosperma* more likely are linked cladistically to myrmecophilous species of *Clidemia* because their anther

connective lacks a dorso-basal tooth and their inflorescences are strongly pseudolateral. Of course, such examples of confusion between species of *Clidemia* and *Tococa* arise because very similar formicaria likely have evolved in both (as well as in several other genera--see discussion under *Tococa*; Judd 1989). A few other members of *Clidemia* show formicaria, but of very different morphology and position, e.g., bilobed ant-domatia at the petiole base occur in *C. allardii*, *C. ciliata*, *C. crenulata* Gleason, and *C. neblinae* Wurd.

The species of *Clidemia* section *Capitellaria*, e.g., *C. involocrata* DC. and *C. capitata* Benth., likely belong among the derived members of the genus due to their pseudolateral inflorescences. This monophyletic group may be distinguished by its capitulate inflorescences, lack of stellate hairs (having small glandular hairs instead--perhaps a reversal), and seeds with \pm smooth "faces" with the papillae in lines along seed-angles.

Clidemia illustrates a common taxonomic pattern within the Miconieae. The basal members of this clade are phenetically very similar to some elements within *Miconia* (especially those species with \pm ovoid anthers opening by a small terminal pore and lacking appendages and/or glands), but these species are connected to morphologically very distinctive species through a whole series of intermediates. The distinctive features of *Clidemia* accumulate gradually within the clade. Thus, a continuum of variation occurs among species with obviously terminal to pseudolateral cymes, nonpapillose to papillose seeds, short to elongate external calyx lobes, etc., with species of *Miconia* section *Octomeris* p.p. being basal, species variously treated as *Heterotrichum* or *Clidemia* being intermediate, and species of *Clidemia* sections *Clidemia* and *Capitellaria* being derived. Traditional evolutionary taxonomic classifications of this complex have tended to recognize the phenetically derived taxa as members of a distinct genus--*Clidemia*, while placing primitive species in *Miconia* on the basis of symplesiomorphic features. Intermediate taxa often have been tossed back and forth between *Miconia* and segregate genera such as *Heterotrichum* and *Clidemia*, depending upon the characters being stressed by the taxonomist working with the group. This pattern can be seen in Wurdack's (1972) placement of the South American species of *Heterotrichum* in *Miconia*, while Standley and Williams (1963) placed the Central American species of *Heterotrichum* in *Clidemia*! Wurdack (1972) stated that he had no opinion as to the best generic placement of the West Indian species of *Heterotrichum*, and these species are often retained in this genus (see Proctor in Adams 1972; Moscoso 1943; León and Alain 1957), despite nomenclatural difficulties (see Wurdack 1972). Thus the same--or very similar--species variously have been placed in three genera. Various taxonomists, e.g., Thorne (1976), Mayr (1969), McVaugh (1943), have proposed rules that may be invoked in delimiting a segregate genus. Yet, these often lead to members of a single clade being placed in different genera, as can be seen in the taxonomic history of this group. Thus, we have chosen (here and throughout) to follow cladistic principles (see Hennig 1966; Wiley 1981;

Bremer and Wanntorp 1978) and to place basal members of the hypothesized *Clidemia*-clade with more specialized members of the same clade on the basis of synapomorphic features.

Clidemia (as circumscribed above) is considered recognizable at the generic level, although some problems remain in the placement of phenetically similar species of *Miconia*. The recognition of *Clidemia* may make *Miconia* paraphyletic. This situation should be rectified by a detailed cladistic analysis of the latter genus--with the eventual removal from *Miconia* of those species found to be basal members of various related genera. At this point a small number of species of *Miconia* cannot be joined with this genus on the basis of synapomorphies, and are kept within the genus purely for convenience. The placement of such species within a metaphyletic (or even paraphyletic) *Miconia* is considered preferable to lumping *Clidemia* (and other segregate genera) into *Miconia*, with the resultant loss of taxonomic information. *Clidemia*, as here delimited (see Appendix), includes several species of *Miconia* section *Octomeris*, those species often (or always) treated as *Heterotrichum*, a few species of *Tococa*, and *Clidemia* sections *Clidemia* and *Capitellaria*, and probably *Myrmidone* Mart.

As discussed by Judd (1986a, 1989), the axillary flowered members of *Clidemia* are not closely related to those with terminal (or pseudoterminal) cymes, and should be treated in *Sagraea* and *Maieta* (Judd 1989). However, there are several terminal-flowered species usually placed in *Clidemia* that are considered to be unrelated to the major complex of this genus discussed above because they possess distinctive synapomorphies of other clades within the tribe, and lack those of *Clidemia*, *sensu stricto*. Several Antillean species of *Clidemia* show strongly 4-lobed hypanthia and ovaries with flattened external calyx lobes, and have the distinctive growth architecture of *Calycogonium*. These species are placed in *Calycogonium*, and are discussed under that genus (see also Appendix). Members of the *Clidemia gracilis* Pittier complex (Judd 1986a) clearly represent an advanced clade within *Ossaea* section *Octopleura* (Griseb.) Cogn., a group derived from (and here placed in) *Miconia* section *Miconia* (see Appendix). These species are discussed under *Ossaea* and *Miconia*. A few species, e.g., *Clidemia japurensis* DC. and *C. alternifolia* Wurd., have narrowly ovate/triangular petals, and are treated here as members of *Leandra* section *Chaetodon* (Triana) Cogn. They are discussed under *Leandra* (see also Appendix).

Macbride (1941: 479) remarked that "*Clidemia* remains . . . a concept rather arbitrarily retained" in the generic classification of the Miconieae, a viewpoint commonly expressed in the literature dealing with this group. The results of the present study (and Judd 1986a, 1989) lend strong support to this view. The genus, as traditionally circumscribed, represents an artificial assemblage, without phylogenetic (or even phenetic) reality, and probably contains at least six distinct and unrelated clades, as outlined above.

Conostegia D. Don

This genus represents a well marked monophyletic group of ca 45 species (Wurdack 1973, 1980; Howard 1989) that range from Mexico to northern South America and the West Indies. The genus is recognizable by its lack of external calyx lobes and inner calyx lobes fused into a stout, \pm conical calyptra (Fig. 1 D-F; Fawcett and Rendle 1926, fig. 134; Gleason 1958, fig. 89; Wurdack 1973, fig. 49; Wurdack 1980, fig. 16). The nonappendaged anthers characteristic of the genus are ovoid, tapered to the apex, and open by a small apical pore. These anther characters lead to the conclusion that this genus did not evolve from within *Miconia*, since members of this genus show various modifications of either pore or connective structure. It is of interest that the flowers of most species of *Conostegia* have distinct pedicels, whereas members of the Miconieae typically have \pm sessile flowers. This feature may indicate that the genus diverged early in the cladistic history of the tribe, retaining this plesiomorphic feature.

The possible isolated position of this genus is reinforced by an analysis of its wood anatomy, although the number of species sampled is small (see Welle and Koek-Noorman 1981). The wood has abundant (mainly apotracheal) parenchyma in tangential bands, 2 to 6 cells wide. These features are considered by Welle and Koek-Noorman (1981) and Vliet et al. (1981) to be apomorphies linking the genus to Blakeeae, *Tibouchina* Aublet, several Merianieae, *Tococa*, and *Tessmannianthus* Markgraf, and separating it from most Miconieae (see Welle and Koek-Noorman 1981: 376). The rays are heterogeneous, exclusively uniseriate, and sometimes composed of some weakly procumbent cells. Most Miconieae have rays mainly composed of square and upright cells, and have bands of pseudoparenchyma consisting of fibers and parenchyma strands, or fibers only (Welle and Koek-Noorman 1981). Druse crystals (plus some rhombic crystals) are characteristic.

Conostegia setosa Triana is noteworthy in having ant-domatia at the base of its lamina (as in *Tococa*).

In summary, *Conostegia* likely is monophyletic and cladistically isolated within the tribe. The group should be maintained at the generic level. It is quite variable as to numbers of floral parts and indumentum. The seed coat is smooth to slightly papillose (Fig. 8 E); petals are \pm blunt.

Ossaea DC.

The genus *Ossaea* is an arbitrary grouping of some of those species of Miconieae with narrowly triangular to ovate petals with \pm acute apices. When

taxonomic groupings are based on potential synapomorphies (or even made phenetically--on the basis of several characteristics), it is evident that petal apex, although of some taxonomic utility, is quite variable within several genera, especially *Sagraea*, *Mecranium*, *Calycogonium*, *Leandra*, and *Miconia*. Wurdack (1962) stated that "the genus is an artificial assemblage of various species groups." Judd (1986a, 1989) demonstrated that the terminal and axillary-flowered members usually assigned to this genus actually are not closely related. The axillary-flowered members of *Ossaea* were placed by Judd (1989) in either *Sagraea* (including the type of the genus *Ossaea*), *Mecranium*, or *Pentossaea*. The species of *Ossaea* with terminal (or terminal and axillary) cymes are discussed in the present paper. These species do not show a suite of apomorphic traits that can be used to delimit them from other genera within the Miconieae; instead, these species are variously considered members of (1) *Calycogonium*, (2) *Leandra* section *Niangae* (DC.) Cogn., (3) *Leandra* section *Chaetodon*, and (4) *Miconia*, as indicated by the particular apomorphies of each. The reasons for the various placements are given in the discussion under these genera. The use of the name *Ossaea* should be abandoned; the type species of the genus is actually a species of *Sagraea* (see Judd 1989), and the group, in its normal circumscription, probably contains at least seven distinct and unrelated clades.

Pachyanthus A. Rich.

Pachyanthus probably is monophyletic because species placed in this group show the synapomorphies of moderate-sized to large, 6-merous (secondarily 5-merous) flowers, \pm robust fruits with persistent, coriaceous, cylindrical-campanulate hypanthia (often tearing into sepal-like segments), and inflorescences with only one to seven (rarely to ca 13) flowers and \pm flattened axes (Fig. 3 A,B,F). The ca 20 species (León and Alain 1957) of this genus have an indumentum of stellate hairs, although these hairs are sometimes reduced. The wood anatomy of the genus may also be distinctive. Welle and Koek-Noorman (1981: 374) suggest that "the combination of oblong intervascular and vessel-ray pits, the predominantly non-septate fibers with pits on radial and tangential walls and the 2-3-seriate rays tempt us to compare *Pachyanthus* with Microlicieae and some Tibouchineae." This view is shared by Vliet et al. (1981). However, their conclusion must be viewed with caution, since only *P. cubensis* A. Rich. was sampled.

The stamens of *Pachyanthus* are \pm ovoid, taper to a small apical pore, and are usually unappendaged (Fig. 3 A), suggesting a divergence basal to the point at which at least most species of *Miconia* originated. *Miconia lundelliana* L.O. Williams (Fig. 3 B) possesses the synapomorphies of the group (see Standley and Williams 1963), and should be transferred to *Pachyanthus* as

suggested by Wurdack (1988). The remaining ca 20 species of the genus (León and Alain 1957) are limited to Cuba and Hispaniola.

A species of this genus has been recorded from Colombia (Cogniaux 1891), i.e., *P. corymbiferus* (Naudin) Cogn. The placement of this species, which was first considered in the monotypic genus *Chalybea* Naudin (Naudin 1851), is certainly incorrect. Like other species of *Pachyanthus*, this taxon has robust, 6-merous flowers with \pm coriaceous hypanthium/ calyx, slightly flattened inflorescence axes, and a similar stellate-dendritic indumentum. However, it is very distinctive due to its many-flowered, axillary inflorescences and bipored anthers with a minute dorso-basal appendage. Wurdack (1988) suggested a relationship with *Huilaea*, a placement that is supported strongly by the fact that *Chalybea* has the apomorphic feature of axillary inflorescences (see Judd 1989). *Chalybea* and *Huilaea* likely are united by the synapomorphy of long-pedunculate inflorescences and 6-merous flowers. However, *Chalybea* differs from *Huilaea* in having a larger number of flowers per inflorescence and often fewer-loculed ovaries (see Wurdack 1988). *Chalybea* and *Huilaea* may eventually prove to be congeneric, but these genera are best kept separate until they have been studied more thoroughly (see comments in Wurdack 1988).

Pachyanthus, excluding *Chalybea*, is best maintained at the generic level. The genus is variable in indumentum and petal shape. The external calyx lobes may be very short to elongate. The seed coat is smooth to minutely roughened (by bulging cells); druses are characteristic.

Tetrazygia Rich. (including *Tetrazygiopsis* Borhidi)

Tetrazygia (including *Tetrazygiopsis*) is an Antillean group of ca 25 species (Howard 1989), one of which reaches south Florida, i.e., *T. bicolor* (Mill.) Cogn. (Fig. 4 D,E). The genus is traditionally based upon a single character--the presence in the fruits of a strongly constricted hypanthium (Fawcett and Rendle 1926, fig. 137). The limits of this genus have been especially troublesome. Borhidi (1977) transferred those species with elongate/conspicuous external calyx lobes to the genus *Tetrazygiopsis*, and also transferred two species of *Miconia* into *Tetrazygia*, i.e., *T. urceolata* (Urban) Borhidi and *T. delicatula* (A. Rich.) Borhidi. (For convenience in the following discussion, the species transferred to *Tetrazygiopsis* are here retained in *Tetrazygia*.) Cogniaux (1891) divided the complex differently, considering the 4-merous species in section *Tetrazygia* and the 5-merous species in section *Miconiastrum* Cogn. *Tetrazygia urbaniana* (Cogn.) Croizat ex Mosc. and the closely related and likely conspecific *T. tuerckheimii* (Cogn.) E. Ekman ex Urban, have occasionally been treated in *Pachyanthus* (Cogniaux 1912); Borhidi (1977) placed these species in *Tetrazygiopsis* section *Pachyanthopsis*

Borhidi, differentiating them from section *Tetrazygia* on the basis of their coriaceous leaves, 5-merous flowers, and 5-loculate ovaries (vs. membranaceous to chartaceous leaves, 4-merous flowers, and 3- [4-] loculate ovaries).

Under the current circumscriptions, both *Tetrazygia* and *Tetrazygiopsis* are probably not monophyletic, and they certainly are delimited only with difficulty, because a few species of *Tetrazygia/Tetrazygiopsis* have only slightly constricted hypanthia, e.g., *Tetrazygia crotonifolia* (Desr.) DC., *T. urbaniana*, and *T. tuerckheimii*, while several phenetically similar species of *Miconia* have a slight to moderate development of calyx/hypanthium constriction, e.g., *M. androsaemifolia* Griseb., *M. obtusa*, and *M. ancistrophora* (C. Wright in Sauvalle) Triana. In addition, several more specialized species of *Miconia*, i.e., those showing various anther specializations, also develop constricted hypanthia, e.g., *M. staminea* (Desr.) DC., *M. amplexans* (Crüger) Cogn., *M. aureoides* Cogn., *M. boissieriana* Cogn., *M. serrulata* (DC.) Naudin, *M. dodecandra* (Desr.) Cogn., *M. mirabilis* (Aublet) L. O. Williams. The above listed species are distributed mainly in sections *Jucunda*, *Tamonea* Cogn., *Octomeris*, and *Adenodesma* Naudin. Although lacking a constricted calyx, some species of section *Laceraria*, e.g., *M. mexicana* and *M. humilis*, are phenetically similar to *Tetrazygia* (see below). Thus, the presence or absence of a constricted calyx/hypanthium cannot be used consistently to delimit the genus *Tetrazygia*, and no additional characters could be discovered in this investigation that support the present generic circumscription. The genus, as presently defined, can only be maintained through selective character weighting--the presence of strongly constricted calyces/hypanthia are stressed in some species, while this feature is ignored in those species possessing *Miconia*-like anthers (see discussion of *Miconia* below)--and a placement of intermediate species in the larger generic entity, i.e., *Miconia*.

The present cladistically oriented investigation, quite surprisingly, gives some support for the maintainence of *Tetrazygia*, although not as presently circumscribed. The species of *Tetrazygia* (as here delimited) possess distinctive glabrous styles that are strongly curved at the apex and have a minute stigma, and have \pm ovoid, unappendaged (or rarely only minutely appendaged) anthers that taper toward a small apical pore (Figs. 3 C,E; 4 D). The latter character may indicate that these species diverged early in the evolutionary history of the tribe, i.e., the species of *Tetrazygia* are likely not related to the majority of *Miconia* species, which have more specialized anthers. The former character may be a synapomorphy linking all species of *Tetrazygia* and several species of *Miconia* (mainly in sections *Octomeris* and *Laceraria*). All species have blunt petals and \pm smooth seeds--both plesiomorphic conditions. Many species of *Miconia* that have this distinctive stigma/style form also often have somewhat constricted calyces. Thus, *Tetrazygia* is maintained here, on a provisional basis, awaiting a more thorough study of the complex of related

species of *Miconia*. It is likely that the genus will eventually be recognized in a broader sense, including several species now placed in *Miconia*.

Basal members of *Tetrazygia* may include *M. androsaemifolia* and *M. pachyphylla* Cogn. (placed by Cogniaux 1891, in section *Amblyarrhena* Naudin), *M. humilis* and *M. mexicana* (placed by Cogniaux 1891, in section *Laceraria*), *M. zemurrayana* Standley, and a distinctive group of West Indian species, such as *M. obtusa*, *M. ancistrophora*, *M. baracoensis* Urban, *M. cerasiflora* Urban, and *M. thomāsiana* DC. (placed by Cogniaux 1891, in section *Octomeris*). The last group is likely monophyletic—all these species show the synapomorphies of lax cymose inflorescences borne on shoots on which the leaves have already fallen. They also all have ovate, blunt-tipped leaves. *Tetrazygia delicatula* exhibits these apomorphies, is phenetically very similar to this species-group, and was placed with these species by Cogniaux (1891); its placement in *Tetrazygia* by Borhidi (1977) surely results in a polyphyletic *Tetrazygia* (as circumscribed by Borhidi). These basal members of the *Tetrazygia* clade show only the apomorphies of a strongly apically curved style with a minute stigma. Many of these species, however, show a slight tendency to have a constricted calyx/hypanthium.

More advanced members of the *Tetrazygia* group may be united by the apomorphy of a strongly constricted hypanthium (Figs. 3 C,E; 4 C-E), which possibly has been reversed in a few species, e.g., *T. urbaniana* (Fig. 4 B). Within this group the 5-merous species with short (or absent) external calyx lobes may be basal; these species include: *T. aurea* R. Howard and Briggs, *T. bicolor* (Fig. 4 D,E), and *T. pallens* (Sprengel) Cogn. (Fig. 4 C). The latter two are obviously closely related and show the synapomorphy of an indumentum of peltate scales. Stellate hairs occur in *T. aurea*, as well as many other species of the genus. A fairly large group of species have the additional synapomorphy of long external calyx lobes, and this group was segregated by Borhidi (1977) as the genus *Tetrazygiopsis* (Fig. 3 C-E; 4 A,B). All these species except for *T. urbaniana* and *T. tuerckheimii* also have 4-merous flowers and this character (although showing homoplasy) may be an additional apomorphy of this group. Species in this complex include (among others): *T. longicollis* Urban and Cogn. (Fig. 3 C-E), *T. hispida* (Sw.) Cogn., *T. laxiflora* Naudin, *T. elaeagnoides* (Sw.) DC., *T. albicans* (D. Don ex Naudin) Triana, *T. brachycentra* (Griseb.) C. Wright, *T. urbanii* Cogn., *T. cordata* Alain, and probably *T. biflora* (Cogn.) Urban. A few species, i.e., *T. crotonifolia*, *T. urbaniana*, *T. tuerckheimii*, have a distinctive appearance due to their reduced, lax inflorescences and distinctive indumentum of stellate hairs with elongate, crisped arms, giving the abaxial leaf surface a ferruginous, cob-webby appearance. These species lack a strong hypanthium/calyx constriction, and may be 4-merous (*T. crotonifolia*) or 5-merous (*T. urbaniana* and *T. tuerckheimii*). They often show the development of only a single pair of leaves per shoot before the production of the terminal cyme, and may be related to the above listed species since they, too, have elongate external calyx lobes. However, it is possible to hypothesize

that these three species were derived from ancestors similar to *T. delicatula*, a link based on their lax inflorescences. This hypothesis requires an independent derivation of elongate external calyx lobes, but this feature is possibly under simple genetic control because long external calyx lobes have evolved many times in the tribe. A few 4-merous species have inconspicuous external calyx lobes; this group includes: *T. angustifolia* (Sw.) DC., *T. urceolata*, and *T. discolor* (L.) DC. *Tetrazygia angustifolia* is distinctive in having only slight curvature of its style, but possesses the characteristic minute stigma. The affinity of these species is poorly understood; they may be derived from the *Tetrazygiopsis* group through a loss of elongate external calyx lobes. It is noteworthy that *Tetrazygia elaeagnoides* may have short to elongate external calyx lobes.

The genus *Tetrazygiopsis* is not recognized here because segregating these species from *Tetrazygia* would make the latter paraphyletic (if the 4-merous species of *Tetrazygia*, sensu stricto, are derived from the 5-merous species of *Tetrazygia*) or polyphyletic (if the 4-merous species of *Tetrazygia*, sensu stricto, are derived from *Tetrazygiopsis*, a 4-merous group, with a loss of elongate external calyx lobes). Borhidi's division of *Tetrazygiopsis* also does not reflect phylogenetic relationships, because *T. crotonifolia* (with 4-merous flowers) is placed in section *Tetrazygiopsis*, while the related *T. tuerckheimii* and *T. urbaniana* (with 5-merous flowers) are placed in section *Pachyanthopsis*. It seems unwise to base named taxonomic groups within *Tetrazygia* on either number of floral parts or length of external calyx lobes because both characters are homoplasious.

Tococa Aublet

Tococa, a genus of ca 50 species (Wurdack 1980), is probably monophyletic, and may be recognized on the basis of stout, \pm straight anthers with a single small pore (apical to slightly adaxially inclined) and connective that lacks appendages except for a minute dorso-basal tooth (Fig. 1 J). Most species have three ovary locules, but some have only two or as many as four (rarely five). Some, probably primitive, species, e.g., *T. subciliata* (DC.) Triana, and a group of species with nearly sessile leaves (*T. nitens* (Benth.) Triana, *T. bolivarensis* Gleason, *T. obovata* Gleason, *T. ciliata* Triana), lack formicaria, but most species have a conspicuous, pouchlike formicaria at the petiole apex or embedded in the blade base (Fig. 1 I; Gleason 1958, fig. 90; Wurdack 1973, fig. 15; 1980, fig. 28). In combination, these serve as distinctive synapomorphies of the members of this genus.

Microphysca Naudin (represented by *M. quadrialata* Naudin), a group characterized by winged hypanthia and/or external calyx lobes (Naudin 1851; Cogniaux 1891), is considered to be embedded within the cladistic structure of

Tococa and cannot be maintained at the generic level (Macbride 1941; Wurdack 1969), because certain species of *Tococa*, e.g., *T. undabunda* J. F. Macbr., *T. gonoptera* Gleason, and *T. stephanotricha* Naudin, also have winged hypanthia. The relationships of *Tococa rotundifolia* (Triana) Wurd., a species previously considered in *Microphysca* (Cogniaux 1891; Wurdack 1969) are problematic. It possesses slightly winged external calyx lobes but the hypanthium is globose. This species may be related to several \pm sessile-leaved and non-formicarial species of *Tococa* as suggested by Wurdack (1969).

The species of *Tococa* possessing wings on their hypanthia and/or calyces often have been recognized as a distinct group, i.e., section *Pterophorae* Naudin; see Naudin (1851), Triana (1871), and Cogniaux (1891).

Clidemia contains a few species with pouchlike formicaria very similar to those of *Tococa* and these two groups often have been confused. These species may be differentiated by their anthers that lack a minute dorso-basal tooth; they also differ from most species of *Tococa* in having pseudolateral inflorescences (as is characteristic of advanced members of *Clidemia*). It is likely that ant-domatia have evolved several times within the Miconieae (Judd 1989). Among axillary flowered Miconieae, such formicaria occur in *Maieta* (including *Clidemia* sect. *Calophysoides*, see Judd. 1986a, 1989), *Sagraea* (if "*Ossaea*" *bullata* actually belongs in this group, see Whiffin 1972), and *Henriettea* (Gleason 1931). Within terminal-flowered Miconieae (including those with pseudolateral inflorescences), similar formicaria evolved in *Tococa* (most species, including *Microphysca*), *Clidemia* (few species, probably including *Myrmidone*), and *Conostegia* (few species). Other kinds of ant-domatia, e.g., swollen branchlet internodes (few species of *Miconia*) or swelling at petiole base-branchlet intersection (several species of *Sagraea* and *Clidemia*), also have evolved within the tribe. Repeated evolution of formicaria is not unlikely considering the probable adaptive significance of these structures (Neto and Asakawa 1987; Benson 1985) and the frequently dense stem trichomes occurring on these plants (Davidson et al. 1989).

The wood anatomy of *Tococa* is fairly distinctive and similar to that of *Conostegia* (Welle and Koek-Noorman 1981; Vliet et al. 1981).

Leandra Raddi

Leandra is a diverse, Latin American genus of some 200 species with several described sections (see Cogniaux 1891; Wurdack 1962, fig. 6; 1980, fig. 62). It traditionally is characterized by its acute/acuminate petals, terminal inflorescences, and often strigose indumentum (Fig. 5 B). The genus is especially variable in seed shape and testa ornamentation (Fig. 9 A-E), and its circumscription and delimitation from *Miconia* and *Ossaea* have been considered problematical. Macbride (1941) claimed that "*Leandra* is scarcely a

natural concept," while Wurdack (1962: 206) stated that the species of *Ossaea* "should probably be inserted at various places in *Leandra*." Macbride also linked these genera, and remarked (1941: 332) that the inflorescence of *Leandra* was "really terminal but some species suggest *Ossaea*." Gleason (1932) also considered *Leandra* closely related to *Miconia*. Wurdack (1962: 171) wrote that "*Leandra* differs from *Miconia* technically only in the acute petals" but added that "many species have a distinct facies unlike that of *Miconia*." Wurdack (1962, 1973) noted that *Platycentrum* Klotzsch and *Pleiochiton* Naudin ex A. Gray, two small generic segregates, are difficult to distinguish from *Leandra*. *Platycentrum* was separated from *Leandra* only by its conspicuously ascending dorsal appendage on the anther connective. However, several species of *Leandra* have dorsally appendaged anthers. At first Wurdack (1973) recognized *Platycentrum*, but stated that the inclusion of the genus in *Leandra* could probably be justified. The discovery of *L. coadunata* Wurd., which effectively bridged the phenetic gap between these two genera, led him (Wurdack 1984) to transfer *Platycentrum clidemioides* Naudin to *Leandra*. *Pleiochiton*, a small group of frequently epiphytic shrubs with short-petiolate, thick leaves, was considered by Wurdack (1962) to be "scarcely distinguishable from *Leandra*."

Not surprisingly, this preliminary survey of *Leandra* suggests that the group, in its present circumscription, is a paraphyletic complex. The traditional treatment of this genus is basically horizontal (see Mayr 1969) with the derived members of several lineages, i.e., *Platycentrum*, *Pleiochiton*, *Ossaea* p.p. (i.e., *Ossaea* II, see Judd 1986a), arbitrarily considered as genera. However, with an expanded circumscription, *Leandra* may be monophyletic. It may be separable from *Miconia* (see below) and should be provisionally maintained at the generic level. The synapomorphy of petals strongly acute to acuminate (and forming a sharply conical configuration in bud) unites these species, although it has been lost in a few specialized members of section *Chaetodon*. The sister group relationships of *Leandra* are likely within the basal complex of *Miconia*, or less likely, within *Miconia* section *Miconia*, e.g., see *M. anisotricha* Triana, which has acuminate petals and elongate multicellular hairs. The second hypothesis requires the loss of the anther appendages typical of *Miconia* (see below) and is considered less likely. The monophyly of *Leandra* requires the inclusion of a distinctive group of West Indian *Ossaea* species (i.e., *Ossaea* II, Judd 1986a), a few species of *Clidemia* (*C. japurensis* DC. and relatives), *Pleiochiton*, and *Platycentrum*.

The cladistically basal members of *Leandra* may include species such as *L. melanodesma* (Naudin) Cogn. (Gleason 1958, fig. 88), *L. laxa* Cogn., *L. subseriata* (Naudin) Cogn., *L. costaricensis* Cogn., and *L. grayana* Cogn. Several of these species have fairly broad, but still acute/acuminate petals. These species have short external calyx lobes, unappendaged anthers, sparse to moderate indumentum of elongate hairs and stellate hairs, and \pm smooth seeds. A species-group likely originating from within this complex (and

phenetically intergrading with it) is characterized by a reduction in the density of elongate multicellular hairs (in some species these hairs being limited to vein-axil domatia or entirely lacking), a usual lack of stellately branched hairs, and anthers with a slightly dorsal thickened anther connective, and usually narrowly triangular and acute petals. Their seeds are non-papillose. Representative species include: *L. debilis* (Naudin) Cogn., *L. riedeliana* Cogn., *L. quinquedentata* Cogn., *L. cornoides* (Schlecht. and Cham.) Cogn., *L. acutifolia* Cogn., *L. sulfurea* (Naudin) Cogn., and *L. cordigera* (Triana) Cogn. Most of these species have been considered members of *Leandra* section *Oxymeris* (DC.) Cogn., although there is no sharp phenetic boundary between these species and those of other sections (Wurdack 1962).

The remaining species of *Leandra* may be united by the apomorphy of a densely strigose indumentum; this hypothesis has to be very tentative because the character is of uncertain polarity and shows homoplasy. These \pm densely strigose species possibly belong to three monophyletic subgroups. The first contains species with the presumed synapomorphy of rounded and conspicuously papillose seeds with a small hilum scar (Fig. 9 B) and with terminal inflorescences that usually show unilateral cymose branches (see Weberling 1988). The species of this complex also lack stellate hairs. Representatives of this distinctive clade, traditionally treated as *Leandra* section *Secundiflorae* (DC.) Cogn. (see Cogniaux 1891; Wurdack 1962, 1973, 1980), include: *L. grandifolia* Cogn., *L. granatensis* Gleason, *L. francavillana* Cogn., *L. mexicana* (Naudin) Cogn., *L. secunda* (D. Don) Cogn., *L. longicoma* Cogn., and *L. dichotoma* (D. Don) Cogn.

The second clade is delimited by angular seeds with an appendage composed of usually large, thin-walled cells (Fig. 9 C). This appendage may be involved in secondary ant-dispersal of the seeds after passage through primary bird dispersers (D. Levey, pers. comm.). Basal members of this group include *L. nanayensis* Wurd. and *L. rufescens* (DC.) Cogn. (as well as other members of the likely paraphyletic *Leandra* section *Tschudya* (DC.) Cogn.). As pointed out by Wurdack (1984), *Leandra* (formerly *Platycentrum*) *clidemoides* has appendaged seeds, and the placement of this species in *Leandra* seems correct. The more advanced members of this group are united by the additional apomorphies of pseudolateral inflorescences and roughened, \pm slightly papillose seeds, and include: *L. lasiopetala* Cogn., *L. aristigera* (Naudin) Cogn., *L. chaetodon* (DC.) Cogn., *Clidemia utleyana* Almeda, *C. alternifolia* Wurd., *C. japurensis*, *C. naevula* (Naudin) Triana, *Ossaea boliviensis* (Cogn.) Gleason, *O. cucullata* Gleason, and *O. araneifera* Markgraf. These species tend to lack stellate hairs, and a few also show a reversal to only sparsely distributed elongate hairs, e.g., *C. alternifolia*; to a smooth testa, e.g., *O. araneifera*; or to unappendaged seeds, e.g., *C. utleyana* and *C. japurensis*. The petals of *Clidemia alternifolia* and *C. japurensis* are narrowly triangular but \pm rounded at the extreme apex (with either a conspicuous or inconspicuous apical projection, respectively) and are very similar to petals of *O. araneifera*, *O.*

cucullata, *L. chaetodon*, *L. aristigera*, etc. The petals of *C. utleyana* are quite blunt at the apex. Only in this species-group, which is well embedded within the clade comprising *Leandra*, has the petal apex reversed to the \pm blunt, seemingly plesiomorphic state. The group is surprisingly uniform, in spite of its containing representatives placed in three genera. The *Leandra* species placed here are typically referred to section *Chaetodon* (Cogniaux 1891; Wurdack 1980). The placement of the members of this clade in three genera in traditional classifications has resulted from an over emphasis on the shape of the petal apex and a confusion of pseudolateral and axillary inflorescences (see Appendix).

The third major clade within those species with \pm densely strigose indumentum may be delimited by the apomorphy of long and conspicuous external calyx lobes (although this feature also occurs in some of the above listed species). Their seeds are \pm non-papillose, although individual testa cells may be bulging (Fig. 9 D). This group, the largest in the genus, may be composed of a basal paraphyletic complex, along with three more specialized clades. Some generalized species in the group include: *L. echinata* Cogn., *L. atropurpurea* Cogn., *L. cardiophyllum* Cogn., *L. adenothrix* Cogn., *L. ionopogon* (C. Martius) Cogn., *L. rhodopogon* (DC.) Cogn., *L. australis* (Cham.) Cogn., and *L. nianga* (DC.) Cogn. (species usually placed in section *Niangae*; Cogniaux 1891). Many of these species have a slight dorsal anther appendage (developed from connective tissue). The elongate multicellular hairs may be smooth to minutely roughened (due to projections of individual cells).

Conspicuously roughened hairs (Fig. 5 C) occur in several species, e.g., *L. carassana* Cogn., *L. dispar* (Gardn.) Cogn., and *L. dasytricha* (A. Gray) Cogn., which are traditionally placed in section *Carassanae* (Triana) Cogn. These species may be cladistically related to a specialized species-group possessing anthers with an elongated dorso-basal connective, inflorescences with condensed axes (and thus clustered flowers) and usually at least slightly roughened elongated multicellular hairs, i.e., section *Leandraria* DC., e.g., *L. crenata* Cogn., *L. cancellata* Cogn., *L. lindeniana* (Naudin) Cogn., *L. aurea* (Cham.) Cogn., *L. polystachya* Cogn., *L. erostrata* (DC.) Cogn., *L. purpurascens* (DC.) Cogn., and *L. lacunosa* Cogn. More specialized members of section *Leandraria* show the additional apomorphies of large bracts associated with capitula and a loss of roughened surface of strigose hairs, e.g., *L. hirta* Raddi, *L. umbellata* DC., *L. bergiana* Cogn., *L. melastomoides* Raddi, *L. involucrata* DC., *L. fragilis* Cogn., *L. parvifolia* Cogn., *L. amplexicaulis* DC., *L. salicina* (DC.) Cogn., *L. scabra* DC., and *L. sericea* DC.

A second group likely showing a sister group relationship to an element within the basal complex of species with elongate external calyx lobes is represented by an assemblage of West Indian species of *Ossaea* (*Ossaea* II in Judd 1986a; Fig. 6) and *Calycogonium krugii* Cogn. (C. section *Krugiophytum*; see Cogniaux 1891; Judd 1986a; and Appendix). These species are united by their hypanthia with stout, thick-based, elongate multicellular hairs, and petals

usually with a stout apical hair. This group also usually lacks stellate hairs, and most species show a reduction in the number of flowers per inflorescence (Fig. 6). Their seeds are \pm non-papillose (Fig. 9 E). Basal members of this West Indian group may include: *Ossaea granulata* Urban, *O. muricata* (Griseb.) C. Wright in Sauvalle, *O. asperifolia* (Naudin) Triana (Fig. 6 A; Fawcett and Rendle 1926, fig. 143), *O. ottoschmidtii* Urban, *O. limoides* Urban, *O. lima* (Desr.) Triana (Fig. 6 E), and *O. turquinensis* Urban. Floral number varies in the group, with both four- and 5-merous species. Species-groups likely derived from taxa within this complex include: *Ossaea shaferi* Britton and P. Wilson, *O. capitata* Urban, and *O. krugiana* Cogn., which have the additional apomorphy of flowers clustered into heads; *Calycogonium krugii*, which has solitary 6-merous flowers with blunt petals; and a group of species with one- to three-flowered inflorescences with long peduncles, usually unappendaged anthers, and petals lacking apical stout hairs (Fig. 6 B-D). The latter complex includes: *Ossaea pauciflora* (Naudin) Urban, *O. hypoglauca* (C. Wright in Sauvalle) M. Gómez, *O. involucrata* (Griseb.) C. Wright in Sauvalle, *O. microphylla* (Sw.) Triana, *O. elliptica* Alain, *O. pulverulenta* Urban, *O. verrucosa* (Griseb.) M. Gómez, *O. hirsuta* (Sw.) Triana (Fig. 6 B-D), and probably *O. inequidens* Urban and E. Ekman. These species usually have stellate hairs and 4-merous flowers. Several have a dense covering of stout, elongate multicellular hairs only on the hypanthia (with such hairs lacking or only sparsely distributed on twigs, leaves, etc.). Several of these species were placed by Cogniaux (1891) in *Calycogonium*. *Ossaea glomerata* (Naudin) Triana and *O. lanata* (Naudin) C. Wright in Sauvalle are also stellate pubescent and may be related to the above taxa; these species are unusual due to the development of both terminal and axillary inflorescences.

The third clade within the complex of *Leandra* with elongate external calyx lobes traditionally is segregated as *Pleiochiton* Naudin ex A. Gray (see Wurdack 1962). These species are only sparsely strigose, usually epiphytic or epilithic climbers with short-petioled, usually coriaceous leaves. The recognition of this genus clearly makes *Leandra* paraphyletic, and its close association with *Leandra* has been suggested by Wurdack (1962).

Leandra shows great evolutionary depth, and is polythetic, since no single apomorphy is present in all species. Despite this diversity, the group may be monophyletic, with the basal synapomorphy of acute or acuminate petals. Additional studies are necessary to clarify its relationship to *Miconia*; however, it seems best to maintain these species at the generic level. No suite of apomorphies could be found to link these species with those of other genera recognized within the tribe. However, some species of *Leandra* section *Chaetodon* are phenetically convergent with members of *Ossaea* section *Octopleura* in having acute petals, pseudolateral inflorescences, and anisophyllous leaves, while other species of *Leandra* have an indumentum similar to some species of *Clidemia*. Within the genus, sections *Oxymeris*, *Nianguae*, and *Carassanae* are relatively generalized and intergrading, while

sections *Leandraría*, *Tschudya/Chaetodon*, and the West Indian *Ossaëa* group are probably monophyletic, derived, and more clearly delimited.

Miconia Ruíz Lopez and Pavón

As discussed above, an element within *Miconia* probably represents the basal complex within the tribe. Macbride (1941) pointed this out, and stated that if a particular species does not fit into any of the related, segregate genera it should be placed in *Miconia*. This diverse genus of ca 1000 species (Wurdack 1980), distributed throughout the neotropics, can be characterized in general by its terminal several-flowered, cymose inflorescences, usually obtuse or rounded petals, usually small calyx lobes not forming a stout, conical cap and with short, inconspicuous external teeth, and nonformicarial leaves (Fig. 7; Fawcett and Rendle 1926, fig. 136). These features are all symplesiomorphies, and therefore the group has been the repository for phenetically primitive (and cladistically basal) species of several clades whose derived members are generically segregated, as has been discussed above. The genus shows great diversity in trichome (see Wurdack 1986), anther (see Cogniaux 1891), and seed (Figs. 9 F and 10) morphology. The sections traditionally recognized have been characterized by differences in various characters of the stamens such as anther shape, method of dehiscence, pore morphology, shape of the filaments, shape and structure of the anther connective, along with shape of the hypanthium/calyx (Fig. 5; Cogniaux 1891; Triana 1871; Gleason 1932, 1940; Macbride 1941; Wurdack 1973, 1980). This pattern of variation has led to instability in generic circumscription, and diverse viewpoints regarding the naturalness of the group. Gleason (1940: 351) wrote that "the range of structure in the stamens, the calyx, and the inflorescence strongly suggests that the genus, as now accepted, is a heterogeneous assemblage greatly in need of segregation," and added (Gleason 1958: 279) that the characters distinguishing several of the segregate genera "are far weaker than those which separate certain sections within the genus." However, Macbride (1941) remarked that it is not at all clear that segregation would serve the purpose of showing the probable evolution and present relationships of these species, and Wurdack (1962, 1973, 1980) said that the sections are not well characterized, and thus, no clear internal discontinuities exist that could serve to delimit units to be segregated.

Additional study of the numerous species of *Miconia*, especially those of South America, is needed before details of phylogenetic relationships within the group can be clarified, and sectional limits redefined. However, it seems reasonably clear that ca. 95% of the species of the genus form a monophyletic group, and cannot be cladistically basal members of various traditionally recognized segregate genera. This conclusion follows from a survey of anther

specializations within the genus. Most species of *Miconia* have at least one of the following derived conditions: expanded connective with glandular hairs, conspicuous dorso-basal appendage with or without gland-headed hairs, a distinctive sterile basal portion of the anther derived from basal portion of anther sacs and connective tissue, dehiscence by a slightly to greatly enlarged terminal pore or by elongated slits, and oblong to obovate anthers (Fig. 5). Within the species with various anther specializations, those with large, \pm curved, ovate anthers opening by a small terminal pore and having a connective that is at least slightly enlarged (and often bearing glandular hairs) are considered cladistically basal. These species are mainly found in sections *Jucunda*, *Tamonea*, *Octomeris*, and *Adenodesma* (Cogniaux 1891). More derived species are placed in sections *Miconia*, *Glossocentrum* (Crueg.) Triana, *Chaenantha*, *Chaenopleura*, *Cremanium* (D. Don) Naudin, and *Amblyarrhena* Naudin.

As discussed above, anther specializations have played a large part in traditional sectional delimitations (see Cogniaux 1891; Macbride 1941). Yet, lines of sectional demarcation often appear arbitrary, and intermediate species exist (Wurdack 1980; pers. observ.). For example, a group of species with elongate hypanthia and floral buds that dehisce by a circumscissile slit may form a monophyletic group. Representative species with these features include: *M. pubipetala* Miq., *M. truncata* Triana, *M. gratissima* Benth., *M. holosericea* (L.) DC., *M. fissa* Gleason, *M. involucrata* Donn. Sm., *M. staminea* (Desr.) DC., *M. tomentosa* (Rich.) D. Don ex DC., *M. ampla* Triana, *M. amplexans* (Crüger) Cogn., and probably *M. plukenetii* Naudin. These species were scattered across sections *Jucunda*, *Tamonea*, and *Adenodesma* by Cogniaux (1891). Species with anthers dehiscent by longitudinal slits (placed by Cogniaux 1891, either in section *Chaenopleura* or section *Chaenantha*, depending on anther shape) or expanded apical pores (placed in section *Cremanium*) probably have evolved more than once. For example, within section *Chaenopleura*, Antillean species such as *M. foveolata* Cogn., *M. rigida* (Sw.) Triana, *M. subcompressa* Urban, *M. ferruginea* (Desr.) DC., *M. domingensis* Cogn., *M. quadrangularis* (Sw.) Naudin, *M. sintenisii* Cogn., *M. stenobotrys* (Rich.) Naudin, *M. krugii* Cogn., and *M. favosa* (Desr.) Naudin are probably not closely related to South American species such as *M. chionophila* Naudin, *M. bullata* (Turcz.) Triana, *M. latifolia* (D. Don) Naudin, *M. integrifolia* Cogn., *M. cernua* Naudin, *M. campii* Wurd., and *M. hymenantha* Triana, because of differences in anther and stigma form. Members of the latter group have anthers with bilobed basal appendages and open by elongate slit-like (rimose) to a gaping apical pore (with protruding septum). These latter species are phenetically similar to members of section *Cremanium*, and may be related to this group (see comments in Gleason 1958). These few examples illustrate the point that sectional boundaries are often vague; their clarification is beyond the scope of this paper. Fortunately, since these species represent various clades within the presumed monophyletic element within

Miconia, it is not necessary to determine their exact cladistic relationships in order to consider the delimitation of *Miconia* from related genera.

Icaria J. F. Macbr. is clearly correctly included by Wurdack (1972) in *Miconia* (within section *Chaenopleura*, as delimited by Cogniaux 1891) because the anthers of *I. ficilis* J. F. Macbr. are specialized and open by longitudinal slits. The presence of filaments that are basally broadened is merely an autapomorphy (at best, since such filaments also occur in other species of *Miconia*); see discussion in Wurdack (1972).

Several species lack any of the derived anther features listed above and are placed in *Miconia* purely for convenience. Such species have unappendaged ovoid anthers opening by a small apical pore, and include species such as *M. nitidissima*, *M. reducens*, *M. schlimii*, and the various species probably related to *Tetrazygia*, e.g., *M. mexicana*, *M. humilis*, and *M. baracoensis* Urban. Detailed cladistic study of the species of *Miconia* may lead to the segregation of these primitive elements (either as members of currently recognized genera, or as newly recognized genera). At this time the species relationships within *Miconia* are still too poorly known to attempt such segregation. Thus, a metaphyletic (likely paraphyletic) *Miconia* is maintained.

The West Indian species of *Miconia* section *Chaenopleura* form a specialized monophyletic group, which can be defined on the basis of its obovate, white anthers opening by two longitudinal slits, and arranged in an actinomorphic fashion (Fig. 7 A,B; Judd and Beaman 1988). Their seeds have a smooth testa (Fig. 10 B). Representatives of this clade include: *M. krugii*, *M. zanonii* W. Judd, Skean, and R. Beaman, *M. coniophora* Urban and E. Ekman, *M. stenobotrys*, *M. barkeri* Urban and E. Ekman, *M. calycina* Cogn., *M. septentrionalis* W. Judd and R. Beaman, *M. jimenezii* W. Judd and R. Beaman, *M. subcompressa*, *M. hypiodes* Urban and E. Ekman, *M. ferruginea*, *M. rigidissima* Urban and E. Ekman, *M. macayana* W. Judd and Skean, *M. desportesii* Urban, *M. favosa*, *M. sintenisii*, *M. foveolata* Cogn., *M. rigida*, *M. quadrangularis*, *M. samanensis* Urban, *M. luteola* Cogn., *M. rufa* (Griseb.) Triana, and *M. selleana* Urban and E. Ekman.

Several species groups usually placed elsewhere need to be transferred into *Miconia* because they possess apomorphies linking them with hypothesized clades in the monophyletic element of the genus. The species currently placed in *Charianthus* are actually cladistic relatives of some species within sections *Miconia* and *Chaenantha* (as is discussed above). The species of *Ossaea* section *Octopleura* (Griseb.) Cogn. and some species of *Clidemia* (*C. gracilis* Pittier and relatives) are also related to a species-group within section *Miconia* as is discussed below.

Several species of *Miconia* section *Miconia*, e.g., *M. carassana* Cogn. and *M. diaphanea* Gleason, have fairly narrow petals with nearly acute apices (although still rounded at the extreme tip). These species also have anthers with a dorso-basal appendage (sometimes bearing gland-headed hairs, see *M. carassana*). *Miconia carassana* also has conspicuously ribbed hypanthia. The

presence of ribbed hypanthia and dorso-basal anther appendages bearing gland-headed hairs are also diagnostic characters of *Ossaea* section *Octopleura*, a group of *Ossaea* species with terminal inflorescences, and some species of *Clidemia* (*C. densiflora* (Standley) Gleason). These two apomorphies are hypothesized to link these phenetically similar species-groups within *Miconia* and *Ossaea*. Some terminal-flowered species of *Clidemia* also possess anthers with a dorso-basal anther connective and fruits with conspicuous ribs, and are tentatively included in this group. Taking *M. carassana* as a provisional out-group, the relationships of these species of *Ossaea* and *Clidemia* were investigated and are briefly outlined here.

The presence of pseudolateral inflorescences and petals with \pm acute apices can be taken as synapomorphies of the group. The various species of *Ossaea* section *Octopleura* likely comprise a paraphyletic and cladistically basal assemblage; representative species include: *O. brenešii* Standley, *O. macrophylla* Cogn., *O. spicata* Gleason, *O. bracteata* Triana, *O. boekei* Wurd., *O. sparrei* Wurd., *O. quinquenervia* (Mill.) Cogn., *O. laxivenula* Wurd. (Wurdack 1980, fig. 38), *O. sessilifolia* (Triana) Wurd., and *O. micrantha* (Sw.) Cogn. The related species of *Clidemia* form a monophyletic group (nested within *Ossaea* sect. *Octopleura*) and recognizable on the basis of a reversal to blunt petals (although a few species have narrow petals that are rounded only at the extreme apex, e.g., *C. densiflora*). *Clidemia densiflora* may be a cladistically basal species within this blunt-petaled clade. More specialized species are characterized by clearly anisophyllous leaves. Species with only this additional apomorphy include: *C. purpurea* D. Don, *C. radicans* Cogn., *C. biolleyana* Cogn., and *C. reitzlana* Gleason. The remaining terminal-flowered *Clidemia* species (considered here) possess the additional synapomorphy of an indumentum of only minute glandular hairs. Among members of this presumably derived clade, *C. gracilis* is likely basal; the remaining species included in this survey show the apomorphic loss of thickened hypanthium/fruit ribs, i.e., *C. ombrophila* Gleason, *C. semijuga* (Gleason) Wurd., and *C. pittieri* Gleason (Gleason 1958, fig. 83). These derived species of *Clidemia* are phenetically very divergent from typical members of *Ossaea* section *Octopleura*, however, they are connected via a whole series of intermediate species, clearly demonstrating that they are members of the same clade. It is recommended that these species of *Ossaea* and *Clidemia* (and relatives) be transferred to *Miconia*, following more detailed revisionary studies of this complex. The inclusion of the species of *Ossaea* section *Octopleura* (along with related *Clidemia* spp.) and *Charianthus* within *Miconia* really only slightly expands the range of variation within the genus since it already includes species with bright red flowers and others with acute petals.

SUMMARY

The basic taxonomic pattern visible within this diverse group may have resulted from rapid diversification from a basal complex. Various successful (i.e., species rich) and phenetically divergent lineages are recognizable within the terminal-flowered members of the tribe, such as *Conostegia*, *Tococa*, *Clidemia*, *Leandra*, and *Miconia*. Other recognizable lineages are quite small, e.g., *Anaectocalyx*, *Calycogonium*, or *Pachyanthus*. However, the cladistically basal members of these genera, regardless of group size, are very often difficult to distinguish from certain species of *Miconia*, a genus that likely contains species that are members of small, phenetically generalized clades, basal members of lineages whose derived species are placed in segregate genera, as well as species showing numerous distinctive apomorphies. As is typical in such situations, the traditional classifications of Miconieae have resulted in a large, more or less phenetically central, paraphyletic, and polymorphic *Miconia* "surrounded" by a series of smaller, monophyletic (or polyphyletic), fairly uniform (or extremely heterogeneous), segregate genera, which are more or less arbitrarily delimited. The level of homoplasy within the tribe is very high, as is easily seen in Table 1. Numerous apomorphic features have evolved in more than one recognized clade.

Although high levels of homoplasy, and the lack of discrete morphological gaps (a hypothesized result of gradual accumulation of apomorphies within various clades coupled with the lack of extinction) have made generic delimitation difficult in the Miconieae, a preliminary analysis of the pattern of synapomorphies has clarified generic limits within the tribe. Twenty genera are provisionally recognized, some of which have circumscriptions somewhat altered when compared to traditional classifications. These genera include the terminal-flowered *Anaectocalyx*, *Calycogonium*, *Clidemia*, *Conostegia*, *Leandra*, *Miconia*, *Pachyanthus*, *Tetrazygia*, and *Tococa*; and the axillary-flowered *Chalybea*, *Henriettea*, *Huilaea*, *Killipia*, *Kirkbridea*, *Loreya*, *Maieta*, *Mecranium*, *Pentossaea*, and *Sagraea*. The placement of the isolated genus, *Catocoryne*, has not been addressed. The evolutionary relationships of the axillary-flowered genera are treated in Judd (1989).

A provisional dichotomous key to terminal-flowered Miconieae is provided below, not only as an aid in identification, but also as a summary of morphological features characterizing each genus (as delimited herein). Alternatively, Table 1 can be used as a polyclave for identification of terminal-flowered Miconieae. In addition, terminal-flowered genera whose circumscription has been substantially altered as a result of this study are described in the Appendix. A key to axillary-flowered genera is presented in Judd (1989).

KEY TO TERMINAL-FLOWERED GENERA OF MICONIEAE

1. Plants creeping, slender-stemmed herbs with leaves 2-5 mm long and wide..... *Catocoryne*.
1. Plants shrubs to trees, or rarely lianas, usually erect with leaves much larger.....2.
2. Internal calyx lobes fused into a stout conical cap which ruptures circumscissily at anthesis; flowers pedicellate; external calyx lobes lacking.....*Conostegia*.
2. Internal calyx lobes free, or if fused than forming a minute, membranous, dome-shaped cap that ruptures \pm irregularly; flowers sessile to pedicellate; external calyx lobes lacking or present...
.....3.
3. Anther sacs basally bifurcate; internal calyx lobes very elongate and individually caducous; external calyx lobes lacking.....*Anaectocalyx*.
3. Anther sacs various, but not basally bifurcate; internal calyx lobes shorter and/or persistent, if deciduous than falling as a unit through the development of a circumscissile slit; external calyx lobes usually present (and minute to elongate).....4.
4. Leaves with pouch-like formicaria at base of blade.....5.
4. Leaves lacking formicaria, or if present than with bilobed formicaria at extreme base of petiole.....6.
5. Inflorescences obviously terminal, or if pseudolateral then hypanthium/calyx usually \pm winged; anthers with small dorso-basal tooth, stout, \pm straight; external calyx lobes usually short and \pm inconspicuous, if elongate than clearly tapering from base to apex.....*Tococa*.
5. Inflorescences pseudolateral and hypanthium not winged; anthers usually lacking dorso-basal tooth, often elongate-slender, \pm curved and tapering toward apex; external calyx lobes usually elongate and \pm terete.....*Clidemia* (myrmecophilous species).
6. Style glabrous, slender, with minute, non-expanded stigma, usually \pm strongly curved distally; twigs usually not conspicuously strigose; hypanthium usually \pm constricted.....*Tetrazygia*.
6. Style glabrous or pubescent, slender to stout, with very slightly to greatly expanded stigma, usually straight to slightly curved; twig indumentum variable; hypanthium constricted or not.....7.
7. Shoots usually producing only a single node bearing leaves prior to initiation of clearly terminal inflorescence; external calyx lobes very often flattened either parallel or perpendicular to floral radii; flowers 4-merous, pedicellate to sessile; hypanthium cylindrical, quadrangular, or clearly 4-lobed; leaves often with conspicuous hair-tuft mite-domatia at junction of midvein with two major secondary veins; hypanthium never densely strigose.....*Calycogonium*.
7. Shoots usually producing several nodes bearing leaves before initiation of clearly terminal inflorescence, or if only one node bearing leaves is produced than inflorescence pseudolateral or flowers greater than 4-merous; external calyx lobes usually \pm terete; flowers 4- to 9-merous, \pm sessile; hypanthium usually \pm cylindrical; leaves usually lacking hair-tuft domatia in axils of midvein and two major secondary veins; hypanthium indumentum variable.....8.
8. Elongate multicellular hairs lacking; inflorescence usually reduced to one (or very few) flowers, with flattened axes; flowers 5- or 6-merous; fruits cylindrical to globose, \pm robust (6-17 mm long), with persistent, coriaceous hypanthium/calyx; inflorescences always terminal.....
.....*Pachyanthus*.
8. Plants without the above combination of characters; elongate multicellular hairs present or absent; inflorescence reduced or not, usually with terete axes; flowers 4- to 9-merous; fruits \pm globose, usually small to moderate-sized (3-12 mm long), with persistent or deciduous, membranaceous to \pm chartaceous hypanthium/ calyx; inflorescences terminal to pseudo-lateral....
.....9.
9. Anthers ovate, stout, straight to slightly curved, opening by minute terminal pore, and lacking appendages (or hairs) except for small dorso-basal tooth; external calyx lobes short; petals blunt; leaves usually \pm sessile; inflorescences terminal; seeds smooth.....
.....*Tococa* (non-myrmecophilous species) ³.
9. Anthers various, but not as above; external calyx lobes short to elongate; petals blunt or acute; leaves sessile to petiolate; inflorescences terminal or pseudolateral; seeds smooth to papillose.....
.....10.

10. Plants lacking the above combination of characters; petals blunt to acute/acuminate, glabrous to pubescent or with apical hair(s); external calyx lobes short to elongate; anthers as indicated in couplet 11; seeds smooth to papillose, occasionally appendaged; twigs conspicuously strigose to glabrous.....11.
11. Petals almost always acute to acuminate at apex (and corolla in a \pm sharply conical configuration in bud); hypanthium never conspicuously ribbed; external calyx lobes short to elongate; plants commonly conspicuously strigose-pubescent, never densely stellate on abaxial leaf surface; anthers usually yellow, short- to elongate-ovoid, and tapering to minute apical pore, lacking appendages or sometimes with short to elongate dorso-basal tooth, connective variously developed, sometimes thickened/elevated..... *Leandra*³.
11. Petals usually \pm blunt at apex (and corolla forming a \pm hemispherical configuration in bud), or if acute then anthers with a glandular-pubescent, dorso-apical tooth and conspicuously ribbed hypanthium; hypanthium ribbed or not; external calyx lobes usually short and inconspicuous; plants only occasionally densely strigose-pubescent, sometimes densely stellate-pubescent on abaxial leaf surface; anthers yellow, white, purple, or pink, short- to elongate-ovate, elliptic, oblong, or obovate, usually with connective variously developed, sometimes prolonged or appendaged at base (often covered with glandular hairs), or with variously developed basal appendage composed of sterile portion of anther sacs and connective tissue, opening by minute apical pore, expanded apical pore (as wide as anther locules or much wider, often with protruding septum), or longitudinal slits..... *Miconia*.

NOMENCLATRURAL CHANGES

We have not attempted to make the numerous nomenclatural combinations implied by this study. Such action would be premature, and should be left to future monographers who have comprehensive understanding of species boundaries in these genera. Below we have made twenty-one nomenclatural changes that are extremely clear and useful to us in current projects. These involve transferring appropriate Hispaniolan, Jamaican and Puerto Rican species to *Calycogonium*, *Clidemia*, *Leandra*, or *Miconia*, transferring *Charianthus* species to *Miconia*, and transferring *Miconia lundelliana* to the genus *Pachyanthus*.

Calycogonium apleurum (Urban and E. Ekman) W. Judd and Skean, comb. nov., *Mommsenia apleura* Urban and E. Ekman, Ark. Bot. 20A (5): 31. 1926.

Calycogonium lomensis (Urban) W. Judd and Skean, comb. nov., *Ossaea lomensis* Urban, Fedde Repert. 13: 467. 1915.

Calycogonium reticulatum (Cogn.) W. Judd and Skean, comb. nov., *Henriettella reticulata* Cogn. in Urban, Symb. Antill. 7: 315. 1912. Often treated as *Ossaea reticulata* (Cogn.) E. Ekman ex Urban, Ark. Bot. 23A (11): 27. 1931.

Calycogonium tetragonolobum (Cogn.) W. Judd and Skean, comb. nov., *Clidemia tetragonoloba* Cogn. in Urban, Symb. Antill. 7: 315. 1912.

³ Some species of these groups/genera are distinguished from *Miconia* only with difficulty.

- Clidemia angustilamina* W. Judd and Skean, nom. nov., for *Heterotrichum angustifolium* DC., Prodr. 3: 173. 1828.
- Leandra alloetricha* (Urban) W. Judd and Skean, comb. nov., *Ossaea alloetricha* Urban, Ark. Bot. 22A (17): 64. 1929.
- Leandra glomerata* (Naudin) W. Judd and Skean, comb. nov., *Sagraea glomerata* Naudin, Ann. Sci. Nat. Sér. 3, 18: 96. 1852. Often treated as *Ossaea glomerata* (Naudin) Triana, Trans. Linn. Soc. 28: 146. 1871. *Ossaea lanceolata* Urban and E. Ekman, of Hispaniola, is closely related (and may be conspecific).
- Leandra hirsuta* (Sw.) W. Judd and Skean, comb. nov., *Melastoma hirsuta* Sw., Prodr. Veg. Ind. Occ. 72. 1788. Often treated as *Ossaea hirsuta* (Sw.) Triana, Trans. Linn. Soc. Bot. 28: 146. 1871.
- Leandra inaequidens* (Urban and E. Ekman) W. Judd and Skean, comb. nov., *Ossaea inaequidens* Urban and E. Ekman, Ark. Bot. 22A (17): 63. 1929.
- Leandra krugiana* (Cogn.) W. Judd and Skean, comb. nov., *Ossaea krugiana* Cogn. in A. DC., Monogr. Phan. 7: 1048. 1891.
- Leandra krugii* (Cogn.) W. Judd and Skean, comb. nov., *Calycogonium krugii* Cogn., Jahrb. Bot. Gart. Berlin 4: 279. 1886.
- Leandra lima* (Desr.) W. Judd and Skean, comb. nov., *Melastoma lima* Desr. in Lam. and Poiret, Encycl. 4: 47. 1797. Often treated as *Ossaea lima* (Desr.) Triana, Trans. Linn. Soc. 28: 147. 1871.
- Leandra limoides* (Urban) W. Judd and Skean, comb. nov., *Ossaea limoides* Urban, Ark. Bot. 21A (5): 50. 1927.
- Leandra pratensis* (Macfad.) W. Judd and Skean, comb. nov., *Ossaea pratensis* Macfad., Fl. Jam. 2: 48. 1850. Often referred to as *Ossaea microphylla* (Sw.) Triana, Trans. Linn. Soc. 28: 146. 1871, based on *Melastoma microphyllum* Sw., Prodr. Veg. Ind. Occ. 72. 1788.
- Miconia coccinea* (Rich.) W. Judd and Skean, comb. nov., *Melastoma coccinea* Rich., Actes Soc. Hist. Nat. Paris 1: 109. 1792. Typically treated as *Charianthus alpinus* (Sw.) R. Howard, J. Arnold Arbor. 53: 401. 1972, based on *Melastoma alpina* Sw., Prodr. 71. 1788.
- Miconia corymbosa* (Rich.) W. Judd and Skean, comb. nov., *Melastoma corymbosa* Rich., Actes Soc. Hist. Nat. Paris 1: 109. 1792. Previously considered as *Charianthus corymbosus* (Rich.) Cogn. in A. DC., Monogr. Phan. 7: 714. 1891.
- Miconia fadyenii* (Hook.) W. Judd and Skean, comb. nov., *Tetrazygia fadyenii* Hook., Hooker's J. Bot. Kew Gard. Misc. 1: 379, t. 12. 1849. Usually treated as *Charianthus fadyenii* (Hook.) Griseb., Fl. Brit. W. Ind. 264. 1860.
- Miconia leblondii* W. Judd and Skean, nom. nov. for *Melastoma nodosa* Desr. in Lam. and Poiret, Encycl. 4: 55. 1797. Usually treated as *Charianthus nodosus* (Desr.) Triana, Trans. Linn. Soc. 28: 99. 1871.

- Miconia purpurea* (D. Don) W. Judd and Skean, comb. nov., *Charianthus purpureus* D. Don, Mem. Wern. Nat. Hist. Soc. 4: 329. 1823, nom. nov. for *Melastoma coccinea* M. Vahl, Eclog. Amer. 1: 48. 1797, a later homonym of *M. coccinea* Rich., 1792.
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APPENDIX

Generic descriptions and species examined.

ANAECTOCALYX: Circumscription not altered as a result of this study; see Wurdack (1973) for description.

Species examined: *Anaectocalyx bracteosa* (Naudin) Triana

CALYCOGONIUM: Evergreen shrubs with determinate shoots; twigs terete to angled, nodose, with a ridge encircling each node, usually producing a single leafy node (or sometimes two nodes) before forming a terminal inflorescence; druse crystals present. Indumentum of conspicuous to very reduced stellate hairs, sometimes intermixed with minute, multicellular, glandular hairs, or slender, elongate-strigose, multicellular hairs with or without glandular apices, occasionally densely covered with ferruginous peltate scales, occurring on stems, leaves, inflorescence axes, and hypanthia. Leaves opposite, decussate, petiolate, coriaceous to chartaceous, flat to strongly abaxially curved; margin serrate to entire, plane to strongly revolute, the teeth (if present) sometimes ending in an elongate multicellular hair; venation acrodromous, suprabasal, with a prominent midvein, usually 1 or 2 pairs of secondary veins (although these occasionally inconspicuous), and numerous percurrent tertiary veins \pm perpendicular to midvein; often with conspicuous mite-domatia formed by a dense tuft of elongate multicellular hairs in the axil of the midvein and 2 larger secondary veins, the hairs sometimes \pm connate, forming a brownish conical structure. Inflorescences terminal (or rarely terminal and axillary) cymes, often reduced to a capitate cluster or only 1-3 flowers. Flowers perfect, 4-merous, pedicellate to \pm sessile. Hypanthium cylindric, 4-angled, or markedly 4-lobed, sometimes constricted above ovary, the indumentum various, but never densely covered with stout, elongate-strigose, multicellular hairs. External calyx lobes 4, inconspicuous to more commonly elongate, flattened either perpendicular or parallel to the floral radii, rarely \pm terete; internal calyx lobes 4, distinct, not calyptrate, broadly triangular. Petals 4, ovate to obovate, with acuminate, acute, to blunt apex, glabrous. Stamens 8, \pm isomorphic, glabrous, geniculate, inserted at apex of hypanthium and deflexed to one side of flower; anthers ovate, straight to curved, dehiscing by a small apical pore, the connective usually non-appendaged, rarely with a slight to moderate, dorso-basal thickening. Ovary \pm inferior, 4- or 2-locular, with axile placentation, the ovules numerous; style cylindrical, curved to \pm straight, glabrous; stigma capitate, papillose. Fruit a berry. Seeds small, rounded to angular-obovate, the testa \pm smooth.

Species examined:

Calycogonium apiculatum Urban & E.
Ekman

Calycogonium apleurum (Urban & E.
Ekman) W. Judd & Skean

Calycogonium calycopteris (Rich.) Urban

Calycogonium domatiatum Urban & E.
Ekman

Calycogonium ekmanii Urban

Calycogonium glabratum (Sw.) DC.

Calycogonium grisebachii Triana

Calycogonium heterophyllum Naudin

Calycogonium hispidulum Cogn.

Calycogonium impressum Urban & E.
Ekman

Calycogonium lomensis (Urban) W. Judd &
Skean

Calycogonium reticulatum (Cogn.) W. Judd
& Skean

Calycogonium rhamnoides Naudin

Calycogonium rhomboideum Urban & E.
Ekman

Calycogonium rosmarinifolium Griseb.

Calycogonium tetragonolobum (Cogn.) W.
Judd & Skean

Calycogonium torbecianum Urban & E.
Ekman

Calycogonium turbinatum Urban & E.
Ekman

Clidemia pterosepala (Urban) Alain

Clidemia wrightii Griseb.

CLIDEMIA: Evergreen shrubs with determinate shoots; twigs terete, nodose, with a ridge encircling each node, producing one to several leafy nodes before forming a terminal inflorescence; druse crystals present. Indumentum of slender, elongate-strigose, multicellular hairs with or without glandular apices (and such hairs usually densely distributed), along with multicellular, minute glandular hairs or stellate hairs, occurring on stems, leaves, inflorescence axes, and hypanthia. Leaves opposite, decussate, sometimes clearly anisophyllous, petiolate, coriaceous, \pm flat; margin entire to irregularly serrate, \pm plane, the teeth (if present) ending in an elongate, multicellular hair; venation acrodromous, basal to suprabasal, with a prominent midvein, usually 1 to 4 pairs of secondary veins (although some of these occasionally inconspicuous), and numerous percurrent tertiary veins \pm perpendicular to midvein; sometimes with formicaria, these pouch-like, smooth or corrugated, and positioned at base of lamina, or bilobed and positioned at base of petiole; mite-domatia usually lacking. Inflorescences terminal cymes, sometimes reduced and capitate, spicate, or even one-flowered, obviously terminating branch to pseudolateral, i.e., soon deflexed to a seemingly lateral position by development of an axillary shoot with the branch forming a sympodium (with usually only 1 leafy node per shoot); inflorescence branches \pm terete; bracts occasionally expanded and persistent. Flowers perfect, 4- to 7-merous, \pm sessile. Hypanthium cylindric, \pm unlobed, only rarely constricted above ovary, with multicellular, elongate-strigose hairs, and minute glandular or stellate hairs. External calyx lobes 4 to 7, usually conspicuously elongated, \pm terete; internal calyx lobes 4 to 7, distinct, not calyptrate, broadly triangular to nearly obsolete. Petals 4 to 7, ovate to obovate, with blunt apex, glabrous (or rarely with few glandular hairs along margin). Stamens 8 to 14, \pm isomorphic, glabrous, geniculate, inserted at apex of hypanthium and deflexed to one side of flower; anther ovate, straight with curved, dehiscent by small apical pore, the connective non-appendaged. Ovary superior to inferior, 3-12-locular, with axile placentation, the ovules numerous; style cylindrical, curved, glabrous to glandular-pubescent; stigma capitate, papillose. Fruit a berry, sometimes robust. Seeds small, rounded to angular-obovoid, the testa usually moderately to strongly papillose, occasionally papillae only in lines along seed-angles, rarely \pm smooth.

Species examined:

- | | |
|--|---|
| <i>Clidemia allardii</i> Wurd. | <i>Clidemia petiolaris</i> (Schecht. & Cham.) |
| <i>Clidemia angustilamina</i> W. Judd & Skean | Schlecht. ex Triana |
| <i>Clidemia biserrata</i> DC. | <i>Clidemia pilosa</i> D. Don |
| <i>Clidemia bullosa</i> DC. | <i>Clidemia pustulata</i> DC. |
| <i>Clidemia capitata</i> Benth. | <i>Clidemia scopulina</i> (Brandege) L. O. |
| <i>Clidemia capitellata</i> (Bonpl.) D. Don | Williams |
| <i>Clidemia ciliata</i> D. Don | <i>Clidemia setosa</i> (Triana) Gleason |
| <i>Clidemia collina</i> Gleason | <i>Clidemia strigilosa</i> (Sw.) DC. |
| <i>Clidemia crenulata</i> Gleason | <i>Clidemia taurina</i> Gleason |
| <i>Clidemia dentata</i> D. Don | <i>Clidemia umbellata</i> (Mill.) L. O. Williams |
| <i>Clidemia erythropogon</i> DC. | (= <i>Heterotrichum umbellatum</i> (Mill.) |
| <i>Clidemia fulva</i> Gleason | Urban) |
| <i>Clidemia heptamera</i> Wurd. | <i>Clidemia urceolata</i> DC. |
| <i>Clidemia hirta</i> D. Don | <i>Miconia araguensis</i> Wurd. (= <i>Heterotrichum</i> |
| <i>Clidemia involucrata</i> DC. | <i>glandulosum</i> Cogn.) |
| <i>Clidemia killipii</i> Gleason | <i>Miconia laevipilis</i> Wurd. (= <i>Heterotrichum</i> |
| <i>Clidemia laevifolia</i> Gleason | <i>racemosum</i> Wurd.) |
| <i>Clidemia matudae</i> L. O. Williams | <i>Miconia macrodon</i> (Naudin) Wurd. |
| <i>Clidemia neblinae</i> Wurd. | (= <i>Heterotrichum macrodon</i> |
| <i>Clidemia octona</i> (Bonpl.) L. O. Williams | (Naudin) Planch. ex Hook. f.) |

Miconia porphyrotricha (Markgraf) Wurd.
(= *Heterotrichum porphyrotrichum*
Markgraf)

Miconia tuberculata (Naudin) Triana
(= *Heterotrichum rostratum* (Naudin)
Gleason)

Myrmidone macrosperma (C. Martius) C.
Martius; probably congeneric with
Clidemia (see text)

Tococa carolensis Gleason, closely related
to *Myrmidone macrosperma* (see
text)

Tococa spadiceiflora Triana

CONOSTEGIA: Circumscription not altered as a result of this study; see descriptions in Wurdack (1973, 1980), Howard (1989).

Species examined:

Conostegia arborea (Schlecht.) Steud.
Conostegia attenuata Triana
Conostegia balbisiana Ser. ex DC.
Conostegia brenesii Standley
Conostegia chiriquensis Gleason
Conostegia formosa Macfad.
Conostegia hirtella Cogn.
Conostegia icosandra (Sw.) Urban
Conostegia lindenii Cogn.
Conostegia macrantha Berg ex Triana
Conostegia micrantha Standley

Conostegia montana (Sw.) DC.
Conostegia oerstediana Berg ex Triana
Conostegia pittieri Cogn.
Conostegia polyandra Benth.
Conostegia procera (Sw.) DC.
Conostegia pyxidata Proctor
Conostegia rhodopetala Donn.-Sm.
Conostegia setosa Triana
Conostegia speciosa Naudin
Conostegia subcrustulata (Berul.) Triana
Conostegia superba Naudin
Conostegia volcanalis Standley & Steyerm.
Conostegia xalapensis (Bonpl.) DC.

LEANDRA: Evergreen shrubs, sometimes epiphytic, rarely lianas, with determinate shoots; twigs terete, nodose, with a ridge encircling each node, producing a single to several leafy nodes before forming a terminal inflorescence; druse crystals present. Indumentum of slender to extremely thick, smooth to minutely roughened, often thick-based, elongate-strigose, multicellular hairs with or without glandular apices, these hairs often densely distributed, occasionally limited to vein-axil mite-domatia or entirely lacking, along with multicellular, stellate or minute glandular hairs, occurring on stems, leaves, inflorescence axes, and hypanthia. Leaves opposite to alternate (due to loss of one leaf of the nodal pair), sometimes strongly anisophyllous, decussate, petiolate to nearly sessile, coriaceous to chartaceous, \pm flat; margin entire to irregularly serrate, plane to revolute, the teeth (if present) ending in an elongate multicellular hair; venation acrodromous, basal to suprabaasal, with a prominent midvein, usually 1 to 3 pairs of secondary veins (although some of these occasionally inconspicuous), and numerous percurrent tertiary veins \pm perpendicular to midvein; rarely with mite-domatia formed by dense tuft of elongate multicellular hairs in vein axils. Inflorescence terminal (or very rarely terminal and axillary) cymes, sometimes capitate, spicate, or even reduced to a single flower, obviously terminating branch to pseudolateral, i.e., soon deflexed to a seemingly lateral position by development of an axillary shoot, with the branch forming a sympodium (with usually one leafy node produced per shoot); inflorescence axes terete, rarely flattened; inflorescence bracts sometimes expanded, persistent to deciduous. Flowers perfect, 4-6-merous, \pm sessile. Hypanthium \pm cylindrical, neither strongly lobed nor constricted above ovary, the indumentum various, but often densely strigose. External calyx lobes 4 to 6, short to more commonly elongate, \pm terete, rarely flattened; internal calyx lobes 4 to 6, distinct, not calyptrate, broadly triangular. Petals 4 to 6, narrowly triangular to ovate (less commonly to obovate), with acuminate to acute (or rarely blunt) apex, glabrous or with a single or dorsal cluster of elongate-strigose, multicellular hairs at to near apex. Stamens 8 to 12, \pm isomorphic, glabrous or rarely glandular pubescent (on filament), geniculate, inserted at apex of hypanthium and deflexed to one side of flower; anthers ovate, straight to curved, dehiscing by small apical pore, the connective not to clearly thickened, non-appendaged or with a short to elongate dorso-basal appendage. Ovary nearly superior to inferior, 2-6-locular, with axile placentation, the ovules numerous; style cylindrical, straight to gradually curved, rarely strongly curved distally, usually glabrous (to glandular-pubescent); stigma capitate, papillose. Fruit a berry. Seeds small, rounded to angular-obovoid, the testa smooth to conspicuously papillate,

sometimes appendaged (due to development of projection composed of large, thin-walled cells at seed's wider end).

Species examined:

- Clidemia alternifolia* Wurd.
Clidemia japurensis DC.
Clidemia naevula (Naudin) Triana
Clidemia utleyana Almeda
Leandra acutifolia (Naudin) Cogn.
Leandra adenothrix Cogn.
Leandra alleotricha (Urban) W. Judd & Skean
Leandra amplexicaulis DC.
Leandra aristigera (Naudin) Cogn.
Leandra atropurpurea Cogn.
Leandra aurea (Cham.) Cogn.
Leandra australis (Cham.) Cogn.
Leandra bergiana Cogn.
Leandra cancellata Cogn.
Leandra carassana Cogn.
Leandra cardiophylla Cogn.
Leandra chaetodon (DC.) Cogn.
Leandra clidemioides (Naudin) Wurd.
Leandra cordigera (Triana) Cogn.
Leandra cornioides (Schlecht. & Cham.) Cogn.
Leandra costaricensis Cogn.
Leandra crenata Cogn.
Leandra dasytricha (A. Gray) Cogn.
Leandra debilis (Naudin) Cogn.
Leandra dichotoma (D. Don) Cogn.
Leandra dispar (Gardn.) Cogn.
Leandra echinata Cogn.
Leandra eggersiana Cogn. (= *Ossaea asperifolia* (Naudin) Triana)
Leandra erostrata (DC.) Cogn.
Leandra fragilis Cogn.
Leandra francavillana Cogn.
Leandra glomerata (Naudin) W. Judd & Skean
Leandra grandifolia Cogn.
Leandra grayana Cogn.
Leandra hirsuta (Sw.) W. Judd & Skean
Leandra hirta Raddi
Leandra inaequidens (Urban & E. Ekman) W. Judd & Skean
Leandra involucrata DC.
Leandra ionopogon (C. Martius) Cogn.
Leandra krugiana (Cogn.) W. Judd & Skean
Leandra krugii (Cogn.) W. Judd & Skean
Leandra lacunosa Cogn.
Leandra laevigata (Triana) Cogn.
Leandra lasiopetalata Cogn.
Leandra laxa Cogn.
Leandra lima (Desr.) W. Judd & Skean
Leandra limoides (Urban) W. Judd & Skean
Leandra lindeniana (Naudin) Cogn.
Leandra longicoma Cogn.
Leandra melanodesma (Naudin) Cogn.
Leandra melastomoides Raddi
Leandra mexicana (Naudin) Cogn.
Leandra multiplinervis (Naudin) Cogn.
Leandra nanayensis Wurd.
Leandra nervosa (Naudin) Cogn.
Leandra nianga (DC.) Cogn.
Leandra parvifolia Cogn.
Leandra polystachya Cogn.
Leandra pratensis (Macfad.) W. Judd & Skean (= *Ossaea microphylla* (Sw.) Triana)
Leandra pulverulenta (DC.) Cogn.
Leandra purpurascens (DC.) Cogn.
Leandra quinqueidentata Cogn.
Leandra rhodopogon (DC.) Cogn.
Leandra riedeliana Cogn.
Leandra rufescens (DC.) Cogn.
Leandra salicina (DC.) Cogn.
Leandra scabra DC.
Leandra secunda (D. Don) Cogn.
Leandra sericea DC.
Leandra subseriata (Naudin) Cogn.
Leandra subulata Gleason
Leandra sulfurea (Naudin) Cogn.
Leandra umbellata DC.
Leandra violascens Pilger (= *Ossaea boliviensis* (Cogn.) Gleason)
Ossaea araneifera Markgraf
Ossaea capitata Urban
Ossaea cucullata Gleason
Ossaea elliptica Alain
Ossaea granulata Urban
Ossaea hypoglauca (C. Wright ex Griseb.) Maza
Ossaea involucrata (Griseb.) C. Wright in Sauvalle
Ossaea lanata (Naudin) C. Wright in Sauvalle
Ossaea muricata (Griseb.) C. Wright in Sauvalle
Ossaea otoschmidtii Urban
Ossaea pauciflora (Naudin) Urban
Ossaea pulverulenta Urban
Ossaea shajeri Britton & P. Wilson
Ossaea turquinensis Urban
Ossaea verrucosa (Griseb.) Maza
Pleiochiton ebracteatum Triana; the genus *Pleiochiton* is likely congeneric with *Leandra*

MICONIA: Evergreen shrubs to small trees with determinate shoots; twigs terete to angled, nodose, usually with a ridge to conspicuous flange encircling each node, producing a single to several leafy nodes before forming a terminal inflorescence; druse crystals present. Indumentum extremely diverse, of multicellular, dendritic hairs, stellate hairs, peltate scales, slender, elongate-strigose hairs with or without glandular apices, and/or minute globular hairs, on stems, leaves, inflorescence axes, and hypanthia (see Wurdack, 1986); such hairs densely to sparsely distributed. Leaves opposite, rarely whorled, sometimes clearly anisophyllous, decussate, petiolate to sessile, coriaceous to membranaceous, flat to strongly abaxially curved; margin entire to strongly and irregularly serrate, plane to revolute, the teeth (if present) sometimes ending in an elongate multicellular hair; venation acrodromous, basal to suprabasal, with a prominent midvein, usually 1 to 3 pairs of secondary veins (although some of these often inconspicuous), and numerous percurrent tertiary veins \pm perpendicular to midvein; rarely with hair-tuft or pouch-like mite-domatia in vein axils. Inflorescences terminal cymes, very diverse in form, sometimes capitate, spicate, or reduced to few flowers, obviously terminating branch to pseudolateral, i.e., soon deflexed to a seemingly lateral position by development of an axillary shoot, with the branch forming a sympodium (with usually 1 leafy node per shoot); inflorescence axes terete to rarely flattened; inflorescence bracts sometimes expanded. Flowers perfect or imperfect (and plants then dioecious), 4 or 5- (to 9)-merous, \pm sessile (to rarely shortly pedicellate). Hypanthium cylindrical to cylindrical-campanulate, rarely strongly lobed, occasionally constricted above ovary, sometimes with thickened longitudinal ribs, rarely winged, occasionally caducous by means of a circumscissile slit, the indumentum various. External calyx lobes 4 or 5 (to 9), usually short and inconspicuous, \pm terete to flattened; internal calyx lobes 4 or 5 (to 9), distinct, and broadly triangular to oblong, sometimes very reduced, or connate into a dome-shaped, irregularly rupturing, membranaceous cap. Petals 4 or 5 (to 9), obovate to ovate or narrowly triangular, with blunt to acuminate or acute apex, sometimes connivent, usually glabrous, but occasionally pubescent (stellate or glandular) or with a dorso-apical elongate-strigose hair. Stamens 4 to 10 (to rarely numerous), anisomorphic to isomorphic, glabrous to glandular-pubescent (on filament and/or anther-connective), geniculate, inserted on apex of hypanthium and radiating around flower (actinomorphic) or deflexed to one side (zygomorphic); anther ovate to obovate, straight to strongly curved, dehiscing by a minute apical pore, expanded apical pore (as wide as anther locules or much wider, often with protruding septum), or longitudinal slits, the connective variously developed, non-appendaged to sometimes prolonged or appendaged at base, or with variously developed basal appendage composed of sterile portion of anther sacs and connective tissue. Ovary nearly superior to inferior, 2-7-loculate, with axile placentation, the ovules few to numerous; style cylindrical, straight to curved, glabrous to variously pubescent; stigma capitate, sometimes greatly enlarged, papillose. Fruit a berry, occasionally robust. Seeds small to large, rounded to angular-obovoid, the testa smooth to conspicuously papillate, rarely appendaged.

Species examined:

- | | |
|---|---|
| <i>Clidemia biolleyana</i> Cogn. | <i>Miconia alternifolia</i> (Griseb.) Alain |
| <i>Clidemia densiflora</i> (Standley) Gleason | <i>Miconia atypifolia</i> Naudin |
| <i>Clidemia gracilis</i> Pittier | <i>Miconia amazonica</i> Triana |
| <i>Clidemia ombrophila</i> Gleason | <i>Miconia ampla</i> Triana |
| <i>Clidemia pittieri</i> Gleason | <i>Miconia amplexans</i> (Crüger) Cogn. |
| <i>Clidemia purpurea</i> D. Don | <i>Miconia andersonii</i> Fawcett & Rendle |
| <i>Clidemia radicans</i> Cogn. | <i>Miconia anisotricha</i> (Schlecht.) Triana |
| <i>Clidemia reitzlana</i> Gleason | <i>Miconia apiculata</i> Urban & E. Ekman |
| <i>Miconia abbreviata</i> Markgraf | <i>Miconia apostachya</i> (Bonpl.) DC. |
| <i>Miconia acuminifera</i> Triana | <i>Miconia argentea</i> (Sw.) DC. |
| <i>Miconia acutifolia</i> Ule | <i>Miconia argyrophylla</i> DC. |
| <i>Miconia adenocalyx</i> Urban & E. Ekman | <i>Miconia asclepiadea</i> Triana |
| <i>Miconia aeruginosa</i> Naudin | <i>Miconia aspergillaris</i> (Bonpl.) Naudin |
| <i>Miconia affinis</i> DC. | <i>Miconia attenuata</i> DC. |
| <i>Miconia alata</i> (Aubl.) DC. | <i>Miconia aurea</i> (D. Don) Naudin |
| <i>Miconia albicans</i> (Sw.) Triana | <i>Miconia aureoides</i> Cogn. |
| <i>Miconia albiviridis</i> Urban & E. Ekman | <i>Miconia bailloniana</i> J. F. Macbr. |
| <i>Miconia alborufescens</i> Naudin | <i>Miconia barbinervis</i> (Benth.) Triana |
| <i>Miconia alpina</i> Cogn. | <i>Miconia barkeri</i> Urban & E. Ekman |

- Miconia basiliensis* Urban & E. Ekman
Miconia biperulifera Cogn.
Miconia borealis Gleason
Miconia brachycalyx Triana
Miconia bracteolata (Bonpl.) DC.
Miconia brenesii Standley
Miconia brevipes Benth.
Miconia bullata (Turcz.) Triana
Miconia burchellii Triana
Miconia buxifolia Naudin
Miconia cabucu Hoehne
Miconia caelata (Bonpl.) DC.
Miconia caesia Cogn. & Gleason
Miconia calvescens DC.
Miconia calycina Cogn.
Miconia campanensis Urban & E. Ekman
Miconia candolleana Triana
Miconia cannabina Markgraf
Miconia capitellata Cogn.
Miconia carassana Cogn.
Miconia caudata (Bonpl.) DC.
Miconia centrodesma Naudin
Miconia ceramicarpa (DC.) Cogn.
Miconia chamissois Naudin
Miconia chionophila Naudin
Miconia chlorocarpa Cogn.
Miconia chrysocoma Gleason
Miconia chrysophylla (Rich.) Urban
Miconia ciliata (Rich.) DC.
Miconia cinerascens Miq.
Miconia coccinea (Rich.) W. Judd & Skean
Miconia concinna Almeda
Miconia condylata Wurd.
Miconia coniphora Urban & E. Ekman
Miconia corallina Spring
Miconia cordata Triana
Miconia coriacea (Sw.) DC.
Miconia cornifolia (Desr.) Naudin
Miconia coronata (Bonpl.) Cogn.
Miconia corymbosa (Rich.) W. Judd & Skean
Miconia costaricensis Cogn.
Miconia crassifolia Triana
Miconia crocea (Desr.) Naudin
Miconia cubatanensis Hoehne
Miconia cubensis (C. Wright ex Griseb.) C. Wright in Sauvalle
Miconia cuneata Triana ex Cogn.
Miconia curvipetiolata Gleason
Miconia cyanocarpa Naudin
Miconia desmantha Benth.
Miconia desportesii Urban
Miconia diaphanea Gleason
Miconia dielsiana Urban
Miconia dipsacea Naudin
Miconia dispar Benth.
Miconia dodecandra (Desr.) Cogn.
Miconia domingensis Cogn.
Miconia egensis Cogn.
Miconia eichleri Cogn.
Miconia elaeoides Naudin
Miconia elata (Sw.) DC.
Miconia elegans Cogn.
Miconia erioclada Triana
Miconia eugeniioides Triana
Miconia expansa Gleason
Miconia fadyenii (Hook.) W. Judd & Skean
Miconia fallax DC.
Miconia fasciculata Gardner
Miconia favosa (Desr.) Naudin
Miconia ferruginata DC.
Miconia ferruginea (Desr.) DC.
Miconia fissa Gleason
Miconia floribunda (Bonpl.) DC.
Miconia foveolata Cogn.
Miconia fragrans Cogn.
Miconia fuertesii Cogn.
Miconia fufuracea (M. Vahl) Griseb.
Miconia glaberrima Naudin
Miconia globulifera Cham.
Miconia gracilis Triana
Miconia gratissima Benth. ex Triana
Miconia guatemalensis Cogn.
Miconia heliotropoides Triana
Miconia hexamera Wurd.
Miconia hirella Cogn.
Miconia hispida Cogn.
Miconia holosericea (L.) DC.
Miconia hookeriana Triana.
Miconia hutchisonii Wurd.
Miconia hyemalis St. Hilaire & Naudin
Miconia hymenantha Triana
Miconia hypiodes Urban & E. Ekman
Miconia ibaguensis (Bonpl.) Triana
Miconia impetiolaris (Sw.) D. Don
Miconia inaequidens Naudin
Miconia involucrata Donn.-Sm.
Miconia ioneuira Griseb.
Miconia jimenezii W. Judd & R. Beaman
Miconia jucunda Triana
Miconia krugii Cogn.
Miconia lacera (Bonpl.) Naudin
Miconia laevigata (L.) DC.
Miconia lanata (DC.) Triana
Miconia lanceolata (Desr.) DC.
Miconia langsdorffii Cogn.
Miconia lateriflora Cogn.
Miconia latifolia (D. Don) Naudin
Miconia leblondii W. Judd & Skean
Miconia ledifolia (DC.) Naudin
Miconia lepidota DC.
Miconia leptantha Urban & E. Ekman
Miconia ligulata Almeda (= *Leandra consimilis* Gleason)
Miconia ligustrina (Sw.) Triana
Miconia ligustroides (DC.) Naudin
Miconia longifolia (Aublet) DC.
Miconia longispicata Triana

- Miconia loreyoides* Triana
Miconia luteola Cogn.
Miconia lutescens (Bonpl.) DC.
Miconia macayana W. Judd & Skean
Miconia macrophylla Triana
Miconia macrothyrsa Benth.
Miconia majalis Cogn.
Miconia mandonii Cogn. ex Britton
Miconia mansfeldiana Urban & E. Ekman
Miconia marginata Triana
Miconia matthaei Naudin
Miconia media (D. Don) Naudin
Miconia megalantha Gleason
Miconia melanotricha (Triana) Gleason
Miconia membranacea Triana
Miconia meridensis Triana
Miconia micrantha Cogn.
Miconia microcarpa DC.
Miconia micropetala Cogn.
Miconia minutiflora (Bonpl.) DC.
Miconia mirabilis (Aublet) L. O. Williams
Miconia monciana Urban & E. Ekman
Miconia monocephala Urban
Miconia multiflora Cogn.
Miconia multiglandulosa Cogn.
Miconia multiplinervia Cogn.
Miconia multispicata Naudin
Miconia muricata (D. Don) Triana
Miconia myriantha Benth.
Miconia neomicrantha W. Judd & Skean
Miconia nerifolia Triana
Miconia nervosa (Sw.) Triana
Miconia nigricans Cogn.
Miconia nitidissima Cogn.
Miconia nodosa Cogn.
Miconia notabilis Triana
Miconia nystroemii E. Ekman ex Urban
Miconia oinchrrophylla Donn.-Sm.
Miconia oligocephala Donn.-Sm.
Miconia orcheotoma Naudin
Miconia ossaeifolia Urban & E. Ekman
Miconia paleacea Cogn.
Miconia pallida Gleason
Miconia papillosa (Desr.) Naudin
Miconia paradoxa (Martius ex DC.) Triana
Miconia pedicellata Cogn.
Miconia pepericarpa DC.
Miconia phaeophylla Triana
Miconia pileata DC.
Miconia pilgeriana Ule
Miconia pinetorum Naudin
Miconia pittieri Cogn.
Miconia plukenetii Naudin
Miconia polygama Cogn.
Miconia prasina (Sw.) DC.
Miconia pseudocentrophora Cogn.
Miconia pseudonervosa Cogn.
Miconia pseudorigida Proctor
Miconia pteropoda Benth.
Miconia puberula Cogn.
Miconia pubipetala Miq.
Miconia pujana Markgraf
Miconia pulvinata Gleason
Miconia punctata (Desr.) D. Don
Miconia purpureus (D. Don) W. Judd & Skean
Miconia pustulata Naudin
Miconia pycnoneura Urban
Miconia pyramidalis DC.
Miconia pyrifolia Naudin
Miconia quadrangularis (Sw.) Naudin
Miconia racemifera Triana
Miconia racemosa (Aublet) DC.
Miconia radulaefolia (Benth.) Naudin
Miconia ravenii Wurd.
Miconia reclinata (Bonpl.) Naudin
Miconia reducens Triana
Miconia rhodantha Wurd.
Miconia rigida (Sw.) Triana
Miconia rigidissima Urban & E. Ekman
Miconia rigidiuscula Cogn.
Miconia rubens (Sw.) Naudin
Miconia rubiginosa (Bonpl.) DC.
Miconia rufescens (Aublet) DC.
Miconia ruficalyx Gleason
Miconia rupestris Ule
Miconia salicifolia Bonpl. ex Naudin
Miconia samamensis Urban & E. Ekman
Miconia sanguinea (D. Don) Triana
Miconia schlechtendalii Cogn.
Miconia schlimii Triana
Miconia sciurea Uribe
Miconia selleana Urban & E. Ekman
Miconia septentrionalis W. Judd & R. Beaman
Miconia semulata (DC.) Naudin
Miconia sessilifolia Naudin
Miconia simplex Triana
Miconia sintenisii Cogn.
Miconia smaragdina Naudin
Miconia sphagnicola Urban & E. Ekman
Miconia splendens (Sw.) Griseb.
Miconia squamulosa (Sw.) Triana
Miconia staminea (Desr.) DC.
Miconia stelligera Cogn.
Miconia stenobomys (Rich.) Naudin.
Miconia stenostachya DC.
Miconia stevensiana Almeda
Miconia striata (M. Vahl) Cogn.
Miconia subcompressa Urban
Miconia tematifolia Triana
Miconia tetrandra (Sw.) D. Don ex G. Don
Miconia tetrasperma Gleason
Miconia tetrastoma Naudin
Miconia tetrazygioides Urban & E. Ekman
Miconia theaezans (Bonpl.) Cogn.
Miconia thyrsoides (M. Vahl) R. Howard
Miconia tiliaefolia Naudin

- Miconia tinifolia* Naudin
Miconia tiri Triana
Miconia tomentosa (Rich.) D. Don
Miconia tonduzii Cogn.
Miconia trianaei Cogn.
Miconia trinervia (Sw.) D. Don ex G. Don
Miconia triplinervis Ruiz & Pavón
Miconia truncata Triana
Miconia urophylla DC.
Miconia uvifera Naudin
Miconia valeriana (Standley) Wurd.
Miconia versicolor Naudin
Miconia virgulata Gleason
Miconia viscidula Urban & Cogn.
Miconia wilsonii Cogn.
Miconia wittii Ule
- Miconia xenoricha* Urban & E. Ekman
Miconia zanonii W. Judd, Skean, & R. Beaman
Ossaea boekei Wurd.
Ossaea bracteata Triana
Ossaea brenesii Standley
Ossaea laxivenula Wurd.
Ossaea macrophylla (Benth.) Cogn.
Ossaea quinquenervia (Mill.) Cogn.
Ossaea robusta (Triana) Cogn.
Ossaea rufibarbis Triana
Ossaea semijuca Gleason (= *Clidemia semijuca*) (Gleason) Wurd.)
Ossaea sessilifolia (Triana) Wurd.
Ossaea sparrei Wurd.
Ossaea spicata Gleason

PACHYANTHUS: Evergreen shrubs with determinate shoots; twigs terete to angled, nodose, with ridge encircling each node, producing one to several leafy nodes before forming a terminal inflorescence; druse crystals present. Indumentum of conspicuous to very reduced stellate hairs, on stems, leaves, inflorescence axes, and hypanthia. Leaves opposite, decussate, petiolate, coriaceous, \pm flat; margin entire, plane to revolute; venation acrodromous, suprabaasal, with a prominent midvein, usually 1 to 3 pairs of secondary veins (although some of these occasionally inconspicuous), and numerous percurrent tertiary veins \pm perpendicular to midvein; mite-domatia lacking or rarely present in axils of midvein and 2 major secondary veins, formed by a tuft of elongate-branched (modified stellate) hairs. Inflorescences terminal cymes, reduced and bearing only 1 to 7 (rarely ca. 13) flowers; axes flattened. Flowers perfect, 5- or 6-merous, \pm sessile. Hypanthium persistent, coriaceous, cylindrical-campanulate (and often tearing into triangular, sepal-like segments), unlobed, not constricted above ovary, with stellate hairs. External calyx lobes 5 or 6, very short to elongate, \pm terete, rarely flattened; internal calyx lobes 5 or 6, distinct, not calyptrate, broadly triangular. Petals 5 or 6, ovate to obovate, with acute, acuminate, or blunt apex, usually abruptly narrowed at base, glabrous. Stamens 10 or 12, \pm isomorphic, glabrous, geniculate, inserted at apex of hypanthium and deflexed to one side of flower; anthers ovate, straight to curved, dehiscing by a small apical pore, the connective thickened but non-appendaged. Ovary \pm inferior, 3- to 5-locular, with axile placentation, the ovules numerous; style cylindrical, curved, glabrous; stigma capitate, papillose. Fruit a robust berry. Seeds small, angular-obovoid, the testa \pm smooth to minutely roughened by bulging cells.

Species examined:

- Pachyanthus angustifolius* Griseb.
Pachyanthus cubensis A. Rich. (incl. subsp. *blancheanus* (Urban) Borhidi)
Pachyanthus discolor J. Norlind
Pachyanthus longifolius Jennings
Pachyanthus lundellianus (L. O. Williams) W. Judd & Skean
- Pachyanthus mayarensis* Urban
Pachyanthus oleifolius Griseb.
Pachyanthus poiretii Griseb.
Pachyanthus reticulatus Britton & P. Wilson
Pachyanthus tetramerus Urban & E. Ekman
Pachyanthus wrightii Griseb.

TETRAZYGIA: Traditional generic circumscription is retained pending more detailed investigation of the complex of related species within *Miconia* (see text); see descriptions in Howard (1989) and Fawcett & Rendle (1926).

Species examined:

Tetrazygia albicans (D. Don ex Naudin)
Triana
Tetrazygia angustifolia (Sw.) DC.
Tetrazygia aurea R. Howard
Tetrazygia bicolor (Mill.) Cogn.
Tetrazygia biflora (Cogn.) Urban
Tetrazygia brachycentra (Griseb.) C. Wright
Tetrazygia cordata Alain
Tetrazygia crotonifolia (Desr.) DC.
Tetrazygia delicatula (A. Rich.) Borhidi
Tetrazygia discolor (L.) DC.
Tetrazygia eleagnoides (Sw.) DC.

Tetrazygia hispida (Sw.) Cogn.
Tetrazygia impressa Urban
Tetrazygia laxiflora Naudin
Tetrazygia longicollis Urban & Cogn.
Tetrazygia pallens (Spreng.) Cogn.
Tetrazygia tuerckheimii (Cogn.) E. Ekman
ex Urban (likely conspecific with *T. urbaniana*)
Tetrazygia urbaniana (Cogn.) Croizat ex Moscoso
Tetrazygia urbanii Cogn.
Tetrazygia urceolata (Urban) Borhidi

The following species of *Miconia* may be basal members of *Tetrazygia*; the systematics of this group needs to be studied in more detail (see text):

Miconia ancistrophora (C. Wright) Triana
Miconia androsaemifolia Griseb.
Miconia baracoensis Urban
Miconia cerasiflora Urban
Miconia humilis Cogn.
Miconia mexicana (Humb. & Bonpl.)
Naudin

Miconia obtusa (Griseb.) Triana
(= *Calyconium obliquum* (Griseb.)
Cogn.)
Miconia pachyphylla Cogn.
Miconia thomasiana DC.
Miconia zemurrayana Standley & L. O.
Williams

TOCOSA: Circumscription of genus not substantially altered as a result of this study; see description in Wurdack (1980).

Species examined:

Tococa acuminata Benth.
Tococa aristata Benth.
Tococa bolivarensis Gleason
Tococa capitata Trail
Tococa caquetana Sprague
Tococa caudata Markgraf
Tococa ciliata Triana
Tococa coronata Benth.
Tococa discolor Pilger
Tococa formicaria Martius
Tococa gonoptera Gleason
Tococa guianensis Aublet
Tococa hirta Berg. ex Triana
Tococa lancifolia Spruce ex Triana

Tococa lasiostyla Cogn.
Tococa longisepala Cogn.
Tococa macrophysca Spruce ex Triana
Tococa mitens (Benth.) Triana
Tococa obovata Gleason
Tococa occidentalis Naudin
Tococa pachystachya Wurd.
Tococa quadrialata (Naudin) J. F. Macbr.
Tococa rotundifolia (Triana) Wurd.
Tococa stephanotricha Naudin
Tococa subciliata (DC.) Triana
Tococa ulei Pilger
Tococa undabunda J. F. Macbr.

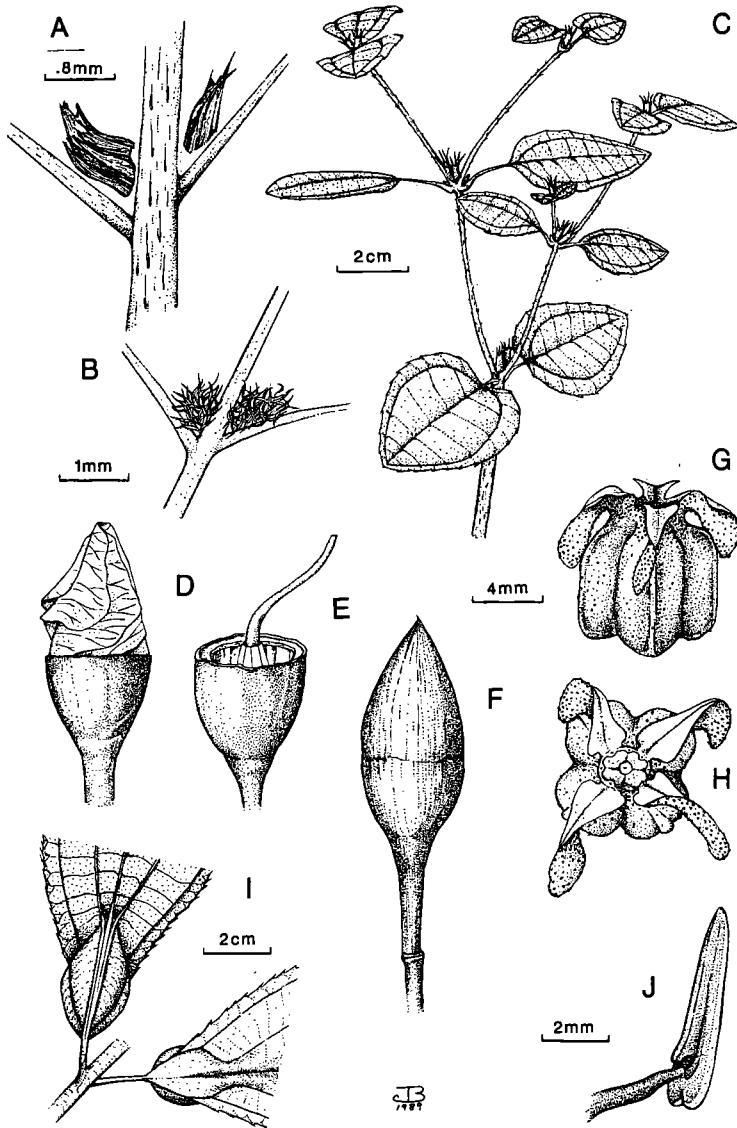


Figure 1. *Calycogonium*, *Conostegia*, and *Tococa*. A, *Calycogonium lindenianum*; mite-domatia formed from \pm connate hairs. B, *C. rhomboideum*; hair-tuft mite-domatia. C, *C. hispidulum*; twig showing distinctive architectural pattern (see discussion in text) and reduced inflorescences. G, H, *C. calycopteris*; note flattened external calyx lobes and 4-lobed hypanthium. D-F, *Conostegia pyxidata* Proctor; note lack of external calyx lobes and inner calyx lobes fused into a stout, conical, circumscissily dehiscent cap. I, *Tococa coronata* Benth.; ant-domatia at base of lamina. J, *T. aristata* Benth.; anther with minute dorso-basal tooth.



Figure 2. *Clidemia*. A,B, *C. hirta*; note sympodial growth with pseudolateral inflorescences and 5-merous flowers. C, D, "*Heterotrichum*" *umbellatum*; note large berry with elongate external calyx lobes, 6-merous flower with blunt petals, and characteristic indumentum. E, F, "*H.*" *angustifolium*; note obviously terminal inflorescence.

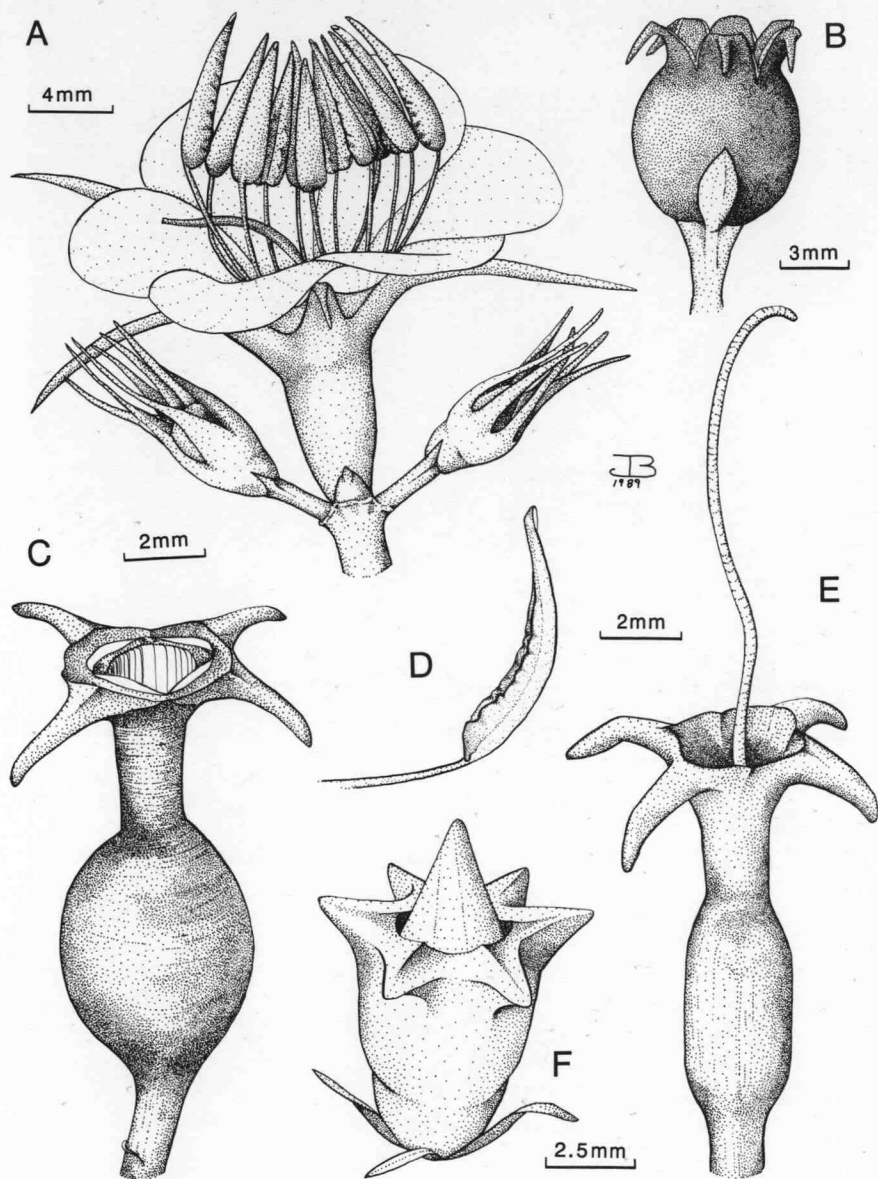


Figure 3. *Pachyanthus* and *Tetrazygia*. A, *Pachyanthus discolor* Naudin; note 6-merous flowers with non-appendaged stamens, reduced cyme. B, *Pachyanthus lundellianus*; large berry with coriaceous (and longitudinally splitting) hypanthium/calyx. F, *P. poiretii* Griseb.; flower bud. C-E, *Tetrazygia longicollis*; note constricted hypanthium and elongate external calyx lobes (C), anther (D), young fruit with apically curved style with minute stigma (E).



Figure 4. *Tetrazygia*. A, *T. tuerckheimii*; note terminal inflorescence. B, *T. urbaniana*; note 5-merous flowers and berries with \pm non-constricted hypanthia. C, *T. pallens*; note constricted hypanthium. D, E, *T. bicolor*; note stylar characters, zygomorphic androecium, and terminal inflorescence.

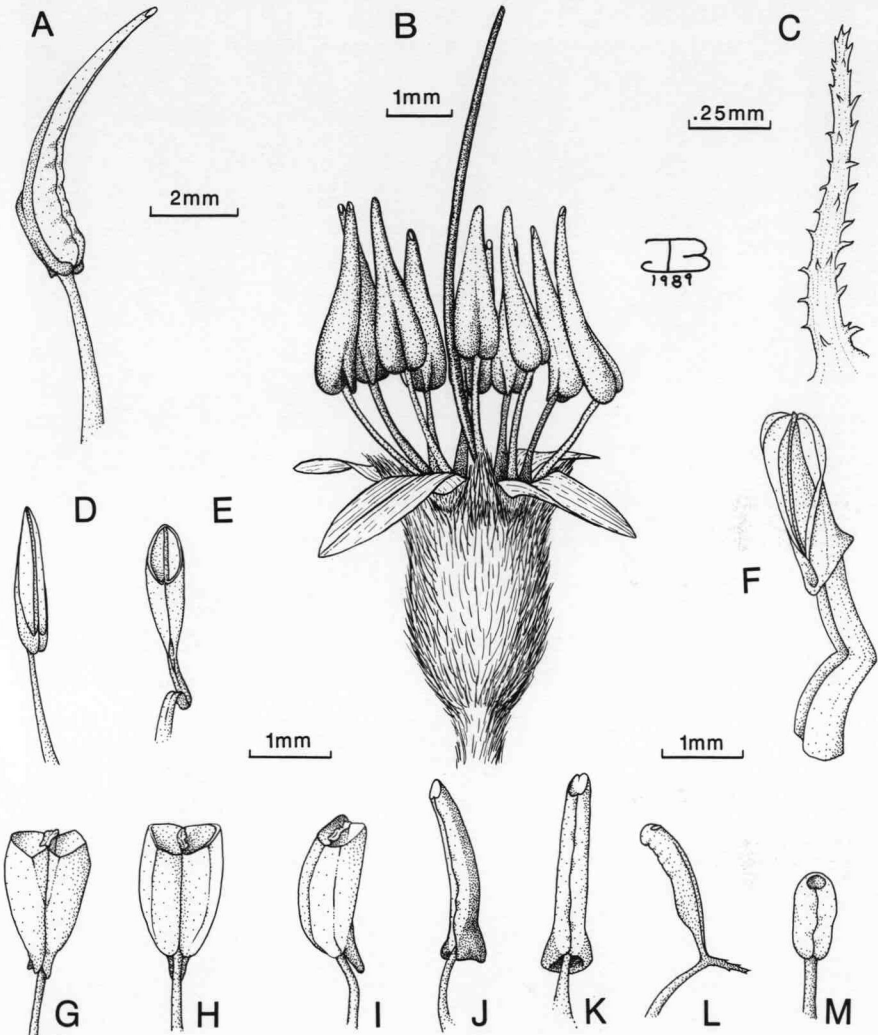


Figure 5. *Leandra* and *Miconia*. B, C, *Leandra aurea*; note anther characters and acute petals (B) and roughened, elongate, multicellular hair (C). A, D-M, *Miconia* anthers: A, *M. dodecandra* Cogn.; D, *M. rigidiscula* Cogn.; E, *M. urophylla* DC.; F, *M. subcompressa*; G, *M. chlorocarpa* Cogn.; H, I, *M. media* (D. Don) Naudin; J, K, *M. laevigata* (L.) DC.; L, "*Ossaea*" *bracteata* Triana (a member of *O.* sect. *Octopleura*, actually a *Miconia*, see discussion in text); M, *M. ciliata* (Rich.) DC.



Figure 6. *Leandra*. A, "*Ossaea*" *asperifolia*; note terminal inflorescence with numerous 5-merous flowers, acute petals. B-D, "*O.*" *hirsuta*; branch with reduced terminal inflorescence (B), 4-merous flower with acuminate petals (C), young fruit with elongated external calyx lobes (D). E, "*O.*" *lima*; note reduced inflorescence, indumentum of thick-based hairs.



Figure 7. *Miconia*. A, B, *M. favosa*; note distinctive androecium (sect. *Chaenopleura*; see discussion in text). C, *M. rubens* (Sw.) Naudin (sect. *Cremanium*). D, *M. laevigata* (L.) D. Don (sect. *Miconia*). E, *M. dodecandra* (Desr.) Cogn. (sect. *Tamonea*). F, *M. tetrastoma* Naudin (sect. *Cremanium*). G, *M. prasina* (Sw.) DC. (sect. *Miconia*).

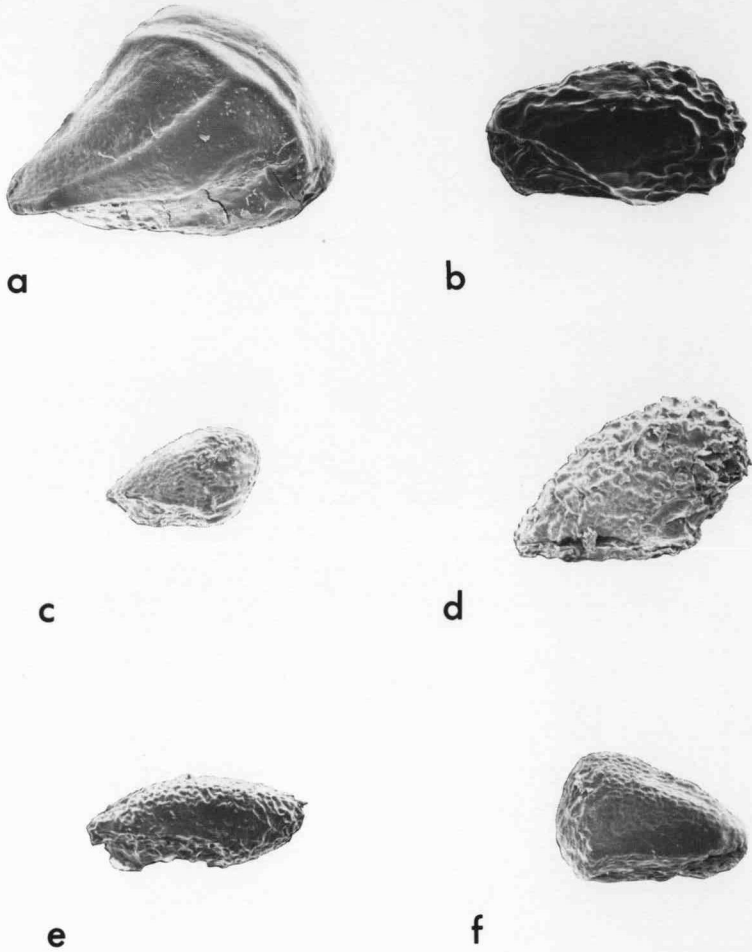


Figure 8. Seeds of terminal-flowered Miconieae: A, *Calycogonium rhamnoides* (Proctor 21389); B, *Miconia macrodon* (Steiermark 54960), a species of *Clidemia*; C, *Clidemia umbellata* (Rehder s.n.); D, *Clidemia hirta* (Judd 5145); E, *Conostegia montana* (Hodge 3441); F, *Tetrazygia crotonifolia* (Judd 2980). See discussion in text.

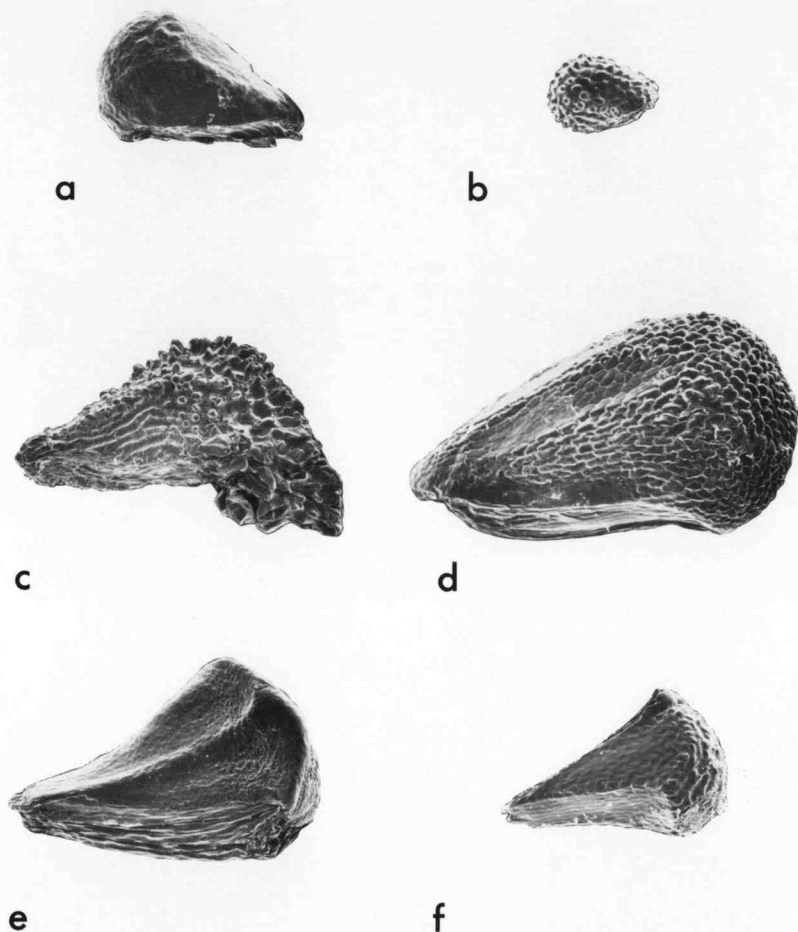


Figure 9. Seeds of terminal-flowered Miconieae: A, *Leandra cornoides* (Hansen and Nee 7600); B, *Leandra secunda* (Zarucchi 1908); C, *Leandra chaetodon* (Schunke 5184); D, *Leandra aurea* (Irvin et al. 25787); E, *Leandra lima* (Skean 1804); F, *Miconia schlimii* (Smith 13). See discussion in text.

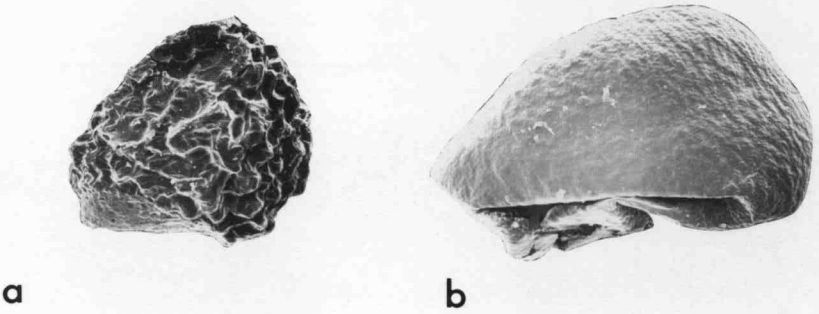


Figure 10. Seeds of terminal-flowered Miconieae: A, *Miconia amazonica* (Ancuash 326); B, *Miconia krugii* (Judd 5121). See discussion in text.

Table 1. Character state values for genera of terminal-flowered Miconieae (as delimited herein); 0 = plesiomorphic state, 1 = apomorphic state, () = occasional to rare condition.

taxa/characters	1*	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
<i>Anaectocalyx</i>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Calycogonium</i>	0	0	0(1)	1(0)	0,1	1	0	0(1)	0	0(1)	0	0	0	0	0,1	0(1)	0(1)
<i>Clidemia</i>	0	0	0	0,1	0	0,1	1(0)	0	0	0	0	0(1)	0(1)	0(1)	0	0	0(1)
<i>Conostegia</i>	0	0	0	0	0,1	0,1	0(1)	0	0	0	0	0	0(1)	0	0	0	0(1)
<i>Pachyanthus</i>	0	0	0	0(1)	1	1	0	0	0	0	0	0	0	0	0	0	0,1
<i>Tetrazygia</i>	0	0	0(1)	0(1)	0(1)	1(0)	0(1)	0(1)	0	0(1)	0	0	0	0	0	0	0,1
<i>Tococa</i>	0	0	0	0,1	0(1)	0,1	0,1	0	0	0	0	0(1)	1(0)	0	0	0	0
<i>Leandra</i>	0	0(1)	0(1)	0(1)	0(1)	0,1	0,1	0	0,1	0	0	0(1)	0	0	0(1)	0	0
<i>Miconia</i>	0	0	0	0	0,1	0,1	0,1	0(1)	0	0(1)	0(1)	0(1)	0	0	0(1)	0(1)	0,1

taxa/characters	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
<i>Anaectocalyx</i>	0	0	0	0	0	0,1	0	1	1	0	1	0	0	0	0	0	0
<i>Calycogonium</i>	0	0	0,1	0	0	0,1	0	0	0,1	1	0	0	0,1	0(1)	0(1)	0	0
<i>Clidemia</i>	0,1	0	0(1)	0	0(1)	0(1)	0	0(1)	1	0(1)	0,1	0	0(1)	0	0	0	0
<i>Conostegia</i>	0	0	0	0,1	0	0	0	0	0	0(1)	0,1	0	0	0	0	0	0
<i>Pachyanthus</i>	0	0	1(0)	1	0	0	0	0	1	0	1(0)	0	0	0	0	0	0
<i>Tetrazygia</i>	0	0,1	0(1)	0(1)	0	0	0	0	1	0,1	0	0	0,1	0	0	0	0
<i>Tococa</i>	0,1	0	0,1	0(1)	0	0(1)	0	0	1	0(1)	0	0	0	0	0	0,1	0
<i>Leandra</i>	0,1	0	0,1	0(1)	0(1)	0,1	0,1	0,1	1	0,1	0(1)	0	0(1)	0	0	0,1	0
<i>Miconia</i>	0,1	0	0(1)	0(1)	0(1)	0(1)	0,1	0(1)	1	0,1	0,1	0,1	0(1)	0	0(1)	0	0,1

*Occurs only in *Catocoryne*, a poorly known genus (see text).

Table 1 Continued

taxa/characters	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51
<i>Anaectocalyx</i>	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0
<i>Calycogonium</i>	0,1	0	0,1	0,1	0	0	0,1	0	0	0	0	0	0	0,1	0	0	0
<i>Clidemia</i>	1(0)	0	0	0	0	0	0	0(1)	0	0	0	0	0	0(1)	0	0	0
<i>Conostegia</i>	0	1	0	0	0	1	0	0	0	0	0	0,1	0	1(0)	0	0	0
<i>Pachyanthus</i>	0,1	0	0(1)	0	0	0	0,1	0	0	0	0	0	0	0(1)	0	0	0
<i>Tetrazygia</i>	0,1	0(1)	0	0	0	0	0	0	0	0	0	0	0	0,1	0	0	0
<i>Tococa</i>	0(1)	0	0	0	0	0	0	0(1)	0	0	0	0	0	1(0)	0	0	0
<i>Leandra</i>	0,1	0	0	0	0	0	1(0)	0	0,1	0,1	0	0	0	0,1	0	0	0
<i>Miconia</i>	0(1)	0	0	0	0	0	0,1	0(1)	0,1	0(1)	0,1	0(1)	0	0,1	0,1	0,1	0,1
taxa/characters	52	53	54	55	56	57	58	59	60	61	62	63	64	65	66	67	
<i>Anaectocalyx</i>	0	0	0	0	0	0	0	0	0	1	0	0?	0?	?	?	?	
<i>Calycogonium</i>	0	0	0(1)	0	0	0	0	0	0,1	1	0	0	0	0	0	?	
<i>Clidemia</i>	0	0	0	0	0	0(1)	0	0(1)	0	1	0(1)	0	1(0)	0	0	0,1	
<i>Conostegia</i>	0	0	0	0	0	0	0	0	0	1	0(1)	0	0	0	1	0	
<i>Pachyanthus</i>	0	0	0	0	0	0	0	0	0	1	1(0)	0	0	1	0	?	
<i>Tetrazygia</i>	0	0	0(1)	0	0	0	1	0	0(1)	1	0	0	0	0	0	0	
<i>Tococa</i>	0	0	1	0	0(1)	0	0	0(1)	0	1	0	0	0	0	0	0	
<i>Leandra</i>	0	0	0,1	0,1	0	0	0(1)	0(1)	0	1	0	0,1	0,1	0	0	0	
<i>Miconia</i>	0,1	0,1	0,1	0,1	0,1	0,1	0	0,1	0	1	0(1)	0(1)	0,1	0	0	0	