

# THE GENERA OF AMERICAN MYRTACEAE -- AN INTERIM REPORT

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## I. INTRODUCTION

Generic concepts developed slowly in the Myrtaceae. At the beginning of the 19th century few species were known, and these were traditionally distributed among ten or twelve genera. Willdenow, for example (Sp. Pl. 2: 935. 1800), knew among the capsular-fruited Myrtaceae 12 species of *Leptospermum*, 14 of *Metrosideros*, and 12 of *Eucalyptus*. The Myrtaceae with baccate fruits he referred to *Eugenia* (30 species), *Psidium* (8 species), *Myrtus* (28 species), *Calyptranthes* (6 species) and *Plinia* (1 species).

The American Myrtaceae, except for the monotypic Chilean genus *Tepualia*, belong to the fleshy-fruited group that since the time of De Candolle has been recognized as a tribe, Myrteae. Outstanding contributions to the knowledge of the species and genera of the American Myrteae were made by De Candolle in 1828 and by Berg in 1855-62, but since Berg's time no one person has had an opportunity to become familiar with the group as a whole. The number of described species is very large, especially in tropical South America, and available herbarium material until recent years consisted chiefly of the classical specimens scattered through European herbaria. Within the last quarter century, however, a considerable amount of new herbarium material has been collected, and a number of regional studies of the American Myrtaceae have been published. The species of the North American continent, of the West Indies, of the Guianas, of the central Andes, of Chile and of the Uruguayan-south Brazilian region have become reasonably well known, and it now seems profitable to assess the work of Berg in the light of modern work on the family, and particularly to evaluate his generic concepts and the concepts of later workers.

Until the time of A. P. De Candolle, most workers accepted without much question the generic limits that had been set forth by Linnaeus, who assigned most of the Myrtaceae known to him to one of three genera (cf. Syst. Nat. ed. 13. 2: 336. 1770):

*Eugenia*: Calyx and corolla 4-merous; drupe 1-locular, 1-seeded.

*Psidium*: Calyx and corolla 5-merous; berry 1-locular, many-seeded.

*Myrtus*: Calyx 5-fid; corolla "sub 5-petala"; berry 3-locular, 1-seeded.

Exactly the same distinctions were used by Willdenow, who added the following genera:

*Calyptranthes*: Calyx truncate, operculate; corolla none; berry 1-locular, 1-4-seeded.

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*Plinia*: Calyx [erroneously said to be "inferus", contrasted to the others which are "superus"] and corolla 4- or 5-merous; drupe sulcate.

Some authors of the early 19th century, notably Kunth (in HBK. Nov. Gen. & Sp. 6: 129–149. 1823, and Sprengel (Syst. Veg. 2: 471, 479–488. 1825) made the genus *Myrtus* a very inclusive one and merged *Eugenia* with it. This was in many respects a logical course, as the original distinction based chiefly on 4-parted vs. 5-parted flowers became quite meaningless when the many newly discovered American species were considered. Sprengel listed 141 species of *Myrtus*, or more than two and one-half times as many as those listed by Willdenow under *Myrtus* and *Eugenia* together.

Thus by 1825 almost nothing was known about generic limits that have since become generally accepted. A few genera marked by some distinctive feature (e.g. *Calyptanthus*) were recognized early, but except for these, until the time of De Candolle, no reasonable way had been found to establish recognizable genera in which to include the rapidly increasing number of known species.

### *Work of De Candolle and Berg*

De Candolle's great contribution was to focus attention on the morphology of the myrtaceous embryo. In the words of Bentham, "Relying upon these characters maintaining throughout the constancy observed in the very few species which he could examine, De Candolle was enabled to make an apparently excellent distribution of the great mass of succulent-fruited Myrteae into . . . three principal groups". The three groups, later characterized by Berg as subtribes, were as follows:

1. MYRCIINAE. Cotyledons broad and thin, foliaceous, very much folded or contortuplicate, more or less surrounded by the elongate, curved, terete radicle. The type genus is *Myrcia*, of which De Candolle (in DC. Prodr. 3: 242–256. 1828) recognized 108 species. About one-fourth of these had previously been described by other authors under *Eugenia* or *Myrtus*. The rest, or about 80 species, were described for the first time in the *Prodromus*. Martius, who had recently returned from Brazil with large collections, made his specimens available to De Candolle for inclusion in the *Prodromus*, and in this way for the first time the size and complexity of the American myrtaceous flora began to become apparent to European botanists. Berg, working only 30 years after De Candolle, recognized about 500 species of what De Candolle would have called *Myrcia*.

2. EUGENIINAE. Embryo thick and fleshy, sometimes apparently homogeneous but often showing the line of separation of two planoconvex cotyledons connected by a short radicle. Most of the species supposed to have this type of embryo were assigned by De Candolle to the genus *Eugenia*, under which he listed 194 species. He recognized also the genera *Syzygium* Gaertn., *Ccaryophyllus* Tourn., *Acmena* DC., and *Jambosa* Rumph., including in all about 60 species of the Old World.

3. PIMENTINAE. Embryo spiral, circular, uncinately-curved or horseshoe-shaped, consisting of a long terete radicle with two very small cotyledons at the inner end. The species of this group known to De Candolle were placed by him in *Campomanesia* (3 species), *Psidium* (42 species) and *Myrtus* (37 species).

By about 1850, when Berg began his revision of the American Myrtaceae, he was able to study many herbarium specimens that had been collected since the time of De Candolle. The majority of these were Brazilian, but in addition he saw many specimens from the Guianas, from the West Indies, and from the Andean region. In a series of publications over a 7-year period, Berg described about 1000 new species and more than 30 new genera in the tribe Myrteae. The sheer volume of this work made it difficult for any subsequent worker to propose innovations in the taxonomy of the Myrteae without a long preliminary period devoted to study of Berg's papers. Very many of the new species proposed by Berg were based upon one or few specimens each, and these specimens were concentrated in the collections

of a few major herbaria (principally those of Berlin, Vienna, and St. Petersburg, but also many in private hands, e.g. the herbaria of Martius, Schlechtendal, Oersted, Sonder, etc.). Thus in the last century hardly anyone except Urban (who published a revision of the West Indian Myrtaceae in 1895) has been well enough acquainted with Berg's species and genera to pass judgment upon any large segment of his work.

Berg's division of the tribe Myrteae was patterned closely after the work of De Candolle, in that he accepted three major groups based upon the structure of the embryo; he proposed also two new coordinate groups including a single genus each.

In what Berg called the subtribe Myrcioideae [i.e. Myrciinae according to modern Codes of nomenclature], he recognized 11 genera; these included *Myrcia* and *Calyptranthes*, both treated by De Candolle in 1828, *Marlierea* (described by Cambessèdes in 1829), and 8 new genera. In the Eugenioideae [Eugeniinae] Berg divided among 15 genera about what De Candolle had assigned to *Syzygium*, *Caryophyllus*, *Eugenia* and *Jambosa*; and in the Pimentoideae [Pimentinae] 16 genera replaced De Candolle's *Campomanesia*, *Psidium* and *Myrtus*.

Perhaps Berg's major contributions to the taxonomy of the Myrteae were his careful and lengthy descriptions, and his recognition of the importance of the structure of the immature ovary. Whereas De Candolle had made reasonable assumptions based on study of the mature embryos of relatively few species, Berg described in detail the flowers of every species he examined. De Candolle necessarily (in the format of the *Prodromus*) provided merely brief diagnostic accounts of each species; Berg's descriptions, on the other hand, can often be used even today to identify an unknown specimen. Dimensions of leaves and flower-parts are usually included. Details of the placentation, the number of locules in the ovary, and the number of ovules in each locule, are usually noted. As it is usually possible to ascertain the number of locules and the number of ovules with relative ease, in dried specimens bearing flowers or even very young buds, Berg was able to apply his knowledge of these characters over a very large assortment of specimens. In the Myrtaceae the ovary, and especially the ovules, are usually very well preserved indefinitely, even in badly moulded or otherwise badly preserved specimens in which the rest of the floral parts have disintegrated to some extent. Even in mature fruits in which the one developing seed has crowded all the abortive ovules against the wall of the fruit, careful dissection will usually reveal the persistent ovules, in two or three groups corresponding to the original locules of the ovary. Berg was therefore able to use the characters of ovule-number and locule-number, often in combination with other features, to establish the principal structure of his classification of the Myrteae. Sometimes the separations effected this way were artificial ones, but for the most part they were not. As a result of Berg's work, for example, it became apparent that all the genera of his Myrciinae, except for one anomalous genus, were bioovulate; most of the genera of Eugeniinae were multiovulate but a fruit rarely matured more than 1-2 seeds; most of the genera of Pimentinae were multiovulate, with several or many small seeds maturing in each fruit.

Berg's generic divisions within the major groups are perhaps less likely to stand the test of time than his delimitations of the subtribes themselves. In his delimitation of genera he relied heavily upon the interpretation of the structures of the calyx and the hypanthium and the changes that take place in them in the developing flower-bud. Thus in each of the three major subtribes he proposed a number of genera comprising a series from those species having the calyx closed or almost closed in bud, to those having an open 4- or 5-lobed calyx. He also attached much importance to the extent of the development of the hypanthium beyond the summit of the ovary; that is, as to whether the stamens seem to be borne at the summit of a cup or tube that extends above the ovary, or on the margin of a nearly flat disk at about the

same level as the summit of the ovary. Berg distinguished *Myrcia* and *Aulomyrcia* on this basis, and on the same basis established the principal division between groups of genera in the Eugeniinae. Although these characters provide useful distinctions at the specific level, and even at the generic level when they are taken together with other correlated characters, it is now clear that they do not in themselves point out fundamental evolutionary lines in the Myrteae.

Recent work in the Myrtaceae, especially those of South America, indicates that Berg described too many genera. Thus his *Cerqueiria* seems to be no more than an extremely modified species of *Gomidesia*, although the anthers of the latter are laterally dehiscent whereas those of *Cerqueiria* are apically 4-porose. Modern workers now for the most part accept the thesis that the species assigned by Berg to the 7 genera *Marlierea*, *Rubachia*, *Calyptromyrcia*, *Aulomyrcia*, *Myrcia*, *Calycampe* and *Eugeniopsis*, belong actually to two principal taxa, *Myrcia* and *Marlierea*; the differences in the division of the calyx, stressed by Berg, prove upon study of new material to be subjective and not well correlated with other features.

Some workers have gone too far, however, in submerging Berg's genera. European botanists, following the lead of Bentham (Jour. Linn. Soc. Bot. 10: 147-166. 1869), have generally until recent years reduced such homogeneous and recognizable taxa as *Ugni*, *Blepharocalyx* and *Myrcianthes* (all to *Myrtus*), and *Plinia*, *Myrciaria*, and *Siphoneugena* (all to *Eugenia*). Bentham's treatment of the American Myrtaceae was indeed somewhat superficial. He was led to prepare his "Notes on Myrtaceae" after having examined carefully all the Australian species in preparation for his flora of Australia which began to appear in 1863. He states that "on former occasions" he has "examined a large number of American and Asiatic species" as well, but his comments on the capsular-fruited members of the family indicate that his knowledge of them was based on recent study of many individual species, whereas his dispositions of the American species and genera seem to have been largely academic, resulting from analyses of Berg's then recently published papers.

As an example the case of *Myrciaria* may be cited. Bentham noted the combination, rare in the Eugeniinae, of the "calyx-tube" [hypanthium] produced above the ovary, and the ovules two in each locule. He went on to say (l.c. 164) "Had these characters been accompanied by any general difference in habit or inflorescence, they might have well served to maintain the genus". It is quite true, as Bentham noted, that in Berg's original circumscription of *Myrciaria* he mistakenly included a number of species of *Myrcia* with "paniculate" inflorescence, but the genus *Myrciaria*, when properly typified, is not on this account to be abandoned; actually the group is well marked by both vegetative and floral characters.

### *Research needs for the future*

In the century that has intervened since the work of Berg and Bentham, there has been no published treatment of the American Myrtaceae as a whole. There are regional studies<sup>1</sup> of the Myrtaceae of the West Indies, of eastern temperate and subtropical South America, and of Chile, in which the matters of proper generic disposition are treated more or less at length. Studies of the myrtaceous floras of other areas, mostly treating relatively small numbers of species and genera, include those of Suriname (Amshoff), Peru (McVaugh), Panama (Amshoff) and Guatemala (McVaugh). Since 1900 more than 20 new American genera of Myrtaceae have been proposed, mostly from the West Indies (by Urban) or from extra-tropical South America (by Kausel). Most of the proposals, except those of Kausel, have been based on studies of limited amounts of new material rather than on adequate comparative studies of regional or revisional nature.

Modern taxonomy demands a synthesis derived from the sum of characters of the

taxa under consideration. As knowledge of a given group increases with time, it becomes easier to look back and see how successive workers have approached more closely to this ideal, or how they have failed. Berg, for example, was able to profit from De Candolle's knowledge of the mature myrtaceous embryo, and at the same time to add his own conclusions relative to floral structure. His taxonomic arrangement, insofar as it was based on combinations of these and related characters, is generally acceptable today; it is where he relied too heavily upon unit characters like the elongation of the hypanthium that his arrangements are most often questioned.

Oddly enough Berg seems not to have attached much importance to the architecture of the myrtaceous inflorescence, although many useful and obvious characters reside in it. Not only is the inflorescence of characteristic form and size in most species, but also it is almost invariably present in herbarium specimens. Although many species change markedly in appearance between flowering and fruiting stages (e.g. by growth and maturation of foliage, elongation of pedicels, loss of pubescence, loss of flower-parts including the calyx), the branching-patterns of the inflorescence usually persist in identifiable form. Differences between genera and indeed between groups of genera, are so constant and so great that one can confidently and quickly identify most of the members of Berg's Myrciinae and Eugeniinae as to subtribe, and often as to genus. I have discussed the principal inflorescence-types elsewhere in detail (ci. *Fieldiana Bot.* 29: 152-161. 1955), and here it may be said only that the most common types are as follows: 1) The raceme, a single primary axis bearing usually several decussate pairs of solitary pedicellate flowers; 2) The dichasium, a primary determinate axis with solitary terminal flower, the whole sometimes one-flowered but usually 3-, 7-, or several-flowered by the development of lateral branches beneath the terminal flower; and 3) The myrcioid panicle, an elongate axis bearing usually several decussate pairs of compound, several-flowered branches.

Berg did not mention inflorescence-characters or vegetative characters in the generic diagnoses published with his revision in *Linnaea*, but in his more extended treatment published in 1857 in the *Flora Brasiliensis* he made some brief remarks about the position and origin of flowers and inflorescence. He also made some effort to distinguish infrageneric taxa in the larger genera. In *Eugenia*, for example, he recognized a number of groups having different inflorescence-types, viz. *Uniflorae*, *Biflorae*, *Glomeratae*, *Umbellatae*, *Corymbiflorae*, *Racemosae*, *Dichotomae* and *Racemosae*.

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<sup>1</sup> URBAN, I. Additamenta ad cognitionem florum Indiae occidentalis. Particula II. Myrtaceae. Bot. Jahrb. 19: 562-681. 1895.

LEGRAND, D. Las Mirtáceas del Uruguay. Anal. Mus. Hist. Nat. Montevideo II, 4 (no. 11): 3-70. pl. I. 1936; Representantes neotropicales del género "Myrceugenia". Darwiniana 11: 293-365. 1957; Las especies tropicales del género *Gomidesia*. Com. Bot. Mus. Hist. Nat. Montevideo 3 (no. 37): 1-30. 1958; Résultats de l'étude de quelques types de Myrtacées sudaméricaines de Cambessèdes dans l'herbier de Saint-Hilaire au Muséum de Paris. Notul. Syst. 15: 259-274. Dec. 1958; Mirtáceas del Estado de Santa Catarina (Brasil). Sellowia 13: 265-363. 15 Dec. 1961; El género *Calyptranthes* en el Brasil austral. Lilloa 31: 183-206. 1962; Sinopsis de las especies de *Marlierea* del Brasil. Com. Bot. Mus. Hist. Nat. Montevideo 3 (no. 40): 1-40. pl. 1-2. 1962.

KAUSEL, E. Revisión de las Mirtáceas Chilenas. 6 pp. Santiago, Aug. 1940; Contribución al estudio de las Mirtáceas Chilenas. Rev. Argent. Agron. 9: 39-68. "Mar." 1942, op. cit. 221-243. "S.p." 1942; op. cit. 11: 320-327. "Dec." 1944; Notas mirtológicas. Lilloa 13: 125-149. 1948 ("1947"); Lista de las Mirtáceas y Leptospermáceas Argentinas. Lilloa 32: 323-368. [Jul-Oct] 1967, reprinted with pagination 3-48.

The group *Dichotomae* of Berg included more than 50 species, most of which are now referred to *Myrcianthes* or to other genera. It remained for Grisebach (Fl. Brit. W. Ind. 236, 240. 1860) to emphasize the difference between the racemose and the dichotomous inflorescence. This author separated *Eugenia* from a newly proposed genus in part as follows:

Inflorescence centripetal, axillary; embryo globose or ovoid, usually undivided, radicle short . . . . . *Eugenia*.

Inflorescence cymose [centrifugal], rarely reduced to single pedicels; central flower sessile, 2 lateral ones pedicellate, inserted into the axils of the bracteoles; embryo annular, the cotyledons distinct, large, incurved-obovate, flat, fleshy; radicle basilar, incurved and approaching the top of the cotyledons . . . . . *Anamomis*.

Consideration of the inflorescence and the characters associated with it, jointly with characters of the flowers and fruit, and with vegetative characters, adds one considerable dimension to the picture of the Myrtaceae, and makes for better delimitation of certain genera that have previously been misunderstood. See, for example, the keys to genera in the *Flora of Peru* (Field Mus. Publ. Bot. 13, pt. 4: 573–582. 1958).

The species of American Myrtaceae are distressingly alike in aspect and in most individual characters, making identification and classification of both genera and species a correspondingly difficult and tedious matter. The leaves are essentially all opposite and entire, and of similar venation throughout; the inflorescences are of a few basic types; the flowers are all much alike except for occasional species in which the stamen-number is drastically reduced, or those relatively few which are set apart by some strong morphological character like the calyptrate calyx of *Calyptranthes*. Distinctive vegetative characters (e.g. bicarinate branchlets, or stalked dibrachiote hairs) occur in but few species; pubescence-types, or the presence or absence of pubescence, sometimes afford useful taxonomic distinctions, but most species lose some or all of their pubescence as they mature. In the absence of more obvious distinctions, the taxonomist of the Myrtaceae is often constrained to consider details of ovarian structure, of placentation, and of ovule number, but even these sometimes fail to provide the evidence necessary for a satisfactory conclusion.

The number of locules in the ovary differs from one group of genera to another, and within individual genera. Among the genera allied to *Psidium* and *Campomanesia* the number is usually 3 or more, but sometimes 2 (cf. Fieldiana Bot. 29: 519. 1963, where there are some speculations upon the direction of a reduction-series in *Psidium*). In the traditional Eugeniinae the number of locules is usually 2; in the Myrciinae it may be either 2 or 3. The number is usually constant in any one species, except that in the pimentoid genera it may vary from 2 to 3, 4 to 5, 6 to 8 or 8 to 10. From a taxonomic standpoint it is important to assess the extent of this variation, and the extent to which it is correlated with specific and generic limits.

The number of ovules in each locule of the ovary is taxonomically significant, but to what extent is not yet fully known. The number is usually only approximately constant within genera or even within species except in those taxa in which it is reduced to 2. There seems to be a general correlation between an increased number of ovules, and increased variation in the number.

A profitable area of investigation may still be found in the details of placentation, and the development of the placentae and the ovules. Berg (cf. Fieldiana Bot. 29: 517. 1963) supposed that the sporophores were parietal in origin in the species of *Psidium* having a 3-locular or multilocular ovary, but as far as I know the differences between these species and those with bilocular ovary have never been worked out. Kausel, in a series of papers culminating in a general discussion in 1956 (Ark. Bot. II. 3: 491–516.), postulated that important taxonomic decisions might be made on the basis of the combination of ovule number, position of placenta (e.g. whether basal or apical), structure of placenta (e.g. whether peltate or merely “warzenförmig”), and morphol-

ogy of the embryo. Amshoff (e.g. in the Flora of Suriname 3: 115 ff. 1951) has attempted to describe differences between species of *Eugenia* on the basis of placental structures, characterizing the ovules as "biseriate", "pendulous", "arranged in a semicircle open above", etc., and the placenta as "peltate, thickened in the middle", "incrassated, semiglobose, in the lower part of the cell", etc. My own observations lead me to think that few valid conclusions as to generic limits can yet be drawn on the basis of information like the above. Many more observations are needed, particularly with respect to comparative embryology; the origins of placental structures; the effects of crowding in the locules and its effect upon the arrangement of the ovules; and in general the extent to which variation may be influenced by factors other than hereditary ones. In species with a variable number of locules, for example, it would be desirable to know the extent to which the number of ovules in each locule varies as the number of locules increases or decreases.

It is still true as it was in the time of De Candolle and in that of Bentham, that the fruits of many species remain unknown. Collectors tend to concentrate upon flowering specimens, and as flowers and fruits are seldom found on the same plant at the same time, it is only the more common species that are well known in the fruiting condition. This may be of little practical importance with respect to species that are readily placed in the proper genus by other obvious features, but in many borderline species and poorly understood genera a knowledge of the structure of the mature seed may be essential to the proper disposition of the taxon. The distinctions between *Plinia*, *Calycorectes*, and *Eugenia*, for example, are not easily made; according to the usual interpretation *Plinia* has free, plano-convex cotyledons, closed buds and 2-ovular locules in the ovary; *Calycorectes* has an undivided embryo, closed buds, and few or many ovules in each locule; *Eugenia* has an undivided embryo, an open lobed calyx and numerous (or sometimes few) ovules. Unfortunately the fruit is unknown in *Plinia* and in *Calycorectes* except in a few species. If it were possible to establish a firm correlation between the free cotyledons and the biovular condition in *Plinia*, the genus might be maintained with more confidence than is now possible, and the distinction between *Calycorectes* and *Eugenia* (if any exist) might be worked out more readily after the elimination of *Plinia* from the complex.

### Cytogenetics

An almost untouched field of investigation is that of the cytogenetics of the American Myrtaceae. I have speculated that some so-called species and other puzzling forms of *Psidium* have arisen as a result of hybridization (cf. Field Mus. Publ. Bot. 13, pt. 4 [Fl. Peru]: 795. 1958; Fieldiana Bot. 29: 524. 1963), but these speculations are without experimental verification. Relatively few of the species of Myrteae are known in cultivation, and because so many of the others are localized tropical species it would be difficult to undertake any systematic cytogenetical program. Observations on chromosome-numbers in a relatively small number of species indicate that there is remarkably little variation in this respect; throughout the entire family the prevailing number is  $x = 11$ . Some polyploids (including one triploid, *Psidium montanum* Sw.) are known, and counts of  $x = 10$ ,  $x = 12$  and  $x = 14$  have been reported. New observations on additional species and genera are urgently to be desired. Chromosome numbers are known for only about 25 species of the entire tribe Myrteae (cf. Moussel, B., in Mém. Mus. Nat. Hist. Nat. [Paris] II. Bot. 16: 91–125. pl. xi–xiv. 1965), and only about half of these are American. For references to earlier work the reader may consult a paper by Atchison, in Am. Jour. Bot. 34: 159–164. 1947, for counts available up to that time; and *Index to Plant Chromosome Numbers*, vols. 1–2, covering the period 1956–64.

## Geographical affinities

In one respect the botanist of the 20th century is in a better position to decide upon specific and generic limits in the Myrteae than were Berg and Bentham. Just as the amount of material available to Berg was much greater than that studied by De Candolle, so has the amount increased enormously in the last century. The knowledge of all groups of plants has increased to such an extent that it is now possible to make some generalizations about the geographical affinities of the floras of Tropical America. On the basis of herbarium material now available, and reasoning to some extent by analogy with other groups of plants, one can now delimit with some confidence the areas in which species of certain genera are most likely to occur. In doubtful cases involving specific limits, also, there are often parallel cases in other plant-families with the same or similar geographical distributions. The genus *Ugni*, for example, is typically Andean in distribution, ranging from Mexico to Chile. On the basis of this distribution (which it has in common with various other genera in different plant-families), and on the basis of some perhaps trivial but constant morphological features that all the widely separated populations have in common, I have no hesitation in regarding this as an independent American genus distinct from *Myrtus* to which Bentham referred it. As to specific limits within the genus, Berg recognized 5 local species in the area from Peru northward, but the differences between these seem insignificant, and their geographical disposition in isolated populations along the Cordillera seems to strengthen the case for regarding them as subordinate taxa of a single species.

Distribution-patterns in South America are becoming apparent for the larger genera also. For example, *Myrcianthes* is well represented in the Andean region and to a lesser extent in Uruguay and southern Brazil, but is almost absent from the Guayana highlands; *Marlierea*, on the other hand, seems to have two centers of abundance, one in the Guayana Highlands and the other in extra-Amazonian Brazil. *Gomidesia*, a genus of some 40 species, is known chiefly in southern Brazil; a few species range as far north as Bahia and one to the Antilles. *Myrceugenia*, including about as many species as *Gomidesia*, is about equally represented in the Chilean — Patagonian province and in the Atlantic sub-tropics of Uruguay and southern Brazil.

## II. PROPOSED REALIGNMENT OF THE AMERICAN MYRTEAE

In a paper which I have repeatedly quoted in the course of the present discussion, George Bentham's *Notes on Myrtaceae* published in 1869, the author pointed out that the embryo-characters described 40 years before by De Candolle were first "supposed not only to be widely and constantly distinct, but also to correspond with differences in the number of parts of the flower, in the texture of the testa, and other minor characters, and they were gladly seized upon as absolute tests of three great genera or subtribes". Bentham went on to say that as more and more species became known, it was becoming increasingly evident that "the embryonic character in the fleshy-fruited Myrteae is . . . more artificial than was supposed, and is only retained for want of a better one". In spite of this caveat, almost all authors for a century have maintained the traditional subtribes of Myrciinae, Eugeniinae and Pimentinae, notwithstanding the fact that they are patently artificial. The recent work of Eberhard Kausel has focussed attention upon this and upon the several small and mostly geographically localized genera that seem out of place in the Bergian subtribes. Kausel has himself proposed a new classification of the Myrteae, in a paper entitled *Beitrag zur Systematik der Myrtaceen* (Ark. Bot. II. 3: 491–516. 1956). He divides



the tribe (which he regards as a family, Myrtaceae, distinct from the capsular-fruited Leptospermaceae), into five coordinate groups (which are nowhere formally described or validly published),<sup>1</sup> as follows:

1. Embryo rich in stored food, germinating hypogaeously, usually spherical or ellipsoid, less often curved and elongate.
2. Embryo undivided. Eugenioideae.
2. Cotyledons large, fleshy, separate; hypocotyl small. Plinioideae.
2. Cotyledon-body large, surrounding the radicle; cotyledon-tips, if present, small, incumbent. Cryptorhizoideae.
1. Embryo poor in stored food, reniform, germinating epigaeously, with long simple or cyclically curved hypocotyl.
3. Cotyledons small, accumbent, or less often united with the hypocotyl. Myrtoideae.
3. Cotyledons large, foliaceous, crumpled and folded together, only exceptionally thin-fleshy and plano-convex. Myrcioideae.

Probably a still better classification could be devised after additional observations on the manner of germination; as Kausel notes, such observations are still all too few. Over-emphasis on the manner of development of the seed, however, may be criticized as much as over-emphasis on any other one character. Kausel, for example, places *Myrceugenella* [*Luma*] with the Myrcioideae (where it is quite out of place when judged by the sum total of all its characters), because the embryo germinates epigaeously in spite of its food-storing cotyledons. He also associates, on the basis of what seem to be empirically chosen characters of the embryo, such dissimilar things as *Legrandia* and *Blepharocalyx*.

I do not believe that the American genera of Myrtaceae can be divided thus simply into subtribes representing natural evolutionary units, though for most purposes (and in most geographical regions) the old artificial classification of Berg may be used for easy reference. It seems preferable to look at the American genera as having resulted from evolutionary specialization along a number of lines, some much more successful than others.

For purposes of argument I have assumed that the evolution and spread of Angiosperms in America has taken place in the way described some years ago by W. H. Camp.<sup>2</sup> According to this assumption the Myrtaceae as a family may have been well established in the southern hemisphere by Cretaceous time. Subsequent evolution has resulted in the development of a large number of species of the capsular-fruited members of the family in Australia (but one genus persisting in America), and probably an equally large number of species of the fleshy-fruited types (the "Myrteae") in tropical America. With the exception of *Eugenia*, and possibly of *Myrtus*, no genus of the Myrteae is known to occur naturally in both Old and New Worlds. It may therefore be taken as a working assumption that the rest of the existing New World genera evolved in tropical America from the original myrtaceous stocks. What were these proto-Myrtaceae like?

#### *Evolutionary specialization in the Myrteae*

Many kinds of specializations are observable in the Myrteae. In general, I read the series as progressing from many parts to few, or none, from free parts to united parts, from green leafy structures to scarious or hyaline bractlike structures, and from indeterminate to determinate growth.

<sup>1</sup> Kausel has recently published an elaboration of his system, including validation of the coordinate groups which he now designates as subfamilies. See *Lilloa* 32: 323-368. 1967.

<sup>2</sup> Distribution patterns in modern plants and the problems of ancient dispersals. *Ecol. Monog.* 17: 159-183. 1947.

In all the American Myrteae, the solitary flower is subtended by a pair of bracteoles; that is, the peduncle is an axillary branch terminated at the first node by a flower. The bracteoles represent the leaves at this node, and branches may develop from the axils of these bracteoles. In many species this last ability seems to have been lost; in others it is facultative. Because the basic pattern of a pedicellate flower subtended by two bracteoles is common to all the species, it may be assumed that such a flower occurred in the primitive Myrteae, and that the different types of inflorescences have evolved through changes in the arrangement of these flowers on the branches. From the condition in which solitary flowers (i.e. 1-flowered peduncles) occurred in the axils of ordinary leaves on indeterminate branchlets, the development of different inflorescence-types seems to have proceeded in several different ways.

It may be inferred that the first step in the development of specialized inflorescences involved the reduction of foliage-leaves to smaller but still green bract-like leaves, and eventually to small bracts that never became green. In all the major evolutionary lines of the Myrteae this has been of common occurrence. Evidences of the reduction of foliar tissue are usually best observed at the lowest one or two nodes of short leafy twigs of the current season. As in many woody plants, the first (lowest) leaf produced may be smaller than the later ones, even when no flower is produced at the same node. When a flower develops with the leaf, at the same node, it seems that the growth of the leaf may be even more retarded. In some species of *Psidium*, for example, the peduncles are mostly scattered along the branchlets in the axils of ordinary leaves, but the leaves subtending the lowermost peduncles are often reduced to half the size of the others, or even to small green bracteoles a few millimeters long. In some other genera the process seems to have gone farther. In many species of *Eugenia* some or all of the peduncles are regularly produced in the axils of small scarious or indurated bracts at the lowermost nodes of leafy branchlets. This may be referred to as the *Stenocalyx* type of flowering; in Berg's genus of the same name (now generally considered a synonym of *Eugenia*), the flowers often develop precociously from a cluster of imbricated bracts surrounding the vegetative bud, and vegetative growth of the leafy axis follows after anthesis; until the branch is well grown, and the subtending bracts have fallen, it is not apparent that the peduncles are in actuality borne at the lowermost nodes of the same branchlet that bears leaves above. The *Stenocalyx* type of flowering may be observed also in several pimentoid genera (e.g. *Campomanesia*) and in *Myrcianthes*.

Associated with these primary reductions in foliar tissue at fertile nodes, further specialization seems to have resulted in the development of groups of flowers, i.e. inflorescences, of different types that can be at least approximately correlated with other characters common to groups of genera.

1) By the growth of flower-bearing, secondary peduncles from the axils of the bracteoles subtending the primary flower. Different stages in this process can still be seen in e.g. some species of *Myrcianthes* and *Psidium*, in which solitary flowers and 3-flowered dichasia may often be found in different axils on the same plant. Presumably further proliferation gave rise to forms with 7- and 15-flowered dichasia. Inflorescences of this kind, i.e. simple axillary dichasia, prevail in the *Psidium* - *Myrtus* complex and in such derivative genera as *Ugni* and *Myrteola*; in *Myrrhinium*; in *Blepharocalyx*; and in *Myrcianthes* and *Reichea*.

2) By the further reduction of leaves to bracts, and the transformation of leafy branchlets with axillary flowers into "racemes", i.e. simple specialized branchlets bearing solitary bracteate flowers at each node. The racemose type of flowering is predominant in the large genus *Eugenia*, in *Calycorectes* and *Myrciaria*, which I take

to be derivatives from eugenioid stock, and in several smaller genera. In many species of *Eugenia*, however, and in *Campomanesia* and other pimentoid genera in which racemes regularly occur, flowering may be partly of the *Stenocalyx* type and partly racemose on the same plant; the relative abundance of the two types of flowering varies from species to species.

There is evidently no fundamental evolutionary separation between 1) and 2) above. In some species of *Eugenia* with normally racemose inflorescence, some or all of the individual flowers may be replaced by 3-flowered dichasia. In *Luma apiculata* the flowers may be solitary or in axillary 3-flowered dichasia, or occasionally the dichasia may be racemosely disposed on very short leafless branchlets. In *Calycolpus* and *Campomanesia* the flowers are usually produced racemosely on short leafless axillary axes, but at least in *Campomanesia* the peduncles often bear 3-flowered dichasia in place of solitary flowers.

Although confusingly different types of inflorescences many occur even on the same plant (as for instance in plants of the *Eugenia florida* — *oerstedeana* complex, where most of the flowering may be of the *Stenocalyx* type, some of the flowers in racemes and even a few in axillary 3-flowered dichasia), it is clear that tendencies toward one type of flowering or another are correlated with other characters that are markers of generic distinctions. In the eugenioid genera almost all the flowers are produced in racemes; a relatively small number of species regularly have some flowering of the *Stenocalyx* type, and very few flowers indeed are produced in the leaf-axils. At the other end of the scale, in such genera as *Psidium*, *Ugni*, and *Myrteola*, most of the flowers (peduncles) are axillary. In some other pimentoid genera<sup>1</sup> the inflorescence-types seem to be specialized in particular ways, e.g. in *Calycolpus* and *Amomyrtus* the peduncles are almost all racemosely arranged but one-flowered, whereas in *Campomanesia* and most of the American species of "*Myrtus*", a fair proportion of the flowering is of the *Stenocalyx* type.

3) By the reduction of leaves to bracts in whole branch-systems, with the production of what I have called the *myrcioid panicle*; cf. Fieldiana Bot. 29: 158–161. figs. 4, 5. 1956. Such a panicle may be 4 or 5 times compound, exhibiting throughout the same opposite and decussate branching that prevails in the leafy branches of the plant. On the same plants may often be observed intermediate stages, in which the small bracts at the bases of the primary branchlets of the panicle are replaced by ordinary leaves, this transforming the one large panicle into a number of smaller ones on a leafy branch. What I take to be vestiges of the primitive flower-arrangement are found at the tips of the branches of the myrcioid panicle, where the flowers are usually solitary and bracteolate, or in 3-flowered dichasia. The panicle is the usual type of inflorescence in *Myrcia* and *Gomidesia*, and in the derived genera *Marlierea* and *Calyptranthes*; in the two last it is often more highly specialized as indicated by the abortion of the terminal bud at the first node, and the consequent development

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<sup>1</sup> Some authors have used *myrteroid* (or its equivalent in other languages) in the sense in which *pimentoid* is used in this paper, i.e. to mean *of or pertaining to the members of the Pimentinae*. Reference is made to the pimentoid genera (cf. also Fieldiana Bot. 29: 172. 1956) and especially to the *pimentoid embryo*. As according to the International Code of Botanical Nomenclature those who maintain the formal designations of subtribes established by Berg will have to take up the name Myrtinae in place of Pimentinae, the term myrteroid might be preferable. I have deliberately used pimentoid, however, as it does have at least a short history, it is more euphonious, and it provides a term applicable to a number of genera that have certain structures in common; on the other hand it may be used without any nomenclatural implication; a genus with pimentoid embryo does not necessarily, or even by implication, belong to the Myrtinae.

of a pair of panicles that are morphologically equivalent to the lower branches of the panicle in *Myrcia*. The myrcioid panicle is also characteristic of *Pimenta*, and in modified form of *Pseudanmomis* and *Pseudocaryophyllus*.

### *Calyx*

The most variable organ in the myrtaceous flower is the calyx. The most common types are those with 5 or 4 distinct lobes, borne at the margin of the staminal disk and at about the same vertical level. In some genera and species the hypanthium is produced vertically into a tube or cup; the stamens and petals are borne on the distal margin of this prolongation, the outer layers of which terminate in the calyx-lobes. Correlated with prolongation of the hypanthium are reductions in size and number of calyx-lobes. It is possible, for example, to demonstrate a large series of intermediate stages between the ample 5-lobed calyx of *Myrcia* and the completely closed bud of *Calyptranthes*. Also correlated are changes in the manner of opening of the calyx at anthesis; the open 5-lobed calyx is ordinarily almost unchanged after anthesis except that the lobes may be reflexed; as the lobes become smaller and the hypanthium elongates, there is more of a tendency for the calyx and hypanthium to split between the lobes when the flowers open, the fissures sometimes extending to the summit of the ovary. The completely closed calyx may open by a calyptra, as in *Calyptranthes* and some species of *Psidium*, or by irregular longitudinal splits, as in *Marlierea*, *Plinia* and *Britoa*. There seems to be no fundamental distinction between the circumscissile, calyptrate calyx and the closed but irregularly splitting calyx, nor does it seem possible to depend primarily upon calyx-characters for the delimitation of genera, as was done by Berg. A few small genera with highly specialized calyx and hypanthium (e.g. *Paivaea*, *Siphoneugenia*) are still defined primarily by reference to these organs.

### *Ovary*

There is much variation in characters of the ovary, but the available data are relatively incomplete and must be interpreted with caution. In the Myrteae the ovary is prevalingly bilocular except for *Myrceugenia* in which the locules are usually 3 in number, and *Campomanesia* and *Psidium* and some related genera in which the number of locules may be 3–5 or as many as 10 or more. Several genera (e.g. *Myrcia*) include series of species with trilocular ovary as well as those with the bilocular type. In general it can be said that in genera which seem to be specialized in several respects, the ovary is usually bilocular; it does not follow, however, that non-specialized species and genera (as indicated by the sum of their characters) are those with multilocular ovary. Presumably the multilocular ovary is a primitive character that has persisted primarily in one line of descent while other characters in the same line (e.g. the flower structure in *Psidium*) have been evolving more rapidly.

### *Ovules*

The number of ovules in each locule of the ovary varies widely, especially between species and genera, but also within individual species. The absolute amount of variation increases markedly with the number of ovules, e.g. in some species of *Psidium* the number may vary from 20–30 or 20–45; in some species of *Myrcianthes* from 10–20 or 15–25; when the number is 10 or fewer it rarely varies by more than 1 or 2, and when the number is 2 (as in *Myrcia* and all the closely related genera; in *Plinia* and *Myrciaria*; and in a few species of *Eugenia*), it is remarkably constant at that level. When reduction in ovule-number occurs, it is usually in genera or species that

are judged to be specialized in other ways also, but the relatively high ovule-numbers in the large genera *Myrcianthes*, *Eugenia*, *Psidium* and *Campomanesia* are to be thought of as unspecialized features that have persisted there.

It is difficult to assess the evolutionary importance that may attach to the placentation and the mode of insertion of the ovules. Writing primarily of the capsular-fruited Myrtaceae, Bentham (Jour. Linn. Soc. Bot. 10: 119, 1869) thought the 'modifications of the ovules and their placentation afford the best generic characters, the most in accordance with minor characters and general habit. I have . . . found no other organs so constant, provided too much weight be not attached to the precise form of the placenta . . .'. Berg was impressed by the peculiar arrangement of the ovules in his group Pimentoideae (that is, especially in *Psidium* and some related genera): in a number of species the ovules are obviously biseriate, on the margins of intruded placentae that Berg took to be parietal in origin. Kausel, as pointed out above, has emphasized the description of details of placentation and the importance of the position of the placenta (e.g. whether apical, central or basal in the cell). As in the great majority of the American Myrteae the placenta is (at least superficially) axile in origin, and as for most species nothing is known of the ontogeny of this structure, it seems premature to speculate upon its degree of specialization in any particular case. It is true that the placentae in some genera assume distinctive forms; the most extraordinary of these are mentioned below in the appropriate places in the text.

### *Cotyledons*

Much importance has been attributed to the cotyledons as indicators of generic relationships in the Myrteae. Reasoning *a priori*, one may assume that thin, separate and more or less leaflike cotyledons represent a less highly advanced type than those that are either 1) Rich in stored food, 2) Partly or wholly united, or 3) Modified in other ways. Thus the embryo of *Psidium*, with small separate cotyledons, may be thought of as primitive in this respect; the somewhat larger and spirally inflexed cotyledons of *Feijoa* [*Acca*] as somewhat more specialized; the very large, thin, crumpled cotyledons of the myrcioid genera as rather highly evolved; and the separate but plano-convex and fleshy cotyledons of *Luma* and *Myrcianthes* as having evolved in a slightly different direction. Presumably the pseudomonocotyledonous embryo of *Eugenia*, resulting from fusion of the separate cotyledons, represents a very old specialization, as it is found in both Old and New Worlds. Among the New World Myrteae are genera (e.g. *Plinia*, *Siphoneugena*) that seem closely related to *Eugenia* except that in most respects they are more highly specialized; in these plants, however, the cotyledons are free, fleshy and plano-convex, suggesting that this last condition may have developed secondarily from some eugenioid type, or alternatively that *Plinia* and *Siphoneugena* represent ancient lineages of which few species have survived.

The integuments that surround the seed differ in thickness and in character from group to group and from genus to genus. The testa is rather uniform throughout the myrcioid genera, cartilaginous, thin and brittle; in *Eugenia* and in general among the genera referred by Berg to the Eugeniinae, it is very thin, membranous or leathery; among the pimentoid genera it may be thin and often glandular-verrucose, or very much thickened, externally lustrous, and bony. It would seem *a priori* that the membranous testa is less specialized from an evolutionary standpoint than the thicker, bony testa, but bony types occur both in Old World and New World species, and presumably developed very early in the history of the family. No one clear line of descent can be demonstrated among the American species with bony seeds, but two principal lines are suggested; see text below.

When all the above morphological criteria are considered, together with other data from morphology, and knowledge of the present geographical ranges of the American genera, it appears that one can reasonably support Camp's thesis of a primary establishment of the family in southern South America, and its subsequent spread, with concomitant evolutionary development, in the American tropics. The genera do not divide themselves readily, however, into well marked subtribes, and in proposing the following classification of the New World Myrteae I have abandoned the traditional classification into Myrciinae, Eugeniinae and Pimentinae, and have attempted merely to suggest certain putative lines of specializations.

#### *Taxonomic subdivision of the Myrteae*

Perhaps 95 percent of the species of American Myrtaceae fit neatly into a relatively few well-defined groups. It is clear, for example, that several hundred species are alike in having at the same time a characteristic inflorescence (the myrcioid panicle), a distinctive embryo (with thin, crumpled and much folded cotyledons), a bilocular (or occasionally, trilocular) ovary, and a highly constant number of ovules (2) in each locule. These species in fact comprise the group Myrciinae which is a very neatly defined group indeed until one considers also the genus *Myrceugenia* (which was included by Berg among the Myrciinae because it has the foliaceous, contortuplicate cotyledons that characterize the rest of the genera). Unfortunately for a neat taxonomic separation, *Myrceugenia* is unlike the rest of the Myrciinae in almost every respect except in the matter of the cotyledons: The inflorescence is not a panicle, the ovules are several or many in each locule, the ovary is usually trilocular, the calyx is usually 4-merous (prevaillingly 5-merous in *Myrcia*), the bracteoles are usually persistent through anthesis (but almost invariably deciduous in the rest of the Myrciinae).

Further consideration shows that *Myrceugenia* fits no better into any of the other traditional subtribes. Although because of the 4-merous and persistently bracteolate flowers many of the species were originally placed in *Eugenia*, they are out of place there because of the trilocular ovary, the myrcioid embryo and the manner, unique as far I know, in which the flowers are produced in many species, i.e. the peduncles are strictly axillary and solitary or, if more than one, then one above another in the axil.

There are about a half-dozen additional genera that, like *Myrceugenia*, appear to combine in unusual ways the characters that have been thought of as traditionally belonging to one or more of the great subtribes. *Nothomyrcia*, for example, has the embryo of the Myrciinae and a bilocular ovary, but its flowers in a raceme; *Amomyrtus* has a pimentoid embryo, and 5-merous flowers in a raceme; *Luma* has 4-merous flowers, the embryo almost of *Myrcianthes* but the cotyledons thinner, and the flowers solitary or in 3-flowered dichasia, or the peduncles produced in short racemes; *Legrandia* has the inflorescence of a *Psidium* or an *Ugni*, 4-merous flowers, bilocular ovary, a stalked peltate placenta with few marginal ovules, and a peculiar massive embryo differing in some respects from that of *Eugenia*; *Amomyrtella* has a pimentoid embryo, 4-merous flowers in short praecocious racemes, and uniquely modified stamens and style.

These genera, except for *Myrceugenia*, are small (1-3 species each), and it is to be noted that they are all confined to temperate or subtropical South America. *Myrceugenia* is disjunct, with a few species in Chile and the rest in the south-Brazilian region; *Nothomyrtus*, *Amomyrtus*, *Luma* and *Legrandia* are Chilean, and *Amomyrtella* is a native of northern Argentina. To the above list might well be added

*Acca* and *Myrrhinium* and even *Blepharocalyx*; all of these have representatives in Uruguay and southern Brazil, and others in the Andes of Peru and/or Ecuador. All are apparently pimentoid in their affinities, but with somewhat atypical embryos, distinctive inflorescences and specialized flowers.

Perhaps these small genera represent evolutionary experiments, combining as they do certain features that are found elsewhere in different combinations, and including some unique features all their own. Certainly their existence and their present geographical localization lead one to speculate that they have been isolated a long time, and that in the meantime other more successful groups have migrated away from the region of the proto-Myrtaceae as the genetic combinations became fixed in larger groups of species, and the principal modern genera became recognizable.

It is worthy of comment in this connection that at the northern end of the axis, in the West Indies, there are several endemic insular taxa that have been treated as independent genera. These differ in one important respect from the anomalous South American genera just discussed; the West Indian taxa for the most part seem to have evolved through specialization of existing genera. *Calypstrogenia* and *Hottea*, for example, both Haitian groups, appear to differ from *Calycorectes* chiefly in the morphology of the calyx; the Cuban *Mozartia* is like *Myrcia* except for an extreme reduction in the number of ovules and locules of the ovary; *Krokia* and *Myrtekmannia*, also Cuban, seem to represent a comparable stage of reduction in the series that includes *Pimenta*. Whether or not taxa like these are in fact genera may remain a matter of opinion, but if they are genera they are not very well marked ones.

There are in the Caribbean region, however, several distinctive taxa that are not so clearly related to other, more widespread genera. *Pseudanamomis* is such a taxon; it belongs neither with *Myrcia*, *Myrcianthes*, nor *Eugenia*, and can hardly be treated logically except as an independent monotypic genus. *Mitranthes* and *Marlieriopsis* seem similarly distinctive, with no obvious relationships among West Indian or South American genera. (See the discussion under the list of imperfectly known genera at the end of this paper.)

It may be, therefore, that such genera as *Pseudanamomis*, *Mitranthes* and *Marlieriopsis* are comparable in age and in evolutionary history to *Myrceugenia*, *Amomyrtus* and the other temperate South American genera included in the circle of Figure 1. If so, it seems likely that *Calypstrogenia*, *Hottea*, *Mozartia*, *Krokia* and *Myrtekmannia* represent the end-products of much later evolutionary development.

The patterns of distribution of the American Myrteae tend to be aligned along a North-South axis. *Myrcianthes*, *Myrteola* and *Ugni* are chiefly Andean, except that the first is represented in the south-Brazilian region also. Primarily in eastern South America, with centers of abundance both north and south of the Amazon, are *Myrciaria*, *Marlierea*, *Siphoneugena*, and probably also *Plinia*, *Calycorectes* and *Calyptranthes*; the species of *Calyptranthes* have multiplied greatly in the West Indies and continental North America, which has tended to make the original South American range of the genus a matter of conjecture. Probably the much larger genera *Myrcia* and *Eugenia* have been established a long time in eastern South America also; both are represented by distinctive species-groups in the south-Brazilian region and by others in northeastern South America and the West Indies, but by relatively few species, and many of these at the western edges of their ranges, in the Andes.

Because so many genera, both large and small, occupy the same distinctive ranges in eastern South America, it may be supposed that at some time in the past the ancestors of the present species ranged rather widely north and south. Very few species however, — perhaps fewer than a dozen — range so widely today; most species in most genera are concentrated either in the highlands (or along rivers) north of the Amazon, or in the plateaus and lowlands of southeastern Brazil. This leads to the

further assumption that although the principal genera may have been established during a time when the vegetation of eastern South America was relatively uniform, the modern species have developed more recently.

From the original complex of proto-Myrtaceae, it seems that several principal trends may be recognized. These are described below, but no attempt is made to group the genera into formal taxa of higher rank. In the paragraphs that follow, and in Figure 1, I have tried to present the concept of an ancient reservoir or gene-pool of myrtaceous stocks, represented today by a series of living small genera that have resulted from isolation or from lack of adaptability. I do not intend to imply that the large and more successful modern groups of genera have arisen from ancestors like *Luma* and *Acca* and the rest, but only that both must have arisen from ancestors now long since extinct, and that the strong correlations of characters like those in the genera related to *Myrcia* must have developed in comparatively recent times, whereas the original gene pool must have produced some random assortments that resulted at an early date in the ancestors of what now seem to be unsuccessful genera.

1) From a group with 5-merous flowers in myrcioid panicles, myrcioid embryo, and bilocular ovary with 2 ovules in each locule, evolution has been evinced mainly in modification of the calyx and hypanthium; specialization of the anthers has occurred in one Brazilian group (*Gomidesia*). In some genera (*Marlierea*, *Calyptranthes*), reductions in the inflorescences and changes in the corolla have taken place.

2) From a group with mostly 4-merous flowers in simple racemose inflorescences, fleshy embryo rich in stored food, and bilocular ovary with several or many ovules in each locule, evolution seems to have proceeded mainly in the direction of reduction in ovule-number, and in modifications of the calyx and hypanthium. From *Eugenia*-like ancestors with massive undivided embryo the Recent species of *Calycorectes* and *Myrciaria* have probably been derived. In *Plinia* and *Siphoneugena*, which are superficially similar to *Calycorectes* and *Myrciaria*, respectively, the cotyledons are distinct (suggesting those of a bean, or those of the *Myrcianthes* group of the Myrteae). Whether this implies parallel evolution from ancestors with different types of embryos, or secondary evolution of the type found in *Plinia* and *Siphoneugena*, I cannot say.

3) From a group with 4- or 5-merous flowers partly solitary and axillary and partly in small dichasia; with distinct plano-convex cotyledons rich in stored food; and with bilocular ovary with several ovules in each locule, evolution seems to have resulted in the production of many local species chiefly along the Andes, and in the predominance of the 4-merous rather than 5-merous flower. What is regarded as the more primitive 5-merous calyx is retained in the monotypic *Reichea*, of Chile, and in a few species of *Myrcianthes* in southeastern Brazil, one in Peru and one in the Guianas. The monotypic Antillean *Pseudanamomis*, with cotyledons somewhat united, 5-merous flowers, and somewhat irregularly branched inflorescence, is regarded as an early offshoot from this line, not from the myrcioid line.

It is tempting to derive this line from something like *Luma* because of the resemblances in embryo-structure, in inflorescence and in number of calyx-lobes between *Luma* and *Myrcianthes*, but in fact the species of *Luma* do not much resemble those of *Myrcianthes* except in these respects, and it is likely that the relationship between the two may not be very close.

From a group probably with 5-merous flowers solitary or in small dichasia, a pimentoid embryo, and numerous ovules in each of several or many locules of the ovary, evolution seems to have resulted in a number of different lines distinguishable



Tabular comparison of the genera included in the circle of Figure 1. See text for explanation.

### MYRRHINIUM

Ovary 2-locular	Embryo pimentoid
Ovules several	Infl. 3x-dichotomous
Fl. 4-merous	Androec. specialized
	Seed bony

Peru & S. Brazil

### NOTHOMYRCIA

Ovary 2(-3)-locular	Embryo myrcioid
Ovules several	Infl. raceme
Fl. 4-merous	

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### ACCA

Ovary 2- or 4-locular	Embryo pimentoid
Ovules several	Infl. of <i>Psidium</i>
Fl. 4-merous	or racemose
	Androec. specialized

Peru & S. Brazil

### MYRCEUGENIA

Ovary 3-locular	Embryo myrcioid
Ovules several	Infl. dichasium or
Fl. 4-merous	fls. superposed

Chile & S. Brazil

### AMOMYRTUS

Ovary 2-locular	Embryo pimentoid
Ovules several	Infl. raceme
Fl. 5-merous	Seed bony

Chile

### LEGRANDIA

Ovary 2-locular	Embryo ± eugenioid
Ovules several	Infl. of <i>Psidium</i>
Fl. 4-merous	Placenta peltate

Chile

### AMOMYRTELLA

Ovary 2(-3)-locular	Embryo pimentoid
Ovules 2	Infl. racemoid
Fl. 4-merous	Seed bony

N. Argentina

### LUMA

Ovary 2-locular	Cot. plano-convex, thin
Ovules several	Infl. dichasium or
Fl. 4-merous	raceme

Chile

by differences in the inflorescence, in the calyx, in the number of locules in the ovary, in the thickness and hardness of the testa, and in the amount of curvature of the embryo in the seed. The inflorescences include all types known to occur in other groups of the Myrteae. Specialization in other respects seems to have proceeded toward reduction of the number of locules and the number of ovules, toward a closed and irregularly opening calyx, and toward a bony as contrasted to a membranous testa.

I have not been able to suggest any wholly satisfactory arrangement of the genera in this assemblage, and have therefore separated them somewhat arbitrarily, and somewhat as Berg did, into one series in which the embryo is often strongly curved or coiled, and the testa of the seed membranous or leathery, and a second in which the embryo is merely uncinately or C-shaped, and the seeds are usually bony with a polished surface. Under this system *Blepharocalyx* is (perhaps artificially) associated with *Campomanesia*, and most of the rest of the genera are placed together in another group.

4) The series that includes the large genus *Campomanesia* is assumed to be relatively unspecialized. The calyx has been modified but little, the number of locules has remained large (the largest in any group of American Myrtaceae), the testa is membranous or leathery, and the inflorescence has not become highly modified. Both racemose and dichasial types of inflorescence are known (the dichasia often 3-flowered, sometimes racemously arranged), and the flowers are often solitary. The embryo is often strongly curved or coiled; I cannot say whether or not this is an evidence of evolutionary advancement. From ancestors like *Campomanesia*, taxa

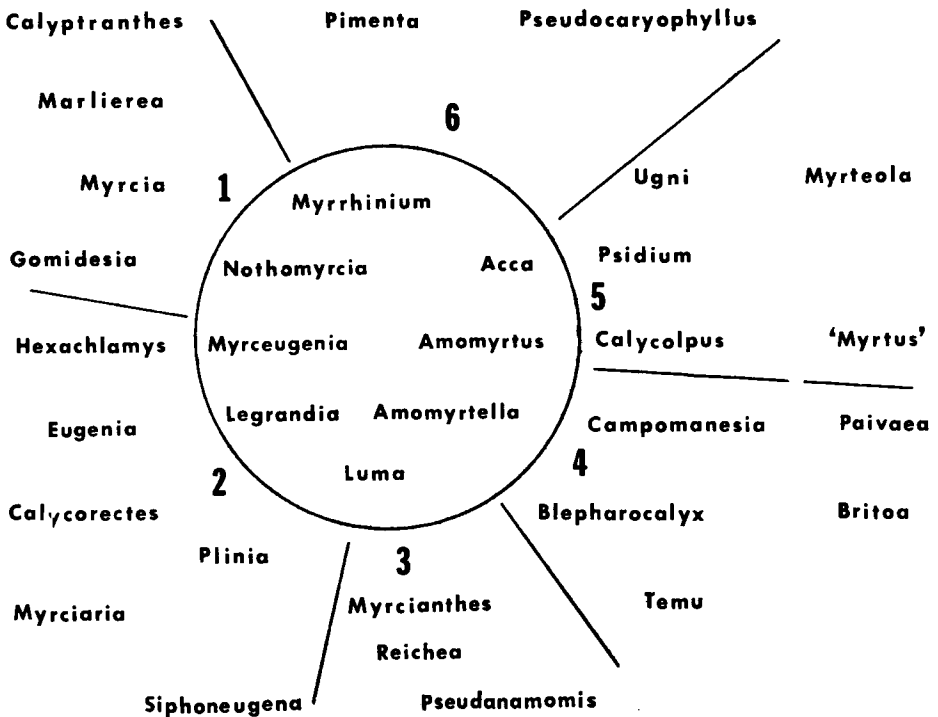


FIG. 1. Genera of American Myrtaceae, tribe Myrteae, arranged according to their supposed evolutionary affinities. The circle includes those genera that seem not to have been involved in any of the major lines of descent; see text for discussion. The numbers refer to numbered paragraphs in the text.

like *Britoa* and *Paivaea* may have been derived through reduction and specialization of the calyx and hypanthium.

The small genus *Blepharocalyx*, on the other hand, seems more highly specialized, and is placed with *Campomanesia* only because of the thin integuments of the seeds, and the strongly coiled embryo. The inflorescence in *Blepharocalyx* is an axillary dichasium (often more than 3-flowered), the calyx is 4-merous and deciduous, the ovary is bilocular, and the geographical range of the genus suggests that it may perhaps better be considered with the other genera in the circle of Fig. 1 (cf. page 371) as one of the early derivatives of an old Myrtaceous stock, with no close modern relatives. In the Chilean group that has been called *Temu*, the calyx-lobes are persistent, and the integuments of the seed somewhat firmer than in *Blepharocalyx*.

5) The American genera with bony seeds and but slightly curved embryo exhibit certain specializations. Like *Campomanesia*, *Calycolpus* has a multilocular ovary and a racemose inflorescence; unlike *Campomanesia*, *Calycolpus* has strictly 1-flowered peduncles, and bony seeds. It is possible that all the American species that have until recently been referred to *Myrtus* represent the end-products of evolutionary series like the one that produced *Calycolpus*. In all these genera, including *Calycolpus*, the flowering is of the racemose or of the *Stenocalyx* type, and the seeds are bony; the number of locules is reduced from 4 or 5 in *Calycolpus* to 2 (or 3) in *Amomyrtus*, *Amomyrtella*, and the West Indian species of "*Myrtus*"; the number of calyx-lobes is usually 5 in *Calycolpus* and *Amomyrtus*, but 4 in *Amomyrtella* and "*Myrtus*"; the ovules are numerous except in *Amomyrtella*, where they are only 2 in each locule.

In *Psidium* and a few other small genera with bony seeds the flowers are prevailingly solitary or in threes (i.e. 3-flowered dichasia), not in racemes; correlated with this is a tendency toward reduction in carpel-number from 5 or more to 3 or 2 (or occasionally 1); extreme modification of the calyx (sometimes with the production of a calyptra) has been correlated with this, and with prolongation of the hypanthium and splitting of the hypanthium in anthesis, and some vegetative specialization (presumably in response to montane conditions) has been correlated with reduction in stamen-number and with specializations in the anthers.

6) Two genera with 4-merous flowers mostly or wholly in myrcioid panicles, and usually bilocular ovary, may be only superficially similar to one another. Specialization in *Pimenta* has resulted in reduction of the number of ovules to 7 or fewer (or to 1 in *P. dioica*); the testa is membranous and the number of locules in the ovary is sometimes reduced to one. In *Pseudocaryophyllus*, as far I know it, the seeds are bony, there are several ovules in each locule, and the ovary is constantly bilocular.

As may be confirmed by reference to Figure 1, the genera assumed to have resulted from the evolutionary changes outlined in group 1, above, are those of the Myrciinae in the sense of most authors, except that I have excluded *Myrcuegenia* and treated it as a member of the heterogeneous group of genera that conform to no recognizable evolutionary pattern. Group 2 includes most of the genera traditionally referred to the Eugeniinae, except for those that I have removed to group 3. Groups 4-6 comprise together most of the genera of the traditional Pimentinae. This last assemblage is probably polyphyletic, as group 2 may also be, and I doubt the wisdom of treating them as subtribes in the formal nomenclatural sense. Similarly it would be futile to attempt to establish any sort of family tree within any of the major groups. In groups 4 and 5 particularly the diversity is so apparent and the kinds of specialization so different from one line to another that it would be impossible to say which of a given

series of genera (e.g. *Campomanesia*, *Calycolpus*, or *Psidium*) was the most highly specialized in general.

### III. ENUMERATION OF THE GENERA

#### TRIBE MYRTEAE

In the arrangement of the genera I have not attempted to follow slavishly any previously published arrangement. No one, as far as I am aware, has attempted an arrangement of all the American genera both old and new, and it would seem a retrograde step to try to intersperse the newly published genera among those in any of the older systems. Obviously if one accepts the concept of evolutionary development of genera, a linear sequence can never be a natural one; on the other hand there are some disadvantages in a strictly alphabetical arrangement. It has seemed best to disturb the traditional arrangement by subtribes as little as possible, and keep together the genera that seem most closely inter-related. The anomalous genera that are included in the circle in Fig. 1 are treated in the text as belonging with the other genera of similar embryo-structure; thus the treatments of *Myrceugenia* and *Nothomyrcia* follow those of the more strictly myrcioid genera; *Legrandia* is treated with the eugenioid genera, and *Blepharocalyx* with the pimentoid genera, although there are some unresolved questions about the morphology of the embryo in these last two taxa. The following synopsis is therefore arranged in a sequence like that of the numbered groups in Fig. 1, except that each numbered group includes one or more anomalous genera from the central circle of Fig. 1. The formal nomenclatural designations of the subtribes are not used except when they are mentioned in the discussion.

#### Group 1. The 'myrcioid' genera

1. <i>Gomidesia</i> . . . . .	376
2. <i>Marlierea</i> . . . . .	376
3. <i>Calypttranthes</i> . . . . .	377
4. <i>Myrcia</i> . . . . .	377
5. <i>Myrceugenia</i> . . . . .	381
6. <i>Nothomyrcia</i> . . . . .	381

This, perhaps the most readily comprehensible of the groups of Myrteae, is essentially the Subtribe Myrciinae of Berg except that *Myrceugenia* is excluded. Berg originally (Linnaea 27: 4-5. 1855) divided the subtribe into a group of ten genera with 2-ovulate locules and the one genus *Myrceugenia* with multiovulate locules. The latter seems to have little in common with the rest of the myrcioid genera except for the characteristic embryo. Of the remaining genera known to Berg, he distinguished two with specialized anther-structure (cf. *Gomidesia*, below) and eight that differed among themselves mostly in modifications of the calyx and hypanthium.

Most of the difficulty in the separation of genera of the myrcioid group has been in the interpretation and proper evaluation of these differences in the calyx and hypanthium. *Calypttranthes* was recognized before 1800 by its closed, circumscissile calyx, and *Marlierea* in 1829 on the basis of its closed calyx that splits open irregu-

larly at anthesis. Berg described 3 new genera (*Rubachia*, *Calyptromyrcia* and *Eugeniopsis*), all characterized by having the buds almost but not quite closed, and opening by a process of splitting irregularly below the small calyx-lobes. *Myrcia* in the broad sense of De Candolle included all the species with an open 5-lobed calyx, but Berg recognized 3 genera here, viz. *Aulomyrcia* (with the hypanthium produced beyond the summit of the ovary), *Myrcia* (summit of the ovary flat, the hypanthium not produced beyond it, and the calyx-lobes separated by acute sinuses), and *Calycampe* (as in *Myrcia*, but the calyx-lobes separated by broad sinuses).

The above generic distinctions, even the best of them, are weak. As I pointed out in 1958 (Mem. N.Y. Bot. Gard. 10: 61-65), there is hardly any real distinction between *Calyptranthes* and *Marlierea*, even though the species that were first known and described seemed sharply separable into two groups on the basis of the circumscissile or non-circumscissile calyx. Now, after examination of much additional material from the Guayana-Guiana region where *Marlierea* has one of its principal centers of diversification, I am inclined to think *Myrcia* is no more distinct from *Marlierea* than the latter is from *Calyptranthes*.

Some authors have attempted to draw the line between *Myrcia* and *Marlierea* on the basis of a 5-lobed calyx in the former, and a 3- to 5-lobed, irregularly splitting calyx in the latter. Apparently neither the manner of splitting nor the number of lobes is consistently correlated with other features. Legrand has pointed out that the distinction between the open and closed calyx in the myrtaceous bud is probably not a fundamental one (Com. Bot. Mus. Hist. Nat. Montevideo 40: 2. 1962).

A few species of *Myrcia*, otherwise typical of the genus, have 4-merous flowers. I have argued elsewhere (cf. Field Mus. Publ. Bot. 13, pt. 4: 746. 1958; Fieldiana Bot. 29: 473. 1963) that the differences between 4-merous and 5-merous flowers are not important in classification even within the single genus *Myrcianthes*. Recent studies in *Psidium* suggest that the calyx in that genus may vary widely within a single species (cf. Fieldiana Bot. 29: 527. 1963). Finally it may be noted that in one group of species of *Myrcia* (sens. lat.), the calyx varies in a way suggesting a considerable degree of plasticity. In *Myrcia inaequiloba*, for example, the calyx-lobes are usually petaloid, 5 in number, including three large inner lobes and two much smaller outer ones, but occasionally the calyx may be 4-lobed, with one of the outer lobes wanting. It may be supposed that the generalized flower of *Myrcia* (and presumably of Myrtaceae) was 5-merous, and the flower of *Myrcia inaequiloba* represents one of the stages in the evolution of the more specialized, 4-merous flower. The few known species of *Myrcia* with 4-merous calyx are all apparently specialized in other respects as well. In *M. minutiflora*, for example, the inflorescence is greatly reduced, sometimes to a single flower; most of the other 4-merous species show gross adaptations to montane habitats.

All these observations tend to support the conclusion that although the calyx, in the American Myrtaceae, may provide useful taxonomic characters at the specific level, generic distinctions based on unit characters of the calyx are likely to be specious ones. Bentham took this point of view in reducing Berg's genera *Rubachia* and *Eugeniopsis* to *Marlierea*, and *Calycampe* and *Calyptromyrcia* to *Myrcia*. In this he has been followed by almost all subsequent students of American Myrtaceae.

Berg, as indicated above, supposed that effective and natural generic limits could be established on the basis of two or three characters only, viz. the degree of longitudinal prolongation of the hypanthium, and the structure and manner of opening of the calyx. Now it is clear that the attractive sharp distinctions between genera simply do not exist. If it were possible to erase from mind all knowledge of the taxonomy and nomenclature of the Myrtaceae, and then to begin again, I suppose that *Calyptranthes*, *Marlierea* and *Myrcia* should be combined into one vast genus. Now, how-

ever, the transfer of several hundred names to *Calyptranthes* (as required by the rule of priority in nomenclature), would not only be impossibly confusing but biologically unsound. These "genera" are, after all, recognizable units; they are taxa; they are assemblages of species in which correlations of evolutionary tendencies can be demonstrated, and as a practical matter we delimit the genera as best we can, recognizing that some or perhaps many borderline species may have to be assigned arbitrarily to one or the other.

The line between *Myrcia* (*Aulomyrcia*) and *Marlierea* is almost impossible to draw satisfactorily in one group of species that have relatively long flower buds with short or rudimentary calyx-lobes that are often reduced to 4 in number. At anthesis the calyx is often ruptured between the lobes by the expanding corolla and stamens, and the lobes more or less separated by the fissures in the spreading and often revolute margins of the hypanthium. At the *Myrcia* end of the series the hypanthium is relatively rigid; it is prolonged little or not at all beyond the summit of the ovary, its margins spread little or not at all in anthesis; the (usually 5) calyx-lobes, distinct from the first, are reflexed from the margins of the hypanthium without any breaks between them. At the *Marlierea* extreme (excluding the species in which the calyx opens by a calyptra as in *Calyptranthes*), the hypanthium is often thin-walled, well prolonged beyond the summit of the ovary, i.e. forming a short broad tube which in anthesis flares at the summit, often to such an extent that the structure as a whole becomes broadly saucer-shaped or even nearly or quite flat (explanate). In the process of spreading, longitudinal fissures may develop in the tube, so that the mature saucer- or disk-shaped hypanthium may consist of 4 or 5 irregularly shaped segments separated by radial fissures; the calyx-lobes in these species persist as appendages at the tips of the larger irregular segments.

The taxonomic difficulties in this are caused by the species that are intermediate between these two extremes. In some species the fissures in the hypanthium tube extend inward beyond the base of the tube proper and involve the staminal ring, so that the mature flower is split from several directions almost to the center, only a small disk around the style remaining entire. These species may be assigned to *Marlierea* without question. In other species the fissures extend to the outer margin of the staminal ring; these suggest *Marlierea*, especially if the other marlierioid features (e.g. deciduous calyx-lobes, calyx-lobes 4 in number; dibrachiate hairs) are present. Sometimes the mechanical breaks between the calyx-lobes are minor ones, evidently involving no more than the thin connecting tissues between the bases of adjacent lobes. Sometimes no clear break between calyx-lobes can be detected, but some or all the lobes are partly or completely deciduous, breaking away from the rim of the hypanthium along a line at base.

The splitting of the hypanthium often seems to be effected by stresses set up in the flower at anthesis when the calyx-lobes separate. In many species of Myrtaceae, in these and other genera, the calyx-lobes are strongly reflexed at anthesis and for a short time thereafter, sometimes returning to a more upright position as the fruit develops. Whether the reflexing of the lobes is caused by differential growth on the two sides, by changes in turgor or by some other changes I do not know, but evidently the change in position is brought about forcibly by changes within the lobes themselves, not merely by expansion in the center of the flower. When the calyx-lobes are well-developed, imbricate in the bud, and slightly narrowed at base, they are usually reflexed from the base without involving any other floral structures. When, on the other hand, the lobes are small and situated near the tip of the bud (that is, when the calyx is partly or nearly closed at tip, narrow at the base of the lobes, and widened below this), then it may be supposed that the longitudinal fissures in the calyx are caused by a combination of the force exerted from within and that put

forth by the calyx-lobes when they are reflexed or recurved; that is, the forces are strong enough to roll back the lobes even if this involves tearing the hypanthium. I have no histological observations to substantiate these speculations. In any event the mere splitting by itself does not seem to be very fundamental. In some species, e.g. *Myrcia guianensis*, individual plants vary in the amount of splitting in a way that seems correlated with the kind of calyx-characters described above.

The splitting of the hypanthium itself seems to be related in a general way to the separation of individual calyx-lobes from the hypanthium. In a considerable group of species the lobes separate completely or partly at anthesis from the undivided tube of the hypanthium. The lobes themselves are often markedly unequal in size (2 often large and petaloid, or the inner pair of 4 larger), thin, separating from the rim of the hypanthium by breaks that extend from the edges toward the center. Most of the species in question have in the past been referred to *Myrcia* or *Aulomyrcia*, but most of them also resemble *Marlierea* in one or more respects (i.e. in having the hypanthium prolonged, with thin and revolute margins, often explanate (though not split) after anthesis; the bracts of the inflorescence persistent; the pubescence at least in part of dibrachiate or laterally attached hairs; the stamens reduced in number; and the flowers 4-merous).

It has thus been necessary to separate *Myrcia* and *Marlierea* somewhat arbitrarily. Species with the calyx relatively unchanged through anthesis have been referred to *Myrcia*, including those with marlierioid features as just described, but few with dibrachiate hairs and none in which the hypanthium ruptures at anthesis. Removal of these anomalous species to *Marlierea* would completely erase the distinction between that genus and *Myrcia*, and I therefore propose to recognize them as a group, constituting an infra-generic taxon in *Myrcia* and making the concept of *Myrcia* (sens. lat.) a more meaningful one. The subgeneric groups will be discussed further below, in the treatment of *Myrcia*.

1. GOMIDESIA Berg, *Linnaea* 27: 6. 1855. *Cerqueiria* Berg, *Linnaea* 27: 5. 1855.

Lectotype species, *G. spectabilis* (DC.) Berg. Legrand (Com. Bot. Mus. Hist. Nat. Montevideo 3 (no. 37): 1-30. 1959) has recently published a synopsis of this group, in which he reduces *Cerqueiria* to the synonymy of *Gomidesia*. He recognizes 43 species of *Gomidesia*, almost all natives of the south-Brazilian region. The diagnostic character of *Gomidesia* is wholly in the anthers; whereas in *Myrcia* the anthers are bilocular, longitudinally dehiscent and explanate, in *Gomidesia* they are incompletely (or in one species wholly) 4-locular; the interior sac of each theca is somewhat displaced distad, and seems to open extrorsely at the tip, and the exterior sac seems to open introrsely at the base. The differentiation in the anthers may be barely perceptible (that is, in species otherwise referable to *Myrcia*), or it may be considerable. In the most extreme situation the anthers have four apical pores (the genus *Cerqueiria*). Bentham summarily reduced *Gomidesia* and *Cerqueiria* to *Myrcia*, on the ground that the differences were "so difficult to appreciate, and so little in accordance with habit". Legrand's work indicates, however, that *Gomidesia* occupies a natural range, mostly in southern Brazil with a few species ranging as far north as Bahia and one only to the West Indies. Although the anther-character is the only thoroughly consistent one distinguishing the genus from *Myrcia*, most of the species are recognizable by the tawny or reddish brown silky, somewhat appressed pubescence that covers the inflorescence and the flowers.

2. MARLIEREA Camb. in A. St.-Hil. Fl. Bras. Mer. 2: 373 [folio ed. 269]. pl. 156. 1829. *Rubachia* Berg, *Linnaea* 27: 11. 1855. *Eugeniopsis* Berg, *Linnaea* 27: 80. 1855. *Krugia* Urb. Ber. Deutsch. Bot. Gesellsch. 11: 375. 1893.

Lectotype species, *M. suaveolens* Camb. Kiaerskou (Enum. Myrt. Bras. 44–51. 1893) recognized both *Rubachia* and *Eugeniopsis* as subgenera of *Marlierea*, coordinate with what he called Subg. *Eumarlierea*. Legrand, in his *Sinopsis de las Especies de Marlierea del Brasil* (Com. Bot. Mus. Hist. Nat. Montevideo 3 (No. 40): 1–39. pl. I–II. 1962), recognized two sections, *Marlierea* (of which *Rubachia* was treated as a synonym), and *Eugeniopsis*. The differences between these two groups are at best subjective, based on the degree of splitting of the hypanthium, and apparently there is no doubt that both *Rubachia* and *Eugeniopsis* are to be included in *Marlierea*. The genus *Krugia* was founded on a single species in which the petals are adherent to a calyptriform segment of the calyx, and break free from the flower with it. Similar situations may be seen in most if not all the species of *Marlierea* that have the calyx opening in this way.

The distinctive features of *Marlierea*, in addition to that of the developing hypanthium, are noted above in the general discussion of the myrcioid genera, and in a recent treatment of the genus as it occurs in the Guayana Highland area of northern South America (Mem. N.Y. Bot. Gard. 10: 61–65. 1958). There are more than 90 known species of *Marlierea*, more than half of which are south-Brazilian, about one-fourth from the Guayana-Guiana region, and the remainder from the Antilles or elsewhere in tropical South America.

### 3. CALYPTRANTHES Sw. Prodr. 5, 79 (nom. cons.). 1788.

Type species, *C. chytraculia* (L.) Sw. (typ. cons.). This genus, like *Marlierea* exclusively American, probably consists of more than 100 species. Like *Marlierea* it has many species in southern Brazil (cf. Legrand, *El género Calyptranthes en el Brasil austral*, Lilloa 31: 183–206. 1962), a smaller number in the Amazonian region, and numerous species in Guayana-Guiana. Unlike *Marlierea* it is well represented in the West Indies (about 100 described species, but probably actually fewer), and in continental North America (cf. McVaugh in Fieldiana Bot. 29: 397–412. 1963).

The distinctive feature of *Calyptranthes* resides in the calyx; the unopened buds are completely closed and often apiculate, opening by a calyptra which usually remains attached by a narrow band of tissue at one side. In certain species, however, a relation to *Marlierea* becomes apparent. In these the bud opens irregularly; one of the divisions is larger than the others, simulating a calyptra, and often remaining attached at one side as in *Calyptranthes*. The smaller lobes may persist or may be deciduous after anthesis. The rim of the hypanthium may remain entire (as usual in *Calyptranthes*) or become irregularly lobulate. These and other features of *Calyptranthes* and *Marlierea* are discussed and compared in the paper cited above (Mem. N.Y. Bot. Gard. 10: 61–65. 1958).

### 4. MYRCIA DC. ex Guillemain, Dict. Class. Hist. Nat. 11: 401. 1827 (preprint 5. 1826); et in DC. Prodr. 3: 242. 1828. *Calyptromyrcia* Berg, Linnaea 27: 34. 1855. *Aulomyrcia* Berg, Linnaea 27: 35. 1855. *Calycampe* Berg, Linnaea 27: 129. 1856.

Lectotype species, *M. bracteolaris* (Poir.) DC. [*M. fallax* (Rich.) DC.]. I have already alluded to the considerable group of species that blur the line between *Myrcia* and *Marlierea*. Even more blurred is the boundary between *Myrcia* and *Aulomyrcia*. It is true that the character emphasized by Berg to distinguish *Aulomyrcia*, namely that of the hypanthium being more or less produced between the summit of the ovary and the insertion of the stamens, is often a conspicuous one. In any limited number of species one can usually define two groups in this way, as was done in the *Flora of Suriname*. If one examines a larger number of species, however, particularly from central and southeastern Brazil where both the supposed genera are most abundant, it becomes evident in the first place that there is a nearly continuous series between



the two extremes, and secondly that it is difficult to find any other characters correlated with the changes in the hypanthium. Some authors have suggested that such characters as pubescence, fruit-shape, and the presence or absence of a "sericeous disc" at the summit of the ovary, may distinguish the two genera. In some areas, as in the Guianas, it does indeed seem that the species of "*Aulomyrcia*" tend to be more nearly glabrous, and to have smaller leaves, than those of *Myrcia* proper. In south-eastern Brazil, on the other hand, extremely specialized vegetative types (e.g. copiously lanate subshrubs with small leaves and large terminal panicles, or shrubs with acicular leaves), include representatives of both "genera" and puzzling intermediates between them. It appears that the prolonged hypanthium may often provide a convenient means of contrasting species, but its evolutionary significance, as shown by correlation with other characters or sets of characters, remains to be demonstrated.

The following subdivision of *Myrcia* is therefore proposed; it is based on prolonged study of the species of northern and western South America, and the Antilles, but conceivably may have to be modified when all the Brazilian species can be considered at the same time.

1. Calyx-lobes 4 or 5, more or less deciduous from the hypanthium at anthesis, often very unequal in size (if 4, the inner pair usually larger; if 5, 2(-3) often larger and petaloid); hypanthium usually glabrous within, and prolonged beyond the summit of the ovary (thus cuplike or tubular in the flower), but its margins not splitting between the calyx-lobes; dibrachiate hairs often present; flowers often glabrous without; inflorescence sometimes reduced to 1 or few flowers. . . . . Sect. 1. *Armeriela*.
1. Calyx-lobes 5, seldom 4, not deciduous from the hypanthium at anthesis, at most somewhat separated laterally by the expanding flower, equal or subequal; hypanthium various, not splitting at the margins; dibrachiate hairs usually not present; flowers glabrous or pubescent; inflorescence freely branched, several- or many-flowered.
  2. Summit of the ovary, and the inner surface of the hypanthium glabrous (staminal ring and inner surfaces of the calyx-lobes sometimes pubescent); hypanthium prolonged beyond the ovary (thus cuplike or tubular in the flower); flowers 5- or 4-merous; ovary 2- or 3- (-4)-locular; fruit globose or subglobose; flowers often glabrous without. . . . . Sect. 2. *Aulomyrcia*.
  2. Summit of the ovary, and the inner surface of the hypanthium, pubescent or hirsutulous; hypanthium scarcely prolonged vertically beyond the ovary, the center of the flower not depressed, or merely somewhat concave; flowers 5-merous; ovary 2-locular; fruit usually oblong-ellipsoid; plants variously pubescent, at least the outer surface of the hypanthium appressed-hairy. . . . . Sect. 3. *Myrcia*.

1. Sect. *Armeriela* McVaugh, sect. nov.

Type-species, *Myrcia inaequiloba* (DC.) McVaugh, comb. nov. <sup>1</sup>

<sup>1</sup> *Myrcia*, sect. *Armeriela* McVaugh, sect. nov., floribus 4 (-5)-lobis, calycis lobis saepe valde inaequalibus tenuibus petaloideisque, plerumque intus pubescentibus, basi ex hypanthii margine partim vel omnino secedentibus, inter se saepe fissis; hypanthium plerumque margine praesertim tenue, per anthesin non fissum, sed saepe explanatum vel late infundibuliforme; ramulorum pili saepe dibrachiati vel lateraliter affixi, rufescentes vel fulvi, saepe sericei; inflorescentiae bractae saepe per anthesin persistentes; a *Marlierea* hypanthio non fisso differt; a *Myrcia* sect. *Myrcia* calycis lobis hypanthioque tenuioribus hypanthio plerumque prolongato, saepe explanato, lobis plerumque inaequalibus, secedentibus, pilis dibrachiatis, bracteis persistentibus, differt.

Typus: *Myrcia inaequiloba* (DC.) McVaugh, comb. nov. *Eugenia inaequiloba* DC. in DC. Prodr. 3: 282. 1828. *Aulomyrcia inaequiloba* (DC.) Amsh. Rec. Trav. Bot. Néerl. 42: 7. 1950.

The name of the section is an anagram of *Marlierea*. The type of the section is chosen deliberately because it is one of a small group of species that are evidently closely interrelated, and that seem to bridge the gap between *Myrcia* and *Marlierea* more nearly than any other species in the section (viz. *Myrcia laevis* Berg, *Aulomyrcia saxatilis* Amsh., *M. graciliflora* Schauer, *M. decorticans* DC.). *Myrcia inaequiloba* and *M. decorticans* are extraordinarily like *Marlierea umbraticola* and *M. gleasoni*, respectively; the two pairs of species are separable only after close study, but according to the classic generic definitions, two of them belong to *Marlierea* and two to *Myrcia*. In the first pair the calyx-lobes merely separate from one another and from the hypanthium, but the hypanthium itself does not split.

Because *Myrcia inaequiloba* was not included by Berg in his genus *Aulomyrcia* it is not available as a possible lectotype of that name. The lectotype of *Aulomyrcia* (see Taxon 5: 137. 1956), *Myrcia multiflora* (Lam.) DC., is a true *Aulomyrcia* in the sense of Berg (i.e. the hypanthium is prolonged and cuplike in flower), but it has a relatively well-developed staminal ring (as in Sect. *Myrcia*), the hypanthium is firm and almost unchanged in anthesis, the calyx-lobes are 5 in number, nearly equal, neither tearing at the base nor separating from the hypanthium; the plant as far as I know has no dibrachiate hairs, and the bracts are deciduous before anthesis.

In the Guiana-Guayana region, the sect. *Armeriela* is represented by about 25 species, including the five mentioned above, and also *Myrcia calycampa* Amsh., *M. guianensis* (Aubl.) DC., *M. minutiflora* Sagot, *M. platyclada* DC., *M. tafelbergica* Amsh., and about 15 species that are so far undescribed or for which no valid names in *Myrcia* have been published.

The lectotype-species of *Calyptrymyrcia*, *C. cymosa* Berg, seems from the description and plate in the *Flora Brasiliensis* (vol. 14, pt. 1: 58. pl. 18. 1857) to represent the widely distributed taxon for which the oldest name is *Myrcia guianensis* (Aubl.) DC. Two other species referred by Berg to *Calyptrymyrcia*, *Myrcia elegans* DC. and *M. spixiana* DC., are also synonyms of *M. guianensis*. The group is characterized by a 3-locular ovary, small leaves with flat or convex midvein, small glabrous flowers with partly deciduous calyx-lobes that are pubescent on the inner surface. There seems to be no valid reason to recognize *Calyptrymyrcia* as a genus. Another synonym is *Aguava* Raf. (*Sylva Tell.* 107. 1838), the lectotype of which is *A. guianensis* (Aubl.) Raf. (= *Myrcia guianensis*). See Taxon 5: 137. 1956. Those who recognize *Aulomyrcia* as a genus distinct from *Myrcia* will have to reckon with the older name *Aguava*.

The two original (and only published) species of *Calycampe*, *C. latifolia* and *C. angustifolia*, are without much doubt conspecific, and probably based at least in part on the same gathering. The calyx-lobes separate to some extent from the hypanthium, and it may have been this that led Berg to describe the calyx-lobes as "basi sinu rotundato ab invicem separata". It seems that Amshoff correctly referred this plant to *Myrcia*, at the same time providing the new name, *Myrcia calycampa*.

## 2. Sect. *Aulomyrcia* (Berg) Griseb.

Since Berg's time most writers on the American Myrtaceae have preferred to treat *Aulomyrcia* as a part of the inclusive genus *Myrcia*, though without much published comment on or justification for such a course. Grisebach (*Fl. Brit. W. Ind.* 234. 1860), when Berg's work was still very new, reduced *Aulomyrcia* to sectional status. Bentham, in the *Genera Plantarum*, commented merely that the hypanthium character was not correlated with habit nor, presumably, with any other characters, and relegated *Aulomyrcia* to synonymy. In this he has been followed by Kiaerskou, Urban, Nie-

denzu, and others. In the *Flora of Suriname* (1951), and in other writings, however, Miss J. G. H. Amshoff has revived *Aulomyrcia*.

The hypanthium (that is, the tissues surrounding the inferior ovary, including the exterior tissues that presumably represent calyx, and the interior ones that presumably represent receptacle and disk, from the summit [margin] of which arise the stamens and petals), is always prolonged to some extent beyond (or laterally from) the summit of the ovary. The extent of such prolongation is measured in a rough way by the distance between the base of the style and the outer edge of the band of stamens. As Bentham wrote (*Jour. Linn. Soc. Bot.* 10: 157. 1869), it is sometimes "very difficult to say whether the interval is perceptible or not". Lateral prolongation of the hypanthial tissues is illustrated in Berg's plates on *Myrcia* in the *Flora Brasiliensis* (pl. 23, 24). When the hypanthium is prolonged vertically (that is when it forms a cup or tube), this feature is often accentuated in pressed and dried specimens, whereas if the prolongation is lateral, pressed flowers often take the form of a flat disk that may appear to represent merely the summit of the ovary surrounded by a broad ring of stamens.

The fundamental similarity between the "cup-shaped" and "disk-shaped" flowers may also be obscured by differences in the size, breadth and thickness of the staminal ring, and by the pubescence on the inner surface of the hypanthium. It is possible to demonstrate a nearly continuous series between species with multiseriate stamens borne on a broad fleshy ring, and species with stamens in 1 or 2 series, borne directly on the nearly unmodified edge of the hypanthium. At the first extreme the staminal ring is so thick that it gives the appearance of a separate structure attached to the inner surface of the hypanthium and giving it a certain amount of mechanical strength as well. Sometimes the broad staminal ring (suggesting in appearance the floral disk of Celastraceae and other families) occupies most of the interior of the flower, nearly covering the base of the style; because the staminal ring tends to be flattened into one plane after the flowers open, it is not always remembered that the stamens arise from the inner surface of the hypanthium, which in the bud surrounds the style and stamens in the form of a short tube, and only at anthesis flattens into its final disk-like form. (cf. Berg's plates on the development of the flower of *Punica*: *Mart. Fl. Bras.* 14, pt. 1: pl. 8, 9).

Berg recognized about 250 species of *Aulomyrcia*, most of them Brazilian. As here restricted, the sect. *Aulomyrcia* is considerably smaller in number of species; in the Guiana-Guayana region it is represented by 12 species only, but these include some of the most widely distributed members of the genus, including *M. citrifolia* (Aubl.) Urb., *M. multiflora* (Lam.) DC., and *M. tomentosa* (Aubl.) DC., and also *M. cuprea* (Berg) Kiaersk., *M. pyrifolia* (Desv.) Ndzu, and others for which no names are presently available. In central and southern Brazil the Sect. *Aulomyrcia* is represented by numerous species, for which there is no recent taxonomic treatment.

The genus *Mozartia* Urb. (*Symb. Antill.* 9: 87. 1923), restricted to Cuba as far as known, includes 7 described species. Alain (*Fl. Cub.* 3: 434-436. 1953) recognizes the genus as valid, and admits six species to the Cuban flora. *Mozartia* is like *Myrcia* in every respect except that the ovary is imperfectly bilocular or unilocular, and the ovules solitary, or sometimes 2 in forms with unilocular ovary. The calyx is either 4- or 5-merous. The hypanthium in the type-species is described as "supra ovarium cupuliformi-productus", and the calyx-lobes as persistent on the fruit, so I have treated it here as related to *Myrcia* sect. *Aulomyrcia*. If *Myrcia* is to include species with both 3-locular and 2-locular ovary, then I see no reason why those with 1-locular ovary should constitute an independent genus for this reason only.

### 3. Sect. *Myrcia*

This section includes the most commonly collected species of *Myrcia* in the Antilles and in northern South America, viz. *M. deflexa* (Poir.) DC., *M. fallax* (Rich.) DC., *M. splendens* (Sw.) DC. and *M. sylvatica* (Mey.) DC. There are an estimated 25 species of the section in South America north of the Amazon, and numerous species in central and southern Brazil. *Cumetea* Raf. (Silva Tell. 106. 1838), typified by *Eugenia coumete* Aubl. [*Myrcia coumete* (Aubl.) DC.], is a synonym (cf. Taxon 5: 139. 1956).

#### 5. MYRCEUGENIA Berg, Linnaea 27: 5 (in clave). Nov. 1855; 131. Jan. 1856.

Lectotype species, *M. myrtoides* Berg. A genus of some 50 species, confined to southern South America. As indicated by Berg's choice of a generic name, *Myrceugenia* superficially seems to fall between *Myrcia* and *Eugenia*. The embryo is like that of *Myrcia*, but the conspicuously bracteolate 4-merous flowers are those of *Eugenia*, the locules of the ovary are multiovulate (as in *Eugenia*); and the inflorescence, if several- or many-flowered, is dichotomously branched. It may be that the characters of *Myrceugenia* are such as to cast doubt upon the naturalness of the division between Myrciinae and Eugeniinae, but the genus itself appears to be a natural one, with a distinctive disjunct geographical range that suggests a long existence for the group as a whole. The Chilean species, about 15 in number, were revised by Kausel (Rev. Argent. Agron. 9: 50-64. 1942), and those of southern Brazil and adjoining areas (34 species) by Legrand (Darwiniana 11: 293-365. 1957). As emphasized by Legrand, the genus differs from both *Myrcia* and *Eugenia* in having usually a 3-locular ovary. The leaves are usually markedly bicolorous, and the midnerve is almost always somewhat excurrent at the apex. The inflorescence (especially in the Chilean species) may be a dichasium; in some Chilean and in most of the Brazilian species the flowers are solitary and axillary (not racemose as in *Eugenia*) or, if 2-4 in an axil, then superposed, i.e. crowded in one vertical row, not in opposite pairs.

According to the assumptions made in the preliminary part of this paper, *Myrceugenia* (and the following genus, *Nothomyrcia*) do not form a part of the main line of evolution of the myrcioid genera, but have been derived directly from ancient myrtaceous stocks; see Fig. 1, and text, p. 367. Bentham (Jour. Linn. Soc. Bot. 10: 153. 1869; et in Benth. & Hook. f. Gen. Pl. 1: 714. 1865) relegated the name to the synonymy of *Myrtus*, to which it has no very close relationship. Bentham likewise considered *Myrceugenia* as a synonym of *Luma* A. Gray, q.v. below. He justified the submergence of *Luma* and *Myrceugenia* on the grounds that neither formed a comprehensible natural taxon. According to the recent studies of Legrand and Kausel, however, all seven of the original species of *Myrceugenia* belong to the genus as currently interpreted; *Luma*, however, was a mixture; four or five of the original species belonged to *Myrceugenia*, two of them wholly or in part to a pimentoid genus akin to *Blepharocalyx*, and one to a Chilean group described by Kausel as *Myrceugenella*, which is eugenioid or as supposed by Kausel intermediate between Myrciinae and Eugeniinae (cf. Rev. Argent. Agron. 9: 42 ff. 1942). Burret (Notizbl. Berlin 15: 522-535. 1941), apparently on the grounds that a majority of the original species of *Luma* (1854) belonged to *Myrceugenia* (1855), listed 54 species under the name of *Luma*, and relegated *Myrceugenia* to synonymy. If, however, the genus *Luma* is typified by the *Myrceugenella* element (i.e. by *Luma chequen* var. *a*) (as suggested in Taxon 5: 142. 1956), there is no nomenclatural conflict between *Luma* and *Myrceugenia*.

6. NOTHOMYRCIA Kausel, Lilloa 13: 147. 1948 ("1947").

Type species, *N. fernandeziana* (Hook. & Arn.) Kausel. The one species, an endemic of Juan Fernández, has a myrcioid embryo, bilocular ovary with about 6 ovules in each locule, and tetramerous flowers in axillary racemes. It has usually been supposed to represent an aberrant species of *Myrcogenia*, from which it differs in the bilocular ovary, racemose inflorescence and deciduous bracteoles. As with so many isolated and monotypic endemic groups, its generic distinctness remains a matter of opinion, but it cannot with reason be assigned to any other genus that I know. Its origin and relationships remain a matter of conjecture; see Fig. 1, and text, p. 370.

Group 2. The 'eugenioid genera'

7. Eugenia . . . . .	382
8. Hexachlamys . . . . .	384
9. Calycorectes . . . . .	385
10. Plinia . . . . .	387
11. Siphoneugena . . . . .	390
12. Myrciaria . . . . .	392
13. Legrandia . . . . .	392

The genera in this group are all referable to the Eugeniinae of authors generally; originally Eugeniinae included also the genera that are enumerated below in Group 3, as well as *Acca*, *Mitranthes* (q.v. below under *Siphoneugena*), and *Aulacocarpus* Berg (now generally considered to be a member of the Melastomataceae). Berg (1855) divided the Eugeniinae into two principal subgroups, the first ("hypanthium supra germen vix productum"), including *Eugenia*, *Phyllocalyx* and *Stenocalyx* (with 476, 19 and 41 species respectively), and the smaller genera *Acca*, *Caryophyllus* (introduced in America) and *Myrcianthes* (2, 1, and 4 species). The second subgroup, ("hypanthium supra germen valde productum"), included members of two Old World groups (*Syzygium* and *Jambosa*), and the seven American genera *Mitranthes*, *Calycorectes*, *Schizocalyx*, *Myrciaria*, *Siphoneugena*, *Hexachlamys* and *Aulacocarpus*. Of these seven *Myrciaria* included 61 species and the others from one to five species each. All the American genera except *Eugenia* were proposed as new by Berg, who thus removed from the too-inclusive *Eugenia* a number of taxa, mostly small in number of species, and not all of them distinctive.

The character of the prolonged hypanthium has proven more useful taxonomically in the eugenioid genera than in the myrcioid ones. Most of the small genera with the hypanthium prolonged beyond the ovary have been accepted by authors following Berg, although not always with a circumscription the same as that of Berg. Among the genera with hypanthium "vix productum" the principal taxonomic problem is that of the separation of *Phyllocalyx* and *Stenocalyx* from *Eugenia*; this is mentioned below under *Eugenia*. *Myrcianthes*, it transpires, is readily separable from *Eugenia* by characters of the inflorescence and the embryo, not by the number of calyx-lobes as supposed by Berg.

7. EUGENIA L. Sp. Pl. 470. 1753. *Greggia* Solander ex J. Gaertn. Fruct. 1: 168. 1788. *Emurtia* Raf. Sylva Tell. 106. 1838. *Epleianda* Raf. Sylva Tell. 107. 1838. *Phyllocalyx* Berg, Linnaea 27: 306. 1856. *Stenocalyx* Berg, Linnaea 27: 309. 1856. *Psidiastrum* Bello, An. Soc. Esp. Hist. Nat. 10: 272. 1881. *Myrcialeucus* Rojas Acosta, Bull. Géog. Bot. 24: 217. 1914.

Lectotype-species, *E. uniflora* L. The American species of *Eugenia*, as most authors have understood the limits of the genus, are alike in having the hypanthium little or not at all prolonged beyond the ovary; the ovary bilocular with several or many ovules in each cell; the embryo apparently homogeneous without a clear division

between the cotyledons; the calyx 4-parted; and the flowers in racemes or solitary at the lower (leafless) nodes of leafy branchlets. There are so many species, and these so diverse in habit and other characters, that it is impossible to characterize the genus briefly except by the more or less technical points mentioned above. There are occasional exceptions to some of these points; although the ovary is very consistently bilocular, the ovules are sometimes as few as 2 in each locule (e.g. in *E. coffeifolia* DC.). The fruit is known in (relatively) so few species that strict generalization is impossible, but I have never seen a species otherwise referable to *Eugenia* except with the so-called homogeneous embryo. The 4-parted calyx is wholly consistent in the American species as far as I know.

The so-called racemose inflorescence, as discussed above in the preliminary part of this paper, evidently represents a rather advanced stage of specialization, when all the leaves of an axillary branch have been replaced by small bracts, and the internodes much shortened. In the American species of *Eugenia*, almost without exception, the flowers are borne in opposite and decussate pairs, on pedicels subtended by small bracts. Usually there are several or many pairs of flowers arising from the same unbranched axis, which is morphologically a branch arising in the axil of a leaf, or at a node that bore a leaf in a previous growing season. Sometimes the raceme-axis is so short that the flowers seem to be umbellate or clustered in the axil; sometimes (as in *E. puniceifolia*, a widespread South American species), the flowers are reduced to a single pair.

In many species of *Eugenia* the flowers are partly in axillary bracteate racemes, and partly in opposite bracteate pairs at the lower nodes of leafy branchlets. It was on this latter character that Berg founded his genera *Stenocalyx* and *Phyllocalyx*. In some species of these supposed genera the flowers are praecocious; that is, they appear before or with the new leaves; because they are grouped in opposite and decussate pairs surrounding the axillary bud that will eventually grow into a leafy branch, and because the modified, non-leafy bracts at the bases of the pedicels are often conspicuously imbricated, they may present a striking appearance while in flower. At maturity, however, when the flowering axis has elongated, and the leafy twig has developed beyond it, the distinctions between this type of flowering and that prevalent in *Eugenia* become essentially non-existent. In *Eugenia patrisii*, for example, a widely distributed South American species, [*Stenocalyx patrisii* (Vahl) Berg], both types of flowering occur; the axillary racemes are often 4–5 mm. long with 4–5 pairs of flowers and the terminal bud abortive, whereas some solitary flowers are also borne at the lower, bracteate, nodes of leafy branchlets. As Bentham said “the inflorescence [of *Stenocalyx* and *Phyllocalyx*] is thus an axillary raceme growing out into a leafy branch — a very vague character depending on the degree of development of the lower floral leaves”. There has been general agreement since Bentham’s time that neither *Stenocalyx* nor *Phyllocalyx* can be recognized as an independent genus. Nomenclaturally speaking this is fortunate, as the lectotype of *Eugenia* is a *Stenocalyx*!

Two genera described by Rafinesque in the *Sylva Telluriana* in 1838, *Emurtia* (p. 106) and *Epleianda* (p. 107) are typified by *Eugenia micrantha* (HBK.) DC., and *E. sinemariensis* Aubl., respectively; see Taxon 5: 139. 1956. The type of *Greggia* Gaertn. is *Eugenia gregii* (Sw.) Poir.

According to Urban (Bot. Jahrb. 19: 640. 1895), *Psidiastrum dubium* Bello, the type and only species of its genus, is a synonym of *Eugenia axillaris* (Sw.) Willd. The plant was described as a native of Puerto Rico. The type and only species of *Myrcialeucus*, *M. odorifolius* Rojas, said to be a native of the Argentinian Chaco, was compared by its author with *Eugenia ligustrina* and *E. uniflora*; it was described as having a red, fleshy, sulcate edible fruit like *E. uniflora*.

Berg, and most subsequent authors, have assumed a close relationship between *Eugenia* and *Myrcianthes* because of general similarities in their flowers, and probably chiefly because of superficial similarities between the fleshy massive, undivided embryo of *Eugenia*, and the equally fleshy embryo of *Myrcianthes*, which, however, consists of two free plano-convex cotyledons and a short radicle. However fundamental the differences between these two types of embryos may be, the methods of flowering are very different in the two genera. No species of *Eugenia*, as far as I know, has the solitary axillary flower that is found in many species of *Myrcianthes*, and the occurrence of three-flowered dichasia is very rare in *Eugenia*. The "pedicels" of some species occasionally may produce a group of 3 terminal flowers instead of the usual one, but this is so rare as to be regarded as an abnormality. Even in the so-called *Eugenia conzattii* Standl., of eastern Mexico, which normally produces some pedunculate 3-flowered dichasia, these are probably not strictly axillary but arise from the lowest node of an abortive axillary branch.

Thus although the distinction between the eugenoid, or "racemose" type of flowering, and the pimentoid<sup>1</sup> or dichasial type, may not be used as an absolute criterion of taxonomic affinity, it seems clear that the racemose type has developed as a eugenoid trait, to the practical exclusion of the other, whereas the pimentoid type is associated with one type of embryo in *Myrcianthes* and its relatives, and another in *Psidium* and related genera. Although the racemose inflorescence occurs in *Eugenia* with a high degree of constancy, its occurrence is not confined to genera of that affinity, as 1-flowered and 3-flowered peduncles may be racemosely arranged in some pimentoid genera, e.g. *Calycolpus* and *Campomanesia*.

The number of American species of *Eugenia* cannot be exactly stated. Berg (in Mart. Fl. Bras. 14, pt. 1: 619. 1859) estimated the number at 537, of which about two-thirds were Brazilian. Many of Berg's species have been reduced to synonymy or transferred to other genera, but also many new species have been described by subsequent authors. According to Urban (Bot. Jahrb. 19: 605-669. 1895) there are about 100 species in the West Indies. Recent studies of the North American taxa (cf. Fieldiana Bot. 29: 413-470. 1963; Fieldiana Bot. 24, pt. 7: 309-374. 1963; Ann. Missouri Bot. Gard. 45: 179-192. 1958) indicate that there are no more than another hundred species on the North American continent. Unpublished data suggest that there may be 75 or more species additional in South America north of the Amazon and east of the Andes. The species of the northern Andes have not been thoroughly studied, but the majority of all Andean species were treated in the *Flora of Peru* (Field Mus. Publ. Bot. 13, pt. 4: 666-745. 1958), where 59 species were listed, including probably no more than 40 that are peculiar to the region. Legrand (Sellowia 13: 306-327. 1961) lists a few more than 50 species for the Brazilian state of Santa Catarina (Berg estimated 17 species for Santa Catarina and Rio Grande do Sul together). The remainder of the flora of central and southeastern Brazil has not been studied as a whole since Berg's time; he estimated a total of 375 species in Rio de Janeiro, São Paulo, Paraná, Minas Gerais and Goiás, and even assuming a considerable overlap, it is probable that there are 250 to 300 species in the region. Thus it seems that in all tropical America there may be at least 500 species, including many that have been discovered since Berg's time.

#### 8. HEXACHLAMYS Berg, Linnaea 27: 345. 1856.

Type-species, *H. humilis* Berg. This is a small group, consisting of three or four species of Paraguay, northern Argentina, Uruguay and southernmost Brazil. It has generally been regarded as a synonym of *Eugenia*. Bentham dismissed it as merely an anomalous, hexamerous form in a large genus with tetramerous flowers. The inflorescence and the seed are essentially those of *Eugenia*. According to Legrand (cf.

<sup>1</sup> So called because this type of flowering prevails among the majority of the species of Berg's subtribe Pimentinae. Strictly dichotomous branching of the inflorescence is characteristic of all the genera, with a few exceptions like *Pimenta* and *Pseudocaryophyllus*.

An. Mus. Hist. Nat. Montevideo II. 4 (no. 11): 59–62. 1936; Darwiniana 9, pt. 2: 302–303. 1950, and Sellowia 13: 275–276. 1961) the flowers are pentamerous, but vary from 4- to 7-merous; the ovary may be 2- or 3-locular. Its status as an independent genus can hardly be determined more precisely without biosystematic investigations.

9. CALYCORECTES Berg, Linnaea 27: 317. 1856. ?*Catinga* Aubl. Pl. Guiane Fr. 511. pl. 203. 1775. *Schizocalyx* Berg, Linnaea 27: 319. 1856, non Weddell, 1854, nec Scheele, 1843. *Schizocalomyrtus* Kausel, Lilloa 32: 367. 1967.

Lectotype-species, *C. grandifolius* Berg. As understood by Berg, the distinguishing features of *Calycorectes* were: Ovary bilocular, many-ovulate; hypanthium prolonged much beyond the summit of the ovary; buds closed, the calyx opening irregularly and splitting into 4–6 lobes. The genus as defined in this way is distinguished from *Eugenia* by the prolongation of the hypanthium into the closed calyx, and by the irregular opening of the calyx. The known species, although apparently not comprising a completely homogeneous group, are alike in a number of ways that seem to reflect an evolutionary trend. Vegetatively the species differ markedly from one another in leaf-size, venation, and quality and quantity of pubescence; the buds in all species have the hypanthium well prolonged beyond the summit of the ovary, and irregularly splitting to the base in anthesis, but in some species the calyx-lobes are as much as half as long as the entire bud, whereas in others they are reduced to mere vestiges and the buds are closed except for a terminal pore. The number of ovules in each locule of the bilocular ovary varies from more than 20 in some species to as few as 3–5. The corolla lobes are usually 4, but are 6 in several species. All the species known to me have in common not only the prolonged hypanthium, but somewhat elongated, oblong or linear anthers, often 1–1.5 mm. long. Similar anthers are found in some species of *Plinia*, and in *Eugenia feijoi*, a species in which the calyx-lobes are loosely connate in the bud, and which may be considered as intermediate in this way between *Eugenia* and *Calycorectes*. In *Calycorectes* also, the bracteoles at the base of the flower are in most species distinct rather than connate, narrow, and often deciduous at or before anthesis; similar bracteoles are found in a relatively few species of *Eugenia*.

In the American Myrtaceae it seems that closed and irregularly opening buds have evolved in several different lines; this has already been discussed above with respect to *Myrcia* and the presumably more specialized genera *Marlierea* and *Calyptanthes*. The distinction between *Myrtus* and *Psidium* has traditionally depended upon these features of the bud and the hypanthium (cf. Fieldiana Bot. 29: 512–518. 1963). In the eugenioid genera the tendency toward prolongation of the hypanthium seems to have been accompanied not only by a gradual reduction in the free parts of the calyx-lobes and the eventual union of the lobes (as in *Calycorectes*), but in some instances by a reduction in the number of ovules in each locule of the ovary (to as few as 3 in *Calycorectes*, 2–4 in *Siphoneugena*, usually 2 in *Plinia* and *Myrciaria*); or by the tendency of the hypanthium-tube to separate from the ovary at anthesis (as in *Myrciaria* and *Siphoneugena*). Of these small genera that have been split out of the inclusive *Eugenia*, *Myrciaria* and *Siphoneugena* are easily recognized in flower or in fruit, by vegetative features as well as by the characters of flowers and fruit.

Some additional evidence bearing on the generic position of *Eugenia*, *Plinia* and *Calycorectes* may be obtained when the fruits of all species are better known. The embryo in *Eugenia* is typically undifferentiated; that is, when the fruit is ripe the interior of the seed is a hard homogeneous mass in which cotyledons, radicle, plumule and other organs cannot be recognized. In *Myrciaria* and *Calycorectes* as far as known, the embryo is like that of *Eugenia*; unfortunately most of the species of



*Calycorectes* are known from flowering specimens only. In *Plinia* the embryo as far as known is like that of *Myrcianthes*, that is with two large separate plano-convex cotyledons like those of a bean; here again the evidence is incomplete, as most species are known only in flower.

It may be, as implied above in the general discussion of evolutionary development in the Myrteae, that the older eugenoid stocks gave rise to two lines, viz. the *Eugenia* — *Calycorectes* — *Myrciaria* line in which the embryo is homogeneous and the reduction in number of ovules accompanied changes in the calyx and hypanthium; and a smaller line, including only *Plinia* and *Siphoneugena*, in which the embryo is of the plinioid type (cf. the discussion by Kausel, Ark. Bot. 3: 500 ff. 1956) with two separate cotyledons, and the reductions in the calyx and in ovule-number parallel those in the other series. This would explain the superficial resemblances between *Siphoneugena* and *Myrciaria*, and between *Plinia* and *Calycorectes*, on the basis of parallelism. An alternative possibility is that the superficial resemblances in each case indicate close evolutionary connections, and that the plinioid embryo has evolved secondarily in each line from ancestors with a eugenoid embryo.

It must be admitted that *Calycorectes* and *Plinia* do not possess really distinctive vegetative characters; they are to be separated in the last analysis only by the number of ovules and by the embryo. Most of the South American species of *Plinia* have sessile or subsessile flowers in sessile clusters subtended by sterile imbricated bracts, but in one Peruvian species the bracts are much reduced and the flowers are pedicellate. As some species with closed buds that have been described in *Calycorectes* (or in *Eugenia*) have as few as 5 or 6 ovules or even as few as 3 in each locule (*Eugenia hexovulata*), the generic distinction between *Plinia* and *Calycorectes*, and that between *Eugenia* and *Plinia* — *Calycorectes* are still somewhat arbitrary. Species in which the hypanthium is not prolonged, and in which the calyx consists of 4 separate lobes both in bud and in flower, are referred to *Eugenia*; species in which the hypanthium is prolonged well beyond the ovary, and in which at the same time the calyx-lobes are usually reduced in size and the calyx opens by splitting at the bases of the lobes, are referred (in the absence of mature fruit) to *Plinia* or *Calycorectes*. There remains a small group of species, viz. *Eugenia feijoi* and its relatives, in which the calyx-lobes are free in bud at the tips only, and cover the developing corolla in the bud, but at anthesis are separated by longitudinal splits in the sinuses, these often extending downward as far as the summit of the ovary as in the irregularly splitting calyx of *Plinia* or *Calycorectes*. It may be supposed that this represents an intermediate condition between the completely closed calyx, and the typical *Eugenia* calyx with 4 imbricate but distinct lobes. It differs from the condition found in some species of *Calycorectes* only because the lobes in *Eugenia feijoi* are always recognizable as such (even if attached by their edges), whereas in *Calycorectes* the calyx splits without reference to the position of the proper lobes.

The known species of *Calycorectes* include one in Mexico, about a half-dozen in northern South America of which three are in the Guianas and adjacent Venezuela and Brazil, and another half-dozen in southeastern Brazil, including *Schizocalyx pohlianus* Berg [*Calycorectes pohlianus* (Berg) Kiaersk.] The calyx in the bud of *Schizocalyx pohlianus* is 4-lobed at apex about to the same extent as that of *Calycorectes australis* Legrand (cf. Mart. Fl. Bras. 14, pt. 1: pl. 35. 1857, and Sellowia 13: 350. 1961).

The genus *Catinga* Aubl. (Pl. Guiane Fr. 511. pl. 203. 1775) can hardly be maintained. Neither of the two original species can be identified from the description alone. Aublet himself never saw flowers of either species; he collected fruiting material of both along a flooded stream ("dans la crique des Galibis") at a time (in May) when the water level was more than 30 feet above normal and only the tops

of the trees could be seen above water. From a study of the protologue it seems that *Catinga* was founded primarily on the character of the large fleshy aromatic fruit ("Drupa globosa, vel ovata, aurantii aut citri formâ, cortice croceo, carnosio...").

Amshoff, in 1947, studied sterile specimens of what she understood to be *Catinga aromatica* and *C. moschata*, among the Aublet collections at the British Museum; on the basis of this she recognized the genus *Catinga* in the *Flora of Suriname*, and described two species under Aublet's names. In 1965 I examined the same Aublet specimens; at that time both *Catinga aromatica* and *C. moschata* were represented by sterile specimens of what I take to be the same species, viz. *Eugenia feijoi* Berg. The fruit of *Catinga aromatica*, as described and illustrated by Aublet, much resembles that of *E. feijoi*, and I have little doubt that the two species are synonymous. This is of academic interest only, as long as the plant is referred to *Eugenia*, because of the existence of the name *Eugenia aromatica* Berg (1856).

If the genus *Catinga* is ever to be maintained it should be typified by the other original species, *C. moschata* (cf. Taxon 5: 139. 1956, where this is designated lectotype-species). Unfortunately it now seems quite impossible to determine the identity of Aublet's plant. Sagot, on the basis of his own field experience, identified *Catinga moschata* with a plant that I should refer to *Eugenia feijoi*, and which Amshoff called *Catinga aromatica* (cf. Fl. Suriname 3: 106. 1951). Sagot supposed that the name *C. aromatica* had been based upon an abnormally long-fruited form of *C. moschata* (Ann. Sci. Nat. VI. 20: 197. 1885). At the same time Sagot contrasted with his "*Catinga moschata* Aubl." a completely different species, and under the mistaken impression that this was the *Calycorectes grandifolius* of Berg, he gave it a new name in *Catinga*, *C. oblongifolia*. The plant he described was the one that was treated by Amshoff in the *Flora of Suriname* as *Catinga moschata* Aubl.

Amshoff (Rec. Trav. Bot. Néerl. 39: 156. 1942) first took up *Catinga oblongifolia* as the valid combination, but nomenclaturally this course is unacceptable; Sagot's name is clearly an illegitimate substitute for *Calycorectes grandifolius*, whatever plant he may have been describing under that name. I have no reason to question Amshoff's later decision (Fl. Suriname 3: 107. 1951) to put *Catinga oblongifolia* into the synonymy of *C. moschata* Aubl., but no more do I have any reason to support such a course. Unless a convincing Aublet specimen of *C. moschata* can be found, the identity of the species must remain in doubt. If *Catinga moschata* proves to be identical with *C. oblongifolia* (i.e. *Calycorectes bergii* Sandw.), then the generic name *Calycorectes* must give way to *Catinga* as already advocated by Sagot in the publication cited above.

#### 10. PLINIA L. Sp. Pl. 516. 1753.

Type species, *P. pinnata* L. As explained above, the distinction between *Plinia* and *Calycorectes* is usually an arbitrary one based on the number of ovules, which are usually 2 in each locule of the ovary in *Plinia*, and 3 or more in *Calycorectes*. In *Plinia* also the buds are closed or essentially so, the very tips of the calyx-lobes sometimes free, approximate in pairs and appressed to the tip of the bud. The embryo in *Plinia* as far as known (i.e. in *P. pinnata* and in *P. costata* Amsh.) has two large, plano-convex cotyledons which are quite distinct or somewhat united at the edges. Almost all the species of *Plinia* agree vegetatively in having the flowers silky-pubescent, often nearly sessile, in small clusters, subtended by conspicuous thin bracts that simulate an involucre.

The known species of *Plinia* include, in addition to the type-species, several described by Urban (mostly on the basis of incomplete material) from the West Indies, one from Costa Rica, about 5 or 6 in northern South America, and one or more in southeastern Brazil. See the *Flora of Suriname* (Vol. 3: 97-99. 1951), *Flora of Peru*

(Field Mus. Publ. Bot. 13, pt. 4: 775–780. 1958), or *Sellowia* 13: 331–332. 1961.

The Cuban species referred to this genus are rather poorly known, and apparently anomalous (cf. Alain, in *Fl. Cub.* 3: 417–419. 1953). Twelve species are admitted to the Cuban flora by Bro. Alain; all except one were originally described by Urban, and six of these are still known from sterile material only. Most of the species are unlike the South and Central American species of *Plinia* in that their leaves are mostly only 2–4 cm. long. It is possible that they are wrongly placed in *Plinia*; if not, they presumably comprise a distinctive section or subgenus.

Kausel (*Ark. Bot.* 3: 506–509. 1956) has transferred to *Plinia*, as members of a newly constituted subgenus *Pliniopsis*, 3 out of 4 of Berg's species of *Myrciaria* of the group *Cauliflorae*, viz. *M. jacobitaba* (Vell.) Berg, *M. cauliflora* Berg, and *M. trunciflora* Berg, on the ground that the cotyledons are discrete and plano-convex and therefore not of the *Eugenia-Myrciaria* type. At the same time Kausel (l.c. 509) proposed a new genus, *Myrciariopsis*, based wholly on *Myrciaria baporeti* Legrand; this differs from *Plinia* subg. *Pliniopsis* mainly in the more lengthy racemes, which may be many-flowered and 30–45 mm. long (cf. Legrand in *An. Mus. Hist. Nat. Montevideo* II. 4 (no. 11): 63. pl. 1. 1936). In *Plinia* subg. *Pliniopsis* the flowers are 3–12 in congested groups. I cannot comment upon Kausel's disposition of these species except to say that in the morphology of the calyx and inflorescence, as well as in the character of the embryo, they are strikingly different from most of the species of *Myrciaria*. Except in the technical character of the embryo they bear little resemblance to the other species of *Plinia*. They are all alike in having a bilocular ovary with 2 ovules in each locule, and 4-merous, racemosely disposed flowers. Further comparative study is needed to establish their generic position more convincingly. Kausel himself (1967) now proposes to treat *Myrciariopsis* as a section of *Siphoneugena*.

Kausel, as noted above (page 361) proposed a new scheme of classification by which *Eugenia*, *Calycorectes* and *Myrciaria* are assigned to one taxon of subfamilial rank (on the basis of having undivided or only slightly divided embryo), whereas *Plinia*, *Myrciariopsis* and other genera with distinct cotyledons are assigned to another subfamily. Under this arrangement the cotyledonary structure assumes paramount importance and other considerations such as flower-structure, inflorescence-morphology, and number of ovules are decidedly secondary. Evidently satisfactory taxonomic disposition of these small south-Brazilian groups having the ovule-number reduced to two or three awaits a comprehensive revision of the *Calycorectes-Plinia-Myrciaria* complex to which they belong.

The identity of the genotype of *Plinia*, *P. pinnata* L., has been a moot question. The binomial was based wholly upon Plumier's *Plinia fructu croceo, odorato* (Nov. Pl. Amer. Gen. 9. pl. 11. 1703). The epithet *pinnata* evidently was used by Linnaeus because the plate appears to represent a plant with alternate, paripinnate leaves (and alternate branching in general). As this type of branching is essentially unknown among the American Myrtaceae, and as no member of the family is known to have compound leaves, the assignment of *Plinia pinnata* to the Myrtaceae requires some justification. Through the kindness of Mlle. Alicia Lourteig and Mme. Gabrielle Duprat, of the Muséum National d'Histoire Naturelle, Paris, I have been able to study Plumier's original drawing and the manuscript accompanying it (Plumier mss. 5: 42), and on the basis of this it now seems that most of the seeming discrepancies can be explained, and that Plumier's plant should be referred to the Myrtaceae, as first proposed by Urban (*Repert. Sp. Nov.* 15: 412–413. 1919). Urban suggested, and I agree, that *Plinia pinnata* L. was the plant that Berg had described under three different names in as many genera (*Marlierea glomerata*, *Myrciaria trinitatis*, *Stenocalyx plumieri*).

The plant shown in Plumier's drawing bears sessile flowers in glomerules scattered along a leafless twig of some size. The fruits are shown on the same stem. The relation of the flowers and fruits to the nodes on the stem is not indicated, but the clusters of flowers appear to be alternately or spirally arranged, not opposite. What seems to be a large (alternate) pinnate leaf with 6 pairs of opposite leaflets is shown as arising from a lateral (alternate) branchlet. The flowers are shown as 5-merous, and from the disposition and number of stamens and style, would seem to be myrtaceous. The fruits are subglobose or a little depressed, and shown with 15 or more rounded longitudinal ridges.

This plant could belong to the Myrtaceae only if the artist had failed to notice that the leaves, branchlets and flower-clusters were all opposite. Then the "pinnate leaf" might be interpreted as a branchlet with 6 pairs of opposite leaves; this was presumably the interpretation made by Urban.

Evidently the plant Plumier described is the one shown in the plate; there are no obvious discrepancies between the details in the drawing and those mentioned in the description. In Plumier's drawings of other Myrtaceae the details of opposite branching of twigs and inflorescences are carefully drawn, and I have been reluctant to suppose that in this one instance he went so far as to show the leaf-arrangement, branch-arrangement and disposition of flower-clusters as alternate throughout. Specimens recently collected on the island of St. Lucia by G. R. Proctor, however, suggest that Urban's identification of *Plinia pinnata* may have been the correct one, and that Plumier's drawing after all may not have been carelessly made. In Proctor's specimens (No. 17999, and to some extent no. 21574) the new leafy branchlets are often unilateral, with little or no evidence on the bark of the main stem that the opposing branchlet has been suppressed. The flower clusters in no. 17999 are borne on leafless twigs 5–8 mm. in diameter. The clusters superficially appear to be scattered along the twigs in random fashion, and even after close scrutiny under a dissecting microscope it is not always possible to demonstrate that any individual cluster arises from a node, nor that such a cluster is opposite a point from which another cluster might arise.

In the light of these modern collections, and in consideration of Plumier's statement that the leaves are in pairs ["ramuli alii . . . paulo magis pedem longi ac quinque aut sex foliorum coniugationis<sup>1</sup> exornati"], one may proceed on the assumption that Plumier's plant was myrtaceous. The leaves in modern specimens are minutely impressed-punctate above and sparingly beset with convex glands beneath, thus apparently fitting Plumier's description ["foliorum . . . innumerisque punctulis paulisper eminentibus exasperatorum"] well enough. There remain the matters of the flowers [described by Plumier as "myrtinis floribus multum similes, sed monopetali, campaniformes . . ."], the calyx ["exiguo et quinquepartito"] and the fruit ["calyce . . . deinde abit in fructum nucis juglandis duplum globosum mollem striatum, croceum, odoratissimum, nucleo tandem foetum nuci myristicae simillimam sed carnosam, et candidam ac tandem internis fossulis excavato resina quadam flavescente plenis"].

The description of the flowers provides perhaps the strongest reason for supposing that Plumier's plant was actually the one now called *Plinia*; in the latter the small petals fall at anthesis, and the irregularly divided calyx-segments become reflexed; after this the pale interior of the prolonged hypanthium, with its marginal ring of stamens, must indeed simulate a monopetalous, campanulate flower.

As to the description of the calyx as 5-parted, I suspect that Plumier mistook the persistent involucre-like bracts that subtend the flower-clusters, for the calyx of a single flower; this is suggested by his drawing of the base of a detached flower; it

<sup>1</sup> Apparently corrected in the original manuscript to *coniugationibus*. — RMcV.

may be that having noted that the supposed calyx-lobes numbered more than 4, he assumed they were 5. This interpretation would fit in with his description of the "monopetalous, campaniform" flower, i.e. he presumably took the hypanthium for a corolla and the subtending bracts for a calyx.

The shape of the fruit, as shown in the original drawing, and the size, shape and disposition of the ridges on it, are well enough matched in modern specimens (e.g. *Proctor 21574*). As for the size of the fruits, those in Plumier's sketch are drawn in such a way that their diameter is approximately the same as the width of the leaves shown with them. The leaves in modern specimens are mostly 2–3 cm. wide. Urban described the fruit of what he then called *Marlierea glomerata* (Bot. Jahrb. 19: 589. 1895) as 20–25 mm. in diameter, and I have seen the fruits in other specimens (e.g. *Hahn 1087*, from Martinique) up to 2.7 cm. in diameter after drying. This indicates that the fresh fruit must be at least 3 cm. in diameter, probably more. I first interpreted Plumier's words "fructum nucis juglandis duplum" to mean "twice as large as a walnut", but perhaps he meant "the double of a walnut"; that is to say "about like a walnut". In French usage today the word *double* still often carries the connotation of a *duplicate*.

11. SIPHONEUGENA Berg, *Linnaea* 27: 344. 1856. *Eugenia* subgen. *Siphoneugenia* [sic] (Berg) Kiaersk. Enum. Myrt. Bras. 174. 1893. *Paramitranthes* Burret, Notizbl. Berlin 15: 541. 1941.

Lectotype-species, *S. densiflora* Berg (cf. *Taxon* 5: 146. 1956). Burret (Notizbl. Berlin 15: 536. 1941) chose as lectotype *S. widgreniana* Berg, stating "als Typus . . . kann man nach der Beschreibung nur *S. Widgreniana* Berg ansehen, deren völlig geschlossener Kelch stets mit einem Deckel aufspringt, während er bei *S. densiflora* . . . nicht geschlossen ist, sondern Kelchläppchen aufweist . . .". The choice of *S. widgreniana* as type seems to have been based largely on erroneous interpretation, as nowhere in Berg's original descriptions (i.e. in *Linnaea*, and in *Mart. Fl. Bras.* 14, pt. 1: 378. 1857) is the calyx described as "completely closed"; on the contrary, both *S. densiflora* and *S. widgreniana* are described as having the calyx 4-lobed, and the same character is mentioned in the generic descriptions. On the assumption that in *S. widgreniana* the calyx was closed, and opened by a calyptra, Burret transferred it to *Mitranthes*, which as noted below has a calyx answering this description. Burret evidently had in mind a bud of the *Calyptranthes* type, circumscissile at the summit, or distal margin, of the hypanthium, whereas Berg described the hypanthium-tube in *Siphoneugena* as "ad verticem germinis [i.e. at the proximal end of the tube] circumscissus et deciduus". This last is the character that sets *Siphoneugena* and *Myrciaria* apart from the rest of the American Myrteae; the elongate hypanthium breaks cleanly from the summit of the ovary, leaving a more or less circular scar on the ovary and fruit. As Burret seems completely to have misunderstood this, his choice of lectotype may be set aside as irrelevant.

Kiaerskou, in his *Enumeratio Myrtacearum Brasiliensium* (i.e. in Warming, *Symb. Fl. Bras. Centr.* 39: 174. 1893), reduced *Siphoneugena* to a subgenus of *Eugenia*, and described a new Brazilian species, *E. chnoösepala*, with three subordinate varieties. Burret, in the paper cited above, typified his new genus *Paramitranthes* by *E. chnoösepala* var. *angustifolia* Kiaersk., and transferred *Siphoneugena densiflora* to *Paramitranthes*. Kiaerskou's material, as indicated by the descriptions in the prologue, and by a photograph of the type of *E. chnoösepala* (at C, Field Mus. Neg. 20940), is clearly a species of *Siphoneugena* in the sense of Berg, so that *Paramitranthes* falls into synonymy. This same view has been taken by Kausel, who has recently (1967) made the appropriate new combinations under *Siphoneugena*.

Thus as I now understand *Siphoneugena*, it includes several species in south-

eastern Brazil and one (*S. densiflora*) that seems to occur both in southern Brazil and in the mountains of Venezuela and the Lesser Antilles. A discussion of the distinguishing features of the genus, and its relationships to *Plinia* and *Myrciaria*, may be found in Fieldiana Bot. 29: 507–511. 1963. Since the publication of that paper I have seen the type of *S. densiflora* (Schüch s.n., in hb. Vindob.), and can report that the 2 locules of the ovary are each 3- or 4-ovulate, not multiovulate as reported by Berg.

Legrand (Com. Bot. Mus. Hist. Nat. Montevideo 3 (no. 36): 4–5, 9–16. 1959 [“1958”]), has taken up the name *Mitranthes* Berg for a group of about 11 species of southern Brazil. To me these seem superficially similar to *Siphoneugena* as well as to *Myrciaria*, and I believe further study should be directed toward the possibility of emending the circumscription of *Siphoneugena* so as to include them. In these species the hypanthium is produced beyond the ovary; the calyx is closed and opens by a calyptra; the ovary is bilocular, with several or many ovules in each locule, and the cotyledons are distinct and plano-convex. Some of the species were originally referred by Berg and others to *Calyptranthes*, *Calycorectes*, or *Siphoneugena*, because of the closed operculate calyx. The only major difference between “*Mitranthes*” in this sense, and *Siphoneugena*, lies in the manner of opening of the calyx; and that organ, as has been pointed out several times in this paper, is by itself not a dependable indicator of generic differences.

Berg included *Mitranthes* (Linnaea 27: 136, 316. 1856) among the eugenioid genera, but it is not clear to me that any of the species known to Berg were eugenioid, with the possible exception of *M. langscorffii*. In Taxon 5: 142. 1956, and again in the *Index Nominum Genericorum* (1957–58), I proposed *Mitranthes browniana* (DC.) Berg as lectotype-species. I had overlooked the fact that Burret, much earlier (Notizbl. Berlin 15: 536–541. 1941) had proposed *M. ottonis* Berg (the only species described by Berg in the original publication in Linnaea), and further had transferred to a new genus, *Mitropsidium*, most of the other species referred by Berg to *Mitranthes*, including *M. browniana*. The choice of *M. ottonis* as lectotype-species was a reasonable one, as Berg had based the genus primarily on the character of the calyptrate calyx, which is evident in *M. ottonis*. Berg was unacquainted with the fruit of any of the original species, so there is no reason to suppose that he suspected any relationship between *Mitranthes* and *Psidium*. The species transferred by Burret to *Mitropsidium* are definitely pimentoid in affinities; I should refer them without question to the genus *Psidium* itself. If as Burret supposed (presumably on the basis of the circumscissile calyx and the trilocular ovary, with multiovulate, bilamellate sporophores), *Mitranthes ottonis* also belongs with the Pimentinae, then the South American species *Mitranthes obscura* (DC.) Legr., [*Calyptranthes obscura* DC.], *Calyptranthes maschalantha* Berg, etc., should be excluded from *Mitranthes*. I have not seen any fruiting specimens of *Mitranthes ottonis*, but from an examination of an isotype, at Vienna, I suppose that it is not related closely to anything in the Eugeniinae. Gross examination, in fact, would suggest that it was a species of *Calyptranthes*, as the buds, the manner of branching, the branching of the inflorescence and the inter-petiole wing-angles on the leafy branchlets are all typical of that genus; only the trilocular ovary with basally located multiovulate placentae is out of place in *Calyptranthes*. Perhaps *Mitranthes ottonis* represents a distinct monotypic Antillean genus; a decision upon this must await the study of fruiting specimens.

After this paper was in the hands of the editor, Dr. George R. Proctor kindly sent me for examination a fine series of Myrtaceae from Jamaica, including flowering and fruiting specimens of what he supposed to be a new species of *Calyptranthes*. It transpired that the ovary in these specimens (Proctor 26471, 26480, 26546, 26726) was 3-, 4-, or 5-locular and mul-

tiouulate, and the calyx closed and circumscissile in bud, exactly as in the original *Mitrnanthes ottonis*. The mature seed (from No. 26726) is of the myrcioid type. In other respects the Jamaican plant, like the Cuban, suggests a large-flowered species of *Calyptnanthes*. After seeing the Jamaican material I have no doubt that *Mitrnanthes* deserves generic standing, and no doubt that the genus is related to *Calyptnanthes* and perhaps a precursor of that group. See also the discussion in the list of imperfectly known genera, at the end of this paper.

12. MYRCIARIA Berg, *Linnaea* 27: 320. 1856.

Lectotype-species, *M. tenella* (DC.) Berg. As thus typified, the group is a very natural and homogeneous one, perhaps more easily recognized as a distinct genus than any other American member of the Eugeniinae. It shares with *Siphoneugena* the character of the 4-lobed, tubular hypanthium which after anthesis is circumscissile at the base; the ovules are 2 in each locule, not 3 or 4 as in *Siphoneugena*, and the embryo, as far as known, is undivided, i.e. as in *Eugenia* proper. These contrasts, and those with *Plinia*, are discussed in a *Revision of Myrciaria Berg, in North America and northern South America* (Fieldiana Bot. 29: 499–504. 1963), in which 7 species are recognized. There are perhaps one or more additional species in the West Indies, and several or many in central and southeastern Brazil; Legrand recognizes 9 species in Santa Catarina (Sellowia 13: 327–331. 1961).

Berg originally included in *Myrciaria* a number of species that were obviously unrelated to the rest — these were, in fact, mostly species of *Myrcia* — and this influenced Bentham (*Jour. Linn. Soc. Bot.* 10: 164. 1869) to relegate *Myrciaria* to the synonymy of *Eugenia*. Neither Grisebach nor Urban recognized *Myrciaria* as a genus, and it was not until more recently that students of the South American flora (in which it is well represented) began to understand it as an independent taxon. In the strict sense, the genus comprises approximately what Berg called *Glomeratae*; the other four groups recognized by Berg as subordinate taxa in *Myrciaria*, viz. *Dichotomae* (3 species), *Paniculatae* (8), *Cauliflorae* (4), and *Uniflorae* (2) are atypical in one way or another, or belong to other genera. The *Cauliflorae* are mentioned above in the discussion of *Plinia*, to which several species have been transferred by Kausel. More recently the same author has proposed the new genus *Paramyrciaria* (*Lilloa* 32: 345. 1967), with one species, *P. delicatula* (DC.) Kausel, said to differ from *Myrciaria* in having distinct cotyledons as in *Plinia*. Most recent writers have set rather narrow taxonomic limits for *Myrciaria*, but Legrand, even in his more recent studies of the Myrtaceae of Uruguay and southern Brazil (cf. *Sellowia* 13: 327–331. 1961) has taken a more liberal view, including in *Myrciaria* not only the *Glomeratae*, but also the *Cauliflorae*, the *Dichotomae* (which are apparently eugenioid, resembling species of *Eugenia* or *Calycorectes*), and *M. (Myrciariopsis) baporeti*, which has long racemes quite unlike anything else known in the genus.

13. LEGRANDIA Kausel, *Rev. Argent. Agron.* 11: 321. 1944.

Type-species, *L. concinna* (R. A. Philippi) Kausel. The type and only species is an endemic of central Chile. Originally described as a *Eugenia*, this plant has the flowers solitary and axillary, 4-merous, subtended by leafy, lance-ovate bracteoles almost 1 cm. long, 4 mm. wide. Because of the inflorescence (which suggests that of *Ugni* or some other pimentoid genus), and the strongly 4-angled branchlets, *L. concinna* is a distinctive species. The embryo is described and figured by Kausel (in the protologue, and in *Ark. Bot.* 3: 498. 1956) as spherical, massive, with the straight, discrete, radicle extending through the mass. Kausel first interpreted the fleshy part of the embryo as the hypocotyl, and the minute lobes at the proximal end of the radicle as cotyledons; he accordingly referred *Legrandia* to the group of the pimentoid Myrtaceae, noting that because of the straight, uncurved embryo it was anomalous in that group. In his later paper he inclined to the opinion, attributed

also to Skottsberg, that the fleshy part of the embryo was of the nature of fused cotyledons surrounding the radicle. Primarily on the basis of this character, Kausel proposed (Ark. Bot. 3: 500. 1956) the group *Cryptorhizoideae*, coordinate with four other principal groups of the Myrtaceae, to include *Legrandia*, *Cryptorhiza* Urb., the small Australian genus *Pilidiostigma* Burret, and *Blepharocalyx* Berg, which latter has by other authors been considered a pimentoid genus.

In summary, *Legrandia* as a genus depends primarily on the combination of the unique features of the embryo, with an inflorescence like that of some pimentoid genera but the ovary bilocular, with 8–10 ovules distributed about the margin of a peltate placenta.

Group 3. *Myrcianthes* and related genera

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Several American taxa of the Myrtaceae are well set off taxonomically from *Eugenia* (to which most of the species were formerly assigned because of the primarily 4-merous flowers), by the tendency of the inflorescence to branch dichasially. The dichasium in its simplest demonstrable form is 3-flowered, consisting of an axillary peduncle terminated by a flower at the first node, and a pair of lateral 1-flowered branchlets arising from the axils of the bracts that subtend the terminal flower. Dichasia with 7, 15, or more flowers are often formed by proliferation, in the same manner, of the lateral branchlets. This manner of branching in the inflorescence is common among the pimentoid genera; it is rare in the myrcioid genera and, as noted above under *Eugenia*, so rare as to be considered an anomaly when it occurs in the species of that genus. Among the so-called myrcioid genera dichasia are known only in *Myrceugenia*, which as noted above has a unique status and probably is not to be considered typically myrcioid.

It is noteworthy that, except for the pimentoid genera, most of the American Myrtaceae that have a determinate, dichotomously branched inflorescence have also an embryo with two distinct, large, and usually fleshy and plano-convex cotyledons. In the genus *Luma* [*“Myrceugenella”*] the cotyledons are thin and flat. Kausel (Ark. Bot. 3: 500, 503. 1956) classifies *Luma* with the myrcioid rather than the eugenioid genera because of the epigealous germination of the seed, which he supposes to be correlated with the small amount of stored food in the thin and leafy, rather than fleshy, cotyledons.

Although it does not seem to me that *Luma* is very closely related in most respects to the principal myrcioid genera, it is interesting to note that in some other characters the species of *Myrcianthes* are more myrcioid than eugenioid. In a few species, e.g. *M. karsteniana* (Berg) McVaugh, *M. osteomeloides* (Rusby) McVaugh, and in *Eugenia pycnantha* Benth. (which is probably a species of *Myrcianthes* but of which the fruit is unknown), the dichasia are forked several times and closely aggregated, forming panicle-like clusters at the tips of the branches. Such branches seem to be transitional in form between the myrcioid panicle and the simple dichasium. Sometimes short lateral branches arising from leaf-axils may consist of several short internodes and as many nodes, each node bearing a pair of many-flowered dichasia. The myrcioid panicle is in effect such a short lateral branch, on which the subtending leaves at the nodes have been reduced to bracts, and on which the dichasial branching is evident only at the tips of the panicle-branches.



The flowers of *Myrcianthes* and related taxa are less strictly 4-merous than those of *Eugenia*. Those of *Pseudanamomis* and *Reichea* are 5-merous, as are those of several species of *Myrcianthes*. Both 4- and 5-merous flowers occur in some species of *Myrcianthes* (e.g. *M. fragrans*, a primarily North American species). In the Myrciinae 5-merous flowers predominate, although 4-merous ones are not rare.

Thus there are several superficial similarities, in the inflorescence, the flower and the embryo, between the myrcioid Myrtaceae as traditionally understood, and the species of the *Luma-Myrcianthes* complex which were formerly referred to *Eugenia* because most of them had 4-merous flowers. Because of these correlated similarities, I have chosen to depart here from the order established by Berg; in a three-dimensional system I suppose the group constituted by *Myrcianthes*, *Reichea*, *Pseudanamomis* and perhaps *Luma*, should lie somewhere near both *Myrcia* and *Eugenia* and at the same time near the pimentoid genera.

14. MYRCIANTHES Berg, *Linnaea* 27: 315. 1856. *Anamomis* Griseb. *Fl. Brit. W. Ind.* 240. 1860. *Pseudomyrcianthes* Kausel, *Ark. Bot.* 3: 504. 1956, in part, perhaps not as to type. ?*Acreugenia* Kausel, *Ark. Bot.* 3: 510. 1956.

Lectotype species, *M. apiculata* Berg. Berg understood this as a group of 4 species with the flowers 5-merous, the inflorescence dichotomously branching, and the embryo with a short radicle and 2 plano-convex cotyledons. All the original species were natives of southern Brazil or Uruguay. Other species of supposed eugenioid affinities, having the flowers in dichasia but the flower-parts in 4's, were assigned by Berg to his group *Dichotomae* of *Eugenia*. In the *Flora of Peru* (Field Mus. Publ. Bot. 13, pt. 4: 745-775. 1958) I discussed the relationship between *Anamomis* and *Myrcianthes*, and took up the latter for a group of about 40 species, mostly natives of the Andean region, but some extending into the West Indies and continental North America. In a somewhat fuller treatment of the genus (*Fieldiana Bot.* 29: 473-497. 1963), I considered all the known species except those of southeastern South America.

Kausel (*Ark. Bot.* 3: 502 ff. 1956) distributed the species of what I should call *Myrcianthes* among several genera. According to his interpretation, those species with a several-flowered dichasium but without a plumule in the embryo, were to be referred to *Anamomis* Griseb.; those with a plumule and a 5-parted perianth were referred to *Myrcianthes*; and those with a plumule but a 4-parted perianth to *Amyrsia* Raf. As I noted in the *Flora of Peru*, it does not seem possible to draw convincing generic lines on the basis of these characters. The name *Amyrsia* Raf. (cf. *Taxon* 5: 137. 1956) is best typified by *Myrtus microphylla* Humb. & Bonpl., although Rafinesque's concept of the genus included some species of *Myrcianthes*.

Certain Andean species that were originally described in *Eugenia* are strictly 1-flowered; the inflorescence is never a dichasium as far as known. They presumably represent species of *Myrcianthes*, as indicated by their general similarity to species that have some of the flowers solitary and others in 3-flowered dichasia. Several of the species with 1-flowered peduncles were treated in the *Flora of Peru* as members of the genus *Myrcianthes*, but formal nomenclatural transfers were not made there unless the species were known in the fruiting condition. At least one species, *Eugenia minimifolia*, was subsequently transferred to *Myrcianthes* when the fruit became known (*Fieldiana Bot.* 29: 492. 1963). An Argentinian species now referred to *Myrcianthes*, *M. mato* (Griseb.) McVaugh, has the embryo typical of the genus, but the peduncles are one-flowered. As there is evidently no fundamental difference between 1- and 3-flowered peduncles, it seems that the generic limit does not depend on the number of flowers, but rather on the realization that both these types are fundamentally determinate at the first node above the leaf-axil, in contrast to the inflorescence of *Eugenia* which may be indeterminate (as in the so-called genus *Stenocalyx*), func-

tionally determinate (when, as usual in *Eugenia*, the terminal bud or buds of a raceme abort), or determinate upon the development of a flower at the tip of an axis of several nodes.

One rather widely distributed species of Uruguay, northern Argentina, Paraguay and southern Brazil, *Eugenia pungens* Berg, was set apart by Kausel as the type of a monotypic genus, *Acreugenia*. In this species the 4-merous flowers, the bilocular multiovulate ovary and the embryo of two distinct plano-convex cotyledons are exactly those of many species of *Myrcianthes* but the flowers are usually a single pair from an abortive axillary axis, i.e. exactly as in *Eugenia*. Because of the embryo character, and because of the similarity in minor characters between this species and other, undoubted species of *Myrcianthes*, I am inclined to believe it belongs with that genus, not with *Eugenia*, and not in a genus of its own. In 1967 Kausel transferred to *Acreugenia* a second species, *Eugenia mato* Griseb., which I had previously transferred to *Myrcianthes*; in this latter species the peduncles are usually 1-flowered, not dichasially branched.

The genus *Pseudomyrcianthes* was set up by Kausel (Ark. Bot. 3: 504. 1956) to include five and perhaps more species formerly referred to *Eugenia*, but which according to Kausel have the flowers solitary or in dichasia (as in *Myrcianthes*) and the embryo homogeneous, with only a partial separation between the cotyledons. The type of the genus is *P. pyriiformis* (*Eugenia pyriiformis* Camb.), in which the inflorescence may be 1-flowered, 3-flowered, or several-times forked. Legrand (Not. Syst. 15: 266. 1958) felt that this species should be retained in *Eugenia*, in spite of the frequency of 3-flowered and several-flowered forms. Some of the species assigned by Kausel to *Pseudomyrcianthes* seems to belong to other genera (e.g. *P. pseudo-mato* is better referred to *Myrcianthes*, as noted in Fieldiana Bot. 29: 493. 1963; and *P. cambessedeanana* is a typical *Eugenia* with racemose inflorescence, as noted in Not. Syst. 15: 269. 1958). When the fruits of all the supposed species of *Myrcianthes* and *Pseudomyrcianthes* in eastern South America are well known, some generic separation may be indicated, but for the moment it seems premature. The placentation in *Pseudomyrcianthes* is described by Kausel as apical, but in fact it does not appear to differ essentially from that in most species of *Myrcianthes*, in which the ovules are usually attached at or above the middle of the locule.

15. REICHEA Kausel, Rev. Mirt. Chil. [1], Aug. 1940; Rev. Argent. Agron. 7: 364. Dec. 1940. *Aspidogenia* Burret, Notizbl. Berlin 15: 521. 1941.

Type-species, *R. coquimbensis* (Barn.) Kausel. The one known member of this genus is confined to the province of Coquimbo in north-central Chile. As described by both Kausel and Burret it is a plant with the inflorescence and the embryo of *Myrcianthes*, but with 5-merous flowers and the placenta peltate with 6–12 marginal ovules. It is described and contrasted with other species and genera, in several publications by Kausel (e.g. Rev. Argent. Agron. 9: 40–42. 1942; Lilloa 13: 129–130, fig. 1. 1948), and in Fieldiana Bot. 29: 476. 1963. As in the case of other Chilean endemics, *Nothomyrcia fernandeziana* and *Legrandia concinna*, taxonomic judgment of generic distinctness is difficult because although each taxon is represented by a single species that is demonstrably different in one or few characters from all the species of genera that seem to be closely related, it is not possible to ascertain the meaning of the differences in terms of genetic constitution; neither is it possible to demonstrate, as it usually is in genera of two or more species, that the taxa retain their generic distinctness even though genetically speaking they may be heterogeneous. The question of the recognition or non-recognition of monotypic genera that are empirically separable from larger taxa is no easier to solve in the Myrtaceae than in any other large natural family.

16. PSEUDANAMOMIS Kausel, Ark. Bot. 3: 511. *figs.* 22, 23. 1956.

Type species, *P. umbellulifera* (HBK.) Kausel. The generic position of this plant has always been in doubt; originally described as a species of *Myrtus*, it has been transferred successively to *Myrcia*, *Eugenia* and *Ananomis*, and independently described as a species of *Myrcianthes* (cf. Urban, Bot. Jahrb. 19: 171–172. 1895). Its proper taxonomic position is evidently near *Myrcianthes* (cf. Fieldiana Bot. 29: 476. 1963). The inflorescence is often a 3-flowered dichasium, but usually is somewhat irregularly branched, producing supernumerary branches near the base of the peduncle or at the base of the central (terminal) flower; the whole may be sub-umbellate as illustrated by Kausel, or the central axis may be prolonged and 3-flowered so that the whole resembles a reduced myrcioid panicle. The embryo is like that of *Myrcianthes* except that the cotyledons are united about one-third their length; the ovules are usually only 5 or 6, rather less than the usual number in *Myrcianthes*; and the calyx-lobes are 5, and deciduous, separating tardily from the hypanthium, as in various species of *Myrcia* but rarely in *Myrcianthes*.

The natural range of *Pseudanamosis umbellulifera* includes Hispaniola, Puerto Rico, and apparently some areas adjacent to the coast in northern Colombia and Venezuela.

17. LUMA A. Gray, U. S. Expl. Exped. [15] (Bot. Phan. 1): 535. *pl.* 66. 1854. *Myrceugenella* Kausel, Rev. Argent. Agron. 9: 42. 1942.

Lectotype-species, *L. chequen* (Molina) A. Gray. In proposing the name *Myrceugenella*, Kausel recognized the priority of *Luma*, but rejected the latter because it had originally been applied to members of three genera, viz. *Myrceugenella* in the sense of Kausel, *Myrceugenia*, and *Temu*. In the protologue of *Myrceugenella*, however, and also in a later paper (Lilloa 13: 127. 1948), Kausel argued that the only acceptable lectotype for *Luma* was *L. chequen* var. *a* in the sense of Gray. As this same variety was proposed by Kausel as the type of *Myrceugenella*, the latter is nomenclaturally superfluous if *Luma* is taken up and typified as above. The lectotypification of *Luma* has been discussed elsewhere (Taxon 5: 142. 1956; cf. *Index Nominum Genericorum*, card no. 39/05011).

This treatment of *Luma* is widely at variance from that of Burret (Notizbl. Berlin 15: 522–535. 1941), who summarily reduced *Myrceugenia* to the synonymy of *Luma*, and referred to *Luma* not only a number of Chilean species that belong to *Myrceugenia* (sensu Berg), but at least six that belong to *Myrceugenella* (sensu Kausel), and also *Nothomyrcia fernandeziana*. At the same time he referred to *Luma* 54 species of the South-Brazilian region; most of these had previously been described as species of *Eugenia* (a few under *Myrceugenia*). Burret did not attempt formal typification of *Luma* or of *Myrceugenia*, merely stating it as his opinion that the two were one and the same, at least after the removal from *Luma* of one or two of the original species. He left in *Luma* the two diverse elements that have been treated by subsequent authors as species of *Myrceugenia* and *Myrceugenella*, respectively; presumably he was influenced, as Kausel has suggested, by Niedenzu's treatment in *Die Natürlichen Pflanzenfamilien*, where these same species, and *Nothomyrcia fernandeziana*, were referred to *Myrceugenia*. Burret's treatment was based on a cursory examination of the material in the Berlin Herbarium; as also noted by Kausel, it is evident that he lacked a thorough critical knowledge of the plants concerned. I have chosen to disregard his implied typification of *Luma* by the *Myrceugenia* element, and to take the position that in addition to *L. apiculata*, *L. chequen*, and 4 other species that he referred properly to *Luma*, there were some 74 species of *Myrceugenia* and other genera assigned erroneously to *Luma*.

The identities of Molina's species of Chilean Myrtaceae, including *Eugenia chequen*,

are always open to question. Kausel (Lilloa 13: 132. 1948) has stated that it is important to consider the vernacular names mentioned by Molina (many of which are still in use), the uses of the plant as originally described, and the works of the older authors mentioned by Molina. With respect to the identity of *Eugenia chequen* (Mol. Sagg. Chili ed. 2. 148, 289. 1810), Kausel states merely that the name *chequen* "no se usa en la actualidad sino solamente para la especie siguiente y para otras especies de hoja pequeña" (Rev. Argent. Agron. 9: 43. 1942).

As understood by Kausel, *Luma* [*Myrceugenella*] includes 4 Chilean species only. The best-known and most widely distributed of these, *L. apiculata* (DC.) Burret, has been described under many different names (cf. Lilloa 13: 131. 1948). All the species are alike in aspect and in morphology, and evidently form together a geographically localized evolutionary unit. In some ways the genus seems close to *Myrcianthes*, e.g. in the 4-merous flowers, in the dichasial branching of many inflorescences, and in the bilocular and multiovulate ovary and the embryo with two broad thin cotyledons. Closer study suggests, however, that the resemblances to *Myrcianthes* have resulted from parallel development, or from very distant evolutionary connections.

The inflorescence in *Luma apiculata*, for example, conforms to no one type; the flowers are often produced in 3-flowered dichasia, but are perhaps more often solitary in the leaf-axils, and in some plants partly in short axillary bracteate racemes. The hypanthium and calyx-lobes are membranous, not fleshy as in most species of *Myrcianthes*; the lobes are glabrous on both sides, not pubescent within as in many Andean species of *Myrcianthes*. The embryo, used by Kausel as a primary character of *Myrceugenella*, consists of two plano-convex but thin, not folded cotyledons, and a terete radicle about as long as the cotyledons (cf. also Fieldiana Bot. 29: 476. 1963 for the contrast between *Luma* and *Myrcianthes*). In short, the species of *Luma* form a closely knit group that seems to have evolved locally, independently of *Myrcianthes*, and quite apart from any other major evolutionary line.

#### Group 4. *Campomanesia* and related genera

18. <i>Campomanesia</i> . . . . .	398
19. <i>Paivaea</i> . . . . .	400
20. <i>Blepharocalyx</i> . . . . .	400
21. <i>Temu</i> . . . . .	401

This and the next two groups (i.e. groups 4–6 of Fig. 1, p. 371) together are approximately equivalent to the Pimentinae in the traditional sense. I have chosen to treat them as three groups of genera because they differ not only in the characters of ovary, embryo, seed-coat and calyx noted by Berg, but also recognizably in the structure of the inflorescence. The differences between groups are not always easy to make out, especially between groups 4 and 5 (those of which *Campomanesia* and *Psidium*, respectively, are the largest genera).<sup>1</sup>

Berg divided the pimentoid genera into two groups, namely those with short, curved embryo ["Embryo uncinato-curvatus, subspiralis, v. semiannularis"], and those with "Embryo spiralis, 2–3-cyclicus". The first included *Psidium*, *Calycolpus*, and other genera with the flowers solitary or in 3's, the locules of the ovary 2–4 or

<sup>1</sup> Since the above text was written I have seen a recent paper which in a way supports the separation between what I call groups 4 and 5. Kausel (Lilloa 32: 338. Jul–Sep 1967) proposes to unite *Campomanesia*, *Britoa* and *Blepharocalyx* in the tribe *Campomanesieae* of his subfamily *Cryptorhizoideae*; *Psidium* and its relatives, according to the same author, are placed not only in another tribe but in another subfamily. I have not been able to obtain sufficient material to verify the observations on embryo-structure that led Kausel to align *Campomanesia* with the little-known *Cryptorhiza* rather than with *Psidium*.

occasionally more, the seeds with hard, bony testa. The second group included the distinctive genus *Pimenta*, and in addition *Campomanesia* and the other genera listed below as possible synonyms of *Campomanesia*. All these (except *Pimenta*) are alike in having the flowers solitary or in 3's, the locules of the ovary usually 4–6 or more, and the seeds with membranous testa.

Bentham correctly pointed out (Jour. Linn. Soc. Bot. 10: 149. 1869) that the distinction between uncinately-curved and spiral, cyclic embryos is not a clear one, but, as he went on to say "it is probable, however, that in most species the seeds have a thinner testa and a longer radicle in proportion to the cotyledons in *Campomanesia* than in *Psidium*". In the *Genera Plantarum* (Benth. & Hook. f. Gen. Pl. 1: 694. 1865) Bentham made the contrast between *Psidium* and *Campomanesia* by means of the embryo-character, by the difference in the number of locules in the ovary, and also by supposed differences in the arrangement of ovules, *Campomanesia* supposedly having the ovules biseriately (rarely 4-seriate), and *Psidium* multiseriately (i.e. irregularly crowded). Study of Berg's work seems to indicate that Bentham misinterpreted the differences in ovule-arrangement as Berg understood them. Berg said of *Psidium* (Linnaea 27: 353. 1856): "Genus maxime naturale, ab auctoribus saepissime cum *Campomanesia* commutatum, facile sporophoris bilamellatis... ab hac distinguendum est, cui semina ad angulum loculorum internum biserialia... sunt". That is, Berg understood the ovules in both genera to be biseriately; he thought those of *Psidium* were produced on "lamellae" of parietal origin, but as in the crowded, multilocular ovary of *Campomanesia* the placentae are not extended into the locules, the ovules appear to be sessile in two rows on the inner angles of the locules, and he described them accordingly.

Thus in the genera of Group 4, as most readily observed in the largest genus, *Campomanesia*, the characters of proportionately long radicle and thin testa are associated. The other genera are grouped with *Campomanesia* because of their possession of the same characters of seed and embryo, but *Blepharocalyx* and *Temu*, at least, are probably not closely related to *Campomanesia*.

18. CAMPOMANESIA Ruiz & Pavón, Prodr. 72. pl. 13. 1794. ?*Britoa* Berg, Linnaea 27: 435. 1856. *Abbevillea* Berg, Linnaea 27: 425. 1856. ?*Acrandra* Berg, Linnaea 27: 435. 1856. ?*Lacerdaea* Berg, Linnaea 27: 437. 1856.

Type species, *C. lineatifolia* Ruiz & Pavón. The genus includes a large central body of species with multilocular ovary, membranous or leathery testa, 1- or 3-flowered peduncles that are often at bracteate nodes on new branchlets, unspecialized and usually 5-merous calyx with relatively thin and often membranous lobes, and thin, veiny leaves. The questions of delimitation of other genera (e.g. *Abbevillea*, *Britoa*) on the basis of differences in calyx-morphology seem to need further study, but the distinctions are subjective at best. Many species are unknown in the fruiting condition, and *Campomanesia* in the traditional sense now includes several groups of species that seem to be out of place among the rest. For example, the group that includes *C. aurea* Berg and *C. cyanea* Berg has exactly the habit of a small-leaved ("Myrtus-like") glabrous *Psidium*; the calyx splits as in *Psidium*, but the ovary is 5–8-locular, and the seeds have a relatively thin testa as in *Campomanesia*. Without knowledge of the number of locules in the ovary, and in the absence of mature seeds, it is often impossible to say whether a given species belongs to *Psidium* or to *Campomanesia*.

As no single character of *Campomanesia*, with the possible exception of the thickness and texture of the testa, permits a ready assignment of an unknown species to this genus rather than to e.g. *Psidium*, it is probable that some species now passing under one name or the other will eventually have to be transferred. In *Campomanesia*

the flowering is usually of the racemose type or the *Stenocalyx* type, but the peduncles may be axillary as usual in *Psidium*; some species of *Campomanesia* have short calyx-lobes like those common among species of *Psidium*, but most species having broad, thin spreading lobes that are pubescent on both sides are probably to be excluded from *Psidium*. Easy separation of these genera upon superficial examination will be feasible only after most of the species have been collected in both flowering and fruiting condition.

Many species of *Campomanesia*, however, are vegetatively distinctive in the same characteristic way. The leaves are ovate-lanceolate, slender-petiolate, thin in texture and with prominent arcuate-ascending lateral veins, the lateral veins usually diminishing distally and curving in to join the next succeeding ones, so that no definite marginal vein is formed; the vein-axils on the lower leaf-surface are often barbate with stiff pale hairs; and the lateral veins at mid-leaf or above are usually considerably more widely spaced than those toward the base of the leaf. Leaves of this kind no doubt suggested to Berg the epithet *malifolia* for one species of *Campomanesia*; they are also characteristic of the type-species, *C. lineatifolia*, and of such species as *C. ciliata* Berg, *C. eugenioides* (Camb.) Legrand, *C. grandiflora* (Aubl.) Sagot, *C. guaviroba* (DC.) Kiaersk., *C. littoralis* Legr., *C. reitziana* Legr., *C. rhombea* Berg, *C. xanthocarpa* Berg, and others; perhaps one-third of the known species of *Campomanesia* including *Abbevillea*.

In certain other groups of species the leaves may be obovate or oblanceolate, and short-petiolate, with strongly ascending nearly straight veins; these closely simulate the leaves of some species of *Psidium*, and I know of no way to distinguish them vegetatively.

All authors since Bentham's time have recognized *Campomanesia* as distinct, but not all have agreed with his verdict that *Abbevillea*, *Acrandra*, *Britoa* and *Lacerdaea* were all synonyms of it. Niedenzu, in the *Natürlichen Pflanzenfamilien*, accepted *Acrandra* (which is distinctive only in having the anthers prolonged into subulate appendages), and *Britoa* (in which the calyx in bud is nearly closed, and opens irregularly at anthesis in the manner of some species of *Psidium*). *Lacerdaea*, as suggested by Berg himself (Linnaea 30: 713. 1861), is a synonym of *Britoa*. *Abbevillea*, distinguished by the undulately margined rather than distinctly thin-lobed calyx, was accepted by Niedenzu as a section of *Campomanesia*. Kiaerskou (Enum. Myrt. Bras. 5—8. 1893) treated *Acrandra* and *Abbevillea* as subgenera of *Campomanesia*, and *Britoa* as an independent genus. Legrand (Notul. Syst. 15: 274. 1958) accepts *Abbevillea* as a subgenus and *Britoa* as an independent genus.

Unfortunately *Campomanesia* as a whole has not been studied since Berg's time. Only two or three species occur in northern South America; only about 10 range as far south as Santa Catarina; the rest of the approximately 80 species recognized by Berg are natives of southeastern and central Brazil, where no comprehensive floristic studies have been undertaken in recent years. Kiaerskou (Enum. Myrt. Bras. 6—17. 1893) published two new species of *Britoa* and 8 of *Campomanesia* from southeastern Brazil, but provided no general treatments of the groups.

The best-known and most widely distributed species of *Britoa*, *B. sellowiana* Berg [*B. guazumaeifolia* (Camb.) Legrand], which is also the type of the genus, is a variable but easily recognized species with rugose leaves, short stout 1-flowered pedicels, dense velutinous pubescence and irregularly rupturing closed buds (cf. Berg, in Mart. Fl. Bras. 14, pt. 1: pl. 53. 1857). It bears little resemblance to most of the other species described by Berg, e.g. *B. dichotoma* (cf. Field Mus. neg. 23351), *B. psidioides* Berg (Field Mus. neg. 23352), or *B. triflora* Berg (Herb. Willd. 95301), all of which look like species of *Campomanesia* with 3-flowered inflorescences and lobed but irregularly opening calyx. Certainly the generic limits in this whole group will bear investigation; there seem to be no large series of species,

as there are in the *Myrcia* – *Marlierea* – *Calyptranthes* complex, in which specialization in the calyx is associated with other modifications. Unless *Britoa* may be recognized as a monotypic genus, it seems that it is not sufficiently distinct from *Campomanesia*.

In a recent paper (Loefgrenia 26: 1–72. Sep. 1967), João Rodrigues Mattos has treated *Britoa* as a subgenus of *Campomanesia*, including *C. guazumaefolia* as the type of a monotypic section, and seven other species in a second section.

19. PAIVAEA Berg, in Mart. Fl. Bras. 14, pt. 1: 614. 1859.

Type-species, *P. langsdorffii* Berg. The only known species was described from São Paulo, Brazil. It is apparently related to *Campomanesia*, but fruit and seed were not seen by Berg, who based the genus on the remarkably modified hypanthium, which is enlarged laterally into a 5-lobed patelliform disk, and the tube of which is considerably prolonged beyond the ovary. The buds are 5-lobed at apex, and at anthesis split longitudinally as far as the summit of the ovary. Bentham (Jour. Linn. Soc. Bot. 10: 150. 1869) doubted “whether this peculiarity is of any more than specific value”, but retained the genus in the *Genera Plantarum* “until its real place shall be ascertained by the examination of the embryo”. Niedenzu (Nat. Pflanzenfam. 3, pt. 7: 73, 74, fig. 39 P & Q. 1893) upheld the genus and published drawings of the bud and flower. As I have not seen any specimens, I include the genus here provisionally.

20. BLEPHAROCALYX Berg, Linnaea 27: 348 (in clave). Jan. 1856; 412. Feb. 1856.

Lectotype-species, *B. acuminatissimus* (Miq.) Berg. Twenty-two species were listed by Berg, including one, *B. salicifolius* (HBK.) Berg, from Ecuador, and the others from Uruguay and southeastern Brazil. The actual number of species may be considerably less than this. Legrand, in his study of the Myrtaceae of Uruguay (Anal. Mus. Hist. Nat. Montevideo II. 4 (no. 11): 25–33. 1936) says that the common Uruguayan species is very polymorphic; he thus treats three of Berg’s species under the same name. In a later paper (Sellowia 13: 338–339. 1961) Legrand suggests that this same species, which he calls *B. tweediei*, is scarcely distinct from *B. salicifolius*. Apparently the genus forms a small natural group with disjunct range like those of *Myrrhinium* and *Myrcianthes*, ranging northward in southern Brazil at least to Minas Gerais and in Argentina to Tucumán and Catamarca. Although listed by Bentham among the synonyms of the inclusive *Myrtus* (Benth. & Hook. f. Gen. Pl. 1: 715. 1865), most later workers who knew the plants have recognized it as an independent genus. Most of the so-called species are remarkably alike in the possession of a bilocular, multiovulate ovary; four-parted flowers with the two pairs of calyx-lobes prominently ciliate (whence the generic name), the outer pair covering the inner in bud, and all the lobes rather cleanly deciduous from the hypanthium after anthesis; the flowers (sometimes solitary) usually in 3-flowered dichasia with the central flower sessile; the embryo (illustrated by Legrand in his 1936 paper cited above) tightly curved or coiled, with membranous, glandular-verrucose testa. The dichasia are sometimes 7-flowered, and in some of the described species the leaves are unlike the nearly glabrous, narrow and acutely pointed ones of the majority, but on the whole this seems to be a homogeneous and easily comprehended group. As pointed out above (page 372) its relationships are obscure. Berg aligned it without question with the pimentoid genera near *Temu* and *Pseudocaryophyllus*, and until recently no one seems to have questioned this disposition of it. Kausel, however (Ark. Bot. 3: 498–503. fig. 6. 1956), on the basis of embryo-characters, refers the genus to his Cryptorrhizoideae, in which the united cotyledons are said to surround the radicle.

Blume (Mus. Bot. Lugd. Bat. 1: 76. 1849), in a note suggesting the need for a revision of the genus *Myrtus*, and the special need for study of the ovary and the

seeds, rather informally proposed two names that have the form of generic names. For the "Genus v. Subgenus" including species with 2- or 3-locular ovary but only two ovules in each locule, "ut *M. excelsa* et *M. ovalifolia* St. Hil., utque probabile, *M?* *Arayan* Humb. et Bonpl." he suggested the name *Calomyrtus*. In the next sentence he continued "Etiam *M. umbilicata* St. Hil. ob alienam seminis structuram diversa est et a reliquis, nomine *Heteromyrtus*, sejugenda, quemadmodum et *M. tomentosa* Ait. et *M. spectabilis* Mihi satis a *Myrto* differunt". Because the rank of *Calomyrtus* is not definitely indicated, it may be regarded as a provisional name, therefore not validly published. The case of *Heteromyrtus* is evidently a little different; the author seems to be putting *M. umbilicata* in a position like that occupied by *M. tomentosa* and *M. spectabilis*, which further on in the same paper (pp. 77, 78) he refers to *Rhodomyrtus* and *Rhodamnia*, respectively. It seems clear from Blume's reference to the "alienam seminis structuram" that he is taking this directly from the protologue of *Myrtus umbilicata* (Camb. in St.-Hil. Fl. Bras. Mer. 2: 296. 1829), in which the author mentioned not only the 3-flowered peduncles and the naked fruit from which the calyx had fallen, but also emphasized the membranous rather than bony covering of the seeds, and the short cotyledons recurved at the apex, and stated his opinion that these characters of the seed and embryo were unusual in *Myrtus*.

The type of *Heteromyrtus*, *Myrtus umbilicata* Camb., is currently accepted as a species of *Blepharocalyx*. Legrand, who saw type-material, regards it as a variety of *B. suaveolens* (Camb.) Burret (cf. Not. Syst. 15: 272. 1958). Thus *Heteromyrtus* Blume (1849) is an earlier name for the genus that has been called *Blepharocalyx* Berg (1856), and unless it can be argued that *Heteromyrtus*, like *Calomyrtus*, was a provisional name for a group of unstated rank, it will be necessary to propose *Blepharocalyx* for conservation.

21. TEMU Berg, *Linnaea* 30: 710. 1861.

Lectotype-species, *T. divaricatum* (Berg) Berg. A Chilean group of two species, summarized by Kausel in *Rev. Argent. Agron.* 9: 64-66. 1942. As a genus this is of doubtful validity; it differs from *Blepharocalyx* in having the calyx-lobes persistent and little or not at all ciliate. The embryo is pimentoid, with testa described by Berg as lustrous and cartilaginous and by Kausel as "sub-leñoso-membranacea"; it is thus not as thin as in *Blepharocalyx*, but not bony as in *Pseudocaryophyllus*. Niedenzu (*Nat. Pflanzenfam.* 3, pt. 7: 71. 1893) treated *Temu* as a subgenus of *Blepharocalyx*, and made the appropriate new combinations based on *T. divaricatum* and *T. cruckshanksii*. As the name *Temu* Berg is untenable because of the existence of *Temus* Molina (cf. *Taxon* 5: 146. 1956), these two Chilean species may be treated for the present with *Blepharocalyx*; if future study makes advisable their separation from that group, a new generic name may be proposed for them.

Group 5. *Psidium* and related genera

22. Calycolpus . . . . .	402
23. Myrtus . . . . .	402
24. Amomyrtus . . . . .	403
25. Amomyrtella . . . . .	404
26. Psidium . . . . .	404
27. Myrteola . . . . .	405
28. Ugni . . . . .	405

This includes the genera with pimentoid embryo, peduncles mostly solitary or 3-flowered, bony seeds, and ovary mostly with 3 locules or fewer. Two possible evolutionary series within it are suggested, one including *Calycolpus* with racemously



arranged and primarily 1-flowered peduncles, and unspecialized calyx, and the other including *Psidium* with mostly solitary and axillary but often 3-flowered peduncles, and a tendency toward modification of the calyx and hypanthium; see text, page 372.

22. CALYCOLPUS Berg, *Linnaea* 27: 378. 1856.

Lectotype-species, *C. goetheanus* (DC.) Berg. All authors since Berg's time have recognized this genus, although some have had misgivings. Bentham (*Jour. Linn. Soc. Bot.* 10: 151. 1869) implied that it was "retained in order the better to draw the line between [*Psidium* and *Myrtus*]". Riley, who revised the genus (*Kew Bull.* 1926: 145–154. 1926), added nothing to existing knowledge of generic distinctness, merely repeating the characters noted by Berg: "It may be distinguished from these genera [*Campomanesia*, *Myrtus*, and *Psidium*] by its sepals, which are patent in the flower-bud, whereas in *Campomanesia* and *Myrtus* they are appressed to the corolla when in bud, and in *Psidium* they form a closed calyx which splits into segments as the flower expands".

Actually the species of *Calycolpus* form a rather homogeneous taxon that is out of place in *Psidium* because of the calyx-characters as described by Berg and Riley, and because of the manner of flowering, which is also unlike that of *Myrtus*. The flowers are produced in very short, axillary racemes, as in the eugenioid genera; there are usually one pair only, from opposite sides of an abortive spur-like axis, but sometimes as many as three or more pairs. The species are also out of place in *Myrtus* because of the large, showy and somewhat fleshy flowers, relatively large leaves, and the 4–5-locular ovary.

Riley recognized 12 species in the genus, but the actual number seems to be about half that. The mostly widely distributed species, *C. goetheanus* [*C. glaber* (Benth.) Berg], ranges from Trinidad and the Guianas to Maranhão and up the Amazon at least to the vicinity of Manaus. The genus as a whole occupies what seems to be a natural range, extending from Central America across the lowlands of northern South America to eastern Brazil.

23. MYRTUS L. Sp. Pl. 471. 1753. *Mosiera* Small, *Man. Southeast. Fl.* 936. 1933.

Lectotype-species, *M. communis* L. Because *Myrtus* represented the generalized type of the pimentoid Myrtaceae, with mostly 1-flowered peduncles, and regular 5-parted flowers with no unusual features either of morphology or in development, many species have at one time or another been assigned to it for want of a better place to put them. Bentham indeed despaired of dividing the Myrteae at all ["After deducting a few monotypic or very small genera presenting more positive abnormal though perhaps artificial characters, the whole of the twelve or thirteen hundred species now known might be almost equally well united into a single genus *Myrtus*, or distributed into the four old genera *Psidium*, *Calyptanthes*, *Myrtus*, and *Eugenia* . . ." (*Jour. Linn. Soc. Bot.* 10: 147. 1869)]. In the *Genera Plantarum* (Benth. & Hook. f. *Gen. Pl.* 1: 714–715. 1865), Bentham relegated to the synonymy of *Myrtus* not only such things as *Ugni* and *Myrteola* (which have 1-flowered peduncles), but also such unrelated groups with more complex inflorescences as *Luma*, *Myrceugenia*, *Blepharocalyx* and *Myrcianthes*.

Berg (*Linnaea* 27: 397–412. 1856) had attempted to limit the group to those species that were more or less similar in aspect, and in characters of inflorescence, flowers and fruit, to the original *Myrtus communis*. His description stresses the 1-flowered peduncles; the 2–4-locular ovary; the hypanthium not produced above the ovary, not splitting between the calyx-lobes at anthesis; the 4–5 free calyx-lobes appressed in the bud; the numerous and usually bony seeds, the pimentoid curved embryo. Of the 34 species known to Berg, about one-fourth were Chilean, and are now all referred to other genera. At least four of Berg's species seem to have been based on plants of

*Myrtus communis* cultivated in America (*M. sparsifolia*, *M. berlandiereana*, *M. oerstedeana*, *M. jacquiniana*). Most of the remainder were described from southeastern Brazil, or based on Sellow's collections from "Montevideo". Burret (Notizbl. Berlin 15: 483–485. 1941) transferred most of the Brazilian species to *Psidium*, and Legrand (Sellowia 13: 339–340. 1961) has accepted several of these in *Psidium*, although recognizing in the flora of Santa Catarina only three species instead of the 11 accepted by Berg.

Thus of the genus *Myrtus* as understood by Berg, almost nothing is left in America. Burret, whose longest published paper on the Myrtaceae (Notizbl. Berlin 15: 479–550. 1941) was an attempt to revise *Myrtus* on a worldwide basis and to establish reasonable generic limits within the complex, concluded that the genus comprises no more than 16 species, of which the type and one other species are Afro-European in origin, and the rest West Indian. Of the West Indian species 12 are natives of the Greater Antilles (9 are Cuban); two occur in Florida, and 1 in the Lesser Antilles. Burret does not discuss the generic limits of *Myrtus* and *Psidium*, or the reasons underlying his transfers from one to another, but apparently he was influenced in the case of the West Indian species by the supposed differences in placentation between the two genera, and habitual similarities to *Myrtus communis*, most of the West Indian species having small 4- or 5-merous flowers and small glabrous or nearly glabrous leaves. As Burret himself noted, neither the generic limits nor the number of species involved can be determined with assurance, because several of the species are based on sterile material.

After examination of a rather limited amount of material of the West Indian species, I am inclined to think they are less closely related to *Myrtus* (that is, to the generitype, *M. communis*) than they are to such American genera as *Calycolpus* and *Amomyrtus*. The flowers are mostly in short racemes or the inflorescence may be partly or wholly of the *Stenocalyx* type, whereas in *Myrtus communis* the peduncles are axillary; the calyx in most species is strictly 4-merous, whereas in *M. communis* it is more often 5-merous; the ovary in the American species is usually bilocular, and the flowers are sometimes in 3's. In some species (e.g. *M. verrucosa* Berg [*Eugenia longipes* Berg]) the calyx shows a tendency to split between the lobes as in *Psidium*.

The one known Mexican species, *Myrtus ehrenbergii* Berg, was transferred by Burret to *Psidium*, but apparently wrongly so, as the calyx is quite unlike that of *Psidium*, and the inflorescence is mostly of the *Stenocalyx* type, as in the West Indian species.

Until the West Indian and Mexican species can be more thoroughly studied their generic position must remain in doubt, but I suppose their relationship to *Myrtus communis* is very slight. Perhaps they represent insular derivatives of something like the ancestors of modern small-flowered *Psidium*s like *P. sartorianum*. Specialization in *Psidium* has resulted in reductions in locule-number and the development of a raceme-like inflorescence in at least one known group of species (cf. Fieldiana Bot. 29: 520. 1963). and in *P. sartorianum* the flowering may be of the *Stenocalyx* type, and the ovary bilocular.

24. AMOMYRTUS (Burret) Legr. & Kausel, Lilloa 13: 145. 1948 ["1947"]. *Pseudocaryophyllus* Sect. *Amomyrtus* Burret, Notizbl. Berlin 15: 514. 1941.

Lectotype-species, *Eugenia darwinii* Hook. f. [= *Amomyrtus luma*, sensu Legrand & Kausel]. This is a group of two Chilean species with racemose inflorescence, 5-merous flowers and pimentoid embryo, referred by Kausel in his first revision of the Chilean Myrtaceae to *Myrtus* (Rev. Argent. Agron. 9: 223–226. 1942). There seems to be no question of the geographical isolation of the group, or of its morphological distinctness. Whether or not it should be recognized as an independent genus is a

question that must be answered subjectively until more is known about the relationships of all the temperate South American Myrtaceae.

25. AMOMYRTELLA Kausel, Ark. Bot. 3: 514. 1956.

Type species, *A. guili* (Speg.) Kausel. This is an extraordinary monotypic group, known only from northern Argentina. Described originally as a species of *Eugenia* because of the 4-merous flowers and the racemose or praecocious development of the inflorescence, it was transferred by Burret to *Pseudocaryophyllus* because of the bony pimentoid seeds, and transferred a little later by Legrand to *Myrtus*. The thin ovate veiny leaves resemble those of *Campomanesia*, even to the barbate axils of the lower surface; the seeds are more like those of *Psidium*; the ovary is 2- or 3-locular, with 2 pendulous ovules arising in the upper part of each cell; the calyx is 4-merous; the hypanthium is produced well beyond the ovary. In the number and proportions of the flower-parts the plant is unique among American Myrtaceae. The stamens are reduced to 20–24 in number; the anthers are disproportionately large, oblong, 1–1.3 mm. long, and as long as or longer than the filaments; the stout columnar style 3.5–4 mm. long is tipped by a peltate stigma 1–1.5 mm. wide. In comparison with the flowers of almost all other American species of the family, these have the anthers of a flower three times as large, on filaments perhaps one-tenth as long as might be expected for the anthers; the style is as thick as the anthers might indicate, but perhaps one-third as long; the stigma is far out of proportion to the thickness of the style, even in the pimentoid genera where capitate stigmas are not uncommon. In a family with so little differentiation observable in the androecium and the style, these flowers are remarkably distinctive. Taken in combination with the other features noted above, they argue convincingly for the generic independence of *Amomyrtella*. Its vegetative and other characters are illustrated by Legrand (*Lilloa* 10: 480. 1944) and by Kausel (in the protologue of the genus).

26. PSIDIUM L. Sp. Pl. 470. 1753. *Guaia* Adans. Fam. Pl. 2: 88, 563. 1763. *Calyptropsidium* Berg, Linnaea 27: 349. 1856. *Psidiopsis* Berg, Linnaea 27: 350. 1856. *Mitropsidium* Burret, Notizbl. Berlin. 15: 486. 1941.

Type species, *P. guajava* L. An American genus of perhaps 100 species, the largest pimentoid group among the American Myrtaceae. The delimitation of the genus, and the difficulties involved in separating *Psidium* from *Myrtus*, were reviewed in *Fieldiana Bot.* 29: 512–518. 1963. In general, species of *Psidium* may be recognized by the pimentoid C-shaped or uncinately embryo; hard or bony seeds; calyx (whether originally open or closed) splitting between the lobes at anthesis; ovary usually 3–4 (rarely 2–7-)locular; placenta usually bilamellate but in bilocular ovaries the ovules often in a single cluster; peduncles usually axillary, the flowering occasionally racemose or of the *Stenocalyx* type.

The feature of the calyprate calyx, relied upon by Berg to distinguish his genus *Calyptropsidium*, and by Burret to distinguish *Mitropsidium*, is apparently less constant than these authors supposed. See the discussion in *Fieldiana Bot.* 29: 525–527. 1963, where it is pointed out that even in the same species, both calyprate and non-calyprate forms may be found. There seems to be no sharp distinction in *Psidium* between groups of species with closed buds and those with open buds.

The genus *Psidiopsis*, comprising a single species, was based on the character of the prolonged tips of the calyx-lobes. As the flowers of the type-species are otherwise like those of *Psidium*, and as no one, as far as I am aware, has pointed out any other distinguishing features, this plant is best regarded as a vegetatively anomalous species of *Psidium*. Burret (*Repert. Sp. Nov.* 50: 57. 1941) transferred it to *Calycolpus*, but without any published justification.

Several species of *Psidium* have become widely dispersed through cultivation. The guava, *P. guajava* L., is one of the best known cultivated plants in all warm regions, and has long been naturalized far beyond its original range, which was presumably in tropical America. The strawberry guava, *P. cattleianum* Sabine, may have been native in southeastern Brazil. The most widespread and taxonomically complex group of the genus is that typified by *P. guineense* Sw.; plants of this complex yield a fruit that is sometimes of good quality but smaller and less desirable than that of the guava. With the above exceptions, the species of *Psidium* occur for the most part as native plants, including a few species each in the West Indies and in continental North America, about 15 additional species in northern South America, a few more in the Andes and a few in southern Brazil; numerous species described by Berg from central and southeastern Brazil have not been adequately studied since his time.

27. MYRTEOLA Berg, *Linnaea* 27: 348. (in clave). Jan. 1856; 393. Feb. 1856, nom. cons. *Amyrsia* Raf. *Sylva Tell.* 106. 1838, nom. rejic. *Cluacena* Raf. *Sylva Tell.* 104. 1838, nom. rejic.

Lectotype-species, *M. microphylla* Berg (*Myrtus microphylla* Humb. & Bonpl. 1808, not *M. microphylla* J. St.-Hil. in Duham. 1800–1801). A small genus, probably of 5 or 6 species, ranging from Venezuela to southern Chile. The species are unique among American Myrtaceae in the combination of shrubby habit; small coriaceous vaccinioid leaves 1 cm. long or less; solitary 4- (rarely 5-)merous flowers subtended by persistent foliaceous bracteoles; few (8–20) or numerous (30–65) stamens with filiform filaments and elliptic-oblong anthers; 3- (rarely 2-)locular ovary; and reniform or hippocrepiform seeds with bony testa and arcuate embryo. For discussion and synopsis of the species see McVaugh in *Field Mus. Publ. Bot.* 13, pt. 4 [Fl. Peru]: 803–809. 1958, and Kausel in *Rev. Argent. Agron.* 9: 230–235. 1942.

Berg seems to have based the genus chiefly upon the 4-merous flowers and the condition of oligandry, neither of which is constant in the group. The species of *Myrteola* are at once distinguishable from those of *Ugni* (which they sometimes superficially resemble) by the stamens, and by the usually 4-merous flowers. The distinction between *Myrtus* and *Myrteola* is not easily made on morphological grounds. Berg pointed out, and Bentham commented upon, the fact that in *Myrteola* the dissepiment of the ovary is incomplete, not reaching the top of the cavity, and this character was used by Niedenzu in the *Natürlichen Pflanzenfamilien* to separate *Myrteola* from *Myrtus*. From an evolutionary standpoint it seems evident that *Myrteola* has arisen independently of *Myrtus*; it is a montane and cool-temperate group that occupies an Andean range like that of various other genera in different families, and there would seem to be nothing gained, nomenclaturally or biologically, by combining it again with *Myrtus*.

28. UGNI Turcz. *Bull. Soc. Nat. Moscou* 21(1): 579. 1848; *Flora* 31: 711. 1848.

Type species, *U. molinae* Turcz. A very natural and homogeneous group of 4 or 5 species, characterized by the small coriaceous leaves, solitary and usually 5-merous flowers subtended by persistent leafy bracteoles, 3–4-locular ovary, seeds reniform or hippocrepiform, with bony testa and arcuate embryo, and anthers sagittate, introrse, basifixed and sometimes winged by the margins of the dilated connective. The genus seems to have two centers of abundance, the one in the mountains from southern Mexico to Peru and the Guayana Highlands, the other in Juan Fernández and Chile from about latitude 33° S. to 45° S. Bentham and Hooker “hesitated much whether we should not admit it as a substantive genus” but finally united it with *Myrtus*. Niedenzu (*Nat. Pflanzenfam.* 3, pt. 7: 65. 1893) recognized its validity, and in this most recent authors have concurred; cf. Kausel, in *Rev. Argent. Agron.* 9: 227–230. 1942; McVaugh, in *Field Mus. Publ. Bot.* 13, pt. 4 [Fl. Peru]: 802. 1958, and in *Fieldiana Bot.* 24, pt. 7 [Fl. Guatemala]: 403. 1963.

Group 6. *Pseudocaryophyllus* and *Pimenta*

29. <i>Pseudocaryophyllus</i> . . . . .	406
30. <i>Pimenta</i> . . . . .	406

The two genera treated here are alike in having the flowers in a myrcioid panicle, although in *Pseudocaryophyllus* the peduncles often bear a dichasium; they are also alike in the possession of a bilocular ovary. Presumably the genera are not very closely related; they are associated only because they are the only pimentoid genera in which the inflorescence resembles that of the myrcioid ones.

29. PSEUDOCARYOPHYLLUS Berg, *Linnaea* 27: 348 (in clave). Jan. 1856; 425. Feb. 1856.

Lectotype-species, *P. sericeus* Berg. As I pointed out in *Taxon* 5: 145. 1956, in proposing *P. sericeus* as the lectotype, Berg probably did not have a valid concept of his new genus, but *P. sericeus* was originally described (as *Myrtus pseudocaryophyllus* Gomes, *Mem. Acad. Sci. Lisboa* 3(1) [suppl.]: 92. pl. 6. 1812) as having 4 persistent calyx-lobes, a dichotomous inflorescence and several very hard seeds; both the description and the illustration suggested pimentoid affinities. Neither Bentham nor Niedenzu accepted *Pseudocaryophyllus*, but Burret (*Notizbl. Berlin* 15: 514–521. 1941) enlarged it, creating a new section (*Amomyrtus*) for 3 Chilean species with 5-merous flowers and racemose inflorescence, and assigning 13 species, including 7 described as new, to his section *Eupseudocaryophyllus*. The latter was described as having the flowers 4- (or 5-)merous, usually in dichasia but rarely solitary; the seeds were not described. The section *Amomyrtus* has since been elevated to generic status, and the section *Eupseudocaryophyllus* seems to have been a mixture; seeds are not described for any of the new species, but at least three of the species assigned to the section (*P. guili*, *P. uniflorus*, and *P. organensis*) are described as having solitary flowers. The others, as far as can be ascertained from Burret's descriptions, have branched inflorescences, 4-merous flowers, bilocular ovary, and usually a small number (2–5) of ovules in each locule. From the description they might all be species of *Blepharocalyx*; all are natives of the part of southeastern Brazil in which *Blepharocalyx* also occurs. I have not seen any of the specimens cited by Burret, and have not been able to form any opinions as to the disposition of his new species except *P. guili*, which is quite out of place in *Pseudocaryophyllus*; see *Amomyrtella*.

The one undoubted species of *Pseudocaryophyllus*, *P. sericeus* Berg [*P. acuminatus* (Link) Burret] is a species of the Brazilian plateau in Minas Geraes, S. Paulo, Paraná and Santa Catarina. Legrand (*Sellowia* 13: 342–343. 1961) also describes from Santa Catarina a second species, *P. crenatus*, which he supposes is related to *P. emarginatus* Burret and *P. hoehnei* Burret, both of São Paulo. I have treated *Pseudocaryophyllus* as distinct because it appears to be a small homogeneous Brazilian group, the species of which have in common the inflorescence and flowers nearly of *Blepharocalyx*, and the bony seeds of *Psidium*. Probably further investigation will show other differences between this group and *Blepharocalyx*; in *P. acuminatus*, for example, the inflorescence when well-developed is not strictly dichotomous, but resembles a short myrcioid panicle.

30. PIMENTA Lindl. *Coll. Bot. pl.* 19. 1821. *Evanesca* Raf. *Sylva Tell.* 105. 1838. *Pimentus* Raf. *Sylva Tell.* 105. 1838. *Amomis* Berg, *Handb. Pharm. Bot.* ed. 3. 1: 339. 1855. *Krokia* Urb. *Symb. Antill.* 9: 468. 1928. *Myrtekmannia* Urb. *Symb. Antill.* 9: 484. 1928.

Type-species, *P. dioica* (L.) Merr. A small group, perhaps of no more than 2 very distinct species, both probably originally West Indian but now widely naturalized

and cultivated in warm regions. The two are alike in having the inflorescence many-flowered, branched as in *Myrcia*, the ovary bilocular, the ovules few in each locule, and the embryo pimentoid with thin testa. Berg proposed to divide these between the genera *Pimenta* and *Amomis*, on the ground that the flower of *Amomis* was 5-parted and the embryo merely curved (“monocyclicus”), whereas the flower of *Pimenta* was 4-parted and the embryo spiral [“spiralis, 2–3-cyclicus”]. Bentham (in Benth. & Hook. f. Gen. Pl. 1: 717. 1865) combined the two genera, stating that the embryo character was not a conclusive one [“Nos tamen certe in *A. acri*, Berg... embryonem interdum 2-cyclium invenimus, etsi saepius minus involutus sit quam in *P. communi*, Lindl.”]. Urban, in his revision of West Indian Myrtaceae, accepted both genera (with one species each) (Bot. Jahrb. 19: 571–576. 1895). In the *Genera Plantarum*, as a primary diagnostic feature of *Pimenta*, the position of the ovules was stressed: “ovulis in loculis 1–6 ab apice pendulis”. In his long paper on Myrtaceae (Jour. Linn. Soc. Bot. 10: 158. 1869) Bentham explained this more fully: “the ovules, a few in number (1 to 4 or perhaps, 6 in each cell) are attached to a placenta suspended from the apex of the cavity, whilst in all the great Myrtoid genera the placenta is adnate to the center of the dissepiment or to the inner angle of the cells”. Actually Bentham was in error here; as correctly described by Urban, the single ovule in *Pimenta dioica* and the 4–7 ovules in *Pimenta (Amomis) racemosa* are borne on placentae arising from the upper part of the dissepiment. There seems to be no fundamental difference between the placentation of *Pimenta* and that of other genera.

Burret (Notizbl. Berlin 15: 509–514. 1941) confirmed Bentham’s observation that the two genera cannot be distinguished by the amount of curvature in the embryo; further he regarded the differences in ovule-number and sepal-number as of little importance as generic characters. He therefore accepted the genus *Pimenta* in the broad sense, as comprising 13 species divided among two sections and four subsections, and including the genera *Krokia* and *Myrtekmannia*. Both *Krokia* and *Myrtekmannia* were originally based on forms with 4-merous flowers and the ovary described as prevalingly unilocular. Burret found that the unilocular ovary was not a constant character of *Krokia*, and he supposed that the allegedly distinctive features of *Myrtekmannia* arose from an abnormality of growth.

Except for *Pimenta racemosa* and *P. officinalis* [*P. dioica*], all the species accepted by Burret are natives of Cuba or Hispaniola, all except one originally described or recognized by Urban. The number of valid species is unknown to me, but a considerable amount of variation does exist among these insular populations, and it seems impracticable to draw convincing generic lines among them on the basis of ovule number, embryo structure or calyx morphology.

Alain, however, in the *Flora de Cuba* (Fl. Cub. 3: 430–434. 1953) takes to the other extreme, recognizing as valid genera not only *Krokia* and *Myrtekmannia* with three species in each, but also both *Pimenta* (2 species) and *Amomis* (3 species).

*Genera incertae sedis*

- 31. Myrrhinium . . . . . 408
- 32. Acca . . . . . 408

The two following genera are treated here at the end of the “pimentoid” groups, because although they are both included among the genera in the circle in Fig. 1, p. 371, their affinities seem to be more with the pimentoid Myrteae than with any others. The inflorescence in *Myrrhinium* is more specialized than that of any genus in the pimentoid group, and the androecium in both *Acca* and *Myrrhinium* is highly specialized in comparison to that of almost any other American member of the Myr-

taceae. The stamens are highly colored, reduced in number but flattened and increased in length, and either twice folded (*Myrrhinium*) or erect (*Acca*) in the bud. In *Myrrhinium* the petals are red, each with a short broad claw that sometimes bears 1–3 erect filiform appendages near its base. The so-called species of *Myrrhinium*, which are almost indistinguishable, range from central Ecuador and Peru, and from northern Argentina to southern Brazil; two species of *Acca* are Peruvian and the other(s) south-Brazilian.

31. MYRRHINIUM Schott in Spreng. Syst. Veg. 4(2): 404. 1827. *Felicianea* Camb. in A. St.-Hil. Fl. Bras. Mer. 2: 375 (folio ed. 270). pl. 157. 1829. *Tetrastemon* Hook. & Arn. in Hook. Bot. Misc. 3: 317. 1833.

Type-species, *M. atropurpureum* Schott. A distinctive genus, of one or perhaps two or three species (cf. Field Mus. Publ. Bot. 13, pt. 4 [Fl. Peru]: 814–816. 1958), made by Berg (Linnaea 27: 4. 1855) the type of a subtribe coordinate with what he called Myrcioideae, Eugenioideae, etc., on the basis of characters of the androecium: The stamens are reduced in number to 4–8, and are twice folded in the bud. On the basis of the other characters of the flower, seed, and embryo, the genus seems to belong in the Pimentinae [“Myrtinae”] to which it was assigned by Niedenzu in the *Natürlichen Pflanzenfamilien*. The plants are readily recognized, either in flower or fruit, by the thrice dichotomous cymes, which are lateral on old wood, 2–3 cm. long, with persistent paired bracts and a central sessile flower in each fork.

32. ACCA Berg, Linnaea 27: 138. 1856. ?*Orthostemon* Berg, Linnaea 27: 440. 1856, not R. Br. 1810. ?*Feijoa* Berg, Linnaea 29: 258. 1858.

Lectotype-species, *A. macrostema* (G. Don) McVaugh (*A. domingensis* Berg). Originally the genus comprised 2 species, both Peruvian, placed by Berg among the Eugeniinae (in the absence of fruit) because of the bilocular ovary and the 4-parted flowers. When mature fruits were eventually collected, it transpired that the embryo in both species was of the pimentoid type. The inflorescence in one species (*A. lanuginosa*) is of the pimentoid (dichasial) type, whereas that of *A. macrostema* is of the eugenoid (racemose) type. The distinctive feature that the two species have in common is the androecium, which consists of a small number (25–50) of stout, flattened, colored (red) stamens 15–22 mm. long, thus considerably longer than the petals.

The genus *Orthostemon* (the name soon changed by Berg to *Feijoa*), with two Brazilian species, was thought by Berg to differ from the rest of the Myrteae by having endosperm in the seed; because of this he erected a group Orthostemonoideae, coordinate with Myrcioideae [i.e. Myrciinae], Eugenioideae, and the others, to include this one genus only. Berg's description [“Semina angulata, albuminosa. Embryo rectus, centralis; cotylae foliaceae, ovatae, planae; radicula elongata”] was regarded by Burret (Repert. Sp. Nov. 50: 57. 1941) as probably having resulted from an error. Burret himself studied ripe seeds of the type-species of *Feijoa*, *F. sellowiana*, and provided the following description: “Semen applanatum, ambitu subreniforme, exalbuminosum. Testa membranacea. Embryo spiraliter involutus, radicula longa, curvata. Cotyledones breviores, angustae, involutae”. On the basis of this description the seeds are typically pimentoid. Kausel took a different point of view (Ark. Bot. 3: 498–499. fig. 4. 1956). He associated *Feijoa* with the myrcioid rather than the pimentoid genera because, although the seed and embryo are pimentoid in size, shape and general morphology, the cotyledons are larger than in most pimentoid genera, and are involute and turned spirally back across the radicle. My own feeling is that any resemblance or evolutionary connection to the Myrciinae is remote; it seems that the sum total of other seed- and embryo-characters provides a more plausible basis

for judging relationships than the one cotyledon-character. In point of fact the small, neatly coiled cotyledons of *Feijoa* bear little resemblance to the broad, crumpled cotyledons of *Myrcia*, except that both are flattened and crowded into the seed.

Berg seems to have been in error in assuming the presence of any considerable quantity of endosperm in the seed of *Feijoa*, although the work of Petit (1908)<sup>1</sup> indicates that there are traces of endosperm in many myrtaceous seeds. Burret, at any rate, finding no endosperm in the seeds he examined, decided that the affinities of *Feijoa* were with the Pimentinae. Largely because of the strong superficial resemblances between the flowers and leaves of *Feijoa sellowiana* and those of *Acca peruviana* [*A. lanuginosa*], and also because of the generally obvious pimentoid structure of the seeds of the two species, Burret advocated the union of the two genera under *Acca*, the older name.

It is difficult to pass judgment upon the correctness of Burret's decision. Certainly *Acca* and *Feijoa* have much in common; they are alike vegetatively, and in the structure of the inflorescence; the seeds of both are pimentoid; their fruits are similar; both have the flowers 4-merous; both have a conspicuous androecium consisting of a relatively few long coarse red stamens. The ovary is 2-locular in *Acca* proper, and is described as 4-locular in *Feijoa*, but comparable differences in locule-number are known in other genera, e.g. *Psidium*.

Several other genera of Myrtaceae (e.g. *Blepharocalyx*, *Myrcianthes*, *Myrrhinium*) have disjunct geographical ranges like that of the inclusive *Acca*, i.e. with some species in the Andean region and others in southeastern Brazil, Uruguay or Argentina.

Whatever may be the taxonomists' decision as to the union of *Acca* and *Feijoa*, the latter name is firmly entrenched. Because of its showy flowers and the edible fruit which has been improved by cultivation, *Feijoa sellowiana* is now widely grown in all warm regions, especially as an ornamental.

#### TRIBE LEPTOSPERMEAE

33. TEPUALIA Griseb. Syst. Bemerk. 31 [Abh. Ges. Wiss. Goettingen 6: 119]. 1854.

Lectotype-species, *T. stipularis* (Hook. f.) Griseb. This, the only known American representative of the capsular-fruited Myrtaceae, comprises a single species, ranging from central Chile south to about latitude 53° (cf. Kausel, Rev. Argent. Agron. 9: 235–236. 1942). According to Kausel (Rev. Argent. Agron. 11: 326. 1944) it is a tree 10–12 m. high. It was considered by Bentham (Gen. Pl. 1: 694. 1865) to be closely related to the Australasian genus *Metrosideros*, differing in the reduced number of ovules and the solitary flowers.

#### IMPERFECTLY KNOWN GENERA

CALYPTROGENIA Burret, Notizbl. Berlin 15: 545. 1941.

Type species, *C. ekmanii* (Urb.) Burret (*Calyptranthes ekmanii* Urb.) The generic characters, as given in the protologue, are as follows: Calyx closed in bud, opening by an operculum; hypanthium not produced above the ovary; ovary bilocular; ovules numerous (probably about 12), arising from the central dissepiment as in *Eugenia*. Burret transferred to *Calyptrogenia* four Haitian species previously described by Urban in *Calyptranthes*, *Calyptropsidium* or *Eugenia*, and one Brazilian species, *Mitranthes riedeliana* Berg. He thought the genus was related to *Eugenia* and *Caly-*

<sup>1</sup> Not seen. A thesis, published in Paris, mentioned by Kausel, and quoted in Netolitzky, F., *Anatomie der Angiospermen-Samen*, pp. 240–241. 1926, under the title of "Struct. anat. fruit et graine Myrt."



*corectes*; he did not see specimens with good fruit, but stated that the embryo "seems to be undivided". Final judgment on the position of these species with closed calyx and multi-ovulate ovary should be put off until fruiting material can be compared with fruiting material of *Mitranthes ottonis* (cf. p. 391), and of species of *Hottea*, which is also a Haitian genus.

CORYNEMYRTUS (Kiaersk.) Mattos, *Loefgrenia* 10: 1. 1963. *Myrtus*, subgenus *Corynemyrtus* Kiaersk. Enum. Myrt. Bras. 18. 1893.

Type-species, *C. corynantha* (Kiaersk.) Mattos (*Myrtus?* *corynantha* Kiaersk.). This is a monotypic group, based originally on a plant having short 2–6-flowered racemes, pentamerous flowers, 3 (–2)-locular ovary, and numerous ovules. The buds were described as clavate, and the hypanthium as patelliform, "integro vel rarius irregulariter fisso". From Kiaerskou's description, and from a photograph of a lectotype (Field Mus. neg. 21053, based on *Glaziou 12721*), I suppose the plant represents one of the pimentoid groups near *Myrtus* and *Psidium*. Mattos does not advance any new evidence that it represents an independent genus, and I see no way to distinguish it convincingly. For the time being it may be treated as a synonym of *Myrtus*.

CRYPTORHIZA Urb. Repert. Sp. Nov. 17: 403. 1921.

Type species, *C. haitiensis* Urb. The generic characters, as given in the protologue, are as follows: Hypanthium not produced above the ovary; calyx 5-merous; ovary bilocular; ovules 6–7 in each locule, the placentae arising from the upper part of the central dissepiment; embryo massive, the cotyledons connate, fleshy, occupying most of the seed, the radicle about as long as the cotyledons and compressed between them. The type of the species was a fruiting specimen (now presumably destroyed) sent to Urban by Buch, supposedly from near Mirbalais, Haiti. From the description of this specimen (leaves short-petiolate and more or less obovate, 3–6 cm. long; inflorescence apparently few-flowered, with flattened axes), I should suppose that the plant was one of the Haitian forms of *Myrcianthes fragrans* (Sw.) McVaugh, in which the calyx is sometimes 5-merous. In a later paper [*Ark. Bot.* 22A (no. 10): 24. 1929], Urban reported that the plant was merely brought to Haitian markets as a condiment, from a source in Prov. Barahona, Dominican Republic. He cited additional collections, stating that the peduncles were axillary or sometimes subtended by small bracts, and usually 3-flowered. Kausel [*Ark. Bot.* II. 3: 500, 502. 1956], made much of the embryo character, even going so far as to propose a taxon of subtribal or subfamilial rank, *Cryptorhizoideae*, to include this genus and three others. Although I have not seen any of the specimens cited by Urban, I am dubious of the validity of the genus *Cryptorhiza*.

GUAPURIUM Juss. Gen. 324. 1789.

Type species, *G. peruvianum* Poir. [*Eugenia guapurium* DC.; *Myrciaria?* *guapurium* (DC.) Berg]. The identity of *Guapurium peruvianum* is unknown, as the type-specimens are sterile, and apparently the species has not been collected again; see *Field Mus. Publ. Bot.* 13, pt. 4: 782–783. 1958. If the plant is a *Myrciaria*, as Berg supposed, and as seems not unlikely, the name *Guapurium* must be taken up for the group now called *Myrciaria*, unless the latter is conserved.

HOTTEA Urb. *Ark. Bot.* 22A (no. 10): 40. 1929.

Type species, *H. miragoanae* Urb. As originally understood by Urban, this genus included three species, all from the Massif de la Hotte, Haiti. The generic characters included the following: Hypanthium not produced above the ovary; calyx closed in

bud, splitting irregularly into two lobes at anthesis; ovary bilocular; ovules about 6 in each locule, biseriate, from the upper part of the dissepiment; cotyledons connate on the margins, otherwise free; radicle very short, mammiform; flowers axillary or several and "umbelliform", pedicellate. Urban compared his new genus to *Calycorectes*, but understood the latter to differ in having the hypanthium produced beyond the ovary, the calyx 4–5-fid after opening, and the ovules more numerous. I have not seen any material of the species included by Urban, and so cannot judge whether or not *Hottea* represents a distinct genus. Six species, all from the mountains of southern Haiti, all described originally by Urban, are listed by Moscoso (Cat. Fl. Doming. 431. 1943). See also *Calyptrogenia*, which is perhaps a synonym of *Hottea*.

MARLIERIOPSIS Kiaersk. Bot. Tidsskr. 17: 281. fig. 11 & pl. 11, fig. A. Preprint, Apr. 1890.

Type species, *M. eggersii* Kiaersk. The type, and only species, was from Dominica, W. I. The plant was described as having the hypanthium produced above the ovary, the calyx closed and splitting at anthesis into 4 lobes, the ovary bilocular with 4–6 ovules in each locule, the seeds discoid-reniform with membranous testa, and curved, almost annular embryo with no trace of cotyledons. Niedenzu, in the *Natürlichen Pflanzenfamilien*, transferred *M. eggersii* to *Mitranthes*, and this was accepted by Urban (Bot. Jahrb. 19: 576. 1895). It is possible that this is the correct disposition of it, but as I pointed out above (page 391), the type of *Mitranthes*, *M. ottonis*, suggests in most respects except the 3-locular ovary some species of *Calyptanthes*. *Marlieriopsis eggersii*, however, presumably is pimentoid in its affinities. The inflorescence, however, is unlike that of any pimentoid genus (or indeed any other genus) that I know. It is a compound panicle, but differs from the ordinary myrcioid panicle in that all the branches, even the long lower ones, are determinate at the first node, i.e. each branch is a 3-flowered (rarely 7-flowered) dichasium. The plant is a most unusual one, and unless the seeds of *Mitranthes* turn out to be very similar to those of *Marlieriopsis*, I am inclined to regard the latter as a distinct genus.

MITRANTHES Berg, Linnaea 27: 136 (in clave), 316. 1856.

Type-species, *M. ottonis* Berg. The typification of this genus is discussed above under the treatment of *Siphoneugena* (p. 391). It is now thought that *Mitranthes* comprises two species, one Cuban and the other Jamaican. Both vegetatively, and in the architecture of the inflorescence and the calyx, these two species have precisely the characters of large-flowered members of the genus *Calyptanthes*. The unique features of *Mitranthes* are the multilocular, multiovulate ovary, combined with an embryo of the myrcioid type and the calyx and inflorescence of *Calyptanthes*. Evidently *Mitranthes* is related neither to the eugenioid genera (as Berg supposed), nor to the pimentoid genera (as Burret supposed), but is instead a relatively unspecialized member of the myrcioid alliance; see the comments above on such isolated small genera in southern South America and in the Antilles.

Now that the embryo of *Mitranthes* is known, it may be possible to determine the generic standing of *Calyptrogenia*, *Hottea*, and *Marlieriopsis* by comparison of their seeds with those of *Mitranthes*. Until then these taxa cannot be satisfactorily placed.

PILOTHECIUM (Kiaersk.) Kausel, Ark. Bot. II. 4: 401. 1962. *Myrtus* subgenus *Pilothecium* Kiaersk. Enum. Myrt. Bras. 21. 1893.

Lectotype species (designated by Kausel), *P. beaurepairianum* (Kiaersk.) Kausel (*Myrtus beaurepairiana* Kiaersk.). Kiaerskou included two species in his subgenus *Pilothecium*; Kausel added three others. All five are natives of southeastern Brazil. They have in common the following: Ovary bilocular, its locules tomentose on the

inner surfaces; flowers tetramerous; inflorescence tending to branch dichasially, and when well developed forming a modified myrcioid panicle very like that described in the present paper for *Marlieriopsis*. Kausel believes *Pilotheceium* to be a genus related to *Pseudanmomis*, and therefore referable in his system to the Plinioideae, but not related to any pimentoid group. He did not cite, and apparently did not study, fruiting material of the lectotype-species, and therefore could not be positive of its systematic position. On the basis of its general structural similarity to another species (*Eugenia ternatifolia* Camb.), however, he assumed that the two were congeneric. The embryo of *E. ternatifolia* was studied, and proved to be of the *Myrcianthes-Pseudanmomis* type, with two large fleshy cotyledons. Presumably Kausel is correct that all five species are out of place in *Myrtus*, but whether or not *Pilotheceium* should be recognized as an independent genus seems doubtful, as its chief diagnostic feature is still the hairiness of the inner surfaces of the ovary. As fruiting material of the type-species is still apparently unknown, any taxonomic disposition of the genus is still provisional.

#### EXCLUDED GENUS

AULACOCARPUS Berg, *Linnaea* 27: 137 (in clave), 345. Jan. 1856.

Lectotype-species, *A. crassifolius* (Benth.) Berg. The type of the genus, originally described as *Campomanesia crassifolia*, probably belongs to the genus *Mouriri* (Melastomataceae); cf. Burret, *Notizbl. Berlin* 11: 150–151. 1931; Morley, *Univ. Calif. Publ. Bot.* 26: 224–225. 1953; *Taxon* 5: 137. 1956. Pittier (Smithson. Misc. Coll. 63, no. 4: 1–4. 1914), suggested that *Aulacocarpus* “must be placed among the Leptospermoideae”, and described a new species from Panama, *A. completens*, which was later transferred by Burret to *Mouriri*.

#### IV. KEY TO ACCEPTED GENERA OF TRIBE MYRTEAE

Because some of the generic distinctions in the Myrtaceae depend upon characters of the embryo and others upon those of the flower and bud, it is practically impossible to construct a usable key for the identification of single specimens of unknown generic position, unless one is willing to go to the length of making a key to all the individual species, which becomes unmanageably long and complicated. When somewhat fewer genera and species are involved, a usable key can be constructed by providing contrasts for some anomalous species only, as was done by Legrand in his *Mirtáceas del Estado de Santa Catarina (Brasil)*; there 20 genera are contrasted, including all those native in eastern South America south of the Amazon except *Paivaea* (*Sellowia* 13: 268–277. 1961). It is also sometimes feasible to provide alternative keys for flowering and fruiting material, as was done for the 14 genera in the *Flora of Peru* (*Field Mus. Publ. Bot.* 13, pt. 4: 572–580. 1958).

Because the inflorescence provides taxonomic characters of a kind, and because the morphology of the inflorescence is usually ascertainable after a little study in any except the most nearly worthless specimens, the primary divisions of the key have been made on this basis. With a knowledge of the structure of the inflorescence and that of the embryo, one can place an unknown, in the majority of cases, at least in the correct group of genera even if flowering material is unavailable. A key based primarily on flowering material becomes chiefly a key to species, because of the greater intra-generic variation in flower-characters. In *Psidium*, for example, the calyx may be 4-lobed, 5-lobed or closed and calyptrate.

The following key is not strictly dichotomous. In a few places there are three choices to be considered. Among the plants with myrcioid inflorescence, for example,

it is necessary to know whether the embryo is myrcioid, or bean-like, or pimentoid. In all such places in the key, attention is called to the existence of an additional alternative.

The following specialized terms are used in the key:

1) Of inflorescences: *Myrcioid*, a compound "panicle", often many-flowered, the central axis usually with several nodes bearing compound and opposite branches, the flowers solitary or irregularly ternate near the tips of these compound branches. *Racemose*, an unbranched axillary axis, usually consisting of several nodes separated by very short internodes, bearing opposite decussate pairs of 1-flowered peduncles subtended by small non-leafy bracts. *Stenocalyx-type*, that in which some or all the 1-flowered peduncles are borne in the axils of small bracts at the lowermost nodes of new leafy branches.

2) Of the embryo: *Myrcioid*, the cotyledons foliaceous, crumpled and folded about the elongate radicle. *Eugenioid*, massive, undivided and apparently homogeneous, without evident division into cotyledons. *Beanlike*, with two large, separate, fleshy, plano-convex cotyledons and a short radicle. *Pimentoid*, the cotyledons small and inconspicuous at one end of an elongate, uncinatate, curved or coiled embryo.

The most recent key to all the genera of American Myrtaceae is that of Niedenzu (Nat. Pflanzenfam. 3, pt. 7: 62 ff. 1893). This author recognized in the Myrteae 32 genera, of which 7 were exclusively palaeotropic, and one (*Aulacocarpus*) non-myrtaceous. Thus the American species were divided among 24 genera, of which some were more inclusive than the corresponding ones in the present paper. More recently published keys to the Myrtaceae of tropical America are regional in scope, including at most about two-thirds of the known genera. The most useful of these, in addition to those listed above, are Kausel's keys to the Chilean genera (Rev. Argent. Agron. 9: 40. 1942, and Lilloa 13: 148. 1948), Amshoff's key to the genera in the flora of Suriname (Fl. Suriname 3, pt. 2: 57-59. 1951). A key to the Cuban genera, including several endemic taxa of rather uncertain status, was published by Bro. Alain (Fl. Cuba 3: 410. 1953).

A key to more than 30 genera, several of which include 100 species or more, can be useful in identification of unknown material in proportion to the completeness of that material, but like all keys it becomes nearly useless in the face of abnormal or poor material. It is not to be expected that species of doubtful generic position, or those thought to be intermediate between accepted genera, can be placed exactly in the following key; such species must be traced individually, with attention to minor or particular characters. The present generic key has been prepared in the hope that it will serve not only the primary purpose of a key, namely identification, but also to some extent will summarize the characters of the genera in easily comprehensible form.

1. Inflorescence myrcioid; bracts and bracteoles rarely present (i.e. deciduous at or before anthesis).
2. Embryo myrcioid, filling the large seed; testa membranous or cartilaginous, fragile; calyx-lobes, if developed, usually 5, sometimes 4.
  - 2a. Ovules several or many in each of 3–5 locules; calyx closed in bud, calyprate, circumscissile; axillary panicles reduced to 1–3 flowers each; Cuba, Jamaica. *Mitranthes*
  - 2a. Ovules 2 in each of 2 or 3 locules.
    3. Anthers with two pairs of pollen-sacs at different levels, the upper seeming to open extrorsely and the lower introrsely; calyx-lobes 5; chiefly southeastern Brazil. *Gomidesia*
    3. Anthers with pollen-sacs all at the same level, opening laterally; calyx various; widespread.
    4. Calyx-lobes normally developed and present in flower and fruit; hypanthium, if produced vertically beyond the summit of the ovary, not splitting between the calyx-lobes at anthesis (the individual lobes sometimes deciduous). *Myrcia*
    4. Calyx modified into a calyptre, or the lobes reduced in size or in number (usually to 4), or very unequal in size; hypanthium noticeably prolonged vertically.
      5. Calyx closed in bud, calyprate, circumscissile; tube of the hypanthium not splitting longitudinally. *Calyptanthes*
      5. Calyx closed in bud or the small lobes free, opening irregularly by the splitting of the hypanthium, the fissures often extending nearly or quite to the summit of the ovary. *Marlierea*
2. [see also 3rd “2”, below]. Cotyledons fleshy, plano-convex, united at one end only; calyx-lobes 5, deciduous; ovary bilocular, the ovules 5–6; inflorescence usually reduced, few-flowered, imperfectly paniculate; West Indies and northern South America. *Pseudanamomis*
2. Embryo pimentoid; ovary bilocular; calyx-lobes, if developed, 4 or 5, persistent.
  6. Calyx-lobes 4; seeds with bony testa; ovules several; inflorescence sometimes determinate, dichotomous; southeastern Brazil. *Pseudocaryophyllus*
  6. [see also 3rd “6”, below]. Calyx-lobes 4 or 5; testa leathery or membranous, not bony; ovules 1 or few; inflorescence always a myrcioid panicle; West Indies and Caribbean lands. *Pimenta*
  6. Calyx closed in the bud, splitting irregularly at anthesis; testa membranous; ovules 4–6; inflorescence a panicle, but each branch a 3-flowered (rarely 7-flowered) dichasium; Lesser Antilles. *Marlieriopsis*
1. Inflorescence 1- or few-flowered (the flowers rarely more than 30), if compound then racemose, or determinate at the lowest node and regularly dichotomous with sessile flowers in the forks.
7. Inflorescence prevailingly racemose, the flowers all in racemes or the flowering partly of the *Stenocalyx*-type.
8. Embryo pimentoid; seeds usually several in each fruit, small, reniform or curved.
  9. Seed with membranous or leathery, glandular-verruucose testa; ovary with 4 or more locules; peduncles 1-flowered or often 3-flowered; flowering often of the *Stenocalyx* type, the peduncles sometimes in racemes; stamens 10 mm. long or less, pale; calyx usually 5-merous, with broad well-developed lobes; southeastern Brazil, a few species in northern and western South America. *Campomanesia*
  9. [see also 3rd “9”]. Seed with membranous or leathery testa; ovary bilocular; calyx 4-merous; stamens 15–30 mm. long, red; Andes of Peru. *Acca*
  9. Seed with bony testa, usually smooth and polished.

10. Ovary with 3–5 or rarely more locules.
11. Peduncles strictly 1-flowered, always in pairs from a very short axillary branch (i.e. racemose); ovary 4–5-locular; calyx open in bud and in flower, with 5 broad and often flaring lobes; northeastern Brazil to Central America. *Calycolpus*
11. Peduncles 1-flowered or 3-flowered, usually in the axils of leaves, but flowering sometimes of the *Stenocalyx* type (or the flowers in sessile (racemose) clusters in a few Central American species); locules of the ovary usually 3 (2–7); calyx often prolonged and modified, sometimes calyprate or with small terminal opening, sometimes 5-lobed; widespread. *Psidium*
10. Ovary bilocular.
12. Calyx 5-merous.
13. Chile; most of the flowers in definite short racemes *Amomyrtus*
13. Widespread (not native in Chile); most of the flowers solitary or in 3's in leaf-axils, the flowering partly of the *Stenocalyx* type. *Psidium*
12. Calyx 4-merous.
14. Filaments about 1 mm. long, equaling or a little shorter than the anthers; ovules 2 in each locule; northern Argentina. *Amomyrtella*
14. Filaments usually 5 mm. long or more, several or many times as long as the anthers; ovules several or many in each locule.
15. Filaments 15–30 mm. long, the style about the same length; Peruvian Andes. *Acca*
15. Filaments and style much shorter, rarely as much as 10 mm. long; eastern S. America and West Indies to Mexico.
16. Hypanthium produced beyond the summit of the ovary; calyx (whether open or closed in bud) splitting longitudinally at anthesis to the summit of the ovary; flowering mostly of the *Stenocalyx* type, or the peduncles in leaf-axils; widespread. *Psidium*
16. Hypanthium hardly if at all produced beyond the summit of the ovary; calyx not splitting between the lobes at anthesis; flowering of the *Stenocalyx* type, or some flowers in racemes, the peduncles usually not axillary; West Indies, eastern Mexico. *"Myrtus"*
8. [See also 3rd "8"]. Embryo myrcioid; bracteoles deciduous; calyx 4-merous; Juan Fernández only. *Nothomyrcia*
8. Embryo eugenioid or beanlike; seed usually 1 (-2), large in proportion to the fruit, with thin testa; bracteoles often long-persistent; flowers prevailing 4-merous.
17. Hypanthium circumscissile at base, cleanly deciduous (with the perianth and androecium) at about the time of anthesis, leaving a circular scar on the ovary and fruit; ovules 2–4 in each locule.
18. Ovary below the deciduous part of the hypanthium prolonged, fusiform or campanulate, usually contracted into a neck in bud and in flower; bracteoles scarcely connate, much shorter than the ovary; ovules usually 4 (-3); cotyledons 2, distinct, plano-convex. *Siphoneugena*
18. Ovary broadened from the base upward, not contracted below the line of dehiscence of the hypanthium, after dehiscence broad and flat, scarcely longer than the involucre formed by the broad connate bracteoles; ovules usually 2; embryo undivided. *Myrciaria*
17. Hypanthium not circumscissile; calyx open, with 4 conspicuous lobes, or partially or wholly closed and opening by irregular fissures; ovules several or many in each locule, occasionally only 2–4.
19. Hypanthium not prolonged beyond the summit of the ovary, the apex of the flower flat or nearly so; calyx-lobes distinct and imbricate in bud and in flower (at most slightly connate near the bases, but the free parts of the lobes then as long as the rest of the bud); embryo eugenioid; ovules usually several, sometimes as few as 2 in each locule. *Eugenia*
19. Hypanthium prolonged into a tube or cup beyond the summit of the ovary, the stamens borne just within the margin; calyx usually with short terminal lobes or completely closed in bud, opening by irregular fissures between the lobes.

20. Embryo eugenioid; ovules numerous, or as few as 3 in each locule; flowers mostly pedicellate, the pedicels not conspicuously bracteate. *Calycorectes*
20. Embryo with distinct plano-convex cotyledons; ovules usually 2 in each locule; flowers mostly sessile or subsessile, in clusters subtended by sterile imbricated bracts. *Plinia*
7. Inflorescence prevailingly dichotomously branched or 1-flowered, the peduncles mostly solitary in the axils of foliage leaves, or a few subtended by small bracts at the lower nodes of leafy branchlets (*Stenocalyx* type).
21. Embryo massive and nearly homogeneous, or with two large plano-convex cotyledons; ovary usually bilocular.
22. Branchlets strongly 4-angled; peduncles 1-flowered; bracteoles sub-petiolate, persistent, up to 1 cm. long; embryo not separable into distinct cotyledons; ovules several, on the margin of a peltate placenta; Chile. *Legrandia*
22. Branchlets not strongly angled; peduncles often branched; bracteoles deciduous, small; embryo of distinct cotyledons.
23. Radicle about as long as the cotyledons; cotyledons plano-convex, fleshy but thin; calyx 4-merous; peduncles 1-flowered or 3-flowered, sometimes in short racemes; Chile and adjacent Argentina. *Luma*
23. Radicle less than half as long as the cotyledons; cotyledons plumply plano-convex; peduncles partly or wholly several-flowered in most species, solitary as far as known.
24. Calyx-lobes 5, deciduous; inflorescence often irregularly dichotomous or umbelliform; ovules 5-6; cotyledons united about one-third their length; West Indies and northern South America. *Pseudanamomis*
24. Calyx lobes 4 or 5, persistent; inflorescence regularly dichotomous with the terminal flowers sessile in the forks; ovules usually more than 6; cotyledons united at base only.
25. Placenta subpeltate, with 6-12 marginal and inwardly directed ovules; calyx-lobes 5; Chile. *Reichea*
25. Placenta sessile, convex or horseshoe-shaped, with usually 8-20 radially directed ovules in a subcapitate group; calyx lobes usually 4, rarely 5; northern Argentina and southern Brazil, northward mostly in the Andes. *Myrcianthes*
21. [See also 3rd "21"]. Embryo myrcioid; ovules several in each locule; ovary usually 3-locular; calyx 4-merous; flowers usually subtended by persistent bracteoles; inflorescence in a few species a dichasium, the flowers usually solitary and axillary, or one above another in the axil; Chile, and southeastern Brazil. *Myrceugenia*
21. Embryo pimentoid; seeds small, often several in each fruit, reniform or curved; ovary often with 3-5 or more locules and several or many ovules in each locule; calyx various.
26. Dichasia lateral on old wood, thrice dichotomous, 2-3 cm. long, with persistent paired bracts and a central sessile flower in each fork; calyx-lobes 4; stamens 4-8, red, 1.5-2 cm. long. *Myrrhinium*
26. Peduncles 1-3 (-7)-flowered; bracts usually deciduous; calyx various; stamens (except in *Acca*) white or very pale pink, 10-13 mm. long or less.
27. Stamens red, 15-20 mm. long or more, much exceeding the petals; flowers solitary or in threes; calyx-lobes 4; Peru and southern Brazil. *Acca*
27. Stamens pale, usually white or cream color, 10-13 mm. long or usually much less; flowers and calyx various.
28. Flowers subtended by persistent foliaceous bracteoles; peduncles 1-flowered, solitary at leafy nodes; shrubs with stiff vaccinioid leaves mostly 2 cm. long or less; seeds bony; fruit 1 cm. in diameter or less; mostly high-montane, Chile to Mexico.
29. Calyx-lobes usually 5; filaments dilated and flattened, the anthers sagittate. *Ugni*
29. Calyx-lobes usually 4; filaments filiform, the anthers not sagittate. *Myrteola*
28. Bracteoles usually deciduous before anthesis, if persistent usually small and not foliaceous; flowers often 3-7 in axillary dichasia, sometimes solitary; leaves usually larger; seeds and fruit various.

30. Calyx-lobes 4, in unequal pairs, ciliate, deciduous after anthesis; flowers usually 3-7 in a dichasium, sometimes solitary, axillary; ovary bilocular; seeds with membranaceous or leathery testa; Andes of Ecuador, and south-Brazilian region. *Blepharocalyx*
30. Calyx closed in bud, or the lobes 4 or 5, not conspicuously ciliate, not deciduous (in *Psidium* the irregular divisions of the hypanthium and calyx sometimes tardily dehiscent from the fruit); flowers solitary, or in 3- or 7-flowered dichasia; ovary bilocular, sometimes 3-4-locular; testa bony or cartilaginous.
31. Peduncles usually twice dichotomous, 7-flowered; calyx 4-merous; testa cartilaginous; Chile. *Temu*
31. Peduncles 1-flowered or 3-flowered, rarely 7-flowered; calyx 4- (5-)merous, or nearly or quite closed in bud; testa bony.
32. Hypanthium produced beyond the summit of the ovary; calyx (whether open or closed in bud) splitting longitudinally at anthesis toward the summit of the ovary; peduncles often 3-flowered; calyx often strongly modified, appendaged, or nearly or quite closed, sometimes 4- or 5-lobed; widespread. *Psidium*
32. Hypanthium hardly if at all produced beyond the summit of the ovary; calyx 4- or 5-lobed, not splitting between the lobes at anthesis; cultivated in America (*M. communis*). *Myrtus*

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