

A RESOLUTION OF THE EUGENIA-SYZYGIUM CONTROVERSY (MYRTACEAE)¹

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A B S T R A C T

Floral anatomy now provides additional, strong evidence confirming the distinctness of the mainly New World *Eugenia s. s.* and the strictly Old World *Syzygium s. l.* Most significantly, species of *Eugenia s. s.* have a transeptal vascular supply to the ovules whereas those of *Syzygium s. l.* have an axile one. Other features of floral histology and vasculature also support such a division. In addition, a review of the taxonomic literature revealed three hitherto neglected organographic criteria—nature of bracteoles, presence or absence of pubescence, and presence or absence of pseudopedicels—that sharply distinguish between *Eugenia s. s.* and *Syzygium s. l.* An ensemble of these and other organographic criteria further demonstrates the basic disparity of these taxa. The organography and histology of flowers of *Eugenia s. l.* are described in detail, with 26 characters contrasting the Old and New World species included in a table.

THE MYRTACEAE are replete with vexing and provocative nomenclatural and systematic problems. The large, protean genus *Eugenia* Linnaeus (1753),³ named in honor of Francois Eugène de Savoie-Carignan (1663–1736), prince of Savoy, Austrian general, and distinguished patron of art, science, and literature, has been one of the most difficult and controversial genera in the angiosperms to define.⁴ Since the time of Linnaeus many species from both the Old and New World have been assigned to *Eugenia*. By 1938 some 2500 species had been described as belonging to, or transferred to, this genus (Merrill and Perry, 1939); by 1950 another 100 binomials had been published under *Eugenia* (Merrill, 1950b); and by 1965 an additional 200 names (as listed in *Index Kewensis*), to which may be added 22 new names in one recent work (McVaugh, 1969) alone. About 35 generic names (validly and invalidly published), based on various Old World

species, have been or could be reduced to *Syzygium* P. Browne ex J. Gaertner (1788) (Schmid, unpublished data). If in turn *Syzygium* is reduced to *Eugenia*, as has been done by many authors (see below), these 35 or more names could inflate the number of generic synonyms of *Eugenia s. l.* to nearly 70 since more than 30 mainly American genera (including the Old World genus *Jossinia* Commerson ex A. P. de Candolle, 1828) have been considered congeneric with *Eugenia s. s.* by various workers. Clearly the genus *Eugenia* has become unwieldy, and a very complicated synonymy and difficult taxonomy are involved.⁵

There are three schools of thought regarding the disposition of *Eugenia* and its Old World segregates (for historical accounts see Kausel, 1956; Merrill and Perry, 1939):

(1) Following Wight (1841) and Bentham and Hooker (1862–67; see Bentham, 1869, for their rationale), who promulgated Wight's then novel treatment of *Eugenia*, many authors (Bailey, 1930, but not 1949; Baillon, 1880; Bullock and Harrison, 1958; Corner, 1952; Fawcett and Rendle, 1926; Gray, 1854; Henderson, 1949; Merrill, initially in 1917; Ridley, 1922; Wilson, 1957, but not 1960) have preferred to retain almost all species of both hemispheres in one immense collective genus *Eugenia sensu latissimo*.

(2) Other workers (Airy Shaw, 1949, 1966), following Niedenzu (1893), who restricted *Eugenia* to largely American species, have favored the segregation of most of the Old World species into a second large collective genus *Syzygium sensu*

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³ Authorities and dates of publication of genera follow the *Index Nominum Genericorum*, which should be consulted for details.

⁴ For especially good taxonomic discussions of the *Eugenia*-*Syzygium* controversy see Amshoff (1958), Bentham (1869), Henderson (1949), Kausel (1956), McVaugh (1956a, b), Merrill (1950b), Merrill and Perry (1939), and Wilson (1957).

⁵ Merrill and Perry (1939) have given the most detailed but far from complete synonymy for *Syzygium*. The most extensive synonymy occurs in Airy Shaw (1966). See Kausel (1957b), McVaugh (1968), and Niedenzu (1893), for example, for generic synonymy of *Eugenia s. s.*

latissimo, or, as did Niedenzu (1893), into two large genera *Syzygium* and *Jambosa* Adanson ex A. P. de Candolle (1828), at the same time denying the validity of most or all of the small generic segregates proposed.

(3) Following A. P. de Candolle (1828, 1842), who accepted *Eugenia*, *Syzygium*, *Caryophyllus* Linnaeus (1753), *Acmena* A. P. de Candolle (1828), *Jambosa*, and *Jossinia*, still other botanists (Amshoff, 1963; Bailey, 1949; Diels, 1922; Guillaumin, 1938; Hosokawa, 1940; Kausel, 1956, 1957b, 1966; Merrill and Perry, see below) have recognized *Syzygium* (sometimes excluding *Jambosa*; or, in fact, accepting *Jambosa* in place of *Syzygium*, as did Blume, 1849–51) for most of the Old World species and have advocated the acceptance of certain small and somewhat distinct segregate genera.

Exemplifying the third school of thought, Merrill and Perry, by virtue of an extended series of works on the Asiatic Myrtaceae (most importantly, 1937, 1938a–c, 1939, 1942a, b; Merrill, 1937, 1939, 1950a, b; Perry, 1950), have had the greatest influence on the taxonomy of *Eugenia s. l.* and its Old World segregates. These authors accepted the very large Old World genus *Syzygium* (including most notably *Jambosa* and *Caryophyllus*, plus some 14 other synonyms listed in their 1939 work). In addition, they reinstated the small Old World genera *Acmena* [including *Lomastelma* Rafinesque (1838) and *Xenodendron* Lauterbach et K. Schumann (1900)—see Merrill and Perry, 1938a] and *Cleistocalyx* Blume (1849) [including *Acicalyptus* A. Gray (1854)—see Merrill, 1939; Merrill and Perry, 1937]. Perry (1950) also accepted the New Caledonian *Piliocalyx* Brongniart et Gris (1865). Merrill (1937, 1950a, b), but not Perry (personal communication, 1970), accepted *Aphanomyrtus* Miquel (1855) [including *Pseudoeugenia* Scortechini (1885)] and *Jossinia*. *Jossinia* represents a small residue of Old World species more closely resembling certain of the American species of *Eugenia* than the Old World species of *Syzygium* (Diels, 1922; Merrill, 1950b) and thus has been included in *Eugenia* as the series *Jossinia* in the subgenus *Eueugenia* (Niedenzu, 1893).

Eugenia, as so defined, "would scarcely appear in the Old World, except for a few introduced species" (Merrill, 1950a, p. 329). Late in his career Merrill (1950b), for reasons not stated, seemed on the verge of accepting additional segregates of *Syzygium*: *Tetraeugenia* Merrill (1917), *Pareugenia* Turrill (1915), and even *Jambosa* and *Caryophyllus*, although earlier he and Perry had considered these taxa (except *Tetraeugenia*) to be congeneric with *Syzygium*.

Most workers, other than those proposing the various segregates, have been reluctant to accept the majority of Old and New World segregate genera of *Eugenia s. l.*, although probably more American segregates, proposed mainly by Berg

(1855–56), are now accepted than Old World segregates. Most recent authors tend to segregate *Syzygium* from *Eugenia s. l.* and occasionally to accept a number of other Old World segregates: most notably, *Acmena*, *Piliocalyx*, *Acicalyptus*, *Aphanomyrtus*, *Cleistocalyx*, *Cupheanthus* Seemann (1865), *Jambosa*, *Jossinia*, and *Pareugenia*. Kausel (1956, 1957a, b, 1960, 1966) represents the extreme liberal view and has accepted some 33 generic segregates of *Eugenia s. s.* and *Syzygium s. l.*, 22 and 11, respectively, whereas Airy Shaw (1966) recognized 16 and 6 segregates, respectively. The segregates accepted by Kausel include such Old World taxa as *Acmena*, *Caryophyllus*, *Jambosa*, *Aphanomyrtus*, *Cleistocalyx*, *Pareugenia*, *Jossinia*, *Cupheanthus*, *Piliocalyx*, *Episyzygium* Suessenguth et Ludwig (1950), *Chloromyrtus* Pierre (1898), *Meteoromyrtus* Gamble (1918), and *Acmenosperma* Kausel (1957a). In fact, Kausel (1956, 1957b, 1966) placed *Eugenia* and *Syzygium* in separate subfamilies, his Eugenioideae and Plinioideae, respectively, and disposed most of the Old World segregates listed above in the Plinioideae, a few in his subfamilies Acmenoideae and Myrtoideae. Melchior (1964) is in essential agreement, but he treated Kausel's subfamilies as tribes.

Only fairly recently have comparative anatomical studies entered into taxonomic consideration. Although the differences between *Syzygium* and *Eugenia* may be somewhat obscure organographically, anatomically these genera appear to be quite distinct. As discussed below, previous work on wood structure (Chattaway, 1959; Dadswell and Ingle, 1947; Ingle and Dadswell, 1953), bark anatomy (Chattaway, 1959), and palynology (Pike, 1956) strongly supports the distinction between the New World species of *Eugenia s. l.* and most of the Old World taxa which are largely referable to *Syzygium s. l.*

The reproductive anatomy of *Eugenia s. l.*, however, has not been investigated in a comparative manner, but it seemed reasonable to expect that such a study, particularly of the flowers, would be of systematic value and might yield evidence paralleling that from previous comparative studies. In fact, it soon became apparent in the initial stages of this research (Schmid, 1970) that there are indeed essential anatomical differences in the flower between the American species of *Eugenia s. l.* and most of its extra-American taxa.

MATERIALS AND METHODS—Methodology, voucher information, and detailed supportive data for many of the statements below are given in Schmid (1971; in press b, c). Thirty-one taxa of *Eugenia s. l.* were examined. These may be conveniently arranged under the following designations:

1) *Eugenia s. s.*—mainly New World, but including the Old World segregate *Jossinia*: *Eugenia acapulcensis* Steud., *E. aeruginea* DC., *E. biflora* (L.) DC., *E. capuli* (Schlecht. et Cham.) Berg, *E. cartagensis* Berg, *E. coffeifolia* DC., *E. confusa* DC., *E. duchassaingiana* Berg, *E. flavescens* DC., *E. florida* DC., *E. gregii* (Sw.) Poir., *E. mandevillensis* Urban, *E. muricata* DC., *E. oerstediana* Berg, *E. pleurocarpa* Standl., *E. salamensis* Donn. Sm., *E. tikalana* Lundell, *E. (= Stenocalyx) uniflora* L., *E. venezuelensis* Berg, *E. whytei* Sprague in Stapf, *E. winzerlingii* Standl., *Jossinia aherniana* (C. B. Rob.) Merr., and *J. palumbis* (Merr.) Diels;

2) *Syzygium s. l.*—exclusively Old World, including such segregates as *Acicalyptus*, *Acmena*, *Caryophyllus*, *Cleistocalyx*, and *Jambosa*: *Acmena smithii* (Poir.) Merr. et Perry, *Cleistocalyx* (= *Acicalyptus*) *myrtoides* (A. Gray) Merr. et Perry, *C. operculatus* (Roxb.) Merr. et Perry, *Syzygium aromaticum* (L.) Merr. et Perry, *S. cumini* (L.) Skeels, *S. jambos* (L.) Alston, *S. malaccense* (L.) Merr. et Perry, and *S. paniculatum* Gaertn.

ORGANOGRAPHY—The following description of *Eugenia s. l.* (*sensu* McVaugh, 1968, and also including *Syzygium s. l.*) is based partly on standard taxonomic works (see Bentham, 1869; Gagnepain, 1917). Reference should also be made to Fig. 24 and Table 1 for characters contrasting *Eugenia s. s.* and *Syzygium s. l.* Details of inflorescence structure are relegated to Fig. 24.

Pubescence—*Syzygium s. l.* is almost entirely glabrous (Henderson, 1949; Merrill, 1950b), whereas *Eugenia s. s.* is predominantly pubescent. For example, only five of the 139 species of *Syzygium s. l.* described in Henderson (1949) but 58 of 60 species of *Eugenia s. s.* in McVaugh (1958)—47 of 54 in his 1963b work—are pubescent. Some of the so-called “glabrous” species of *Eugenia s. s.* are actually very sparingly pubescent.

Pedicels and bracteoles—The flowers are sessile, subsessile, or usually pedicellate. An articulation generally separates the pedicel (if present) and flower. McVaugh (1963b) reported pedicels up to 20 mm long for *Eugenia aeruginea* and *E. winzerlingii*, but most species he described in this work have pedicels less than 5 mm long. Two (sometimes 4, Merrill and Perry, 1939) bracteoles, situated opposite the ends of the septum and above the articulation, subtend each flower. In *Syzygium s. l.* bracteoles (and bracts) are mostly inconspicuous and very fugacious (Henderson, 1949; Perry, personal communication, 1971), whereas in *Eugenia s. s.* they are generally conspicuous and persistent (McVaugh, 1963b) but sometimes deciduous at or before anthesis (e.g., *E. salamensis*, *E. uniflora*). For example, five of 150 species of *Syzygium s. l.* listed in Merrill and

Perry (1939) (5 of 103 in their 1942a work), but 76 of 93 species of *Eugenia s. s.* in McVaugh (1969) (35 of 46 in his 1958 work and 40 of 47 in his 1963b work) have persistent bracteoles.

Size of buds—Floral buds near the stage of anthesis range from very small to gigantic, being up to 3 cm long in *Syzygium malaccense* (McVaugh, 1963b).

Pseudopedicel—Many species have the lower portion of the inferior ovary gradually narrowed into a slender pedicel-like base (Fig. 24, upper right). I designate this a “pseudopedicel” since it resembles a pedicel, although actually it is part of the flower. I believe my term is more descriptively restrictive than the entirely comparable “pseudostalk” of Henderson (1949) or the “pseudostipe” of Wilson (1957).

The pseudopedicel can only be designated on a topological basis. Its proximal part is anatomically indistinguishable from the distal part of the pedicel, except, of course, where traces depart to the bracteoles. Thus, proximally the pseudopedicel is well separated from the pedicel only by the bracteoles and articulation (if present), but distally it merges into the rest of the flower.

Most species of *Syzygium s. l.* have a pseudopedicel according to Henderson (1949), who reported one for 113 of 122 species. Pseudopedicels are very rare in *Eugenia s. s.* (McVaugh, personal communication, 1971), but one is present in *E. stipitata* (McVaugh, 1958).

Floral tube⁶—The floral tube of *Syzygium s. l.* is often much prolonged beyond the summit of the ovary (e.g., *Acmena smithii*) or little or not so (e.g., *S. aromaticum*). The floral tube of *Eugenia s. s.* is little or not at all prolonged beyond the ovary (e.g., up to 1.1 mm in *E. salamensis* var. *hiraefolia*). American species of the *Eugeniinae* with a prolonged floral tube are usually referred to *Siphoneugena*, *Calycorectes*, or *Myrciaria*.

Parianth parts⁷—The calyx and corolla are consistently tetramerous in *Eugenia s. s.* (McVaugh, 1958, 1963b, 1968, 1969) but occasionally pen-

⁶ In Schmid (1971) this character was defined in a taxonomic sense. However, in some cases the top of the ovary may be depressed and the peripheral parts of the ovary may thus line part or all of the so-called “floral tube.” Therefore, in such cases, which would generally not be apparent from macroscopic examination, part of the so-called “prolongation of the floral tube beyond the ovary” may actually include some ovarian tissue.

⁷ I use the terms “sepals” and “petals” according to taxonomic convention and, hence, without morphological connotation. Morphologically, if one adheres to the appendicular concept of the inferior ovary (Eames, 1961), the petals and sepals extend to the base of the epigynous flower, and distally “petal lobes” and “sepal lobes” would be present rather than the “petals” and “sepals” designated by taxonomists.

tamerous (or other) in *Syzygium s. l.* Jayaweera (1957), for example, found 95.5% of 3000 flowers of *S. malaccense* to be tetramerous for both calyx and corolla. Two sepals occur at points opposite the ends of the septum, the other two opposite the dorsal positions of the carpels. The petals alternate with the sepals. The perianth parts, especially the petals, are usually conspicuous, but sometimes minute (e.g., *Acmena smithii*), particularly in *Syzygium s. l.* The calyx lobes are distinct and usually persistent in *Eugenia s. s.* Those of *Syzygium s. l.* are obscure and deciduous to distinct and persistent; these extremes represent a rather shaky generic distinction between *Syzygium s. s.* and *Jambosa*.

In *Syzygium s. l.* the perianth is often calyptrate. Half (69 corolline versus 1 calycine) of the species listed in Henderson (1949) have calyptrae. Those few species of *Syzygium s. l.* with calycine calyptrae are sometimes segregated as *Acicalyptus*, *Cleistocalyx*, or *Piliocalyx*. *Jambosa* has free petals whereas *Syzygium s. s.* has the petals coherent into calyptrae, but this presumed generic distinction also frequently breaks down. Calyptrate species of *Eugenia s. s.* do not occur since such would invariably be referred to *Calycorectes*.

Stamens—Most species of *Eugenia s. l.* have numerous stamens, as many as 500 reported for the Peruvian *E. scalariformis* (McVaugh, 1958). Those few species of *Syzygium s. l.* with 4–8 stamens are occasionally segregated as *Aphanomyrtus* (Amshoff, 1963; Kausel, 1957b; Merrill, 1937, 1950b) or as the probably closely related *Tetraeugenia* with four stamens (Merrill, 1917). Stamens of *Eugenia s. l.* are usually free. However, *Paraeugenia*, a segregate of *Syzygium s. l.*, was proposed for those forms with united stamens. Since there are intermediate forms linking all these segregates with other species in *Syzygium s. l.*, these genera have generally been rejected.

The stamens are borne on a flat disc surrounding the base of the style or on the margins or inner surface of the floral tube (if this is present). *Syzygium s. s.* is supposed to be distinguishable from *Jambosa* on the basis of an inconspicuous versus conspicuous staminal disc, respectively, but many exceptions occur.

According to Merrill and Perry (1938b, c, 1939), stamens of *Eugenia s. s.* are much less incurved in bud than those of *Syzygium s. l.*

Anther sacs are mostly parallel and longitudinally dehiscent but divaricate and terminally dehiscent in the Old World segregate *Acmena*. Anther connectives each with a terminal secretory cavity are considered typical of the Myrtaceae (Erdtman and Metcalfe, 1963; Weberling, 1966). However, the anthers of a few species (e.g., *Eugenia flavescens*, *Jossinia aherniana*, *Cleistocalyx myrtoides*) lack secretory cavities.

Nectaries—These are rarely described in the taxonomic literature. Brown (1938) rightly emphasized that nectaries should be studied in living material because they become greatly distorted in dried specimens. An ovarian annular type of nectary is present in *Syzygium aromaticum*, *S. jambos*, *S. malaccense*, and *S. paniculatum* (Schmid, in press b).

Ovary—The ovary is inferior and very consistently bilocular. Some species occasionally have trilocular flowers (e.g., *Eugenia confusa*, *E. winzerlingii*, *Acmena smithii*, *Cleistocalyx operculatus*, *Syzygium malaccense*) or very rarely unilocular (e.g., *Jossinia aherniana*) or multilocular ones (e.g., quadrilocular in *E. stipitata*, McVaugh, 1958). A prominent compitum, the canal or space connecting two or more ovarian loculi (Carr and Carr, 1961), is usually present. Rastogi (1951) confused the compitum with the phyletic beginning of true parietal placentation. In *Syzygium s. l.* the ovary is often spongy, with tissue containing large intercellular spaces. This condition apparently does not occur in *Eugenia s. s.*

Ovules and seeds—The anatropous, usually bitegmic (Davis, 1966; Mauritzon, 1939) ovules are several to many per locule, rarely as few as two per locule (e.g., *Eugenia coffeifolia*). Placentation is axile. Only one or two ovules (very rarely more) per ovary develop into the often quite large seeds. Cotyledons are usually fused (pseudomonocotyledonous) in *Eugenia s. s.* but usually divided in *Syzygium s. l.*—although fused in *Acmena*.

Style—The apex is usually simple, very rarely bifid (e.g., the African *Eugenia aschersoniana*, *E. mossambicensis*, Amshoff, 1958). The style is frequently quite long and thus usually doubled back in the bud.

HISTOLOGY—**Secretory cavities**—Secretory cavities ("oil glands," "oil cavities," "secretion reservoirs," "oil cells," etc.) are a characteristic feature of the Myrtaceae and are responsible for the well-known aromatic properties of its taxa. Vertical secretory ducts occur in a few genera (e.g., *Angophora*, *Eucalyptus*, and *Spermolepis* of the subfamily Leptospermoideae—Carr and Carr, 1969; Ingle and Dadswell, 1953).

The secretory cavities of *Eugenia s. l.* are spherical to ovoid and achieve a maximum dimension of about 350 μ in flowers of *E. mandevillensis* and *Syzygium malaccense*. Secretory cavities in the Myrtaceae have been described as being schizogenous, obliotoschizogenous, schizolysigenous, and lysigenous (Carr and Carr, 1970). However, a careful reinvestigation with new techniques is in order since these differences in inter-

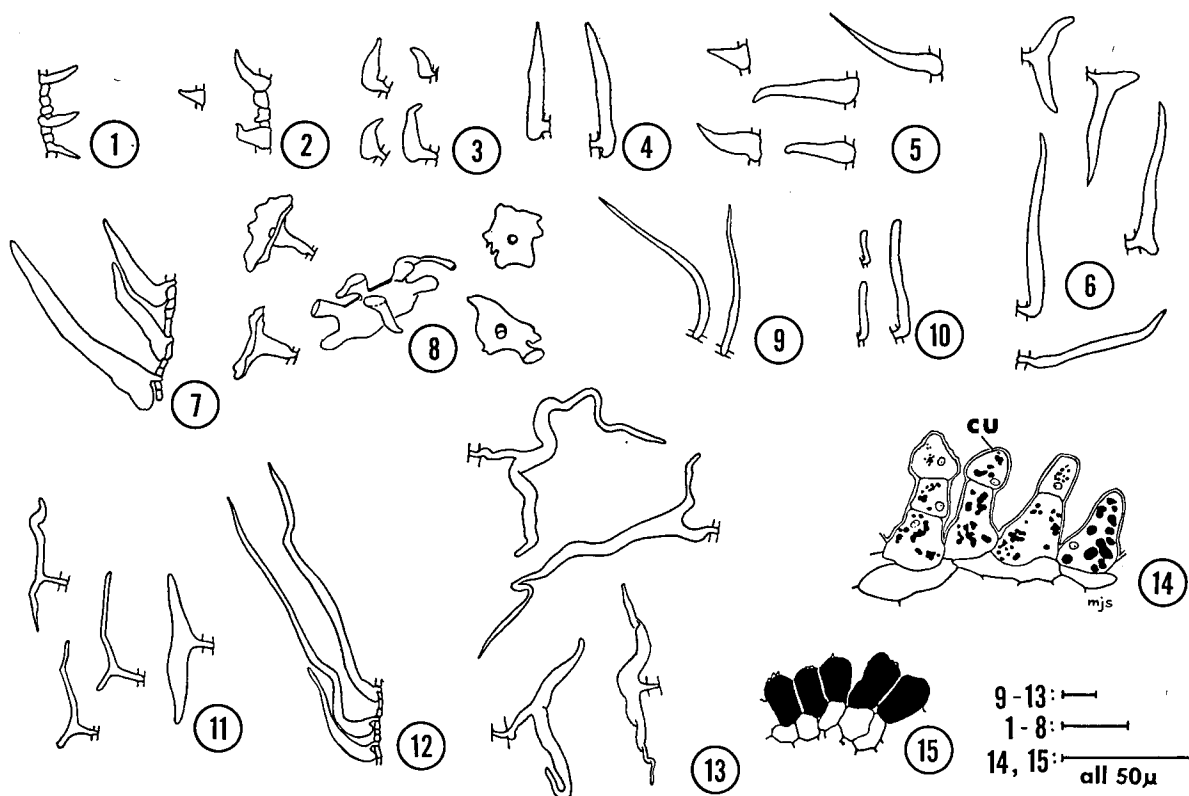


Fig. 1-15. Various types of trichomes (hairs in Fig. 1-13, papillae in Fig. 14, 15) on floral organs of *Eugenia s. l.* Trichomes (except Fig. 6, 8, 14, 15) oriented so that distal end of flower or appendage is toward top of page.—Fig. 1, 2. *E. capuli*, floral tube (Fig. 1, Gentle 5044, MICH), sepal (Fig. 2, Breedlove 14407, MICH).—Fig. 3-5. *E. florida* (Steiermark & Gibson 95781, MICH), floral tube (Fig. 3, 4), margin of sepal (Fig. 5).—Fig. 6. *Jossinia aherniana* (Velasco s. n., US), staminal disc, all hairs from an area less than 1 mm².—Fig. 7. *E. muricata* (Pires et al. 50887, MICH), floral tube.—Fig. 8. *E. gregii* (Hahn 641, MICH), floral tube; side, bottom, and top views of hairs respectively.—Fig. 9. *E. mandevillensis* (Proctor 19686, MICH), staminal disc.—Fig. 10, 11. *E. pleurocarpa* (McVaugh 15322, MICH), sepal (Fig. 10), floral tube (Fig. 11).—Fig. 12. *E. biflora* (Steiermark & Wurdack 31, MICH), floral tube.—Fig. 13. *E. salamensis* var. *salamensis* (Carter & Chisaki 1209, MICH), floral tube.—Fig. 14, 15. *Acmena smithii* (Schmid 1968-A2, MICH), transection of petal (Fig. 14), showing papillae with tannin globules and cuticle (cu); transection of filament (Fig. 15), showing papillae filled with tannin.

pretation seem partly due to technical difficulties in tissue preparation (Carr and Carr, 1970).

A stamen with a terminal secretory cavity is characteristic of the Myrtaceae, as noted above. At the species or series level, the distribution of oil cavities has been considered to be of taxonomic significance in vegetative structures of *Eucalyptus* (Carr and Carr, 1969; Welch, 1920). However, this seems not to be the case in the Myrtaceae I examined. The distribution and number of secretory cavities is quite variable, even between different buds from the same plant, and thus of little use taxonomically except in the few cases where cavities occur in unusual places (e.g., adjacent to the loculi in *Eugenia mandevillensis*).

Secretory cavities of various species of *Eugenia s. l.* are not distinguishable from one another. Winton and Winton (1939) came to the same conclusion after examining various cultivars of the Myrtoideae.

Trichomes—A variety of trichomes is encountered in *Eugenia s. l.* (Fig. 1-15). Usually the hairs are simple (Fig. 1-3, 5, 9, 10) or weakly to strongly dibrachiate (malpighian) (Fig. 4, 6, 7, 11-13). Funnel-shaped (infundibuliform) hairs (Fig. 8) occur in *E. gregii*. Many hairs are attached by a small peg (Fig. 4, 6-8, 12, 13), but others have the large basal part of the cell embedded in the epidermis (Fig. 1, 2, 5). The hairs on a plant often vary considerably. Those depicted in Fig. 6 were found within an area less than one mm². Much of the apparent variability is presumably due to different ontogenetic stages.

The hairs of the Myrtaceae are reported to be exclusively unicellular (Hummel and Staesche, 1962; Metcalfe and Chalk, 1950). I found no evidence to contradict this (Fig. 1-13). Papillae (Fig. 14, 15), however, may be multicellular, as on the petals of *Acmena smithii* (Fig. 14). Hairs of various myrtaceous genera have been described

as bicellular, but actually there is a single protoplast which withdraws into the lower part of the cell, the upper part being shed after a septum forms between the two parts (Uphof, 1962).

As in most species of American Myrtaceae (McVaugh, 1968), in *Eugenia* the initial pubescence usually disappears soon after flowering (McVaugh, 1963a, b). Presumably the distal parts of the hairs break off by the mechanism just noted. In addition, at least in herbarium material, those hairs attached merely by small pegs (Fig. 4, 6–8, 12, 13) seem especially susceptible to breakage.

The presence or absence of pubescence, its type, and its distribution afford useful taxonomic distinctions both in the American Myrtaceae and in *Eugenia s. s.* (McVaugh, 1963a, b, 1968). *Syzygium s. l.* is mostly glabrous whereas *Eugenia s. s.* is mostly pubescent.

Tannin⁸—The Myrtaceae are characteristically tanniferous (Metcalf and Chalk, 1950). The flowers of *Syzygium s. l.* are moderately to very tanniferous, those of *Eugenia s. s.* usually only slightly so.

Distribution of tannin in my material does not seem to be taxonomically significant. In a number of species (e.g., *Acmena smithii*, *Syzygium paniculatum*) much tannin occurs in the epidermal and subepidermal layers and particularly in the stamens and style. It is tempting to relate this distribution of tannin to a protective function against snails, insects, and pathogens, as presumed by earlier botanists (see Eyde, 1966, for references and a detailed discussion of the occurrence of tannin in flowers). It would seem particularly important for a plant to evolve protective devices for its fertile parts. Tannin also frequently occurs in phloem parenchyma cells (significance: protection against aphids?).

Crystals—Numerous druses, but relatively few prismatic crystals, usually occur in some or all of the floral parts, depending upon the species and perhaps even the individual. Raphides are absent. Anthers, in particular, often contain dense clusters of druses (e.g., *Acmena smithii*, *Syzygium aromaticum*). Matthews and Knox (1926) and Namikawa (1919) suspected that the calcium oxalate of crystals might play a role in causing dehiscence of the anther by breaking down cells in the connective. However, the fact that anthers of some species (e.g., *S. jambos*) apparently lack crystals militates against this assumption, at least for the group I studied.

Sclerenchyma—Pass (1940) discussed in considerable detail the distribution of sclereids in

⁸ In keeping with botanical precedent, I consider the darkly staining cells or parts of cells to be tanniferous, although no attempt was made at chemical identification.

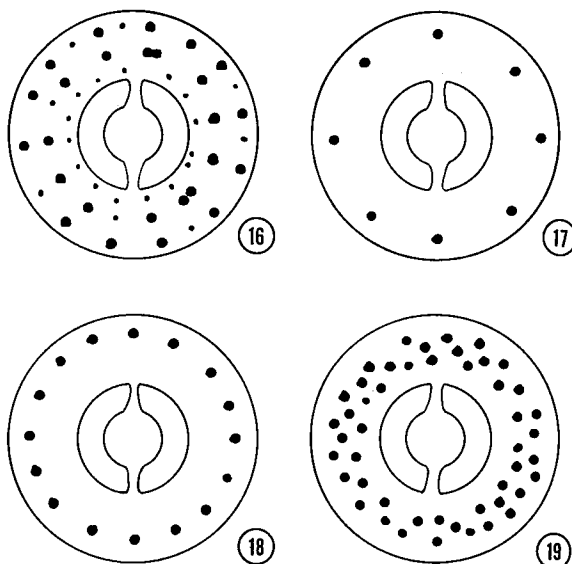


Fig. 16–19. Variation in bundle arrangements.—Fig. 16. Polycyclic, with two or more concentric rings of bundles.—Fig. 17, 18. Monocyclic, with a single ring of bundles; Fig. 17 with a definite number; Fig. 18 with an indefinite number.—Fig. 19. Zonocyclic, with many bundles dispersed in a banded ring, definite concentric rings of strands as in Fig. 16 not apparent.

flowers of 25 species of Myrtaceae, in which he found three patterns (excluding the seed): (1) sclereids present in flowers, and sometimes also in the buds; (2) sclereids present only after anthesis, during fruit maturation; (3) sclereids absent from all reproductive stages.

I found sclerenchyma (sclereids and/or especially phloem fibers) only in flowers of *Syzygium s. l.* In the larger flowers sclerenchyma, especially fibers, occurs throughout the floral tube and ovary; in several cases it occurs even in the sepals but never in the petals, stamens, or style. This distribution suggests that evolution of sclerenchyma in certain species might have paralleled the evolution of zonocyclism, which seems to have resulted as numbers of stamens increased as an adaptation to bird pollination (Schmid, 1971).

VASCULATURE—There is so much variability in floral vasculature, both between different species and within a single species (even between different flowers of the same plant), that generalized descriptions of vasculature were not prepared. Nevertheless, the following features of vasculature seem salient.

Floral tube—The major vascular bundles of the floral tube exhibit the following patterns in the Myrtaceae (Schmid, 1971; in press b, c):

(1) Monocyclic (not “unicyclic,” which is a Latin–Greek hybrid): with a single ring of bundles

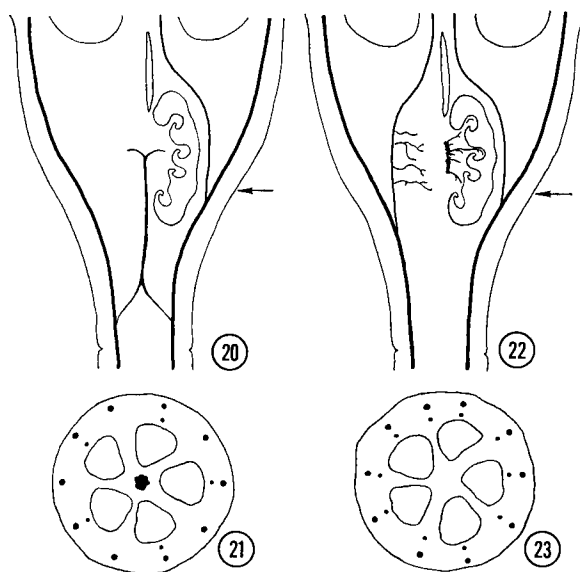


Fig. 20–23. Generalized diagrams of axile (Fig. 20, 21) and transeptal (Fig. 22, 23) ovular systems in Myrtaceae. Arrows at Fig. 20 and 22 indicate approximate levels of transections shown in Fig. 21 and 23, respectively.

(Fig. 17, 18); e.g., *Acmena smithii*, *Cleistocalyx operculatus*, all species of *Eugenia s. s.* and *Jossinia*.

(2) Polycyclic: with two or more concentric rings of bundles (Fig. 16); e.g., *Eucalyptus* (Carr, Carr, and Milkovits, 1970), also *Alangium* of the Alangiaceae (Eyde, 1968). Bundles may or may not occur along definite radii.

(3) Zonocyclic (Greek *zōnē*, meaning belt, girdle, zone): with many bundles dispersed in a banded ring, definite concentric rings of strands not apparent (Fig. 19); e.g., *Cleistocalyx myrtoides*, all species of *Syzygium s. s.*

Only types 1 and 3 occur in *Eugenia s. l.*, but there are intermediate types. For example, *Syzygium aromaticum* is monocyclic proximally, zonocyclic distally (Schmid, 1971, in press b). Two variations occur in the monocyclic pattern: (a) usually eight major bundles present, as in all species of *Eugenia s. s.* and *Jossinia* (Fig. 17); and (b) an indefinite number of bundles present, as in *Acmena smithii* and *Cleistocalyx operculatus* (Fig. 18).

It is best to apply these terms to regions of the flower in the vicinity of the loculi since all zonocyclic flowers are monocyclic in their very base, before the strands have divided.

Floral tube versus perianth parts—Many species of *Eugenia s. s.* (e.g., *E. biflora*) display a very regular relationship between the major bundles of the floral tube and the vasculature to the perianth members. *Syzygium s. l.* and other spe-

cies of *Eugenia s. s.* exhibit irregular patterns. A regular relationship clearly seems related to monocycly with a definite number of bundles (Fig. 17) (Schmid, 1971).

Stamens—A single strand, sometimes only one or two vessel elements thick (e.g., *Eugenia venezuelensis*), supplies each stamen. Distally the strand typically expands, often considerably, in the connective, where it frequently abuts against a large terminally situated secretory cavity. The shape of this distal expansion may be a potentially useful taxonomic character.

Ovular supply—The species of *Eugenia s. l.* display two pathways of vasculature supplying the ovules, transeptal and axile (Fig. 20–23). In the transeptal ovular system, the vascular supply to the ovules is from the sides, via the peripheries of the septa (Fig. 22), and there is no vascular tissue in the center of the ovary below the placenta (Fig. 22, 23). By contrast, in the axile ovular system, the vascular supply to the ovules is through the center of the gynoecium, via the bases of the septa (Fig. 20), and all transections of the lower parts of the ovary will reveal vascular tissue in the center (Fig. 20, 21). The axile supply occurs in *Syzygium s. l.* whereas the transeptal one occurs in *Eugenia s. s.*

I purposely avoided designating bundles related to the ovular supply as “ventral carpellary bundles” since I am uncertain of the homology between ventral bundles in other families and those bundles of *Eugenia s. l.* comprising the axile and transeptal systems.

I use the adjective “axile” rather than “axial.” The former is without morphological implications, “axile” simply indicating a central position for the vascular supply to the ovules (as opposed to a lateral or transeptal one); in contrast, “axial” could be construed as meaning that the placentae may be cauline in nature (see Jackson, 1928). In spite of Eames’ (1961, p. 235) decree that “no placentae are morphologically cauline,” whether carpels, particularly their placentae, are of an appendicular (foliar) or axial (cauline) nature has by no means been conclusively decided. Moe-liono (1970), for example, presents detailed arguments for an axial interpretation of placentae in the Caryophyllales.

Style—In many species of *Eugenia s. l.* the number of styler bundles as seen in transection increases toward the styler apex. This, of course, is partly due to branching of bundles. However, often there are distally occurring styler bundles without any basal connections. Possibly such “free-floating” strands result from the rapid expansion of the style. Fusions between styler bundles frequently occur.

The bundles often expand near the apex of the

style, generally forming two arcs or even a continuous ring of vascular tissue. Arber (1931, p. 36), incredibly, believed a similar situation in the Cruciferae to be "connected with the hindrance to further flow of sap when the distal region of the organ is approached." Melville (1962) discussed such stylar vascular expansions ("brushes") in terms of a "dichotomous branch system" and invoked an intricate hypothesis in support of his gonophyll theory.

Rastogi (1951) found five stylar bundles in *Eugenia jambolana* (= *Syzygium cumini*) and interpreted these as indicating a pentacarpellary nature for the stylar region, with three of the carpels in the presently bicarpellary ovary having been lost. By Rastogi's (1951) reasoning the 5–13 bundles in the base of the style of *Acmena smithii* would necessitate a very elaborate phylogeny.

In contradistinction to these philosophers, I believe the branching and distal expansion of stylar bundles to be functionally related to the secretion of stigmatic fluid and to the concomitant receptivity of the stigma for pollen.

Other features—Other features of the vasculature of *Eugenia s. l.* are even more variable. Generalization thus is difficult. The nature of some of this variability is evident from the detailed descriptions in Schmid (1971; in press b, c). The considerable variability in level and manner of origin of the dorsal carpellary bundles of *Syzygium s. l.* is detailed in Schmid (in press a).

DISCUSSION—It is evident from the nomenclatural and taxonomic history outlined above that there is a plethora of discordant opinion regarding the validity and disposition of the various Old and New World segregates of *Eugenia s. l.* The Old World segregate genera have perhaps been more controversial than the New World ones or the former, at least, have received the greater attention.

It is perhaps tempting on the basis of phyto-geographical considerations alone to accept the division of *Eugenia s. l.* into at least two genera: the mainly American *Eugenia* and the exclusively Old World *Syzygium*. However, obtaining valid organographic justification for their taxonomic recognition has been extremely difficult because of their immensity and diversity. Authors wishing to split up *Eugenia s. l.* have, of course, proposed various criteria that they believed effectively separated these and additional groups, but unfortunately these distinctions have never been made on a worldwide basis. In fact, there exist no monographs on *Eugenia s. l.* or even *Syzygium s. l.* other than regional ones. Examination of the keys authors have used to separate *Eugenia*, *Syzygium*, and their respective segregates can be very misleading because a few commonly intro-

duced species have skewed the extent of their differences—e.g., the New World *E. uniflora* and the Old World *S. cumini*, *S. jambos*, *S. malaccense*, and *S. paniculatum* obviously do not adequately reflect the weltering procession of the many other taxa in their hemispheres.

Perhaps largely for these reasons, the distinguishing characters used by Merrill and Perry (1937, 1938a–c, 1939, 1942a, b), Merrill (1937, 1939, 1950a, b), Perry (1950), and other authors, have been rejected as inconsistent by more conservative botanists (Airy Shaw, 1949; Bailey, 1930, but not 1949; Henderson, 1949; Merrill, initially in 1917; Wilson, 1957, but not 1960), some of whom have worked in different geographical areas and have reverted to the Bentham and Hooker (1862–67; Bentham, 1869) concept of a "super" genus *Eugenia* to include everything.

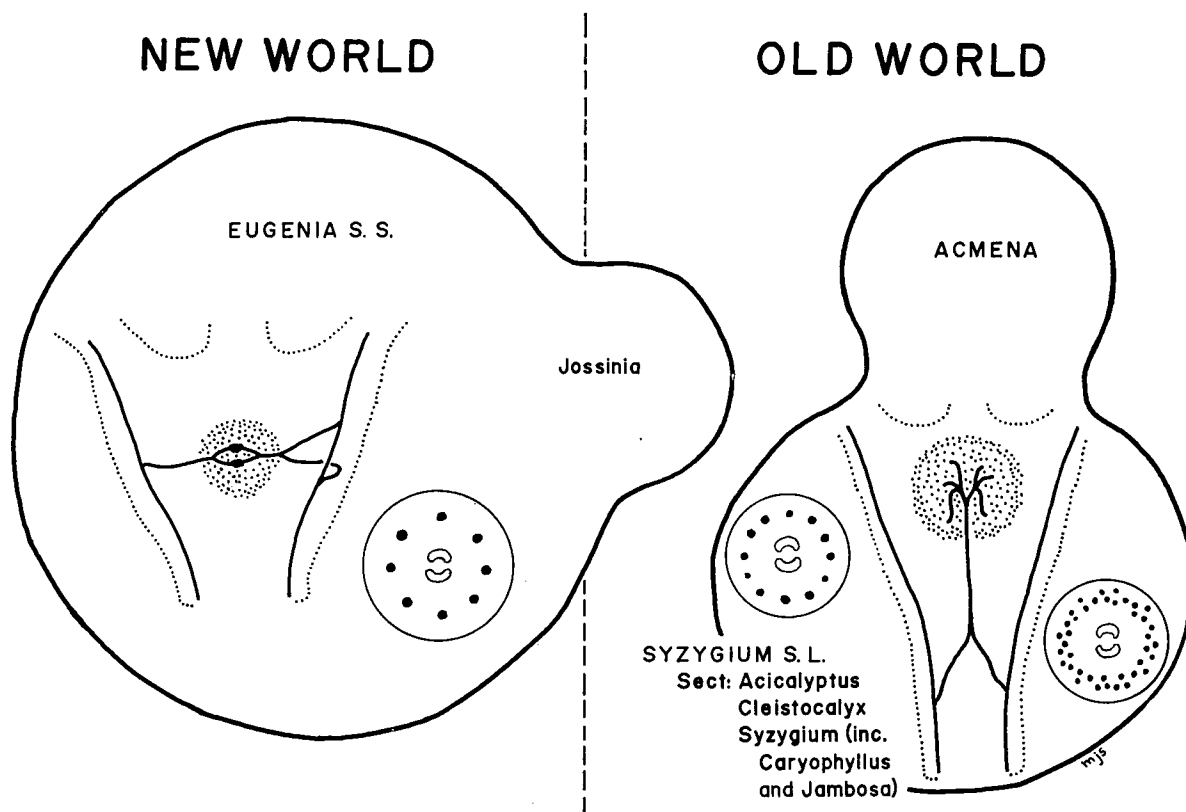
In recent times Merrill and Perry, by virtue of the extended series of papers just cited, have had the greatest influence on the taxonomy of *Eugenia s. l.* and its Old World segregates. Departing from most previous workers by placing greater emphasis on fruit rather than on floral characters, Merrill and Perry (1938b, c, 1939) suggested that the Old and New World species could be effectively distinguished as follows (descriptive terms from their 1939 paper):

Syzygium: (1) dried fruit not too easily broken; (2) testa roughish and more or less loosely adhering to the pericarp; (3) cotyledons of embryo distinct, usually attached near the middle of the opposing faces, concealing the hypocotyl within; (4) floral tube ("calyx limb") prolonged beyond the ovary; (5) stamens much more incurved in bud than in *Eugenia*; (6) inflorescence largely centrifugal, with the panicles branching by threes or with secondary cymes.

Eugenia: (1) pericarp easily crushed, thinner than in most Old World taxa; (2) testa smooth, chartaceous to cartilaginous, and mostly lustrous, free from the pericarp (and adherent to the cotyledons); (3) cotyledons united, the embryo undivided and thus pseudomonocotyledonous; (4) floral tube less prolonged than in *Syzygium*; (5) stamens much less incurved in bud; (6) inflorescence centripetal, with one-flowered pedicels (or peduncles) solitary, clustered, or in a short raceme.

Merrill and Perry regarded characters (2) and (3) as "the basic distinctions between the two genera" (1938c, p. 206), but they also stressed (1939) that both floral and fruit characters are essential for the elucidation of *Eugenia s. l.*

Subsequent workers (Amshoff, 1958, 1963; Bailey, 1949; Kausel, 1956, 1957b, 1966; Melchior, 1964) have generally accepted these distinguishing characters, particularly that of the divided versus undivided cotyledons. In fact, Kausel (1956, 1957b, 1966), a splitter *par excellence*, used only this character of the embryo



CHARACTER

*PUBESCENCE VEG. AND/OR REPRO. PARTS
 *POSITION OF THE INFLORESCENCE
 MATURATION FLOWERS ON INFLORESCENCE
 *STRUCTURE OF THE INFLORESCENCE
 *BRACTEOLES SUBTENDING FLOWERS
 SIZE OF BUD NEAR STAGE OF ANTHESIS
 *PSEUDOPEDICEL (ATTENUATE FL. BASE)
 PROLONGATION FLORAL TUBE ABOVE OVARY
 *VARIATION IN NUMBER PERIANTH MEMBERS
 MAGNITUDE OF THE PERIANTH PARTS
 DURATION OF THE LOBES OF CALYX
 DISTINCTNESS OF THE LOBES OF CALYX
 *COROLLINE OR CALYCINE CALYPTRAE
 INCURVATION OF STAMENS IN THE BUD
 POSITION OF LOCULI IN THE OVARY
 *DISCRETENESS OF THE COTYLEDONS
 SURFACE OF THE SEED-COAT
 AMOUNT SCLERENCHYMA IN THE FLOWER
 TEXTURE OF THE OVARIAN TISSUE
 AMOUNT OF TANNIN IN THE FLOWER
 ARCHITECTURE OF VASCULAR SYSTEM
 *LARGE BUNDLES OF THE FLORAL TUBE
 NUMBER BUNDLES IF PATTERN MONOCYCLIC
 FLORAL TUBE BUNDLES AND PERIANTH PARTS
 *PATHWAY OF VASCULAR SUPPLY TO OVULES
 CONNECTIONS OF THE DORSAL BUNDLES

EUGENIA S. S.

MOST SPECIES (ca 90%)
 PREDOMINANTLY LATERAL
 CENTRIPETAL
 SOLITARY FLOWERS OR
 USUALLY RACEMES
 MOSTLY PERSISTENT AND
 CONSPICUOUS (ca 80%)
 VERY SMALL TO MODERATE
 RARELY PRESENT (ca 1%)
 NONE TO SLIGHT
 CONSTANT (4 + 4)
 USUALLY LARGE AND
 CONSPICUOUS
 USUALLY PERSISTENT
 DISTINCT
 NEVER
 LESSER
 MIDDLE
 USUALLY FUSED
 SMOOTH
 NONE
 COMPACT
 USUALLY SLIGHT
 CLOSED
 MONOCYCLIC
 DEFINITE, USUALLY 8
 OFT REGULAR RELATIONSHIP
 TRANSEPTAL
 FREQUENT TO OTHER
 CARPELLARY BUNDLES

SYZYGIUM S. L.

VERY FEW SPECIES (ca 5%)
 USUALLY TERMINAL
 CENTRIFUGAL
 SOLITARY FLOWERS OR USUALLY PANICLES OR CYMES
 MOSTLY FUGACIOUS AND
 INCONSPICUOUS (ca 95%)
 VERY SMALL TO VERY LARGE
 MOSTLY PRESENT (ca 90%)
 NONE TO MUCH
 RATHER VARIABLE (4-5 + 4-5)
 MINUTE TO LARGE AND
 CONSPICUOUS
 DECIDUOUS OR PERSISTENT
 OBSCURE TO DISTINCT
 OFTEN (ca. 50%), MOSTLY
 COROLLINE
 GREATER
 NEAR TOP
 USUALLY DISTINCT
 ROUGH
 NONE TO MUCH
 USUALLY SPONGY
 MODERATE TO VERY MUCH
 OPEN TO CLOSED
 MONO- TO MOSTLY ZONO-
 CYCLIC
 INDEFINITE
 IRREGULAR RELATIONSHIP
 AXILE
 NOT UNITED WITH OTHER
 CARPELLARY BUNDLES

Fig. 24. Diagram and table of organographical and anatomical differences between *Eugenia s. s.* and *Syzygium s. l.* Tabulated characters elaborated in text; those deemed most significant marked with asterisk. Other important differences occur in bark, wood, and pollen (see text). Diagrams of flowers depict patterns of bundles in floral tube (transections) and ovular vascular supply (longisections, the plane of septum facing viewer). Taxa arranged to show suggested taxonomy.

TABLE 1. Quantification of several generic differences^a

Character	<i>Eugenia s. s.</i>	<i>Syzygium s. l.</i>	
Pubescence present on vegetative and(or) reproductive parts	ca 90 %	ca 5 %	} of species
Bracteoles persistent	ca 80 %	ca 5 %	
Pseudopedicel present	ca 1 %	ca 90 %	

^a Compiled from data in Henderson (1949), McVaugh (1958, 1963b, 1969), Merrill and Perry (1939, 1942a), and Perry (1950). Actual values rounded off to nearest 5 % and biased toward similarity between the taxa.

to place *Eugenia* and *Syzygium* in separate sub-families.

However, Henderson (1949), Wilson (1957), and McVaugh (1958, 1963b) in essential agreement with these two workers, rejected the segregation of *Syzygium* from *Eugenia* since they found the degree of fusion of the cotyledons and the extent of adherence of the testa to the pericarp to be quite variable. The former character varied even within a single species; the latter varied depending upon whether living, dried, or dried-and-boiled material was examined. In addition, Amshoff (1958) noted that the African members of *Eugenia s. s.*, which Merrill (1950a, b) would have included in *Jossinia*, resemble the American species in having a pseudomonocotyledonous embryo but differ in having the testa "probably adhering to the pericarp," the presumed character of *Syzygium* (Merrill and Perry, 1938b, c, 1939). All the evidence, however, indicates that the degree of union of the cotyledons, while somewhat variable within a taxon, may still be useful in distinguishing between many Old and New World forms, although certainly by itself it is not a good generic character. In light of the studies of Henderson (1949) and Wilson (1957), however, the extent of adherence of the testa to the pericarp (or, conversely, to the cotyledons) seems to be a worthless character.

Taxonomists have generally used various characters of the inflorescence and flower, particularly of the floral tube and perianth, in attempts to delimit *Eugenia s. s.* and *Syzygium s. l.* However, there are so many species with intermediate character states that one or a few character differences should not be expected to separate these taxa. For example, the prolongation of the floral tube beyond the ovary, one of the most favored characters of taxonomists, is absent in *S. aromaticum* but ranges up to 1.1 mm in *E. salamensis* var. *hiraefolia*, which is the converse of the presumed generic distinction. Nevertheless, it seems that a multitude of characters might adequately sort out either genus. Figure 24 presents a diagrammatic representation and a tabulation of the differences between *Eugenia s. s.* and *Syzygium s. l.* If one can eliminate the possibility of a given plant being

an adventive, perhaps the surest single distinguishing feature indicated in Fig. 24 is where the plant lives—by itself, however, hardly a valid basis for generic distinction.

Many of the organographic characters listed in Fig. 24 have been emphasized previously, but a few, particularly those concerning pubescence, bracteoles, and pseudopedicels, deserve broader appreciation since their specific aspect is quite diagnostic (Table 1). For example, Henderson (1949, p. 14) stated that "the great majority of species [of *Syzygium s. l.*] are glabrous in all their parts," but, as shown above, most species of *Eugenia s. s.* have pubescent vegetative and/or reproductive parts. However, Merrill (1950b, p. 358), in comparing the sparingly pubescent *Jossinia* with the "characteristically entirely glabrous" *Syzygium*, is the only worker I know who has utilized this rather obvious distinction. Secondly, the nature of the bracteoles as a diagnostic feature, mostly persistent in *Eugenia s. s.* (McVaugh, 1963b) but mostly fugacious in *Syzygium s. l.* (Henderson, 1949; Perry, personal communication, 1971), also seems to have escaped the attention of most taxonomists. Only McVaugh (1963b) used this feature in a key to these taxa. Finally, the usual presence of a pseudopedicel in *Syzygium s. l.* (Henderson, 1949) but its general absence in *Eugenia s. s.* (McVaugh, personal communication, 1971) has been used as a distinguishing character by only a few workers (Guillaumin, 1938; Hosokawa, 1940; McVaugh, 1963b; Nienzenzu, 1893).

In my opinion, the totality of organographic characters tabulated in Fig. 24 (see also Table 1) is adequate to differentiate nearly all species of *Eugenia s. s.* and *Syzygium s. l.*, particularly if the hitherto neglected features concerning pubescence, bracteoles, and pseudopedicels are emphasized. In addition, both Henderson (1949) and Merrill and Perry (1939) suggested that good distinguishing characters might be found in inflorescence structure. Consequently, the over-all ensemble of organographic differences (Fig. 24) would seem sufficient by itself to warrant the taxonomic acceptance of these two groups. However, there is fairly extensive additional evidence from anatomy and palynology now available, including new data from floral anatomy presented here, that further demonstrates the basic disparity of *Eugenia* and *Syzygium*.

Anatomically, the two genera appear quite distinct. Moll and Janssonius (1918) indicated that their arrangement of species on the basis of wood structure does not support the subdivision of *Eugenia* into *Jambosa*, *Syzygium*, etc. However, the more comprehensive studies of wood by Ingle and Dadswell (1953; also the preliminary report by Dadswell and Ingle, 1947) reenforce the concept that at least two genera are represented within *Eugenia s. l.*: (1) "*Eugenia A*" (a designation

of Ingle and Dadswell, 1953), including the New World species plus several Old World species possibly referable to *Jossinia*; and (2) the quite different "*Eugenia* B," including *Acmena*, *Cleistocalyx*, *Syzygium*, and a number of Australasian species described under *Eugenia* but probably referable to *Syzygium* because of similar wood (Ingle and Dadswell, 1953). Chattaway (1959) also studied wood of *Eugenia s. l.*, upheld the distinction between "*Eugenia* A" and "B," and included seven additional species in "*Eugenia* A" and 12 in "B." Evidence from bark anatomy (Chattaway, 1959) and palynology (Pike, 1956) also supports the separation of "*Eugenia* A" and "*Eugenia* B." Unfortunately, the cytological evidence is so scanty and inconclusive that it is thus far of no help (see Fedorov, 1969; Moussel, 1965, for literature).

My studies (Schmid, 1971) show that there are also some profound anatomical differences in the flower between the mainly American species of *Eugenia s. l.* (Ingle and Dadswell's "*Eugenia* A") and most of the extra-American species ("*Eugenia* B"). These differences are listed in Fig. 24.

Syzygium s. l. has an axile ovular system whereas *Eugenia s. s.* has a transeptal one (Fig. 20–24). I consider this character to be a basic one indicating the generic discreteness of these taxa. In fact, Eyde (1967, p. 177), who discussed the significance of these types of ovular supply and their occurrence in various angiospermous families, regarded the transeptal ovular system to be "a family character of [the] Cornaceae" and used it to exclude such taxonomically puzzling genera as *Curtisia*, *Corokia*, *Melanophylla*, and *Kaliphora*.

Figure 24 gives a number of other anatomical differences between the flowers of *Syzygium s. l.* and *Eugenia s. s.* The fact that the former tend to be moderately to strongly tanniferous, whereas the latter tend to be only slightly so, suggests that these taxa may also differ chemically. The occurrence of sclerenchyma in flowers of several species of *Syzygium s. l.* and its absence in *Eugenia s. s.* may be related to floral size and perhaps the concomitant adaptation to ornithophily or chiropterophily (Schmid, 1971). These modes of pollination have been reported for *Eugenia s. l.* (Grant, 1950; Knuth, 1904; van der Pijl, 1936, 1956; Porsch, 1941; Werth, 1900).

Thus on the basis of the facts from both vegetative and especially reproductive anatomy, it is difficult to escape the conclusion that there are at least two largely allopatric, co-ordinate groups embraced by *Eugenia s. l.*: the strictly Old World genus *Syzygium s. l.* and the mainly New World genus *Eugenia s. s.* Furthermore, this anatomical evidence warrants the taxonomic acceptance of these two groups despite the fact that the gross organographic differences between them are not entirely clear-cut. The fact that the anatomical

and organographical differences are largely correlated with geographical separation in the Old and New World strongly indicates that we are dealing with two long-separated lines of evolution.

The transeptal type of ovular system occurs rather infrequently in angiosperms (Eyde, 1967; Schmid, unpublished data). In the Myrtales a transeptal ovular supply is known only in the Oliniaceae (Rao and Dahlgren, 1969), Onagraceae (Baehni and Bonner, 1948, 1949; Bonner, 1948; Carlquist and Raven, 1966; van Tieghem, 1875), Punicaceae (Berg, 1857–59, pl. 8, 9; Sinha and Joshi, 1959; Tung, 1935), Thymelaeaceae (Heinig, 1951), and Myrtaceae. In the Myrtaceae most genera of the subfamily Myrtoideae have a transeptal ovular supply (Schmid, 1970; unpublished). However, only an axile system apparently occurs in the Leptospermoideae. I discovered an axile system in *Eucalyptus micrantha*, *Leptospermum scoparium*, and *Tepualia stipularis* (Schmid, 1970). In addition, published figures indicate only the axile supply to be present in the following Leptospermoideae: *Angophora* (Petit, 1908), *Baeckea* (Rastogi, 1951), *Callistemon* (Polunina, 1958), *Calothamnus* (Petit, 1908), *Eucalyptus* (Baccarini, 1884; Carr et al., 1970; Niedenzu, 1893; Petit, 1908; Zucconi, 1958), *Leptospermum* (Rastogi, 1951), *Melaleuca* (Baccarini, 1884; Leins, 1965), and *Metrosideros* (Baccarini, 1884). The ovular system in series *Corymbosae* of *Eucalyptus* (Carr et al., 1970) may be somewhat intermediate between the axile and transeptal types, but the very clear diagrams of *Eucalyptus* in the little-known paper by Baccarini (1884) show a very definite axile system.

In view of its sporadic occurrence in the angiosperms and in the Myrtaceae, the transeptal supply clearly seems to be derived. However, this does not necessarily mean that *Syzygium s. l.*, with an axile ovular system, is ancestral to *Eugenia s. s.*, with a transeptal system. If the other characters listed in Fig. 24 are evaluated by the traditional dogmas of anatomy and organography, it is evident that presumably primitive and presumably derived characters are fairly well combined in each of the two genera. Thus, the many organographic similarities between *Eugenia s. s.* and *Syzygium s. l.*, which have made life so difficult for the working myrtalean taxonomist, presumably resulted from parallel evolution in the two groups after they had arisen from the same ancestral stock, an ancestor no doubt with an axile ovular system. The divergence of *Eugenia* and *Syzygium* apparently occurred in the distant past, and neither genus is directly ancestral to the other. This echoes the situation of the two main lines in *Eucalyptus* (Carr and Carr, 1962). The Myrtaceae, indeed the Myrtales as a whole, are well represented in both Paleogene and Neogene deposits of India, and *Syzygium* is known from the Miocene of India (Lakhanpal, 1970). The con-

siderable variation in organography and vasculature of *Eugenia s. l.* suggests that the complex may still be undergoing rapid evolution.

In Fig. 24 I purposely displayed the taxa I recognize as "clusters" rather than as "phylogenetic lines"; the rationale for the circumscription of these taxa is given in Schmid (1971; in press b). With a literal interpretation of vasculature (see Schmid, in press a, for the pitfalls of this), and particularly with a penchant for reduction series, a botanist might attempt to contrive a phylogenetic scheme for the species of *Eugenia s. l.* reported here. However, in view of our present state of ignorance about the Myrtaceae, I believe that unbridled phylogenetic speculation would accomplish little and would probably lead to error. Finally, the recent papers of Carlquist (1969) and Eyde (1971) remind us that consistent differences in histology or vascular patterns can adequately serve as useful taxonomic markers although their phylogenetic or even functional significance remains obscure.

NOTE ADDED IN PROOF—The analysis of an additional 19 species of *Eugenia s. s.* (including the segregate *Jossinia*) and an additional 21 species of *Syzygium s. l.* (including samples of such segregates as *Acmena*, *Caryophyllus*, *Cleistocalyx*, *Aphanomyrtus*, *Piliocalyx*, *Pareugenia*, *Tetraeugenia*, *Pseudoeugenia*, *Acmenosperma*, *Xenodendron*, *Acicalyptus*, and *Jambosa*) substantiates the anatomical differences listed in Fig. 24. A few of the large-flowered American species of *Eugenia s. s.*, however, have sclerenchyma in the flowers (this perhaps to be expected from a functional viewpoint), and a number of species have very tanniferous flowers.

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