

EVOLUTION IN THE MYRTACEAE – EVIDENCE FROM INFLORESCENCE STRUCTURE

BARBARA G. BRIGGS and L.A.S. JOHNSON*

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Synopsis

A review of relationships of the Myrtaceae, and other families commonly referred to the Myrtales, results in a restricted view of the Order and tentative recognition of Lythrales as distinct. Within the Myrtaceae an informal classification into alliances, suballiances, and infra-alliances is presented, based on evidence from all available sources, particularly embryo and trichome types. Seven alliances (approximating to tribes) are recognized in the subfamily Leptospermoideae, and six in the Myrtoideae. The 144 generic groups recognized are listed, often with comment on their status and relationships. Realignments include the placement of *Osbornia* (*Osbornia* alliance) in the *Myrtoideae*, *Basisperma* in the *Kania* suballiance of the *Metrosideros* alliance, *Eucalyptopsis* (with *Allosyncarpia*) and *Eucalyptus* s. lat. (10 generic taxa) as separate alliances, *Baeckea* et aff. (*Baeckea* suballiance) in the *Chamelauctum* alliance, *Paivaea* in the *Cryptorhiza* alliance, and *Syzygium* et aff. in the *Acmena* alliance (separate from the *Eugenia* alliance).

The primitive inflorescence in Myrtaceae follows an opposite-decussate pattern with flexibility in the development of apical buds of major terminal and lateral axes, these either producing vegetative growth or terminating in a flower; branches lateral to a flower-terminated branch also end in flowers. This flexibility cuts across the division of inflorescences into closed (anthotelic) and open (blastotelic) types. From a primitively flexible condition there has been a limitation of inflorescences (uniflorescences) to lateral or terminal positions, and a stabilization to anthotelic panicles or to units equivalent to the lateral branches of panicles. The chief trends, repeated in parallel in many groups, have been: stabilization of position and form, demarcation, reduction of branching, some elaboration of branching (often by accessory axes), phyllotactic change (from opposite-decussate to disjunct-opposite or disperse), and reduction in number and length of internodes. Where the branching systems of different orders are qualitatively different, a distinction between *uniflorescence* (in this case anthotelic) and *conflorescence* (here blastotelic) is useful. Many cases involve aggregation of the latter into *superconflorescences*. The inflorescence features of each of the recognized genera are summarized and some functional aspects are discussed.

The approach to inflorescence analysis adopted rejects the typological basis of W. Troll's system, but draws upon his descriptive studies and organography. Some new terms are introduced in order to permit more logical (but not theory-limited) description and comparison of inflorescence types.

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*National Herbarium of New South Wales, Royal Botanic Gardens, Sydney, Australia, 2000.

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1. INTRODUCTION

A great diversity of inflorescence form is apparent in the Myrtaceae — in the Australian members alone, Bentham (1867) referred to panicles, corymbs, umbels, cymes, spikes, heads, and solitary flowers. Authors such as Bentham (1869), Merrill and Perry (1939), McVaugh (1956a, 1968), Carr and Carr (1959), Dawson (1968a, 1970b, 1970c, 1972b, 1972d), and Johnson (1972, 1976) have appreciated the importance of inflorescence features in phylogenetic or classificatory studies in the family. However, the inflorescences of many genera have not been described with any attempt at comparative interpretation, and the extent of reduction and aggregation of inflorescences in many groups has not been recognized.

We attempt here to contribute to several diverse subjects:

- (i) the probable primitive inflorescence condition in the Myrtaceae, together with the phylogenetic trends that have led to the present diversity;
- (ii) a survey of inflorescence features in all genera, and some review of phylogenetic relationships in the light of inflorescence conditions;
- (iii) the relationships of Myrtaceae with other families and the affinities, in turn, of the families that have been placed in the Myrtales in recent systematizations of the higher-level taxonomy of the angiosperms;
- (iv) generic and suprageneric classification within the Myrtaceae;

- (v) the systematization of inflorescence analysis and the development of logical descriptive terminology of inflorescences.

Of these, (i) and (ii) are the primary aims of the study; (iii) is included to determine whether conditions in allied families throw light on the primitive condition in Myrtaceae and also for its intrinsic interest; (iv) is necessary to provide some systematic framework for the presentation of our findings; and (v) arises from problems found in applying existing systems of inflorescence analysis and description.

The survey of inflorescence conditions in Myrtaceous genera requires considerable discussion both of the systematic framework and of inflorescence features. This necessitates a sequence of topics that is unfortunately not equally logical for all aspects. The affinities of the Myrtaceae and relationships within the family are treated first, followed by various general and particular aspects of inflorescences.

We have examined herbarium specimens or (in a minority of genera) fresh material, and have recorded features from a wide and representative range of species of all available genera. Sometimes the observations are incomplete because the available material was fragmentary or very limited in range of seasonal stages or because the inflorescences were partially obscured in mounted herbarium specimens. Unfortunately we were not able to re-examine material in some cases where observational discrepancies or the need for changes in concept became apparent late in the study. Particular attention was given to species doubtfully included in the genera to which they are currently referred or considered by other authors to be aberrant. Material was studied at the following institutions: Australian and some non-Australian taxa at the National Herbarium of New South Wales; Central and South American species at the herbaria of the University of California (Berkeley), the Rancho Santa Ana Botanic Garden (Claremont), and the Missouri Botanical Garden (St. Louis); Pacific species at the Bernice P. Bishop Museum (Honolulu); and various groups not readily located elsewhere at the herbaria of the Royal Botanic Gardens at Kew and Edinburgh. We could not, in general, check the identities of the many hundreds of specimens studied but these were compared with others filed under the same names, at specific and generic level, in an attempt to avoid gross misidentifications. The publications of McVaugh (1956a, 1956b, and particularly 1968) have been of great value in the generic placement of American species.

2. AFFINITIES AND THE SYSTEMATIC FRAMEWORK

2.1 *Which families are allied to the Myrtaceae?*

Concepts and circumscriptions of the Myrtales, and of more inclusive groups including Myrtaceae, have varied over the years. Here it will be sufficient to consider the more comprehensive treatments since the early 1960s and to set out (Table 1) the family placements in the systems of Melchior (1964), Cronquist (1968), Takhtajan (1969 and, more fully, 1970), and Thorne (1976), together with relevant indications of opinion by Corner (1976), in his survey of seed structure in dicotyledons, and to review these in the light of such other evidence as is available. The study by Young and Watson (1970), based on a phenetic numerical analysis without interpretation or reference to evolutionary direction, results in placing Myrtaceae with Cactaceae; Melastomataceae near Rutaceae; and Onagraceae with Convolvulaceae, Violaceae, Oxalidaceae, and other strange bedfellows. We cannot take this kind of arrangement seriously nor can we accept the methodology, the comparability or sufficiency of data, or the approach to the theory and practice of taxonomy embodied in Young and Watson's paper.

TABLE 1
Families that have been included in Myrtales

Family	Melchior	Cronquist	Takhtajan	Thorne	Corner	Suggested Placement
Myrtaceae (incl. Heteropyxidaceae)	M	M	M	M	"Myrt. gr."	M
Psiloxylaceae	—	—	—	—	—	M
Melastomataceae (incl. Memecylaceae)	M	M	M	M	"Myrt. gr."	M
Oliniaceae	M	M	M	M	—	M
Penaeaceae	Thymelae.	M	M	M	"Myrt. gr."	M
Lythraceae	M	M	M	M	"Lythr. gr."	Lythr.
Sonneratiaceae	M	M	M	M	"Lythr. gr."	Lythr.
Punicaceae	M	M	M	M	"Lythr. gr."	Lythr.
Trapaceae (= Hydrocaryaceae)	M	M	M	M	"Lythr. gr."	Lythr.
Combretaceae	M	M	M	M	"Lythr. gr."	Lythr.
Onagraceae (= Oenotheraceae)	M	M	M	M	"Lythr. gr."	Lythr.
Crypteroniaceae	M	M	Saxifrag.	M	—	Lythr.
Haloragaceae (incl. Gunneraceae?)	M	Halorag.	Hippurid. (= Halorag.)	Corn.	"Halorag. gr." (Lythr./M)	aff. Lythr./M
Rhizophoraceae s. lat. (incl. Anisophylleaceae and Legnotidaceae?)	M	Corn.	M	Corn.	"Myrt. gr." (excl. Legnotidaceae)	aff. The.? (heterogeneous?)
Thymelaeaceae (incl. Gonystylaceae?)	Thymelae.	M	Thymelae. (aff. Euphorbi.)	M	Thymelae. (aff. Malv. — Euphorbi.) (but not typical)	aff. Euphorbi. or Malv.
Lecythidaceae (incl. Barringtoniaceae)	M	Lecythid.	M	The.	"Myrt. gr."	Dilleniidae? (not M)
Theligonaceae (= Cynocrambaceae)	M	Halorag.	Theligon.	Rubi.	aff. "Centro- spermae" (Caryophyll.)	Rubi. (in Rubiaceae)
Dialypetalanthaceae	M	M	Gentian.?	?	—	aff. Gentian. or Rubi.
Cynomoriaceae	M	Santal.	Santal.	Santal.	—	Santal.? (not M)
Hippuridaceae	M	Halorag.	Hippurid. (= Halorag.)	Corn.	—	aff. Solan.

Comparison of suggested placement with those by Melchior (1964), Cronquist (1968), Takhtajan (1970), Thorne (1976), and Corner (1976). Key: M = Myrtales, other orders abbreviated by omission of ending "-ales"; Myrt. gr., Lythr. gr., Halorag. gr., respectively = Myrtaceae, Lythraceae, and Haloragaceae groups; "—" family not mentioned. Thorne treats Sonneratiaceae, Punicaceae, and Crypteroniaceae as subfamilies of Lythraceae, and includes Hippuridaceae within Haloragaceae. Corner regards Legnotidaceae as probably distinct from Rhizophoraceae and as being a doubtful member of his Myrtaceae group.

Information on general flower and fruit morphology is largely omitted in this paper, but is taken into account by us and by various authors cited. Greater detail of chemical, anatomical, seed, pollen, and embryological features can be found in the works cited in this section and in references therein. Comment on inflorescences in the families considered here is given in a later section (4.2) together with necessary discussion of their bearing on classification.

2.1.1. Exclusions: families of distant or doubtful affinity

Two families can readily be eliminated from further consideration. Hippuridaceae and Cynomoriaceae each constituted a separate suborder in Melchior's system and were included by him with an expression of doubt. As pointed out by Hegnauer (1964: 227), the Mediterranean family Cynomoriaceae has been referred to Myrtales only because of a supposed relationship with Hippuridaceae. It is placed in Santalales by Cronquist, Takhtajan, and Thorne, though not resembling any other

member of that order in pollen morphology (Erdtman, 1952) and virtually unknown chemically (Hegnauer, 1964); the characters of the single species (a leafless parasite) show no particular resemblance to those of any supposed member of the Myrtales. Hippuridaceae, as Hegnauer (1966: 238, 267) very firmly states, can hardly belong with the Haloragaceae (or the Myrtales). The presence of pseudo-indicans (i.e. iridoid compounds) and absence of ellagic acid (and indeed of tannin-substances in general) are chemical characters strikingly different from those of all the other families under consideration, and appear to be of particular phylogenetic significance (Kubitzki, 1969). They support the relationship with Solanales indicated by Pulle (1952), who placed the family in a monotypic order Hippuridales (which does not, of course, correspond with Takhtajan's use of "Hippuridales" for an order containing Haloragaceae). The unitegmic and tenuinucellate ovules are consistent with this. The absence of ellagic acid contra-indicates Thorne's assignment of the Hippuridaceae to the Cornales.

The monotypic Brazilian *Dialypetalanthus*, treated as a separate family of the Myrtales by Melchior and by Cronquist, and dubiously referred to Gentianales by Takhtajan, is among Thorne's few "*taxa incertae sedis*"; affinity with Loganiaceae or Rubiaceae has been suggested by other authors. Its characters (especially the definitely 2-seriate arrangement of rather numerous stamens, large stipules, absence of intraxylary phloem, and seeds with oily endosperm) do not suggest any close relationship with Myrtaceae, nor is there convincing evidence of affinity with other families listed in Table 1. Chemical information is lacking, but if ellagic acid were found to be absent and iridoid substances present, then an affinity with Gentianales or Rubiales would be supported and relationship with any "Myrtalean" group contra-indicated — and *vice versa*.

Melchior included Theligonaceae (Cynocrambaceae) because they "show evident relationships" with Haloragaceae and do not belong to the Centrospermae (Caryophyllales). It appears that he was correct only in the latter statement (despite Takhtajan's referral of the group to the Caryophyllidae), since morphological evidence (Wunderlich, 1971) indicates that the sole genus *Theligonum* belongs in the Rubiaceae. Support is given chemically by the presence of anthocyanins (rather than betalains as in the Caryophyllales) as well as of iridoid compounds (Fairbrothers *et al.*, 1975, and references therein), and ultrastructurally by the existence of starch-accumulating (S-type) sieve-tube plastids (Behnke, 1975) as in Rubiales (and many other groups) rather than protein-accumulating (P-type) plastids as in Caryophyllidae. Iridoid substances are absent from Myrtales s. lat., but do occur in Cornales to which Thorne refers Theligonaceae; the distribution of plastid-types in these orders appears still to need investigation.

Lecythidaceae are placed by Cronquist as an order of his subclass Dilleniidae (corresponding generally to Thorne's superorder Theiflorae), and Thorne includes the family in his broadly-conceived Theales. Takhtajan also comments on a possible relationship with that group, while retaining the family tentatively in his Myrtales. Embryological features, centrifugal stamen development and lack of intraxylary phloem are all given as reasons for exclusion from the Myrtales; we have given weight to these features in following this exclusion. Corner, while including Lecythidaceae as one of his "Myrtales in the strict sense" on seed structure, also recognizes that in the tenuinucellate ovules and centrifugal androecium there is a resemblance to Theaceae. Nevertheless the Lecythidaceae lack iridoid compounds, which are present in Theales in the narrower sense though not in all orders of the Dilleniidae (Theiflorae). Ellagic acid is present as in the Myrtales and Lythrales and also in the Dilleniales and Theales.

Comparative pollen morphology is as yet inconclusive (Walker and Doyle, 1975). On the whole it seems most likely that the Lecythidaceae belong with the Dilleniid group of orders.

We would also exclude Thymelaeaceae from Myrtalean affinity, despite their possession of intraxylary phloem and vested pits (characters that occur in some other groups as well, e.g. Asteridae, and need closer comparative histological study). Chemically (Hegnauer, 1973), Thymelaeaceae differ importantly from the Lythrales and Myrtales: they lack ellagic acid (indeed tannin-substances in general are almost absent), but contain characteristic coumarins. Hegnauer considers that the toxic substances in Thymelaeaceae indicate a metabolic resemblance of a very particular kind with Euphorbiaceae, and a relationship with that family is probably indicated despite the presence in it of galli- and ellagitannins. Corner firmly places Thymelaeaceae, on seed structure, in his Malvalean complex, which he relates to Euphorbiales and not to the Dilleniid group. Takhtajan likewise suggests a Euphorbialean affinity for Thymelaeaceae, and palynology "helps to confirm the relationship", though particular resemblances must be due to parallelism (Walker and Doyle, 1975). *Gonystylus*, included by most recent authors in Thymelaeaceae, lacks intraxylary phloem, but shows some general anatomical resemblances to Thymelaeaceae (Metcalf and Chalk, 1950); it is little-known chemically (Hegnauer, 1966), but, whether or not it is segregated as Gonystylaceae, it has no particular bearing on the relationships of Myrtales.

To us, the various groups assigned to Rhizophoraceae seem not to constitute a very convincing family assemblage. The tribe Anisophylleae differs from the remainder in disperse rather than opposite-decussate phyllotaxy and in complete lack of stipules, as well as in being strongly aluminium-accumulating (Hegnauer, 1973). The non-mangrove genera differ in wood anatomy from the mangrove group as well as among themselves (Metcalf and Chalk, 1950; van Vliet, 1976). Corner finds the seeds of the mangrove genera and of *Carallia* (which is in a different wood-anatomical group, see above) to have a thick testa as in Myrtaceae, and retains these as Rhizophoraceae s. str.; the only two other genera examined by him (*Gynotroches* and *Pellacalyx*) have a thin testa but a specialized outer epidermis in the tegmen, and he refers these to the separate family Legnotidaceae. Rhizophoraceae as a whole lack the internal phloem and vested pits of the Lythrales and Myrtales; they are said to have centrifugal androecial development (cf. Lythrales, below); some of the non-mangrove genera (including *Carallia*) have toothed leaves with the theoid tooth-type (Hickey and Wolfe, 1975), otherwise unknown in families of supposed Myrtalean affinity. This limited occurrence of the theoid tooth-type is the very shaky basis of Hickey and Wolfe's tentative referral of Myrtales to the Dilleniidae (the general venation patterns could well be convergent, as these authors remark). Cronquist and Thorne both refer Rhizophoraceae to their concepts of Cornales. On the basis of leaf-teeth (Cornales have rosoid teeth) and chemical constituents (Rhizophoraceae lack iridoid compounds, the reverse of the situation in the Cornales s. str. though not in all the families referred to Thorne's probably heterogeneous Cornales), this seems unlikely to be correct; perhaps part at least of the Rhizophoraceae s. lat. are derived from a Dilleniid stock, though not from Theales (which have iridoid compounds). Whether any of the Rhizophoraceae s. lat. are related to Lythrales or Myrtales, and whether they should be treated as one, two, three, or four families, cannot be decided without further study.

Haloragaceae (considered here to be close to or to include Gunneraceae but *not* Hippuridaceae — see above) also lack internal phloem and vested pits (Metcalf

and Chalk, 1950). The leaf-teeth are of rosoid type (Hickey and Wolfe, 1975), in contrast to those of Rhizophoraceae but apparently in agreement with Onagraceae and Trapaceae (see below), as well as with Cornales, where the family is placed by Thorne. The family lacks iridoid compounds (present in Cornales s. str.), and chemically (when Hippuridaceae are excluded) shows general resemblance to the Lythrales and Myrtales, in the vicinity of which it was placed by Cronquist and by Takhtajan. The seeds are endospermic, unlike those of Lythrales and Myrtales, and lack any thickening of either testa or tegmen* (Corner, 1976). The ovules are bitegmic and crassinucellate. On balance, Haloragaceae are probably an offshoot of the Rosid stock, possibly with an origin not too distant from that (those?) of the Lythrales or Myrtales, but not to be included in those orders.

2.1.2 *The Lythrales and Myrtales*

We are now left with the twelve families listed first in Table 1. None of the cited authors mentions Psiloxylaceae or *Psiloxylon*. All of the remainder (though not always in family rank) are included in Myrtales by Cronquist and by Thorne; Melchior excludes only Penaeaceae, and Takhtajan only Crypteroniaceae. Thorne's concept of Myrtales includes only one of the families here excluded, namely Thymelaeaceae, and his order Myrtales is the only member of his superorder Myrtiflorae, regarded as close to the Rosiflorae (Thorne has no higher categories within his "subclass Dicotyledoneae"). Takhtajan's superorder Myrtanae comprises his Myrtales and Hippuridales (= Haloragales, together with the clearly unrelated Hippuridaceae, see 2.1.1) and falls within his subclass Rosidae, but it is noteworthy that he places Thymelaeaceae far away to constitute an order of his superorder Malvanae in the subclass Dilleniidae. Cronquist has no superorders, but his treatment agrees with Takhtajan's in so far as he regards Haloragales as close to Myrtales within a subclass Rosidae. Extraordinarily, he also regards Proteales as close to Myrtales, because of a supposed link through Thymelaeaceae and Elaeagnaceae. So far as we can see, the morphological and chemical evidence does not support a close relationship of Thymelaeaceae with Myrtaceae (see 2.1.1), Proteaceae (Johnson and Briggs, 1975), or Elaeagnaceae (Hegnauer, 1966; Thorne, 1976); nor does it support Cronquist's and Takhtajan's referrals of Elaeagnaceae to Proteales or a neighbouring order (Johnson and Briggs, 1975).

Affinity among these twelve families is supposedly indicated by their common possession of intraxylary (internal) phloem (bicollateral bundles) and vested intervacular pits, as well as a series of features of vegetative, floral, and pollen morphology (Thorne, 1976). Carlquist and Debuhr (1977) mention septate crystalliferous parenchyma, a tendency for rays to be narrow-multiseriate plus uniseriate with predominantly erect ray cells, and the presence of amorphous deposits in ray cells, as additional features of wood anatomy by which "the order Myrtales can be defined". They include essentially all of the above families in their concept.

These do indeed all appear to possess intraxylary phloem and vested pits (Metcalfe and Chalk, 1950), but as remarked above (2.1.1) those features occur together also in other families, including the chemically different Thymelaeaceae and various Asteridae (e.g. Apocynaceae, Convolvulaceae, Solanaceae, Loganiaceae), and separately in still others (e.g. intraxylary phloem in Basellaceae, vested pits in

*In the seed-coat, the *tegmen* is developed from the inner integument, the *testa* from the outer integument.

Malpighiaceae), so that they must clearly have arisen more than once. The distribution in dicotyledons of the other features mentioned by Carlquist and Debuhr needs checking. The twelve families (so far as known) possess a number of chemical features in common also (e.g. presence of ellagic acid, absence of iridoid substances and of isoquinoline alkaloids — Hegnauer, 1964-73; Kubitzki, 1969), although none of these is exclusive to the group.

Morphologically, however, some of the supposed resemblances do not hold, and there are indications that the complex consists of two groups. Corner (1976), largely from a study of seed structure, divides the "Lythrales-Myrtales" into three groups. He excludes the Haloragaceae (with "simplified" seed-coats), and also the families grouped around Combretaceae, Lythraceae, and Onagraceae (with tenuinucellate ovules; seeds with a fibrous tegmen and with or without a sclerotic mesotesta), from "Myrtales in the strict sense". In the latter he includes Melastomataceae, Myrtaceae, Penaeaceae (but Oliniaceae are not mentioned), and Rhizophoraceae ("excluding Legnotidaceae"), as well as Lecythidaceae. These have seed-coats with a sclerotic mesotesta, but lack any specialized development of the tegmen.

Clearly, such a classification cuts across those of other authors, especially Cronquist and Thorne, which are based on other features. In particular, Rhizophoraceae and Lecythidaceae lack intraxylary phloem; the latter (and probably Rhizophoraceae as well) differ from Myrtaceae also in their centrifugal androecia. Corner's Lythraceae-group and also the Lecythidaceae have tenuinucellate ovules in contrast to the rest of his Myrtales s. str. and to the Haloragaceae, in all of which the ovules are crassinucellate.

It is of particular interest that Mayr (1969) describes (*contra* Thorne, 1976) centrifugal androecium development in Lythraceae (in *Lagerstroemia*, the only polyandrous genus studied) and Punicaceae, together with a general developmental similarity to these families in the flowers of the non-polyandrous Onagraceae. She observes that "die Myrtaceen weichen in allen wesentlichen erscheinenden, untersuchten blütenmorphologischen Merkmalen von den übrigen bearbeiteten Familien, den Lythraceae, Punicaceae und Onagraceae ab". These considerable differences of the Myrtaceae from the other three families named coincide with the ovule and seed differences stressed by Corner, and (in general) with at least one chemical character, the nature of the chief reserve materials in the seeds: starch in Myrtaceae (but also in Trapaceae!), fatty oils in Lythraceae, Punicaceae, Combretaceae, and Onagraceae (also in Rhizophoraceae and Thymelaeaceae), the condition in the other families being unrecorded.

Apart from secondary tooth-like cilia or ill-defined crenulations in some Myrtaceae, leaf-teeth occur amongst these families only in Onagraceae and Trapaceae. Curiously, these families are not mentioned by Hickey and Wolfe (1975), who give the impression that the only toothed-leaved "Myrtales" are some Rhizophoraceae (see 2.1.1); but Onagraceae have toothed leaves and, so far as we can determine from our observations, the teeth are of rosoid type (as indeed they are in Haloragaceae, as reported also by Hickey and Wolfe). The teeth in Trapaceae are curiously two-pronged, but each double tooth appears to be a derivative of the rosoid type. Trapaceae are now often considered closer to Lythraceae (e.g. by Thorne, 1976) than to Onagraceae, but Lythraceae have entire leaves. The starchy seeds of Trapaceae may be a special development associated with the large fruits and the mode of life of these aquatics. In general, this small Northern Hemisphere-family seems to belong with the Lythraceae group rather than near the Myrtaceae.

All told, there seems to be reason to treat these families as falling into two orders: Myrtales *sensu stricto*, and Lythrales. Despite the centripetal *versus* centrifugal androecial development, there are probably grounds (chemistry, leaf-tooth type, general floral morphology) for considering them both as early offshoots of the Rosid group that have lost any trace of divided leaves. Walker and Doyle (1975) remark on the "rosid palynological trends" in the Myrtales s. lat. Corner's suggestion that the Lythrales may have originated from Myristicaceous or Rutaceous stock is not supported chemically: Lythrales lack the isoquinoline alkaloids characteristic of the Magnoliid and Rutaceous groups and, conversely, possess ellagic acid as a constituent. Corner also suggests, however, that the distinctive fibrous tegmen of the Lythrales may have been lost in the Myrtales s. str.; certainly the development of ovules and seeds, as well as of the androecium, needs further study throughout the Lythrales and Myrtales, and in other possibly allied families in the Rosid and Dilleniid lines.

A feature possibly linking the Lythrales and the Myrtales s. str. (and Haloragaceae?) is the presence of rudimentary stipules, as reported by Weberling (1956, 1958, 1960, 1963) in a number of the families that have been referred to the Myrtales, though, curiously, they are wanting in Melastomataceae. Weberling describes single small stipules at each side of the leaf-base in Oliniaceae, Penaeaceae, Sonneratiaceae, and Onagraceae, as well as in Haloragaceae s. str. (excl. Gunneraceae) and Lecythydaceae (the last two not being regarded here as members of Myrtales or Lythrales); in Myrtaceae, Punicaceae, Trapaceae, Combretaceae, and Lythraceae s. lat. several stipular lobes ("*Stipularzipfel*") tend to occur in a transverse row across the leaf-base. Clearly the disposition of these types is at variance with the seed and other characters mentioned above, and also with inflorescence types (4.2), and the significance of the character is difficult to assess. It is of interest that rudimentary stipules do not occur in Thymelaeaceae. The presence of groups of stipular lobes is quite easily seen in many Myrtaceae of both subfamilies, though they are often not present in all parts of the plant. They appear to be absent in the *Eucalyptopsis* and *Eucalyptus* alliances, except sometimes at the cotyledonary node of certain eucalypts (Carr and Carr, 1966).

Eyde (1975) suggests that comparative studies of vascular supply to the ovules may be useful in working out affinities amongst families referred to Myrtales. Both axile (e.g. in our *Acmena* alliance) and trans-septal vascularization (e.g. in *Eugenia* s. str.) are found in Myrtaceae (Schmid, 1972a, b, c), and Eyde reports trans-septal bundles to be general in Onagraceae.

It may be significant that the families of Myrtales s. str. are predominantly southern in distribution, whereas there is a much stronger northern representation in those of the Lythrales.

Several families require a brief special mention:

Within Lythrales, the family Crypteroniaceae, formerly considered to consist of a single genus *Crypteronia*, is enlarged by van Beusekom-Osinga and van Beusekom (1975), and by van Beusekom-Osinga (1977), to include several genera formerly referred to Melastomataceae and other families. The case for this hardly seems to be convincingly borne out by the associated studies of anatomy by van Vliet and Baas (1975), or of pollen by Muller (1975). If the new grouping is indeed well-founded, it would raise the question of cross-relationships between Melastomataceae (Myrtales s. str.) and Lythrales, since *Crypteronia* is regarded by Thorne (1976) and others as included in or very close to Lythraceae (see 4.2 for comment on inflorescences).

The two small African families Penaeaceae and Oliniaceae possess anatomical

features (Mújica and Cutler, 1974; Carlquist and Debuhr, 1977), stipules (Weberling, 1963), and (in the case of Penaeaceae at least) seeds consistent with placement in the Myrtales s. str. Rao and Dahlgren (1969) suggest that Oliniaceae may be related to Rubiaceae, but the features described by them do not support this view at all strongly. These authors (Dahlgren and Rao, 1969) also studied Geissolomataceae, a South African monotype that has sometimes been thought to be allied to Penaeaceae and hence to other Myrtales. Dahlgren and Rao give anatomical (e.g. lack of intraxylary phloem) and morphological reasons for excluding the family from Myrtales. They suggest a relationship with Oleales; Thorne (1976), on the other hand, refers Geissolomataceae to the suborder Bruniineae of his enlarged Pittosporales. Weberling (1963), however, pointed out the existence of small stipules as in many Myrtales s. lat., in contrast to Pittosporales-Bruniineae and to Oleaceae, though not to the stipuliferous Salvadoraceae (placed in Oleales by Thorne).

Psiloxylaceae are discussed below (4.2)

2.2 *Suprageneric affinities within the Myrtaceae*

Some systematic arrangement has been necessary to organize and present the results of the survey of inflorescences, but it would perhaps be premature to introduce here a new formal system of suprageneric taxa. We have arranged the genera in informal alliances, suballiances, and infra-alliances, partly because previously published suprageneric names give very different status to assemblages that we consider to merit approximately equal rank. The names of the alliances have been chosen to correspond with the earliest previously published names in tribal rank, to provide essential continuity of nomenclature if the system is later formalized. Unfortunately, this results in some alliance names not being based on either the best-known or the least specialized genus included (e.g. *Chamelaucium*, *Cryptorhiza*, and *Acmena* alliances). Fig. 1 gives a synoptic view of the suggested phylogeny and Table 2 summarizes the arrangement, together with some information on distribution, fruit, embryo, germination, and trichomes. Information on oil-glands in embryos of the two subfamilies is from Petit (1908). In the *Eucalyptus* alliance, although oil-glands are laid down in the embryo, the schizogenous oil-spaces and oil secretion do not develop until after germination begins (Carr and Carr, 1970). Further details of distribution, especially within Australia, are given by Johnson and Briggs (in press). We have checked representative examples of embryo-types, and the information given on trichomes is largely based on our observations.

Table 3, which is presented after the discussion of various inflorescence features, lists all the genera that we recognize (with whatever degree of certainty as to their status), arranged according to their alliances and subsidiary groupings. The genera are listed alphabetically in Appendix III, with reference to their systematic position.

The characters of the embryo and fruit have rightly been considered as particularly significant in determining major divisions within the family, and were emphasized by de Candolle (1828), Berg (1855-61, many publications, see Stafleu and Cowan, 1976: 185), Bentham (1865, 1869), Merrill and Perry (1938, 1939), Burret (1941a, b), and Kausel (1956, 1957a), but still need further comparative study. So also do floral morphology, anatomy, chemistry, and (within some alliances) karyology. In the past, trichomes have been neglected in the characterization of major groups; they are discussed separately (2.2.2). Some further features distinguishing, or predominating in, alliances and suballiances will be evident from Table 3 and the notes thereto (8.2), as will some of the doubts and problems concerning them.

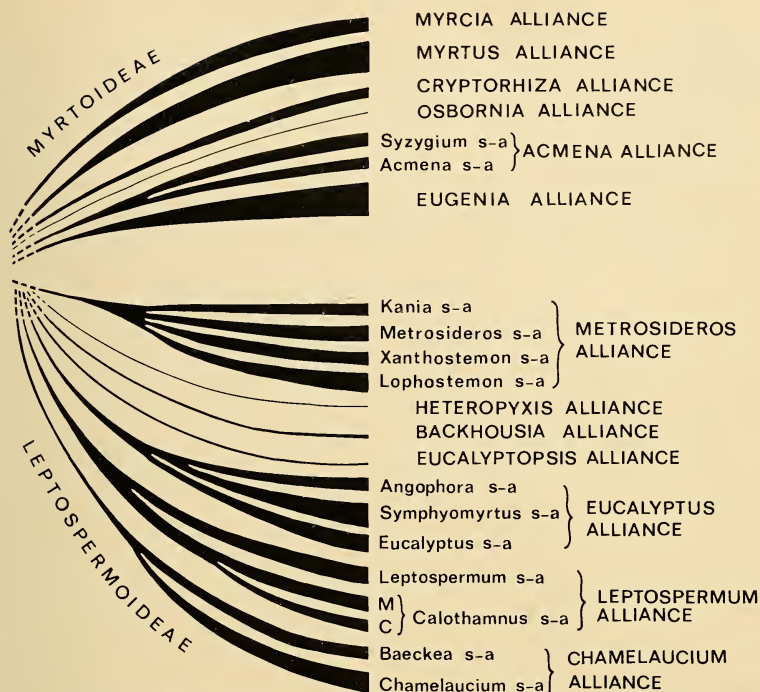


Fig. 1. Suggested general phylogeny of the Myrtaceae. Widths of band-ends convey only a general impression of the diversity of the groups. s-a = suballiance; M = *Melaleuca* infra-alliance; C = *Calothamnus* infra-alliance.

2.2.1 Comparison with previous systems

Two subfamilies have long been recognized in the Myrtaceae. On the whole, these seem to represent natural groups, although the more primitive members of each are more similar than their extreme developments might lead one to expect, and we have here transferred one genus, *Osbornia*, from Leptospermoideae to Myrtoideae. Kausel (1956, 1967) separated the capsular-fruited genera as a distinct family, Leptospermeaceae, which he did not treat in detail. Within his restricted concept of Myrtaceae, he accorded subfamily rank to a number of the groups (some previously treated as subtribes) that we treat as alliances within the Myrtoideae. The Myrtaceae, as generally recognized (and including *Kania* and *Heteropyxis*), appear to us to constitute a very coherent and well-defined family.

The alliances recognized in the Leptospermoideae are here compared briefly with treatments by other authors. We may begin with Niedenzu (1898), who included all except our *Chamelaucium* alliance in a tribe Leptospermeae.

A.I *Metrosideros* alliance. Recognized by Niedenzu as subtribe *Metrosiderinae*. In recognizing the *Kania* suballiance we are in agreement with the grouping of genera suggested by Dawson (1972d), but have added *Basisperma*, which Dawson did not

TABLE 2
Major divisions of the Myrtaceae

Taxon	No. generic Taxa	Distribution	Fruit	Embryo and Copleyons (in seed)	Germination	Trichomes*
A. Subfamily LEPTOSPERMOIDEAE	72	SE. Asia, Australia, Pacific, outliers in S. Africa and Chile	Commonly dehiscent, pericarp usually dry	Straight or folded; oil glands absent or not yet functional. Copleyons foliaceous, often small	Phaneroecylar where known	Standard or multicellular
I. METROSIDEROS ALLIANCE	25	Pacific, Malasia, N. and E. Aust., also gen. aff. <i>Mearnsia</i> ("Metrosideros" sect. <i>Crysalia</i> , i.e. <i>M. angustifolia</i>) in S. Africa and <i>Tepualia</i> in Chile	Usually dehiscent with dry pericarp (indehiscent and succulent in <i>Kjellbergiodendron</i>)	Straight or variously folded or bent. Cots \geq hypocotyl	Phaneroec.	Standard
i. <i>Kenia</i> suballiance	(4)					
ii. <i>Metrosideros</i> suballiance	(10)					
iii. <i>Xanthostemon</i> suballiance	(3)					
iv. <i>Lophostemon</i> suballiance	(8)					
II. HETEROPYXIS ALLIANCE	1	SE. Africa	Dehiscent, few-seeded, ovary superior	Straight. Cots oblong, plano-convex, slightly $>$ stout hypocotyl	?	Standard
III. BACKHOUSIA ALLIANCE	2	E. Australia	Indehiscent, few-seeded, pericarp not succulent	Bent. Cots foliaceous, folded or convoluted	Phaneroec. (<i>Choricarpia</i> pers. comm. Peter G. Wilson)	Standard
IV. EUCALYPTOPSIS ALLIANCE	2	N. Aust. and New Guinea	Dehiscent	Large, straight. Cots broad, flat, contorted, much $>$ short hypocotyl	?	Uniseriate, multicellular, often branched, blunt, thin-walled
V. EUCALYPTUS ALLIANCE	10	Major concentration Aust.; some species of (i) and (ii) in E. Malasia; <i>Arillastrum</i> (f) in New Caledonia	Dehiscent	Bent. Cots thin, broad, deflexed and convoluted, usually much longer than hypocotyl, which is \pm covered by cots	Phaneroec.	Uni- or multicellular, various (see 2.2.2), often absent
i. <i>Agaphora</i> suballiance	(4)					
ii. <i>Symphomyrtus</i> suballiance	(3)					
iii. <i>Eucalyptus</i> s. str. suballiance	(3)					
VI. LEPTOSPERMUM ALLIANCE	14	Major concentration SW. Aust.; well represented in E. and S. Aust.; a few genera also in W. Pacific and SE. Asia	Dehiscent	Straight or curved. Cots thin or plano-convex, sometimes convoluted, $>$ hypocotyl	Phaneroec.	Standard
i. <i>Leptospermum</i> suballiance	(4)					
ii. <i>Calothamnus</i> suballiance	(10)					
a. <i>Melaleuca</i> infra-alliance	(5)					
b. <i>Calothamnus</i> infra-alliance	(5)					

TABLE 2 — continued.

Taxon	No. generic taxa	Distribution	Fruit	Embryo and Coseyledons (in seed)	Germination	Trichomes*
VII. CHAMELAUCIUM ALLIANCE	18	Aust., major concentration SW. Aust.; <i>Egletes</i> also with a few spp. to SE, Asia and New Caledonia	Dehiscent (f) or indehiscent (ff), pericarp not succulent	Straight (f) or with small bent neck bearing cot(s) (f). Cots small, ovate or linear, much < thick hypocotyl	Phaneroc.	Usually absent; multicellular when present or (in <i>Platanthus</i>) unicellular but scarcely standard
i. <i>Breynia</i> suballiance	(5)					
ii. <i>Chamaelirium</i> suballiance	(13)					
B. Subfamily MYRTOIDEAE	72	Major concentrations S. and C. America, SE, Asia, E. Aust., W. Pacific; <i>Myrtus</i> pantropical; <i>Myrtus</i> Mediterranean to Iran, minor of Sahara	Indehiscent, pericarp usually succulent	Various, see under the alliances. Often with oil glands	Phaneroc. or cryptoc.	Standard or very rarely multicellular
I. MYRCIA ALLIANCE	7	S. and C. America	Indehiscent	Cots foliaceous, crumpled and folded around elongate hypocotyl	Phaneroc.	Standard
II. MYRTUS ALLIANCE	29	S. and C. America, E. Aust., New Zealand, New Caledonia, Malasia; a few spp. to S. China; <i>Myrtus</i> isolated in Mediterranean	Indehiscent	Curved or coiled. Cots small, much < elongate hypocotyl	Phaneroc.	Standard
III. CRYPTORHIZA ALLIANCE	7	S. and C. Amer., <i>Platostigma</i> in E. Aust.	Indehiscent	Straight or curved. Cots fused, solid mass enclosing hypocotyl and radicle	Cryptoc.	Standard
IV. OSBORNIA ALLIANCE	1	N. Aust., E. Malasia; on sea-coasts	Indehiscent, pericarp not fleshy	Straight. Cots broad, flat, separate, much > short hypocotyl	Phaneroc.?	Standard
V. AGENA ALLIANCE	8	S. and SE. Asia, Malasia, N. and E. Aust., islands of W. Pacific; <i>Syzygium</i> spp. also in Hawaiian Islands and Africa	Indehiscent	Cots large, plano-convex, fleshy, almost or completely separate (f) or partly fused or closely interlocked and penetrated by the ramifying funicle (ff)	Cryptoc., or phaneroc. in some only of (f)	Multicellular when present, usually absent
i. <i>Syzygium</i> suballiance	(4)					
ii. <i>Armena</i> suballiance	(4)					
VI. RUGENIA ALLIANCE	20	Mostly S. and C. America; <i>Eugenia</i> also from Africa to S. and E. Asia and NE. Aust.; <i>Metroxylum</i> in India; <i>Sterro-coryum</i> in New Caledonia	Indehiscent	Cots as <i>Syzygium</i> alliance type (f) or massive and ± completely fused	Cryptoc. (except <i>Luma</i> phaneroc.)	Standard

*Trichome types are described in 2.2.2.

study. A subtribe Kaniinae was established by Weberling (1966) to accommodate *Kania* alone. The other three suballiances, which may require redefinition, correspond in part to groupings informally suggested by Dawson (1970-1977) and by Peter G. Wilson with J. T. Waterhouse (personal communication).

A.II *Heteropyxis* alliance. Implicitly recognized by Melchior (1964) as a subtribe. Not included in the Myrtaceae at the time of earlier comprehensive treatments. Stern and Brizicky (1958) suggested that "*Heteropyxis* should be placed in Leptospermeae as a subtribe, Heteropyxineae". Such a subtribe was described by Fernandes (1971), but the correct spelling of the name would be "Heteropyxidinae". Fernandes reported the chromosome number $2n = 24$ in *H. natalensis* Harv., whereas $x = 11$ is the base number in the great majority of the family. He added the occurrence of $x = 6$ in *Darwinia* as evidence for the origin of $x = 12$ by polyploidy. This argument is untenable in view of the existence of apparent reduction series from 11 to 6 (Smith-White, 1959) in the highly specialized *Chamelaucium* suballiance, to which *Darwinia* belongs, and the great dissimilarity of that group from *Heteropyxis*.

A.III *Backhousia* alliance. Niedenzu recognized a subtribe Backhousiinae. We have altered the circumscription by removal of *Osbornia* to the Myrtoideae and the inclusion of *Choricarpia* (genus established since 1898). *Choricarpia* has generally been compared with *Syncarpia*, but Ingle and Dadswell (1953) and Bamber (1962) drew attention to the considerable dissimilarity in wood and bark anatomy. Their information supports our conclusion, on general morphological grounds, that *Choricarpia* is very different from *Syncarpia* and is in fact related to *Backhousia*. Affinity with the latter has been independently suggested by Peter G. Wilson and J. T. Waterhouse (personal communication).

A.IV *Eucalyptopsis* alliance. Genera described subsequent to any comprehensive treatment. *Eucalyptopsis* is not allied to *Pleurocalyptus* (*Metrosideros* alliance) as was suggested by White (1951), who described the former. *Eucalyptopsis* and *Allosyncarpia* have no particular relationship to either *Eucalyptus* or *Syncarpia*, despite their unfortunately chosen names.

A.V *Eucalyptus* alliance. Corresponds with subtribe Eucalyptinae of Niedenzu, apart from our addition of *Arillastrum*. See also 8.2.

A.VI *Leptospermum* alliance. Largely equivalent to subtribes Leptosperminae and Calothamninae in Niedenzu's treatment. We remove *Baeckea* together with its allies, and place the *Melaleuca* and *Calothamnus* infra-alliances in the same suballiance, partly on account of similarities in inflorescence and despite the more specialized anthers in *Calothamnus* and associated genera. Therefore our *Leptospermum* and *Calothamnus* suballiances are not coincident with Niedenzu's subtribes.

A.VII *Chamelaucium* alliance. The *Baeckea* suballiance was included by Bentham (1867), by Niedenzu, and in turn by Melchior (1964) as a subtribe (Baeckeiinae) of the Leptospermeae; the genera of the *Chamelaucium* suballiance constituted the tribe Chamelaucieae (as "Chamaelaucieae") of these authors, being accorded higher taxonomic status than our other alliances. The *Chamelaucium* suballiance is a distinctive and coherent assemblage, probably best regarded as an evolutionary grade with its origin amongst early members of the *Baeckea* suballiance. The diversity of chromosome numbers, $n = 11, 9, 8, 7, 6$ (Smith-White 1950, 1954, 1959), contrasts with the general stability in the rest of the family, in which $n = 11$, or rarely 12, 22, or 24.

The suprageneric affinities of the Myrtoideae have received more attention recently than those of the Leptospermoideae, but development of a satisfactory classification in detail must await further study and assessment of relationships of a number of the genera. The group as a whole was treated by Niedenzu (1898) as subfamily Myrtoideae, consisting of the single tribe Myrteae; by Melchior (1964) as a subfamily of 7 tribes; by McVaugh (1968) as a single tribe, Myrteae, including a number of informal groups; but Kausel (1956) treated it as a family consisting of 5 subfamilies. (References to these authors hereinafter are to be taken to refer to these particular publications unless otherwise indicated.) Within this framework the alliances that we recognize have been treated as follows (see also 8.2):

B.I *Myrcia* alliance. Recognized by Niedenzu (subtribe Myrciinae), Kausel (subfamily Myrcioideae), Melchior (tribe Myrcieae), and McVaugh ("myrcioid genera").

B.II *Myrtus* alliance. Recognized by the first three authors as Myrtinae (but *Feijoa*, syn. *Orthostemon* Berg non R. Br., excluded as Orthostemoninae), Myrtoideae, and Myrteae respectively, but most of the American members distributed by McVaugh into informal groups clustered around *Psidium* and *Pimenta*. Some genera formerly included here were segregated by Kausel in his Cryptorhizoideae (see below).

B.III *Cryptorhiza* alliance. This grouping, tentatively recognized here, was set up by Kausel (as subfamily Cryptorhizoideae), who was followed in this by Melchior (tribe Cryptorhizeae). Its distinctive embryo character certainly requires further investigation, including developmental study and survey of embryo conditions in additional genera of the subfamily. McVaugh was not convinced that this is a natural assemblage, and distributed its members among several informal groups. Kausel at first included only *Cryptorhiza*, *Legrandia*, *Pilidiostigma*, and *Blepharocalyx*. Later (Kausel, 1967) he enlarged it to include *Campomanesia* and *Britoa* (together with *Blepharocalyx* in a separate tribe, Campomanesieae, which he considered might also encompass *Marlieriopsis* and "*Eugeniomyrtus*" (= *Myrtus* subgenus *Eugeniomyrtus* Kiaersk., not published at generic rank; we have seen no material of the single species "*M.*" *warmingiana* Kiaersk.). We have also tentatively included *Paivaea* because of its similarity to *Campomanesia*, despite absence of information on embryo features.

B.IV *Osbornia* alliance. Not previously recognized; genus referred (e.g. by Niedenzu) to Leptospermoideae, where it was placed in Backhousiinae. Its pericarp is leathery rather than fleshy, but the fruit is indehiscent; features of leaves, flowers, and embryo suggest Myrtoidean affinity.

B.V *Acmena* alliance. Included by Niedenzu in the Eugeniinae, together with members of the *Eugenia* alliance. *Syzygium* and its allies (*Acmena* alliance) and those genera of the *Eugenia* alliance with separate cotyledons were later separated (Kausel, 1956) as Plinioideae. Subsequently, Kausel (1957a) segregated the genera of the *Acmena* suballiance as a subfamily (Acmenoideae) characterized by the branched intrusive funicle. Melchior followed Kausel's later (1957a) treatment, recognizing Plinieae and Acmenae in addition to Eugeniaceae. The *Syzygium* suballiance has not previously been recognized at a suprageneric level, although other authors (e.g. Schmid, 1972c; Legrand, 1975) have been well aware of the distinctiveness of the *Syzygium-Acmena* group as a whole.

B.VI *Eugenia* alliance. Recognized (at levels equivalent to the *Myrcia* alliance) by all four authors, but Kausel excluded the genera with plinioid embryos and placed them, together with the *Acmena* alliance (q.v.), in his Plinioideae. Melchior followed

Kausel's arrangement, but at tribal level. McVaugh included some of the plinioids among his "eugenoid" genera, but placed others in a separate group "*Myrcianthes* and related genera".

2.2.2 Trichome features characterizing Myrtaceous alliances

The "standard" Myrtaceous trichome type, found in four alliances of the Leptospermoideae and in five alliances of the Myrtoideae (Table 2) is acute, rather thick-walled, and unicellular (with no basal cell). Variations within this type are curled, bent, basally saccate, and 2-armed ("biramous") hairs. Rarely the hair is expanded and flattened distally, becoming lobed, umbrella-like, or funnel-shaped. Infundibuliform hairs occur in material of uncertain identity, distributed under the invalid name "*Campomanesia hypoleuca* Hort. ex Gentil.", cultivated in Zaïre, *Thomas 686* (NSW*); Schmid (1972a) reports them in a species of *Eugenia*. A "membrane" is commonly formed across the lumen near the cell base, enclosing the shrunken protoplast (Uphof, 1962); this often gives a misleading impression that the hair consists of more than one cell. The hairs within the ovary of *Pilotheicum* need investigation.

The remaining four alliances lack "standard" Myrtaceous hairs, with the possible exception of *Eucalyptus* s. str. in the *Eucalyptus* alliance and *Pileanthus* in the *Chamelaucium* alliance, but possess trichomes or emergences of other types in at least some members (Table 2). Further features are as follows:

Eucalyptopsis alliance: The description (Blake, 1977) of *Eucalyptopsis* as "perfectly glabrous" appears correct for some specimens, but others (e.g. NGF 17297, in NSW) bear short, often branched, multicellular hairs, which resemble those of *Allosyncarpia*. Standard Myrtaceous hairs are not found. An undescribed and almost glabrous species of this alliance (see 8.2) also has very short trichomes of this general type, at least in some of the axils within the inflorescence.

Eucalyptus alliance: Johnson (1972) drew attention to differences in trichome types. None of the taxa possess an indumentum of "normal Myrtaceous trichomes". They exhibit one or other of the following conditions: (a) trichomes completely absent, (b) trichomes non-"standard" and scattered on surface, (c) trichomes similar to standard form but found only in clusters on special sites on the epidermis, and (d) trichomes non-standard but clustered as in (c). The hair (and bristle) types described are found in only a minority of species in certain supraspecific taxa, as follows:

Angophora suballiance: *Arillastrum* is glabrous when adult; juvenile stages should be studied, since hairs in this alliance are often present only on juvenile growth. Coarse multicellular bristle-glands, enclosing a protruding oil-gland, are found in *Angophora*, "*Blakella*", and "*Corymbia*". These structures are described as glandular hairs by Carr *et al.* (1970) but, since they do not give rise to external secretions in the manner usually associated with glandular hairs, the term "bristle-glands" is preferred. This was used by Johnson (1972), who drew attention to their general occurrence in *Angophora*, "*Blakella*", and "*Corymbia*". Some species of *Angophora* also bear blunt, rather thin-walled, uniseriate, multicellular hairs. "*Corymbia*" produces unicellular hairs that are also usually blunt and rather thin-walled; sometimes ("*Eucalyptus ferruginea* Schau.) such hairs are found only upon protruding oil-glands. Hairs of similar type also occur in some species of "*Blakella*" (e.g. "*E. gilbertensis*" (Maiden & Blakely) S.T. Blake), radiating from prominent oil-glands or bristle-glands.

* Where reference specimens are cited the herbarium in which they are held is indicated by the symbols used in Holmgren and Keuken (1974).

Symphomyrtus suballiance: Juvenile shoots of almost all species of *Eudessmia* have blunt, thin-walled, unicellular hairs in radiating clusters over flat or scarcely prominent glands. *Symphomyrtus* and "*Telocalyptus*" lack trichomes (although the former rarely has pluricellular papillae over glands).

Eucalyptus suballiance: "*Gaubaea*" is glabrous, but juvenile shoots of "*Idiogenes*" may exhibit poorly developed, very short, blunt, unicellular hairs. Much of *Eucalyptus* s. str. is glabrous, but juvenile plants of Series *Capitellatae* and *Olsenianae* (Johnson and Blaxell, in press) have trichomes reminiscent of "standard" Myrtaceous hairs, these being acute, thick-walled, and unicellular. They occur in distinctive radiating clusters over prominent oil-glands.

Members of the *Chamelaucium* alliance are almost all glabrous except for the denticulations or "cilia" frequently occurring on margins of leaves, bracts, or petals (sometimes sharply keeled leaf midribs are similarly denticulate abaxially). These denticulations are often multicellular but, even when unicellular, they lie in the plane of the surface and appear to constitute a minutely laciniate margin, rather than projecting from the plane of the epidermis as in the "normal" Myrtaceous indumentum. Stout multicellular hairs occur on the stems of *Hypocalymma xanthopetalum* F. Muell. and on the perigynium of *Balaustion*. The stiff but silky hairs on the perigynium of *Pileanthus* resemble "standard" hairs except for the somewhat bulbous base and minute apical notch (extending only part way through the wall). Multicellular emergences amongst the stamen bases of some *Baeckea* species, although sometimes called trichomes, are quite dissimilar from the trichomes in Myrtaceous indumenta.

The *Acmena* alliance also lacks "standard" hairs, most members being entirely glabrous. Trichomes occur in a few New Guinea species of *Acmena* and *Syzygium*, e.g. *S. porphyrocarpum* (Greves) Merrill & Perry, and material distributed as *S. puberulum* Merrill & Perry (NGF 12355, 13159). The inflorescence axes and perigynia of these are densely clothed with multicellular trichomes, which are uniseriate or multiseriate (particularly towards their bases), variable in size, and usually blunt; the cells are rather thin-walled, and in *S. porphyrocarpum* contain much tannin.

At least some of the hair types appear to be independent developments, and the presence of trichomes in Myrtaceae can be regarded as indicating relationship only when they are similar in general type.

2.2.3 *The recognition of genera in Myrtaceae*

The last comprehensive treatment of the family to include a full listing of the genera recognized was that of Niedenzu (1898), who accepted 72 genera. Since that time there has been much revision of generic limits as well as description of previously unknown groups, transfer to the family of a few genera previously placed elsewhere, and exclusion of at least one genus wrongly included when first described (*Platyspermatium* Guillaumin, 1950). We do not by any means always accept the narrowest generic concepts proposed, nevertheless 144 groups of generic level are provisionally accepted (but see addendum). These are listed in Table 3 (p. 206), arranged according to their alliances and, as far as practicable, in systematic sequence within the alliances. That table also summarizes our observations on the inflorescences of each genus and is accompanied by notes on the placement and affinities of many genera, as well as on additional inflorescence features. A few of the "genera" are undescribed (except at species level) and several have hitherto been recognized only as infrageneric taxa. Recent work has rendered untenable the most inclusive generic delimitations used in past treatments, but many groups await detailed investigation and some are known only from very incomplete material.

Table 3 is tentative at various points, both as to the recognition and as to the placement of taxa. Although we have examined material widely, we have not been able to search the literature exhaustively or to form opinions in all cases from examination of specimens. The inherently unsatisfactory result of projecting a many-branched phyletic "tree" on to a linear sequence has added to the problems of listing the genera.

The genera are numbered for convenience of reference, and these numbers are also sometimes used elsewhere in this account. Author citations for generic names are omitted (except where essential to avoid ambiguity), being available in Shaw (1973). The only names listed as synonyms are some that have been in fairly common use in recent decades; other synonyms will be found in the standard works cited and, in particular, we have mostly not listed New World generic names for which we accept the synonymization by McVaugh (1968).

In placing genera we have had regard to published classifications and information therein, but have taken particular account of trichomes, androecium, embryo, and wood anatomy.

Space prevents reference to the reasons for the many particular inclusions, exclusions, and placements in the list, but some of the more significant are noted below. Genera that we have not examined, or have studied insufficiently in these respects to form any opinion, are marked * in the following notes. Where we have examined material and also cite references, our conclusions, although sometimes tentative, rest at least partly on our observations, as well as on the information or arguments in the references cited.

(a) Genera included that have frequently been referred to other families:

1 *Kania* (Weberling, 1966)

26 *Heterophyxis* (Stern and Brizicky, 1958; Fernandes, 1971)

(b) Genera recognized at variance with other recent treatments — see Notes to Table 3 (8.2) under the following generic taxa:

7-14 components of *Metrosideros* s. lat.

32-40 components of *Eucalyptus* s. lat.

87 *Mosiera*

89 *Psidiopsis*

119 *Acicalyptus*

128 *Acreugenia*

132 *Paramyrciaria*

133 "*Pliniopsis*"

(c) Genera recognized with particular doubt — see 8.2 under the following:

30 *Allosyncarpia*

69 *Homoranthus*

70 *Rylstonea*

85 *Feijoa*

90 *Corynemyrtus**

108 *Myrtella*

114 *Cryptorhiza**

127 *Pseudomyrcianthes**

136 *Pilotheceum*

141 *Meteoromyrtus*

144 *Hottea*

(d) Genera excluded from Myrtaceae:

Aulacocarpus (Central America); Melastomataceae, included in *Mouriri* (see McVaugh, 1968).

Platyspermation (New Caledonia) (see Erdtman, 1952); among "*taxa incertae sedis*" (unplaced as to family) of Thorne (1976).

Psiloxylon (Mauritius); *Psiloxylaceae* (see Croizat, 1960). The unisexual flowers, entirely superior ovary (indeed virtually stipitate), and the large, lobed, sessile stigmas differ markedly from the Myrtaceae condition; a conceivable common ancestor of *Psiloxylon* and the Myrtaceae would be decidedly un-Myrtaceous, in contrast to such an ancestor for the genera included in the family in the present paper. *Psiloxylon* has intraxylary phloem (Metcalf and Chalk, 1950: 125), but little is known of chemical constituents or seeds. We place it tentatively within Myrtales s. str.

3. THE ANALYSIS OF INFLORESCENCES*

The work of Wilhelm Troll (1954, 1957, and particularly 1964, 1969) goes far beyond that of all earlier authors in its analysis and systematization of inflorescence structure. We have nevertheless found some of his concepts inappropriate for the description and comparison of Myrtaceous inflorescences, and indeed we cannot accept a number of fundamental aspects of his approach to inflorescence analysis (Appendix I). We adopt his terminology only when it is essentially descriptive; otherwise it would not be clear whether or not terms carried their Trollian theoretical implications. Consequently we have introduced certain neologisms, despite the notoriously complex inflorescence terminology already existing, in an attempt to present comparisons of inflorescences in language that is logical, precise, and relatively theory-free. These new terms, which are further discussed in Appendix I, arose in the study of a single plant family, although a large one with diverse inflorescences, but we consider them applicable to inflorescence studies generally, with the reservations that are always necessary in biomorphological terminology.

3.1 *The seasonal growth unit and anthotelic*

In order to provide a frame of reference for specifying the relative positions of nearby axes, we define a SEASONAL GROWTH UNIT (SGU) as a shoot, or branched system of shoots, formed within a single growing season and arising (terminally or laterally) from an axis formed in a previous growing season. Such units within perennial plants are therefore separated from each other by older portions of stem — "older wood" in cases such as the Myrtaceae. Although they are commonly annual, this is not a necessary condition and the degree of demarcation from a former season's growth (e.g. by a zone of scars indicating that there has been an over-wintering bud) may vary greatly. Ramiflorous or cauliflorous inflorescences, arising laterally from old wood, themselves constitute SGU's distinct from new leafy shoots, whether or not the latter are also floriferous.

Various terms have been used elsewhere to designate axes or inflorescences terminated by flowers, in contrast to those that produce flowers only laterally. Troll's term "monotelic" is bound to his particular typological theory and hence distinctly inappropriate, and such terms as "closed" or "determinate" are special applications of words that do not necessarily convey any notion of termination by a flower. We have therefore adopted the following as a precise and logical terminology without theoretical connotations: ANTHOTELIC (from Greek, ending in a flower) applies to

*Some new terms are introduced, and some others may not be generally familiar; they are defined in Appendix II.

inflorescences (or parts of inflorescences) or axes that have also been known as “determinate” or “monotelic”; BLASTOTELIC (ending in a bud or sprout) is used for those without a terminal flower, i.e. “indeterminate” or “polytelic” inflorescences or axes. Within the latter type a further distinction is useful: AUXOTELIC (growing at the end) applies to blastotelic inflorescences or axes that continue growth beyond the flowering region, and ANAUXOTELIC (not growing at the end) to those that terminate in an abortive vegetative apex.

3.2 Terminology of inflorescence types

In allied taxa, or sometimes within a single genus or species, inflorescences commonly show different degrees of elaboration. Generally a common plan runs through such inflorescences, but they differ in the degree of branching and/or in the number of internodes or their elongation, so that different terms (defined in Appendix II) apply to such variously elaborated inflorescences. It has nevertheless seemed appropriate, for the Myrtaceae, to use such terms as *panicle*, *thyrsoid*, *metabotryoid*, *botryoid*, *dichasium*, *triad*, and *monad* when reporting inflorescence conditions, even though many taxa present an array of several such types. It is necessary to stress that *panicle* is used in Troll's sense of “*Rispe*” (Appendix II, Fig. 3), and *not* for a branched “indeterminate” inflorescence as by many English-language authors.

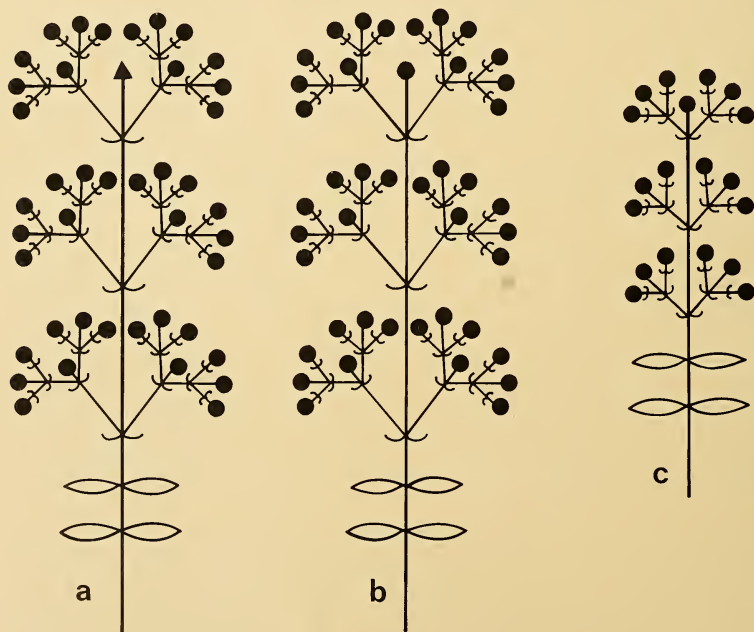


Fig. 2. (a) Thyrsoid (main axis blastotelic), (b) thyrsoid (all axes anthotelic), and (c) metabotryoid (degree of branching may be less than shown at upper nodes of main axis).

Of these terms, *thyrsoid* (as a noun, and in our sense) and *metabotryoid* are newly introduced. A THYRSOID (Fig. 2b) or "determinate thyrse", being anthotelic, bears the same relation to a thyrse (Fig. 2a) as a botryoid does to a botryum in the terminology of Troll (1954: 52). A METABOTRYOID (Fig. 2c) differs from a botryoid in that some at least of its lateral axes produce triads (dichasial groups of 3 flowers) rather than only monads (single flowers). Metabotryoids may result from the phylogenetic (or conceptual, i.e. typological) reduction of either a thyrse (with more elaborated dichasial branches) or a panicle, and it is therefore inappropriate to include them within the thyrse category.

Inflorescences are herein assigned to categories according to the highest degree of branching attained in any part of them. For example, an anthotelic inflorescence in which the lateral branches are 7-flowered or >7-flowered dichasia toward the base, triads in the middle, and monads toward the apex, would be classed as a thyrse.

When appropriate, anthotelic branches (partial inflorescences) forming parts of panicles or thyrses may be described as (lateral) dichasia, triads, etc.

3.3 *Conflorescences*

Inflorescence systems in the Myrtaceae and certain other families commonly involve two or more levels of organization that differ qualitatively in the pattern of branching and the development or arrangement of phyllomes. In order to designate units of a particular level, we have applied the terms *uniflorescence* (U), *conflorescence* (C), and *superconflorescence* (C²). In Myrtaceae and groups with comparable inflorescence patterns, a UNIFLORESCENCE is taken to be an anthotelic branch system (within the SGU) that is lateral to a blastotelic axis. The term is considered to be applicable also more generally to a floriferous branch system of characteristic pattern that is qualitatively different in some way from the axis on which it is borne. A CONFLORESCENCE is then a floriferous branch system of which the main axis bears uniflorescences. A SUPERCONFLORESCENCE (a somewhat looser concept) is a functional aggregation of conflorescences, not necessarily within a single SGU.

Such distinctions do not, of course, apply to inflorescences of all types, and these terms are therefore often inapplicable. Thus we do not use them in those taxa with flexibility as to anthotelic or blastotelic development of axes of a particular order (4, 5), although parts of the branching systems of such taxa may be appropriately equated with uniflorescences. Where the anthotelic inflorescence is terminal on a major axis of the SGU the terms are also inapplicable, since the whole inflorescence is in some ways equivalent to a uniflorescence, whereas in other respects its lateral branches resemble uniflorescences. In such cases there is no distinction between the R₂ and a₁ (see 3.4).

In the case of Myrtaceae, the uniflorescence almost always has opposite and decussate phyllotaxy and branching. Conflorescences have the same phyllotaxy as the vegetative regions of the plant; this is commonly also opposite (sometimes ± disjunct-opposite) and decussate, but some taxa within the Leptospermoideae consistently have disperse (spiral) phyllotaxy.

To emphasize the difference between simple and compound situations, we have described uniflorescences using the names for the different inflorescence types, but have used (for example) *racemiform*, *thyrsiform*, or *spiciform* to describe conflorescences resembling racemes, thyrses, and spikes respectively. These adjectives are used for cases in which the main axis grows on (whether before, during, or after flowering), as well as in anauxotelic conflorescences.

Whether a distinction between uniflorescences and conflorescences is useful in a particular angiosperm group depends, of course, on its inflorescence structure and phylogenetic history of inflorescence modification. Very different from the inflorescences of Myrtaceae are those of Proteaceae (primitively racemose with blastotelic uniflorescences and disperse phyllotaxy), but a distinction between unit inflorescences and aggregations of such, i.e. conflorescences, proved useful in that family also (Johnson and Briggs, 1975). In Myrtaceae, Johnson (1972, 1976) previously applied the term "conflorescence" to systems of umbellastral "uniflorescences" in *Eucalyptus* s. lat., but some reinterpretation of detail is necessary as a result of the present study (see 8.2, A.V *Eucalyptus* alliance and genera 31–40).

3.4 Terms designating axes

It has proved necessary to refer to certain axes of uniflorescences or of conflorescences:

a_1 : The main or primary (first-order) axis of a uniflorescence.

peduncle: The proximal internode below the prophylls of the a_1 ; recorded as "present" in Table 3 if clearly developed, although sometimes short. Where a uniflorescence cannot be distinguished, this term is considered inapplicable.

ANTHODIUM (Fig. 3): The internode between the flower and the ultimate node of the axis that it terminates (sometimes this internode is not elongated). In Myrtaceae and elsewhere the term "pedicel" has sometimes been applied to the anthodium. However, when there are metaxyphylls (see 3.5) or prophylls immediately below the flower, "pedicel" has sometimes been applied to the penultimate internode. Schmid (1972a, b) adopted the latter usage and referred to the ultimate internode as a "pseudopedicel". Henderson (1949) and Wilson (1957) had used "pseudostalk" and "pseudostipe" for this structure. Schmid (1972a) indicates that when the anthodium [our terminology] is elongated it is anatomically indistinguishable from the distal part of the penultimate internode, so there seems no clear reason to regard the anthodium as "part of the flower" (Schmid, 1972a) rather than as an internode of the axis below the flower. The transition from the tapering perigynium base to the anthodium is nevertheless externally very indistinct in many Myrtaceae. Similar conditions, with varying elongation of the anthodium distal to prophylls or "bracteoles", are found in many families; there seems no reason to call such a flower-stalk a "false" pedicel, since it is merely the last infrafloral internode of the axis concerned. Elsewhere, authors have sometimes used "pedicel" or "*Blütenstiel*" indiscriminately to denote the whole "flower-stalk" above the ultimate branch-bearing node, thus including one, two, or even several internodes (and in this respect often varying between side and median flowers).

R_z : The branch from which the a_1 arises (a_1 is lateral to R_z). The symbol R_z refers to the ultimate (z) branch or *ramus*. The R_z is the main axis of the conflorescence.

R_y : The branch from which the R_z arises laterally. In some taxa (e.g. frequently in *Leptospermum*) where the R_z and R_y are capable of continued growth, a branch may be an R_z in one season and then produce laterals that are themselves R_z 's in a subsequent season, thus an axis that is the R_z in relation to one conflorescence may be an R_y in relation to a conflorescence produced in a later growing season. In a few cases, especially when short shoots (brachyblasts) are borne ramiflorously or cauliflorously, branching may reach a level of complication higher than that of superconflorescence, so that one may designate the branch bearing compound brachyblasts as an R_x .

In those genera with anthotelic frondose branches, the same axis functions as a_1 and R_2 , and we avoid these designations as inapplicable.

In well-defined uniflorescences the a_1 does not bear foliage leaves. We have generally noted whether the R_2 is frondose (leafy), bracteose, or frondobracteose, the last indicating a gradual transition from leaves to bracts. Whether the R_2 grows on beyond the flowering region (auxotelic, in contrast to anauxotelic), either before or after flowering, is also recorded.

3.5 Bracteoles: *prophylls and metaxyphylls*

The term "bracteole" has elsewhere been applied to various bract-like structures that are not always equivalent, and is thus insufficiently precise. It is often applied to (one or) two distal "empty" phyllomes (i.e. leaf-organs lacking axillary buds or with such buds not developing further) on an axis terminating in a flower. When the axis is PRONODATE (Appendix II), then the "bracteoles" are also the *first* phyllomes upon it and thus correspond to *prophylls* (*Vorblätter*) as designated by Troll (1964, 1969). The most distal phyllomes (whether or not they are also the most proximal and therefore are *prophylls*) on an anthotelic axis may not be empty; in that case they are not usually termed bracteoles, even though they correspond with bracteoles elsewhere in all respects other than the expansion of the buds in their axils. Nevertheless, it is often useful to indicate whether empty phyllomes are present below the terminal flower of an anthotelic axis. Troll (who does not use the term "bracteole") refers to such phyllomes, if they are distal to the last non-empty phyllomes (*Tragblätter*, our PHEROPHYLLS, see Appendix I), as *Zwischenblätter* ("betwixt-leaves") and we have adopted this term in the Greek-derived equivalent METAXYPHYLLS (Fig. 3). It may be extended to cover the rather rare cases of phyllomes distal not to *prophylls* but to empty *prophylls* (e.g. on an unbranched plurinodate axis); also we adopt Troll's convention that *prophyllar* "bracteoles" (i.e. at the proximal node of the axis) are not regarded as *metaxyphylls*, even though they may be entirely similar in appearance and function (so far as protection of the flower-bud is concerned) to actual *metaxyphylls* elsewhere in the same inflorescence. (Very rarely there may be more than one pair of *metaxyphylls*.) The somewhat artificial distinctions arise chiefly from the different and equally valid reference points: the bottom of the branch-shoot for the *prophyll*; the flower for the "bracteole"; the flower together with lower nodes for the *metaxyphyll*.

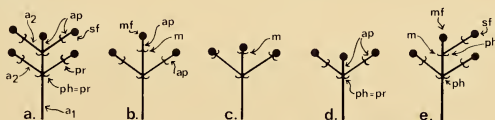


Fig. 3. Botryoid, triads, anthopodia, and metaxyphylls. ap = anthopodium, m = metaxyphyll, mf = median flower, ph = prophyll, pr = prophyll, sf = side flower.

(a) 2-nodate botryoid, anthopodia developed (+), metaxyphylls absent (-). a_1 and a_2 = primary and secondary axes (respectively) in cases where the whole structure shown is a uniflorescence.

(b) Branches at 2nd node not developed so that the relevant *prophylls* of (a) become *metaxyphylls* in (b), and the botryoid becomes a *metaxytriad*; anthopodia +, metaxyphylls +.

(c) As in (b) but anthopodia not developed.

(d) Triad, anthopodia +.

(e) Relatively uncommon condition, where, as a result of development of only one lateral axillary axis, one member of the distal pair of bracts could be regarded as a *metaxyphyll* but the other as a *pherophyll*.

Metaxyphylls do not occur in strict dichasia where the axes are, by definition, uninodate (or at least pronodate). In paniculate systems we generally interpret their presence as indicating reduction of the inflorescence from a type with greater potential for branching. In Myrtaceae a pair of "bracteoles" (prophylls) is almost always associated with solitary flowers (monads), and generally with side flowers (flanking a median flower in a triad). Any bracts between the last branching and the median flower are metaxyphylls.

Inflorescences of the form of triads (Tr) but having metaxyphylls (Fig. 3) are distinguished (Tr*) in the summary of inflorescence conditions in Myrtaceae (Table 3). Similarly M* refers to monads with more than one node on the a_1 . These plurinodate triads and monads (METAXYTRIADS or METAXYMONADS), unlike normal triads and monads, cannot result from the reduction of strictly dichasial systems, but derive rather from paniculate or botryoidal inflorescences.

4. THE PRIMITIVE MYRTACEOUS INFLORESCENCE

4.1 *The general primitive condition in dicotyledons*

Troll (1964, 1969), Weberling (1965), and Stebbins (1974) all stress the division of flowering-plant inflorescences into two principal types: (a) the determinate or monotelic, and (b) the indeterminate or polytelic. (These are respectively (a) *anthotelic* and (b) *blastotelic* in our terminology.) Those authors give examples interpreted as reflecting evolutionary change from the former to the latter in various families and genera. The examples include cases where formerly anthotelic inflorescence types become blastotelic through suppression of terminal flowers and/or change in the pattern of development of the distal region of the inflorescence, e.g. botryoids can give rise to botrya (racemes). Inflorescences of apparently similar "indeterminate" type can result also from aggregation and subsequent reduction of anthotelic inflorescences lateral on a blastotelic shoot, for instance, a racemose structure may arise from a conflourescence of 1-flowered uniflorescences; if the blastotelic main axis regularly fails to grow on (i.e. is anauxotelic) then the resulting inflorescence may be indistinguishable from a "classical" raceme or spike, i.e. from a botryum. Cases of the first type (suppression of flower development distally) involve change in inflorescence-type without change of order (i.e. degree of complexity); those of the second type (aggregation) involve the origin of an *apparent* first-order condition by reduction of a second-order system in which the anthotelic elements form part of the higher-order blastotelic system.

In discussing evolution of anthotelic systems, Troll (1969: 254) accepts views proposed by Nägeli that the panicle may be the basic general inflorescence type in angiosperms (the panicle here being defined broadly to include the thyrsoid).

Such considerations of the general primitive dicotyledonous condition (and of subsequent derived types) are relevant, but cannot be taken as a conclusive argument for any particular condition being primitive within an individual family.

4.2 *Inflorescences in families allied to Myrtaceae*

Families included in the Myrtales in recent treatments are considered above (2.1 and Table 1), where five families are referred to the Myrtales s. str. and seven to the Lythrales. In addition, the Haloragaceae are considered as probably allied to the Lythrales/Myrtales, while seven other families are excluded from this affinity.

Omitting the Myrtaceae from discussion at this stage, the three Myrtalean families for which there is adequate information include anthotelic SGU's in at least

some genera. Panicles (Melastomataceae and Olianiaceae) and botryoids (Penaeaceae) sometimes terminate frondose branches; but there are also smaller inflorescences (including axillary monads), which may result from reduction trends similar to those described below in Myrtaceae (6.2). Accessory branching (6.3.2) is common in Melastomataceae. *Psiloxylon* (Psiloxylaceae) has small axillary racemiform inflorescences; these are perhaps anthotelic (botryoids?), but the limited available material (all dried) is insufficient to determine whether the apparently terminal flower is indeed truly so. Disperse phyllotaxy in the inflorescence (as well as in vegetative regions) and general recaulescence of the bracts increase the difficulty of interpretation. Although we have not definitely observed "bracteoles" in *Psiloxylon*, prophylls (bracteoles of side flowers) are present on inflorescence axes in the other three families. As will be seen below, these inflorescence conditions are largely in agreement with those considered as basic in Myrtaceae.

In contrast to the Myrtales s. str., the Lythrales present a heterogeneous array of inflorescence types. Panicles and a range of fewer-flowered (but still anthotelic) inflorescences in Lythraceae, botryoids in Punicaceae, and solitary flowers in Sonneratiaceae are at least sometimes terminal on frondose branches. Prophyllar bracteoles accompany side flowers and solitary flowers in these families. Botrya (blastotelic) and branched systems of botrya, or single flowers axillary to foliage leaves on blastotelic axes, characterize Combretaceae, Crypteroniaceae s. str., Onagraceae, and Trapaceae. Moreover, these four families all appear to lack prophyllar bracteoles.

Our observations for Crypteroniaceae are limited to *Crypteronia*; material of the other genera included by van Beusekom-Osinga and van Beusekom (1975) in their enlarged concept of the family has not been available for study, and the descriptions of inflorescences (van Beusekom-Osinga, 1977) are in terms too general to determine whether any of them differ in structural plan from that of *Crypteronia*. The inclusion by Thorne (1976) of Crypteroniaceae at subfamilial level (Crypteronioideae) in his Lythraceae is contra-indicated by the discordance of inflorescence types; the other three subfamilies (Lythroideae, Sonneratioideae, and Punicoideae — mentioned above by their names in family rank) are anthotelic.

Thorne regards the Lythraceae s. lat. as the least specialized of the families that he includes in the Myrtales. As shown below in the discussion of Myrtaceae, blastotelic systems can be derived from anthotelic ones. However, in Myrtaceae this has not involved loss of prophyllar bracteoles. Derivation of the Combretaceous type of inflorescence from that found in Lythraceae would have involved several changes: reduction of branching, loss of anthotely, and loss of prophyllar bracteoles. Inflorescence types suggest the division of the Lythrales into two major subgroups; further study is needed to determine whether such a division is supported by other features (see 2.1.2 on the possible significance of leaf-teeth in Trapaceae and Onagraceae; this agrees with the inflorescence grouping).

Inflorescences in other families considered above (2.1) are as follows: in Haloragaceae there is a range from panicles and complex thyrsoids to thyrsoids and monads (Orchard, 1975); the basic type appears to be anthotelic, and prophyllar bracteoles are present. *Gunnera* requires investigation of inflorescences, and indeed of family position (Weberling, 1956). Rhizophoraceae s. lat. include dichasial and paniculate branching systems with frequent loss of median flowers, particularly at the lower nodes. Inflorescences in both mangrove and some non-mangrove genera appear to be basically anthotelic, with prophyllar bracteoles. The irregular bifurcating inflorescences of *Cerriops* and the highly condensed brachyblast systems of *Gynotroches*

require further analysis, as do the inflorescences of the disperse-phyllotactic Anisophylleae. Inflorescences of Thymelaeaceae are diverse and require study, although at least some appear to be anthotelic (e.g. 7-flowered heads in *Phaleria*) and some show prophyllar bracteoles. The Lecythidaceae have botrya with prophyllar bracteoles. Hutchinson (1959) illustrates a panicle with prophyllar bracteoles in the Dialypetalanthaceae, which is consistent with the suggested position in or near Rubiales. Material of the remaining families has not been available for study.

One should bear in mind that anthotelic inflorescences of basically paniculate form are found in other groups for which no particular relationship with Myrtales is suggested, e.g. Rurales, Oleales, Rubiales (Troll, 1969: 2-3, and our own observations). The Rosales and Saxifragales also have basically anthotelic inflorescences (but with secondary departures from that condition); thus this feature in the Myrtales, Haloragales, and part of the Lythrales is generally consistent with a Rosid relationship (see 2.1.1).

4.3 Views of other investigators

Contrasting views relevant to the nature of the primitive Myrtaceous inflorescence have been presented by McVaugh (1956, 1968) and by Dawson (1970b). More recently Dawson (1976) has put forward another contrasting interpretation. Our own conclusions do not agree fully with those in any previous account.

McVaugh (1968) considered that, in the primitive condition, "solitary flowers (i.e. 1-flowered peduncles) occurred in the axils of ordinary leaves on indeterminate branchlets", each flower having two (prophyllar) bracteoles. He concluded that dichasia had arisen by elaboration, secondary peduncles developing from the axils of the bracteoles of the primary flower. The "racemose" arrangement, as in many *Eugenia* species, was explained as resulting from reduction of the subtending leaves (frondose pherophylls) to bracts, with some aggregation of the solitary flowers. He interpreted the panicle ("the myrcioid panicle") as arising from "reduction of leaves to bracts in whole branch systems"; he did not specifically mention that this would involve a switch from the indeterminate (blastotelic) to the anthotelic condition. Previously, however, (McVaugh, 1956) he had taken the view "that the primitive myrtaceous inflorescence is assumed to be one in which the primary axis, and each of the subordinate axes, is terminated by a flower". His discussion at that time referred to some of the difficulties of interpreting and delimiting inflorescences, but did not clearly recognize the problem of establishing the relationship between blastotelic and anthotelic inflorescence types.

Carr and Carr (1959), in discussing *Eucalyptus* s. lat., are among other authors who interpreted inflorescence conditions somewhat similarly to McVaugh (1968), implying that there had been a build-up of essentially dichasial unit inflorescences by elaboration from the single-flowered condition.

Troll (1969: 2) included the Myrtaceae in a listing of characteristically monotelic (anthotelic) families; thus he clearly did not accept the *axillary* flower as basic.

Dawson at first (1970b) regarded the panicle as the basic inflorescence type, noting that

"It is often difficult to define an inflorescence and even more difficult to distinguish a simple from a compound inflorescence. In this series of papers a group of flowers in which the main axis terminates in a flower is regarded as a

simple inflorescence, but when the axis terminates in a vegetative bud the inflorescence is regarded as compound."

Later, however, Dawson (1976) concluded that the basic inflorescence type in *Metrosideros* s. lat. is a dichasial cyme, and that paniculate inflorescences in this group are therefore compound. We are more in agreement with his earlier than his recent views, but would stress the further aspect of "flexible" development, which prevents the primitive condition from being clearly characterized. Nevertheless, Dawson's rule of thumb, quoted above, serves to distinguish between uniflorescences ("simple") and conflorescences ("compound") in the majority of genera — although not in those discussed below under 5.

4.4 *Myrtaceous vegetative morphology*

To understand inflorescence systems, it is essential to look at the flowering shoots in the context of the general vegetative growth patterns of the group concerned. To this end, we present a synopsis of the exomorphological vegetative conditions that may reasonably be inferred, on a comparative basis, to have existed in primitive Myrtaceae. Such relatively unspecialized conditions were presumably adapted to more or less mesic forest habitats, in which the less specialized members of the family still occur, irrespective of the possibility that still earlier ancestors inhabited less mesic sites, according to the hypothesis of Stebbins (1974). These basic conditions, which in some cases are still the most common, can be seen as forming a starting point for numerous vegetative specializations, many of which are also listed below to illustrate the trends and diversity in the family. Certain features of leaves and hairs not of direct relevance to inflorescence systems are also included.

BASIC CONDITION. — DERIVED CONDITIONS.

Cotyledons 2, free, foliose. — Cotyledons folded, lobed, thickened, reduced, or fused.

Germination phanerocotylar. — Cryptocotylar.

Taproot with laterals. — Adventitious roots, sometimes from upper branches (e.g.

Metrosideros spp.), or from slender stems of root-climbers (*Mearnsia* spp.) and of creeping chamaephytes (e.g. *Darwinia glaucophylla* B. Briggs).

Primary stem capable of continued monopodial growth; if this is damaged the replacement stems also monopodial. — Sympodial growth; multinodate axis terminates in anauxotelic bud with acrotonic innovation shoots continuing growth (e.g. *Metrosideros* s. str.; Dawson, 1968b), also, more commonly, partial facultative sympodality associated with flowering regions.

Perennial, woody. [No herbaceous forms, no stem succulents.] — No departures from these conditions.

Leptocaul habit, trunk ± erect, growth ± arborescent, no special modifications of branching. — Shrubby habit, low shrubs, chamaephytes sometimes with prostrate stems (e.g. *Darwinia* spp.). — Root-climbers and epiphytes (e.g. *Mearnsia* spp.). — Production of lignotubers from axils of cotyledons or first few leaves; buds producing new stems arising from lignotubers (mallee habit, especially some of *Eucalyptus* alliance), or more rarely from roots (*Eudesmia* sp. = "*Eucalyptus*" *tetrodonta* F. Muell.) or underground stems ("*Corymbia*" spp.). — Suffruticose habit (Legrand, 1950; White, 1977) from woody underground stems (e.g. *Hexachlamys* sp., some African *Eugenia* spp.). — Ability to sprout from epicormic buds buried in the bark of trunks (e.g. *Tristaniopsis*, *Syncarpia*, most of *Eucalyptus* alliance). — Brachyblasts, vegetative as well as lignogenous.

- Some branching from uniseriate accessory buds (usually phylloscopic).* — Loss of accessory buds.
- Seasonal resting buds not highly developed.* — Perulate resting buds terminating seasonal growth and/or in axils.
- Verticillate phyllotaxy (see Appendix II) with leaves opposite and decussate throughout.* — Ternately verticillate (e.g. *Allosyncarpia*, *Cupheanthus* spp.). — Disjunct-opposite phyllotaxy (e.g. most of *Eucalyptus* alliance but virtually absent in *Arillastrum* and *Angophora*, weakly developed in “*Gaubaea*”). — Disperse (spiral) phyllotaxy (e.g. common in *Xanthostemon* and *Lophostemon* suballiances, *Heteropyxis* and *Leptospermum* alliances). In a few *Symphyomyrtus* spp. the juveniles exhibit disperse phyllotaxy, later reverting to disjunct (see 8.2, No. 36). Reversion to opposite phyllotaxy following spiral phyllotaxy in seedling stage (*Xanthostemon* spp.). — Plagiotropic leaf arrangement due to twisting of internodes or petioles (e.g. *Mearnsia* spp., especially in root-climbers).
- Internodes not of two alternating lengths.* — Nodes bearing foliage leaves (above elongated internodes) alternating with nodes bearing small scale-like phyllomes (above very short internodes), resulting in frondose leaf-pairs being positioned above each other, not at right-angles (decussate) (e.g. *Calypttranthes* spp.).
- Stipule-lobes minute, several in a transverse intrapetiolar row, ± cylindrical or bristle-like.* — Loss (e.g. *Eucalyptus* alliance) or some degree of modification of stipules.
- Foliage leaves dorsiventral, mesomorphic but not herbaceous.* — Similifacial or ± centric (e.g. *Darwinia* spp., *Chamelaucium*). — Enlargement from ± centric to expanded with secondary anomalous venation (e.g. *D. citriodora* (Endl.) Benth.).
- Leaves not deciduous.* — Imperfectly dry-season-deciduous (e.g. some of *Eucalyptus* alliance, viz. spp. of “*Blakella*”, *Symphyomyrtus*, “*Telocalyptus*”).
- Not heterophyllous.* — With serial leaf modification (“leaf spectrum”) within SGU; juvenile leaves more generalized in dorsiventrality and venation than adult leaves; this sequence ± repeated on reversion shoots, produced after damage to main shoots. — Leaves in flowering region much reduced and/or caducous.
- Mesophyllous, ± unspecialized.* — Leaves very large (e.g. “*Corymbia*” spp., *Syzygium* spp., *Cupheanthus*). — Microphyllous or nanophyllous (many *Leptospermoideae*, some *Myrtoideae*). — Pungent (e.g. *Leptospermum* spp., *Acreugenia*), or with drip-tips (especially various *Myrtoideae*).
- Leaf margins entire.* — Margins minutely-laciniate or “ciliate” (e.g. some of *Chamelaucium* alliance); quasi-dentate or crenulate (*Symphyomyrtus* spp.). Never with well-defined, vascularized teeth.
- Leaf venation pinnate, brochidodromous with tendency to develop intramarginal veins.* — Venation with very close parallel laterals spreading from midvein (e.g. *Metrosideros nervulosa* C. Moore & F. Muell., *Angophora* spp., “*Corymbia*” spp., *Decaspermum* sp.). — Some main lateral veins ± parallel to midvein and equally prominent (e.g. *Eucalyptus pauciflora* Sieber ex Spreng.). — Intramarginal and secondary intramarginal veins prominent and ± approaching midvein; leading to basal acrodromous venation (e.g. *Melaleuca* spp., *Rhodamnia*).
- Not glaucous.* — Leaves and shoots glaucous or pruinose (e.g. some of *Eucalyptus*, *Leptospermum*, *Chamelaucium*, and *Acmena* alliances).
- Trichomes unicellular, acute.* — Trichomes 2-armed or infundibuliform (still unicellular). — Trichomes absent (e.g. *Acmena* alliance, many of *Eucalyptus*

alliance). — Quasi-stellate arrangement of trichomes (e.g. juvenile *Eudesmia*, *Eucalyptus* spp.). — Trichomes pluricellular (uniseriate) (e.g. *Eucalyptopsis* alliance, *Angophora*). See also 2.2.2.

Bristle-glands absent. — Bristle-glands present (*Angophora* suballiance, see 2.2.2).

Terpenoid-containing, schizogenous oil-glands present in leaves, young stems, and floral structures. — Incomplete development, almost complete loss.

— Enlargement or proliferation of glands, and sometimes ducts.

4.5 *The primitive Myrtaceous inflorescence — a flexible system*

Earlier in our investigation we considered that the basic condition was a frondo-bracteose panicle, terminal upon a leafy shoot (anthotelic) and with no sharp transition between vegetative and flowering regions (Fig. 4). The diversity of other inflorescence types was seen as the result of reduction of panicles, often accompanied by aggregation. These views now appear to require substantial modification in the light of the situations described below (5). Our present conclusions involve some sharp contrasts with the general concepts of Troll, but owe much to him in that they arise largely from comparison of our findings with his analysis of inflorescences. We are also in accord with his stress on the relation of inflorescences to the branching systems of the vegetative regions of the plant.

An arborescent plant with a growth system as described above (4.4), being many-branched and leptocaul (whatever its more remote ancestors may have been), would not terminate its aerial growth once and for all in an overall flowering (hapaxanthly). Rather, many of its shoots would eventually, under certain internal and external stimuli, pass into a flowering phase while other shoots would remain wholly vegetative. The shoots remaining vegetative might be "leaders" determined by their position in the general architecture of the tree, or might be in a lateral position but in shade.

Present conditions in the Myrtaceae and allied families strongly indicate that, in the ancestors of this group, when the flowering phase was attained, some multinodate frondose shoots would have ultimately terminated in an apical flower. At the nodes beneath such a terminal flower the phyllomes would probably be more or less reduced (*hypsophylls*) but grade proximally into normal foliage leaves. [Both *hypsophylls* and *pherophylls*, respectively equivalent to *Hochblätter* and *Tragblätter* as defined by Troll (1954, 1957), are commonly included in the less precise category of "bracts".] Such *hypsophylls* and foliage leaves would be the *pherophylls* of axillary but usually fewer-noded shoots, themselves also usually ending in flowers. These shoots might themselves branch in the same manner, and so on, the shortest branches having only the single prophyllar node before ending in a flower. In Troll's terminology the branches would constitute a series of *paracladia* of successive orders. Such a system of anthotelic multinodate or plurinodate shoots would constitute a panicle (or a typological derivative of a panicle if less branched or fewer-noded, see 6.2).

However, since the extent of the anthotelic branching system at any time would be ill-defined, depending on whether particular branches had entered the flowering phase, in many cases the bounds of an "individual" panicle could not be clearly specified. (The difficulties of applying Troll's *synflorescence* concept in such cases are discussed in Appendix I, together with other reasons for not adopting it.) In trees of moist forests the seasonal growth units (SGU's), whether vegetative or florigenous, are themselves not always clearly demarcated by resting stages, thus increasing the difficulty of defining the limits of "an inflorescence" (or of a *synflorescence*).

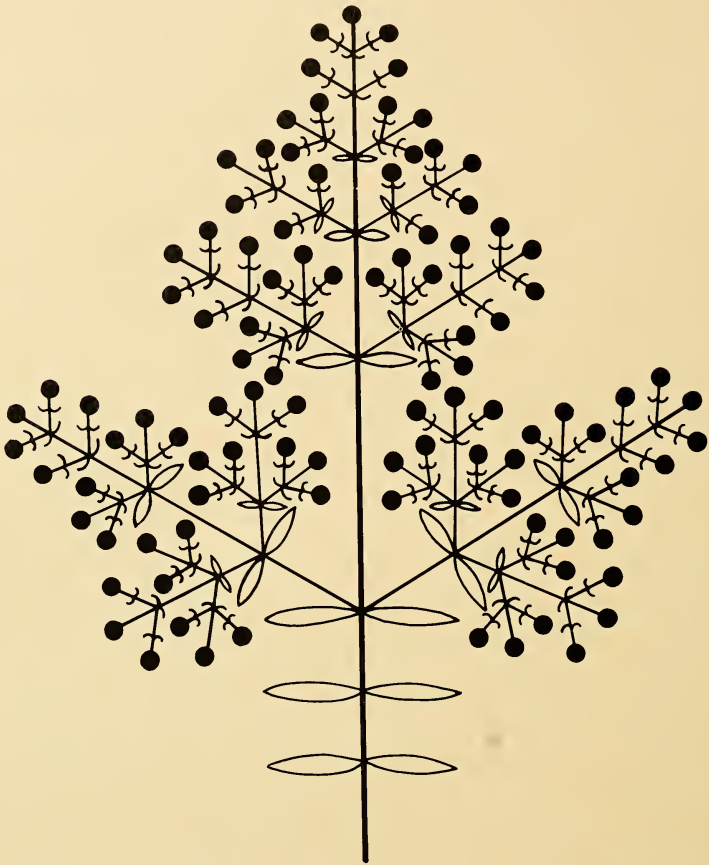


Fig. 4. Frondobracteose panicle. In this, as in subsequent figures, all structures are represented diagrammatically as if in the same plane, although the actual phyllotaxy is opposite and decussate (or disperse and spiral in other taxa). Accessory branching (see Fig. 5) is not shown, although this may be a primitive condition in the Myrtacean line.

It is likely that the tree as a whole would have partially monopodial branching (from auxotelic shoots), augmented by sympodial branching from the development of axillary buds proximal to (or even among) branch regions that had entered the flowering phase; this is the case in many living Myrtaceae.

Comparative study suggests to us that the ancestral Myrtaceous condition was of the essentially flexible nature postulated above, as indeed it remains in certain living

members of the family. In these, when a shoot comes into the flowering stage, the shoot apex may possess the potential either to produce vegetative growth or to terminate in a flower. In the following account we shall refer to SGU's on the understanding that sometimes even these are not very well defined.

The variable potential of the apices may affect the main axes of the SGU and also the secondary or higher-order axes, but the latter generally have a greater likelihood of becoming floriferous. Likewise, terminal and axillary buds arising from a previous SGU (i.e. from older wood) may be similar in their potentialities for development, but commonly they differ in the extent of branching and/or growth, so that lateral buds often produce anthotelic axes while terminal buds develop vegetative axes, which in turn produce anthotelic laterals.

Evidence for this flexibility comes from the observations (i) that a number of genera, in both of the subfamilies and a majority of alliances, show such instability within species or sometimes within individuals, and (ii) that where the inflorescence pattern has stabilized this may be to either a terminal condition (anthotelic SGU) or, much more commonly, to anthotelic lateral flowering branches (uniflorescences) of a blastotelic SGU.

A basically flexible condition seems likely to have been the starting point for separate trends, in many evolutionary lines, to stabilized patterns of inflorescence position and development. The great majority of these lines show increased distinction between auxotelic main leafy stems and anthotelic floriferous lateral branches within the SGU. However, flexible conditions persist in a number of genera, while in others the trend has resulted in the floriferous SGU's themselves being regularly anthotelic. As further developments, such anthotelic SGU's may be more or less sharply distinguished from purely vegetative SGU's and may be produced terminally, laterally, or in both positions, from an earlier SGU. Perhaps only in "*Telocalyptus*" (*Eucalyptus* alliance) and in most species of *Syzygium* and its allies of the *Acmena* alliance are all flowering SGU's anthotelic. Except for the *Leptospermum*, *Chamelaucium*, and (perhaps) *Eugenia* alliances, all alliances have some members that retain anthotelic major axes, though in most cases these are greatly in the minority.

5. ANHOTELIC/BLASTOTELIC FLEXIBILITY

We may consider certain examples in some detail as illustrative of the flexible anthotelic/blastotelic condition. Since both flexible conditions and more or less fixed anthotelic SGU's are often found in closely related taxa, it will be convenient to discuss the anthotelic cases together with further examples of flexibility before treating general trends of inflorescence modification and aggregation.

These are based on examination of a wide range of herbarium specimens, and in some cases fresh material, from which representative examples are selected for illustration.

5.1 *Flexibility* in *Decaspermum paniculatum* (Lindl.) Kurz

We have not observed any anthotelic first-order axes within an SGU but the second-order and higher-order axes may produce:

- (a) both terminal and lateral paniculate shoots, so that the whole (or at least the distal region) is a panicle and ends in a flower, or
- (b) lateral paniculate shoots only, the apical bud retaining the capacity for continued growth (auxotelic).

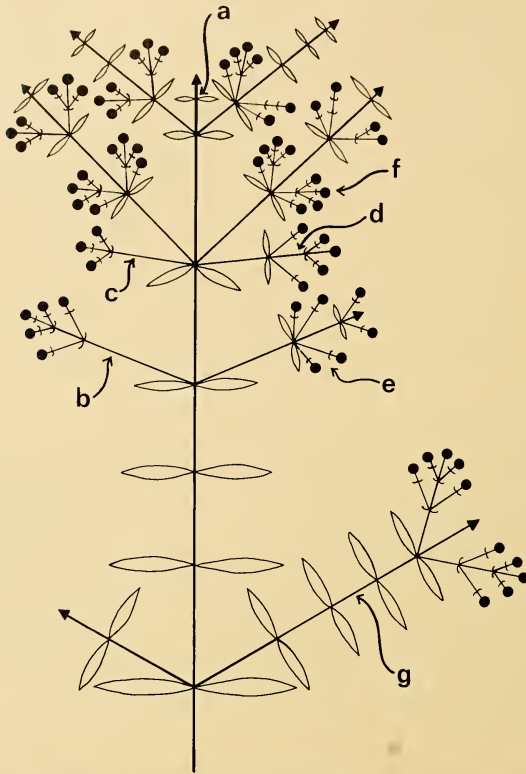


Fig. 5. Flexibility of inflorescence development in *Decaspermum paniculatum*. The primary axis of the SGU (a) is blastotelic (and auxotelic); most of the secondary axes are also blastotelic and auxotelic, but (b) is anthotelic. At any node the major lateral axis may be accompanied by a phylloscopic accessory axis; often the major branch is blastotelic and the accessory is anthotelic (c, d), or both may be anthotelic (f). Accessory axes may show the same degree of branching as the main laterals at that node (e), or be less branched (f). The secondary axes vary from frondose (g), or frondulose (d), to bracteose (b).

Terminal flowers are more common on third-order and higher-order branches than on second-order axes within the SGU. In both cases (a) and (b) the inflorescence system and its parts may be frondose or bracteose and either extensively ramified, few-flowered, or even (on higher-order branches only) reduced to a single flower. Fig. 5 illustrates a somewhat extreme case of flexibility in *D. paniculatum*. Although presented diagrammatically the figure shows the actual branchings, leaves, bracts, etc. of part of the following specimen: Castlewood, Johore, Malaysia — *NSW 13876* (NSW).

Several other *Decaspermum* species also show similar variability, but some are more stable and lack anthotelic leafy shoots.

5.2 Flexibility in *Angophora*, "*Corymbia*", and *Eudesmia* within the *Eucalyptus* alliance

An even greater flexibility is shown within *Angophora* and "*Corymbia*" (*Angophora* suballiance), and *Eudesmia* (*Symphyomyrtus* suballiance), in that inflorescences may also terminate the main stems of the SGU. Four developmental patterns are found in *Angophora* (Fig. 6), and these, or variants of them, cover most of the conditions in the *Angophora* suballiance, though only some of them occur in *Arillastrum* and "*Blakella*".

(a) *Anthotelic*. The terminal flower may be the central flower of a dichasial umbellaster or may be a single flower flanked by two 3-flowered or 7-flowered umbellasters (these often with reduced "peduncles"), and further dichasial umbellasters are borne at the more proximal nodes, so that the whole inflorescence constitutes a thyrsoid or a metabotryoid (Fig. 6a).

(b) *Anauxotelic with late failure of terminal bud*. The appearance of the flowering branch system is much as in (a), but with a terminal abortive bud. This bud then commonly appears to consist of vegetative rather than floral organs. The lateral umbellasters may then be regarded as uniflorescences. (Fig. 6b).

(c) *Anauxotelic with early failure of terminal bud*. The terminal bud of the frondose SGU fails before the development of a floriferous region, and one or more lateral buds then form thyrsoids, which are commonly bracteose. One such lateral thyrsoid may continue the general direction of growth of the original axis, so that its axillary position is seen only by careful inspection. (Fig. 6c).

(d) *Auxotelic*. The axis of the SGU retains its capacity for continued vegetative growth while producing lateral umbellasters, which in this case can be regarded as uniflorescences (U's, see 3.3). (Fig. 6d).

Cases (b), (c), and (d) together constitute the blastotelic condition. Types (b) and (c) appear to be the most common in *Angophora*, but the frequency of (a) and (b) varies from species to species, e.g. (a) is rare (if present?) in *A. costata* (Gaertn.) J. Britten.

Figure 6 is based on the following specimens (all in herb. NSW); the actual leaves, flowers etc. are represented diagrammatically, the positions of fallen flowers and bracts being attested by the presence of scars: (6a) *A. subvelutina* F. Muell., Upper Hastings River, N.S.W., *Maiden NSW 138369*, xi.1897; (6b) *A. costata*, N of Booti Booti, N.S.W., *Johnson NSW 123726*, x.1953; (6c) *A. costata*, 20 miles [c. 30 km] N of Ipswich towards Esk, Qld, *Tindale NSW 123727*, xii.1968; (6d) *A. costata*, Botanic Gardens, Sydney, *Camfield (?) NSW 140338*, c. 1896.

In *Eudesmia* the anthotelic condition is uncommon, but it occurs in *E. sp.* ("*Eucalyptus*" *gamophylla* F. Muell.) and hybrids ("*Eucalyptus*" *gamophylla* × *odontocarpa* F. Muell.). The other variants in *Eudesmia* are discussed at 8.2 (No. 35).

The earlier representation of eucalypt inflorescences by Johnson (1972, 1976) did not allow for flexibility as to anthotely and blastotely in the angophoroids and *Eudesmia*. It requires modification in other respects (see 8.2: A.V *Eucalyptus* alliance, 31-40).

5.3 Additional cases of flexibility or stabilization of major axes on the anthotelic pattern

Genera with flexible conditions or anthotelic major axes are listed below. To assist reference to the systematic framework and inflorescence summary (Table 3),

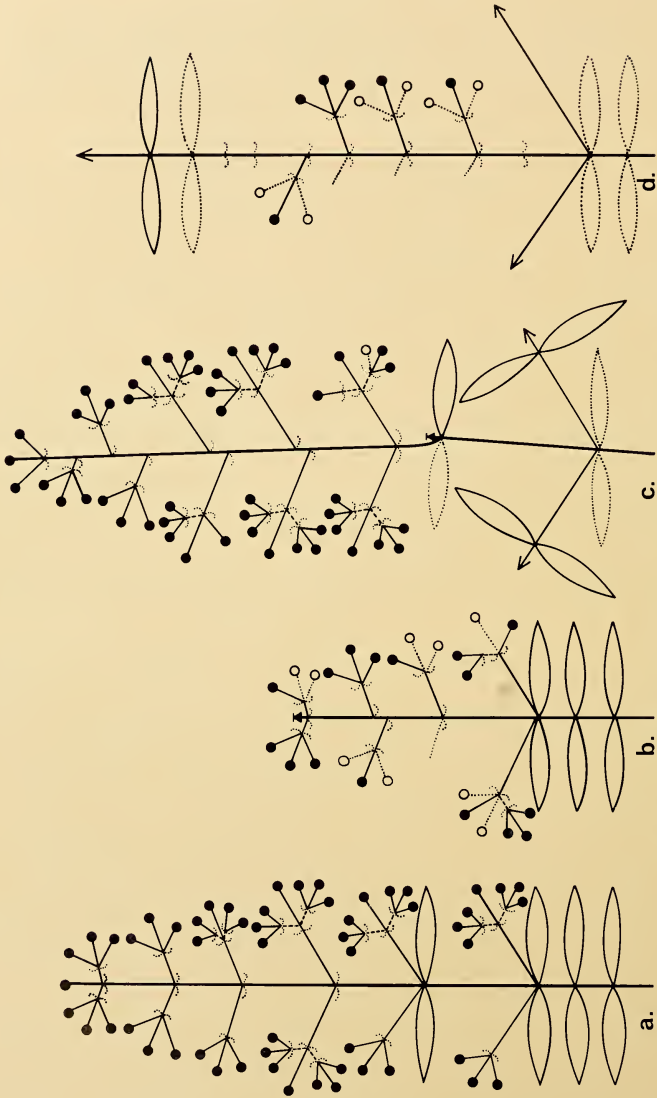


Fig. 6. Flexibility of inflorescence development in *Angophora*. Anthotelic (a) and blastotelic (b, c, d) conditions (see text). Some flowers (open circles), bracts, and axes (dotted lines) are represented only by scars on the specimens. Non-elongated internodes are shown by dashed lines. In this and subsequent diagrams an arrow-head indicates auxotely; a short arrow-head with cross-bar indicates anauxotely.

the genera are numbered as in that table; some further information is also given under 8.2 below.

3. *Cloëzia*. This genus includes (a) species with anthotelic main axes of SGU's, (b) intermediate types in which the main axes are blastotelic but the laterals are variably anthotelic or blastotelic, and (c) a stabilized condition with lateral uniflorescences only. The species with panicles or thyrsoids have types (a) or (b), whereas those with the more reduced metabotryoids, botryoids, triads, or monads are of type (c). The uniflorescence/conflorescence (U/C, see 3.3) distinction applies only in type (c).

7. *Mearnsia* s. strictiss. (= *Metrosideros* section *Mearnsia* (Merr.) Dawson). Panicles, thyrsoids, metabotryoids, and botryoids may terminate frondose main axes of SGU's, or may be lateral on a frondose R_2 or on a bracteose short-shoot R_2 .

14. *Metrosideros*. A rare case of flexibility has been seen in the normally blastotelic *Metrosideros* s. str. (see 8.2).

18. *Whiteodendron*. The SGU is sometimes clearly blastotelic, bearing lateral uniflorescences that appear to be reduced panicles or metabotryoids (a_1 with 2 nodes, differing from 7-flowered dichasia in the presence of metaxyphylls below the central flower); however, the central flower of such U's very often fails to develop, and there is some doubt about the structure. In other cases the main axis of the SGU appears to end in an arrangement of flowers similar to a lateral U, but (in the limited and imperfect material examined) no developed flower has been observed in the terminal position.

19. *Kjellbergiodendron*. Lateral panicles or thyrsoids certainly occur. Available material also strongly suggests, but does not fully establish, that certain terminal structures are large panicles rather than conflorescences of many lateral botryoids or thyrsoids. (In this and several other critical cases the extreme distal region has unfortunately proved susceptible to damage during specimen processing or during growth.)

26. *Heteropyxis*. Panicles are generally terminal, but a few lateral panicles on blastotelic axes may perhaps also occur. Weberling (1963) describes this genus in terms of Trollian synflorescence concepts, which are appropriate only when it is considered in isolation.

27. *Backhousia*. *B. bancroftii* F. M. Bail. & F. Muell. and *B. anisata* J. Vickery have panicles and metabotryoids respectively; these may either terminate frondose SGU's or be lateral to frondose R_2 's. The other species regularly have lateral dichasia.

29-30. *Eucalyptopsis* and *Allosyncarpia*. In *E. papuana* C. T. White panicles commonly terminate main axes of SGU's but sometimes occur laterally on a frondose, auxotelic R_2 , at times themselves constituting SGU's arising from old wood. In *Allosyncarpia ternata* S. T. Blake the major flowering axes, themselves terminal or lateral within the SGU, bear triads laterally in whorls of three. These axes have not been observed to terminate in a flower, but comparison with *Eucalyptopsis papuana* suggests that they correspond with the anthotelic axes of the panicles of that species. Indeed the situation, if stabilized as non-anthotelic, could represent the establishment of a conflorescence (blastotelic) condition wherein the conflorescence is equivalent to the whole anthotelic inflorescence in *Eucalyptopsis*. In an undescribed species of this alliance from Queensland the inflorescence is generally similar to that of *Allosyncarpia*, except that the branching is not ternate but opposite as in *Eucalyptopsis* and that the umbellasters are sometimes more than 3-flowered, though not as commonly so as in *E. papuana*. The apparently contrasting conditions in these three clearly related

species are then equivalent to the extremes of anthotelic and blastotelic conditions such as occur in a case of flexibility within a species or individual.

37. "*Telocalyptus*". Major axes of flowering SGU's are regularly anthotelic, in contrast to conditions in other members of the *Eucalyptus* alliance, which are facultatively or regularly blastotelic.

73-76. *Calyptranthes* and *Marlierea*; possibly rarely also *Myrcia* and *Gomidesia*. These genera, particularly the first two mentioned, may perhaps present a difficulty in interpretation rather different from that in most other genera (but cf. 30. *Allosyncarpia*). McVaugh (1968: 364-5) describes a frequent condition of *Marlierea* and *Calyptranthes* involving "the abortion of the terminal bud [of the primary axis of the panicle] at the first node and the consequent development of a pair of panicles that are morphologically equivalent to the lower branches of the panicle in *Myrcia*". We observed such situations, but were unable to determine with certainty whether the aborted bud corresponds to the apex of a vegetative short shoot or to that of the main axis of a panicle. Such buds were not aborted flower buds, but this would not be expected in either case — the axis of the panicle, had it continued growth, would have formed further bracts and nodes before terminating in a flower. Less often the abortion is observed at the second node of the a_1 , or similar abortion is repeated at the first node of each a_2 , producing four (partial) panicles (or metabotryoids, etc.). Comparison with congeners suggests that abortion within the primary panicle has indeed been involved and that the whole assemblage therefore corresponds with a uniflorescence in allied taxa, although it could now fall within the definition of a conflorescence or, in some cases, even a superconflorescence.

In addition, *Myrcia* shows clear examples of flexibility. Although in most species of this large genus the SGU's are blastotelic and bear lateral uniflorescences of varying degrees of branching (panicles to monads), there are a few in which we have recorded terminal panicles, thyrsoids, or botryoids.

78. *Nothomyrcia*. The single species is usually blastotelic with racemiform C's, each of which forms an SGU axillary on a frondose R_y and bears a number of small, crowded, non-floriferous bracts at the base. Rarely, the equivalent branches are anthotelic, thus constituting botryoids (e.g. *Solbrig et al.* 3809, UC). Racemiform C's or botryoids are sometimes lateral on short shoots, which are probably the bases of old uniflorescences or conflorescences.

81. *Pseudocaryophyllus*. Most species examined bear lateral panicles or triads (and uniflorescences of intermediate degree of elaboration may perhaps occur), but terminal thyrsoids have also been noted.

109. *Marlieriopsis*. Thyrsoids and metabotryoids are lateral or perhaps sometimes terminal on wood of a previous season; commonly on wood that still retains foliage leaves, but rarely also on wood formed two seasons previously. Although they arise in the axils of persistent leaves, these appear to constitute separate anthotelic SGU's since they bear one or two pairs of scars at the base, probably indicating the position of perules and hence the existence of a resting bud stage.

116. *Osbornia*. This bears monads or triads, sometimes with additional bracts on the main axis suggesting reduction from more ramified structures. They may be either terminal or lateral on the main and lateral axes of the SGU.

117-119, 121-124. The *Acmena* alliance (both suballiances but no information about *Cupheanthus* in this regard): *Syzygium*, *Cleistocalyx*, *Acicalyptus*, *Acmenosperma*, *Piliocalyx*, gen. nov., and *Acmena*. In this group of genera a few species (e.g.

Syzygium coolminianum (C. Moore) L. Johnson) have blastotelic SGU's that bear lateral uniflorescences. However, in the great majority, the flowering SGU's are regularly anthotelic, bearing terminal panicles, etc. It is common for many SGU's to be short shoots, arising on the old wood from resting buds, and proceeding into the flowering phase without a proximal frondose portion. In some species the terminal flower buds may show facultative abortion, but not conversion to vegetative buds; i.e. they exhibit abortive anthotely, not blastotely. The essentially anthotelic condition of flowering SGU's characterizing most species of this group of genera is in contrast with that in *Eugenia*, with which *Syzygium* and its allies have been considered congeneric even by some relatively recent authors (Henderson, 1949; Corner, 1976).

136. *Pilotheceum*. Our observations from very limited material, together with the illustrations of Kausel (1962), indicate flexibility similar to that of some species of *Decaspermum* (5.1) in the lateral branches of the SGU; no anthotelic principal axes were observed.

6. TRENDS OF INFLORESCENCE MODIFICATION

6.1 *Stabilization and demarcation*

From the postulated primitively flexible inflorescence structure (still preserved in some taxa), multiple trends appear to have led to constancy of terminal or lateral position (of the largest actual anthotelic units) with respect to the main axes of the season's growth. Frondobracteose conditions, showing a gradual transition from the foliage leaves to the floral bracts, were probably primitive and there has been a sharpening of the distinction between the vegetative and flowering regions. The latter may be bracteose or may produce caducous foliar organs, even on otherwise frondose axes.

Throughout the Myrtaceae, stabilization has led to regular production of inflorescences that are (i) panicles or reduced derivatives of panicles, or (ii) equivalent to parts of paniculate systems. Reduction series occur from panicles to smaller anthotelic inflorescences (6.2), but in many other cases it is difficult to determine whether such smaller inflorescences are due to reduction of the whole of a larger anthotelic inflorescence (e.g. panicle, metabotryoid, botryoid) or to flexibility of development. For example, in *Decaspermum* (Fig. 5) the difference between a botryoid and a group of monads appears to be due to flexibility, namely a switch between termination in a flower and growing-on of the axis (i.e. between anthotely and auxotelic blastotely). Generally it seems probable that axes (a_1 's) of lateral uniflorescences are homologous with the lower lateral branches, rather than with the main axes, of panicles terminal on anthotelic SGU's. Equivalence to the main axis would imply an elaboration and change of the overall pattern of seasonal growth (and hence the extent and "tely" of the SGU) to bring these axes into lateral positions. Indeed, such a change would mean that a season's growth would come to include the equivalent of several former (anthotelic) SGU's, these being borne laterally on a blastotelic main axis. This seems unlikely to have happened widely and is suggested by few examples, though it may have occurred in part of *Syzygium* (*S. coolminianum*, see 5.3).

Flowering is often restricted to part only of the SGU. Uniflorescences or conflorescences in some taxa may be borne at most nodes (pantotonically) but in others the arrangement is characteristically acrotonic, mesotonic, or basitonic. The "*Stenocalyx*" arrangement described by McVaugh (1968) refers to basitonic,

auxotelic, racemiform confluences as seen, for example, in some species of *Eugenia*, *Myrcianthes*, and *Campomanesia*.

A clearly differentiated inflorescence of relatively constant position has been a prerequisite for many other evolutionary developments, in particular those involving reduction and aggregation.

6.2 Reduction of branches and branching

As we have seen, smaller inflorescences may be derived by way of anthotelic/blastotelic flexibility, followed by fixation of blastotelically in some axes of a flowering SGU. Thus what would, in the anthotelic state, be regarded as an expanded panicle may be partitioned into smaller units. For instance, Figs. 5 and 6 display thyrsoids, dichasia, botryoids, metaxytriads, metaxymonads, triads, and monads, showing various degrees of partitioning and reduction. In this section we shall rather deal with reduction in inflorescences, whether they be terminal or lateral on an SGU, without departure from anthotelically within them. Although the expanded panicle is here taken as the starting point, the same processes may apply in the further reduction of the already limited inflorescences derived by partition.

Reduction from a paniculate condition may occur in:

- (A) number of nodes on axes of various orders,
- (B) degree of branching, *and/or*
- (C) number of flowers (by abortion) without reduction in degree of branching.

Most often, on multinodate axes and particularly in large inflorescences, reduction in degree of branching does not occur alone but is associated with, or follows, reduction in number of nodes. This results in the axes of highest remaining order each retaining only a single node with its two empty prophylls. Such a balanced reduction of nodes and degree of branching is here designated (AB). In smaller inflorescences, and only in a minority of cases, (B) may predominate so that the reduction in number of nodes is less complete. The axes of highest remaining order are then plurinodate, bearing at least one pair of empty hypsophylls in addition to the prophylls.

Many particular reductions can be inferred by comparison of related taxa, and in some cases individual specimens may display several stages, even within an SGU. Examples of the most frequent sequences are given below. These may be combined in a variety of ways. (Inflorescence designations are followed by reference to relevant figures.)

(i) Panicle (Fig. 7a) is reduced by process (AB) to a panicle in which all lateral branches are botryoids (not illustrated); thence in turn by (A) to a metabotryoid (7b); by (AB) to a botryoid (7c); by (A) to a triad (7i); and by (AB) to a monad (7j).

(ii) Panicle (7a) is reduced by (A) affecting all axes except the a_1 , to a thyrsoid (Fig. 2b); thence, by (AB) affecting dichasial lateral branches, to a metabotryoid (7b).

(iii) Botryoid (7c) is reduced by (B) affecting upper nodes and by (A) not keeping pace with (B), to a metaxytriad (7g); thence by (B) to a metaxymonad (7h); and by (A) to a normal monad (7j).

(iv) Metaxytriad (7g) reduced by (A) to a normal triad (7i).

(v) Metabotryoid (7b) reduced by (A) to a 7-flowered dichasium (7e).

(vi) Panicle (7a) reduced by (A) to a high-order dichasium (7d); thence by (AB) to a low-order dichasium (7e); and by (AB) to a triad (7i).

(vii) Dichasium (7d) reduced (by (C) affecting median flowers) to a dichasium in which the median flowers at lower-order branchings are suppressed (7f). One may compare the condition in many Rhizophoraceae (see 4.2).

(viii) Dichasium (7d) reduced (by (C) affecting side flowers) to a modified dichasium in which the higher-order branchings are pseudomonochasial (not illustrated, see Appendix II: *pseudomonochasium*).

(ix) A range of inflorescence types may be reduced, by (B) predominating in at least some parts of the inflorescence, to conditions in which non-branching nodes occur at various points (not illustrated).

Metabotryoids, botryoids, small dichasia, triads, and monads can be derived by a variety of paths, and one can arrive at their precise origins only by comparative study of related taxa, if at all. No fossil series is likely to be found to give more direct evidence of sequences of this kind.

The most common sequence has followed a pattern of alternating (or concurrent) narrowing and shortening, broadly of the $AB \rightarrow A \rightarrow AB \rightarrow A \rightarrow AB$ type, as for example in the *Syzygium* suballiance, which shows a range from panicles through metabotryoids, botryoids, and triads to monads, but, so far as known, no high-order dichasia or thyrsoids. We have not found thyrsoids and dichasia to be frequently present in the same genus, although both do occur in *Myrrhinium* and in *Pilotheicum*. In these, the dichasia apparently represent shortened thyrsoids, but in the *Angophora* suballiance dichasial uniflorescences are equivalent to the lateral dichasial branches of terminal or lateral thyrsoids (see 5.2 and Fig. 6). The same may apply to *Eudesmia* (*Symphomyrtus* suballiance) in part, but dichasial umbellasters in some *Eudesmia* species are equivalent to (less reduced) metabotryoidal umbellasters, which themselves may be derived from thyrsoids.

Most often, although thyrsoids show node reduction to dichasial form in their lateral branches, they are associated in the same genus with metabotryoids and botryoids, i.e. the reduction is confined, in the taxa concerned, to the a_2 's and their branches, whereas the a_1 remains multinodate.

A few genera show evidence of reduction from a paniculate condition along both a "narrowing-then-shortening" path and a "predominantly shortening" path. Thus, both longish panicles and dichasia of seven or more flowers are known in *Backhousia*, while both botryoids and dichasia of seven or more flowers occur in *Myrrhinium* and *Blepharocalyx*.

Reduction in the number of flowers (process C) has rarely become phylogenetically fixed without corresponding reduction in the degree of branching. The dichasia of some species of *Backhousia* do show regular abortion of central flowers at lower branchings and the thyrsoids of (8) gen. aff. *Mearnsia* ("*Adnatae*" = spp. such as "*Metrosideros*" *queenslandica* L. S. Sm.) show similar abortion at certain nodes. Troll (1969: 256) drew attention to the facultative suppression of central flowers in panicles of *Syzygium aromaticum* (L.) Merr. & Perry ("*Eugenia caryophyllata*"). In some species of the *Eucalyptus* alliance the ultimate (and sometimes penultimate) branching has switched in part from dichasial to pseudomonochasial, presumably associated with crowding in the primordial stages of the more floriferous umbellasters (Carr and Carr, 1959).

6.3 Increase of branching

6.3.1 Elaboration of normal branching pattern

Inflorescence reduction appears far more frequent than elaboration, but there is

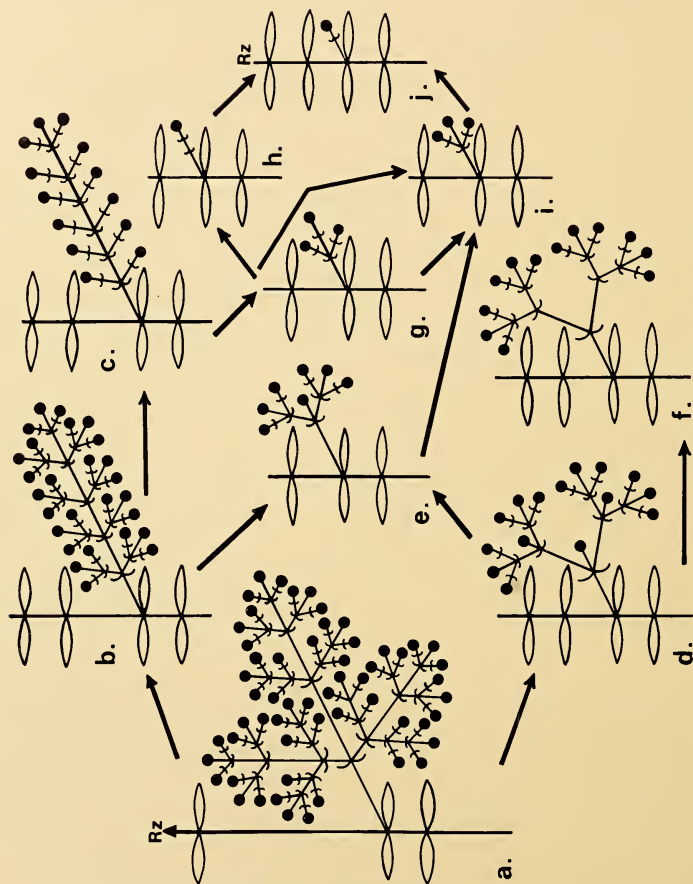


Fig. 7. Sequences of reduction from (a) panicle to (b) metabotryoid, (c) botryoid, (d) dichasium, (e) small dichasium, (f) dichasium with abortion of median flowers, (g) metaxytriad, (h) metaxymonad, (i) triad, and (j) monad (see text).

no reason to suppose that the primitive Myrtaceous condition was an inflorescence as highly branched and floriferous as the largest now found, e.g. in species of "*Telocalyptus*" (37) or of *Pimenta* (82). Whilst *developmentally* (organogenetically) it is true that branching proceeds by a building-up process in every case (however condensed this may be in the shoot primordia), *phylogenetically* we consider that the reduced conditions are in general secondary.

Low uniflorescence flower-numbers are most often associated with highly modified bracts, specialized flowers, aggregated systems (conflorescences or super-conflorescences), and other specializations. These usually permit little flexibility of growth, and are associated with condensed growth patterns in which primordia of all branches are laid down before the inflorescence (or often the conflorescence) buds unfold. Such conditions are, of course, often manifestly adaptations to advanced pollinator associations or to seed-dispersal or seed-protection mechanisms associated with specialized fruit-types.

Conversely, many-flowered anthotelic systems are usually more flexible in branch or node number, and their developmental patterns are more "open", allowing the possibility of some inflorescence elaboration beyond that of the ancestral condition, if such elaboration is favoured by selection. Conflorescences of many small uniflorescences may themselves have varying degrees of constraint on open-ended development.

Some taxa do show a degree of flexibility in reduced uniflorescences, if these are not very highly specialized. In such cases, where structural modifications do not prevent it, a facultative capacity is retained for development beyond the prevailing levels of branching or node number (e.g. some *Baeckea* spp.).

6.3.2 Accessory branching

A rather different, but obvious and widespread, type of "elaboration" is the presence of accessory axes or uniflorescences (Fig. 5). We believe accessories to be a primitive feature within the family, for they occur in both subfamilies and in 10 of the 13 alliances recognized, as well as in at least one other Myrtalean family, namely Melastomataceae. Accessories are unknown in the *Leptospermum*, *Chamelaucium*, and *Osbornia* alliances, which are among the most specialized in the family. The accessory axes are generally phylloscopic (Troll, 1969), i.e. situated between the main axillary axis and the subtending pherophyll, but both phylloscopic and axonoscopic accessories sometimes occur at the same node, with several axes in a vertical series in the axil. Accessory axes may be present in the vegetative as well as the floriferous regions. Uniflorescences may be accessory to leafy branches, and single flowers accessory to large panicles or to other well-developed uniflorescences.

6.4 Phyllotactic change

Opposite and decussate leaf arrangement is the basic and most widespread condition in Myrtaceae, but some members of several Leptospermoid alliances have disperse phyllotaxy, as noted in Table 3. In much of *Eucalyptus* s. lat., and in some other genera, the members of a leaf-pair in adult plants (but usually not in juveniles) are separated by an *intranode* or elongation of the nodal regions (Jacobs, 1955). This condition is here termed DISJUNCT-OPPOSITE phyllotaxy. Rarely, as in *Allosyncarpia*, *Ballardia*, *Cupheanthus* spp., and occasionally in vigorous regeneration shoots of some species of the *Eucalyptus* alliance, each node bears a whorl of three leaves (ternate phyllotaxy).

Whereas the foliar phyllotaxy generally continues in all blastotelic shoots, and therefore in the R_2 's of conflorescences, the basic opposite and decussate phyllotaxy is commonly preserved in the branching pattern of the uniflorescence or in anthotelic inflorescences; dichasial rather than monochasial systems are therefore general. For instance, in *Lophostemon*, most species of *Xanthostemon*, and some species of *Melaleuca* and allied genera, the vegetative phyllotaxy is disperse (spiral), but opposite and decussate phyllotaxy is retained in the uniflorescences. This is true also of *Leptospermum* and its allies, but less obvious since the uniflorescences are almost always reduced to monads in which the opposite condition is observable only in the prophylls ("bracteoles").

On the other hand, in those species of *Xanthostemon* formerly referred to *Nani*, the uniflorescences are often somewhat irregularly branched and depart more from the opposite and decussate condition than does the foliage. Table 3 and section 8.2 record other instances of disjunct-opposite phyllotaxy and of recaulescence (defined in Appendix II). Concaulescence is rarer, but is occasionally found in those groups that tend to some irregularity in the uniflorescence or anthotelic inflorescence.

6.5 Shortening and differential growth of internodes

Phylogenetic shortening of internodes is, of course, achieved developmentally by suppression of internode elongation. Such trends may affect all axes, resulting in sessile flowers as in the whole *Calothamnus* suballiance, or may selectively affect axes of a particular order. Shortening of higher-order axes, producing clusters of sessile flowers at the periphery of a branched inflorescence, is seen in *Eucalyptopsis*, *Allosyncarpia*, *Heteropyxis*, and some *Syzygium* species. In the umbellasters (usually dichasial) of the *Eucalyptus* alliance (5.2), axial elongation is in general completely suppressed except usually for the proximal internode ("peduncle"), the anthopodia ("pedicels", above the most distal bracts or branchings), and for some degree of intranode elongation in certain species of *Symphyomyrtus* sect. *Adnataria* (Carr and Carr, 1959; Johnson, 1972). Several *Backhousia* species show similar reduction except that the shortened internodes are not entirely obsolete. In the uniflorescences of *Syncarpia* and *Choricarpia* all axes are reduced except the "peduncle". The result in *Syncarpia* is a flattened 7-flowered dichasial grouping of a central flower flanked by two triads, and at the fruiting stage these are embedded, by concrescence of the perigynia, in an enlarged and woody "compound fruit". In *Choricarpia* the dichasial cluster (perhaps sometimes condensed-paniculate), of 15 or more flowers, is globose but not lignified in fruit. These two genera are much more different than their names and previous taxonomic treatment would suggest. Fusion of the shortened axes and the floral perigynia has arisen, clearly independently, in the head-like umbellasters of *Syncarpia*, *Choricarpia subargentea* (C. T. White) L. Johnson, *Allosyncarpia*, and *Symphyomyrtus lehmannii* Schau. ("*Eucalyptus*" *lehmannii* (Schau.) Benth.).

Increased or differential elongation of internodes is also observed in some taxa, leading for example to corymbiform patterns, as in some of the *Angophora* suballiance. A similar phenomenon is observed in conflorescences in such genera as *Verticordia*, *Pileanthus*, and *Actinodium* (*Chamelaucium* suballiance).

7. AGGREGATION OF UNIFLORESCENCES AND MODIFICATIONS OF CONFLORESCENCES

The distinction between uniflorescences ("unit inflorescences") and conflorescences has already been mentioned (3.3). Conflorescences are extremely

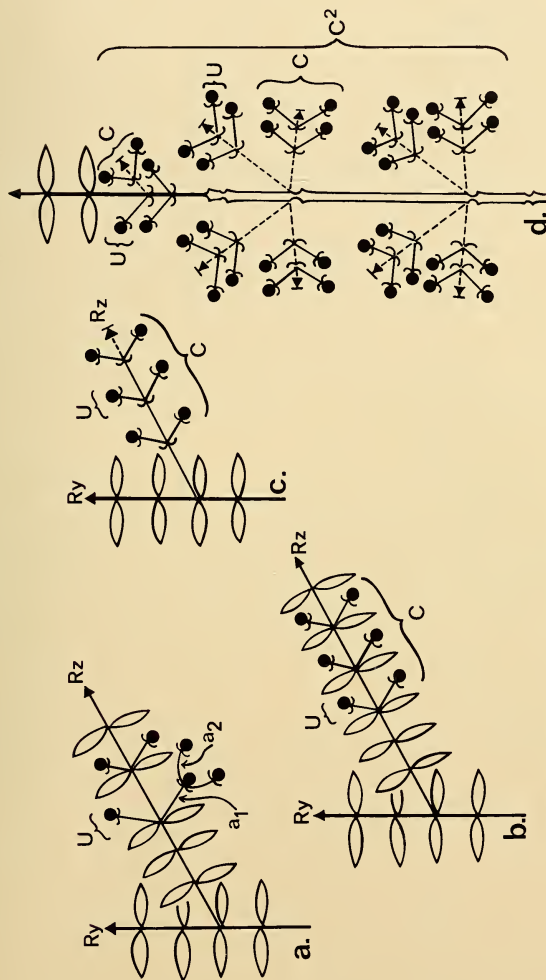


Fig. 8. Confluences in *Eugenia* s. str.
 (a) Uniflorous (U) triads (very rare in *Eugenia*) or monads.
 (b) Racemiform auxotelic confluence (C) of monads.
 (c) Confluence axis (Rz) reduced to a bracteose, racemiform, anauxotelic short shoot (lateral to Ry).
 (d) Ramiflorous example with condensed fasciculiform-racemiform confluences arising from axillary buds (some of them accessory) on secondarily thickened confluences arising from produced monads (U 's), as well as very short C 's, in a bracteose region at the base of the frondose axis of the blastotelic current SGU. Axes that do not elongate are represented by broken lines.

widespread and have been subject to many of the same trends of modification as uniflorescences. In addition to the taxa recorded (Table 3) as having specialized conflorescences, many that lack any high degree of conflorescence specialization nevertheless show some grouping of uniflorescences at nearby or successive nodes. In some taxa, a further aggregation and/or reduction has led to compound groupings of higher order, *superconflorescences*.

The more notable conflorescence types occur in genera with much-reduced uniflorescences, and all the examples discussed concern triads or monads. Where the uniflorescences are less reduced — panicles, thyrsoids, metabotryoids, botryoids, larger dichasia — only more loosely organized conflorescences are found. In the *Eucalyptus* alliance the uniflorescences are usually umbellastral condensed dichasia (or sometimes umbellastral metabotryoids); they are variously arranged in conflorescences as shown by Johnson (1972, 1976), subject to the modified interpretations indicated below (8.2: 31–40).

This discussion and Table 3 do not include as conflorescences the even less defined situations where adjacent leafy shoots are sufficiently coordinated in their growth to form a loose but functionally significant massing of flowers although, in a more general (topological rather than functional) sense, any part of a blastotelic SGU (or in some cases a blastotelic branch within an SGU) that bears lateral uniflorescences may be regarded as a conflorescence, and its main axis as an R_2 . The modifications of conflorescences are illustrated by the following examples. Except for Fig. 8d, which is taken from a particular specimen, the figures are schematic only.

7.1 *The eugenioid racemiform conflorescence*

Uniflorescences in *Eugenia* s. str. are monads, except in a few species that produce occasional triads (e.g. the Floridan *E. dichotoma* DC.) and a few others that probably do not belong to the genus (see 8.2, No. 140). The uniflorescences are borne in racemiform conflorescences on leafy branches (Fig. 8a, b), or the conflorescence axis (R_2) may be reduced to a bracteose short shoot (Fig. 8c). Particularly in ramiflorous or cauliflorous species, the R_2 may be so reduced as to be inconspicuous (Fig. 8d), bearing a dense cluster of monads. Similar racemiform conflorescences are a feature of many Myrtoideae with monad uniflorescences. Particularly in basitonic species of *Eugenia*, the conflorescences are often in loose or relatively well-defined aggregations, i.e. superconflorescences.

Figure 8d depicts a ramiflorous example from *E. capuli* (Schlecht. & Cham.) Berg (Micos, San Luis Potosi, Mexico, *Pringle 3966*, NSW). Condensed racemiform C's, each of them a separate SGU, with one or several small perular bracts at the base, arise from each of two (rarely one or three) superposed axillary buds, one or more thus being accessory. These buds are axillary to foliage leaves and/or arise from wood formed in a previous season (penultimate or earlier SGU). Sometimes a phylloscopic accessory C may be situated below a frondose branch arising in the same axil. Frondose SGU's on the same shoot sometimes also produce lateral monads (U's) or short C's in a basitonic position. In some other species short shoots (brachyblasts) with completely unelongated internodes arise laterally on the old wood and produce monads (axillary to bracts on the brachyblast), each of which appears to be in a separate SGU. Available material has been insufficient for us to determine whether these SGU's each consist of a monad alone or of an extremely short brachyblast (R_2) bearing a monad laterally; the latter would be expected in view of the generally blastotelic conflorescences of *Eugenia*. The primary brachyblasts also produce definitely blastotelic branches (which are also brachyblasts), and thus highly con-

densed short-shoot systems (compound brachyblasts) may persist, and remain floriferous, on the old wood for several years. The axes in such a cluster may therefore include a_1 's, R_2 's, R_y 's, and R_x 's.

7.2 *Conflorescences of the Chamelaucium suballiance*

The conflorescences of this group of about 13 genera show a spectacular diversity in appearance, concealing a basic uniformity. The same uniflorescence is common to all: a pedunculate monad with prophylls ("bracteoles") but without antherpodium. The uniflorescence in this alliance and the common condition for *Eugenia* are identical — indeed a striking convergence reached through extreme reduction. In several genera the prophylls are fused (e.g. *Verticordia*, *Pileanthus*, some *Calytrix* spp.) or imbricate; they serve to protect the floral buds up to a fairly late stage of development, the calyx-lobes being small or petaloid and therefore ineffective in this regard.

Thryptomene and *Micromyrtus* show no substantial modification of this arrangement (Fig. 9a), although the functional attraction of the small flowers is enhanced by their occurrence at the many rather closely spaced nodes in the floriferous region. Throughout the suballiance the R_2 is relatively little modified. A minority of species in *Chamelaucium* and *Verticordia* show some development of anauxotelic floriferous shoots but, even in these species, the R_2 may sometimes grow on after flowering.

Although a few species of *Darwinia* show little or no conflorescence specialization (Fig. 9b), most have groups of two or more pairs of very shortly pedunculate monads in dense heads, commonly with the R_2 growing on after flowering (Fig. 9c). The prophylls (subtending leaves) of the U's are inconspicuous, but a few pairs of adjacent leaves are often greatly enlarged, petaloid, and coloured. The Western Australian species show a sequence from (for example) the little-modified *D. thymoides* Benth., through *D. virescens* (Meissn.) Benth., where the petaloid leaves are about as long as the perigynia ("floral tubes"), to the pendulous "bells" (Fig. 9d) of *D. meeboldii* C. A. Gardn. ("Mondurup Bell") or *D. speciosa* (Meissn.) Benth., in which individual flowers are hidden by several series of long petaloid leaves and the R_2 .

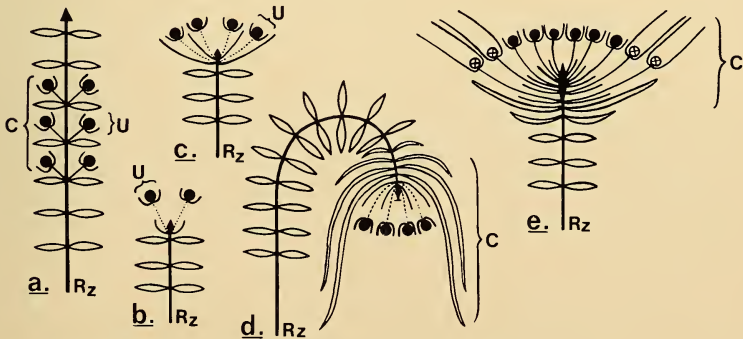


Fig. 9. Conflorescences in the *Chamelaucium* alliance (see text).

(a) Least modified condition, as in *Thryptomene* and *Micromyrtus*.

(b, c, d) Various degrees of modification in *Darwinia* (R_2 sometimes auxotelic).

(e) Capitulum-like corymbiform conflorescences of *Actinodium*, with proximal (outermost)

ray-like sterile U's.

is anauxotelic, so that the conflorescence with its involucre of coloured leaves closely mimics a single large flower.

Equally remarkable in appearance are the daisy-like, densely corymbiform pseudanthia of the monotypic *Actinodium* (Fig. 9e), in which the "rays" of the capitulum-like conflorescences consist of several rows of modified sterile flowers. The axis of the conflorescence is somewhat swollen but not flat, and variation in the length of the peduncles of the monads brings the flowers to approximately the same level, although the outermost arise c.2-5 mm below the innermost. The R_z may end in an aborted vegetative apex (anaxotelic) or may grow on after flowering (auxotelic).

7.3 *Conflorescences and superconflorescences in the Calothamnus suballiance*

Uniflorescences in the majority of genera of the *Calothamnus* suballiance are triads, although this arrangement is often obscured by their condensed internodes, lack of anthopodia, and crowding in the dense, usually auxotelic, spike- or cluster-like conflorescences (Fig. 10a). The perigynium and ovary of some *Calothamnus* species are partly embedded in the conflorescence axis (R_z) but the three-flowered groupings are relatively easily discernible. The uniflorescences are reduced to monads in *Callistemon* (Fig. 10c), in some species of *Melaleuca* (Fig. 10b-e), and in *Lamarchea* and *Eremaea*. Monads also characterize some so-called "*Callistemon*" species of New Caledonia (e.g. *C. pancheri* Brongn. & Gris), which combine *Callistemon*-like flowers with *Melaleuca*-like leaf venation, and which apparently warrant generic segregation (genus 46) or perhaps transfer to *Melaleuca*. In most genera, including many species of *Melaleuca*, the R_z is auxotelic, growing on as a frondose shoot either before or after flowering (Fig. 10a-c); in some *Melaleuca* spp. (e.g. *M. lateriflora* Benth.) the short conflorescences, of several monads, are anauxotelic and form a superconflorescence on the auxotelic R_y (Fig. 10d).

Of particular interest is *Melaleuca exarata* F. Muell. (Fig. 10e), which has numerous flowers each embedded in the corky bark, forming an extended spike-like arrangement. This species exemplifies a further extreme of reduction and aggregation: the whole apparent "spike" is a superconflorescence (its axis an R_y), each individual flower represents a conflorescence reduced to a single uniflorescence, itself a monad, and the numerous bracts around the base of each flower give evidence of the highly compound arrangement.

The conflorescences are themselves reduced to single flowers also in *Lamarchea* and *Eremaea*. In *Lamarchea* these monads occur singly, laterally (but not evidently so) on a short-shoot (brachyblast) R_z , which is so reduced that one sometimes cannot discern any abortive apical bud, but which retains several empty bracts near the base of the flower (i.e. the base of the monad U). In *Eremaea* the R_z is also very short, but its apical bud is usually discernible and occasionally grows on after flowering. The conflorescences may occur singly, or a few at nearby nodes in a very loose superconflorescence.

7.4 *Conflorescences and superconflorescences in Hypocalymma*

In this Western Australian genus of the *Baeckea* suballiance (*Chamelaucium* alliance), the inflorescences superficially resemble spiciform conflorescences (as found in the *Calothamnus* suballiance), but examination shows that the aggregations are commonly of a higher order than is at first apparent.

The uniflorescences are monads borne at the lowest one or two nodes of brachyblasts; rarely in *H. speciosum* Turcz. these shoots have been observed to be

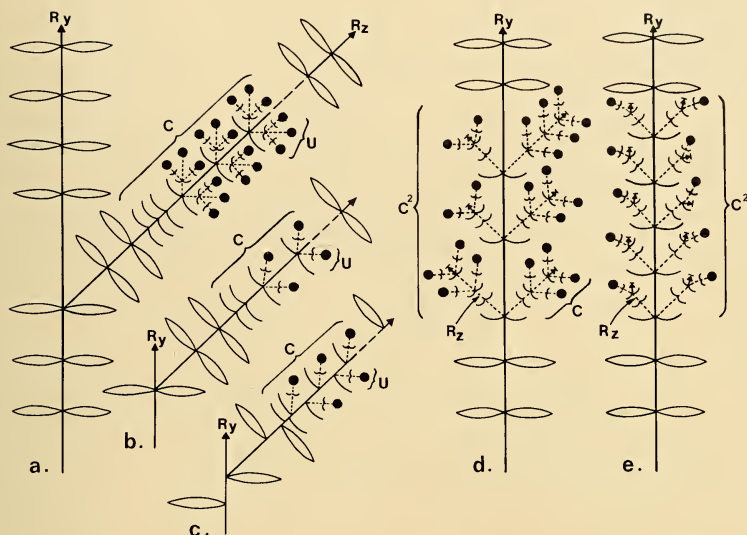


Fig. 10. Spiciform confluences and superconfluences in the *Calothamnus* suballiance. (See text for further explanation.) *Calothamnus* shows type (a); various species of *Melaleuca* show all types (a-c); *Callistemon* shows type (c).

(a) Confluence of triads. Below the confluences there are often perular bracts (as shown) or the scars of such bracts.

(b) As (a) but the U's reduced to monads.

(c) As (b) but with disperse phyllotaxy.

(d) Superconfluence: the lateral clusters of flowers are very short bracteose confluences on anauxotelic axes.

(e) As (d) but the lateral confluences reduced to monads, e.g. *Melaleuca exarata*.

auxotelic (Fig. 11a). The two or four monads on such a brachyblast constitute a confluence, and these C's usually occur at several adjacent nodes in the floriferous region, forming a spiciform superconfluence. The R_z and the peduncles of the monads are so greatly condensed that the clusters of two or four flowers (Fig. 11b, c) are sessile or subsessile in the axils of leaves on the main axis (R_y). The R_y is frondose but the R_z is nearly always bracteose. Functionally, unlike those of the *Calothamnus* alliance, the confluences and superconfluences of *Hypocalymma* are not compound "brush-blossoms" (see 9) but merely aggregations of flowers with showy petals.

7.5 Confluences and superconfluences in *Leptospermum*

The uniflorescence is a monad except in the cases of *L. mjoebergii* Cheel (section *Fabricia*) and *L. sp. aff. brachyandrum* (F. Muell.) Druce (section *Leptospermum*). Both of these seldom-collected northern Australian species have triads and monads, often on the same shoot (Fig. 12a).

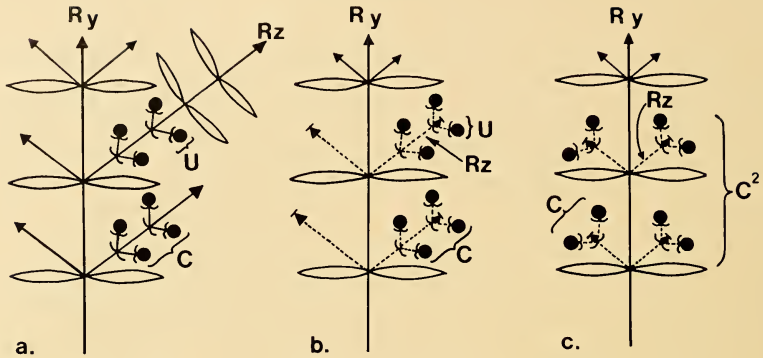


Fig. 11. Conflorescences and superconflorescences in *Hypocalymma*.

(a) Uncommon condition without obvious superconflorescence specialization, and in which the conflorescence axes are auxotelic.

(b) Superconflorescence: the four flowers of each condensed conflorescence are sessile in the leaf axils, and the conflorescence axes are anauxotelic.

(c) As (b) but the conflorescences reduced to two flowers only.

When the U's of *L. sp. aff. brachyandrum* ("Brass's Purple-barked Turkey-bush") from the Kennedy Range, North Queensland, have more than one flower, they often also have an extra non-floriferous node on the a_1 proximal (prophyllar) or distal (metaxyphyllar) to the branching node; in some cases there may be such an extra node on the a_2 (observed in cases where there is no extra node on the a_1). The very small bracts on the binodate axes may appear at first to be superposed rather than decussate, but careful examination indicates that this is probably due to crowding and distortion in the very tight buds. These uniflorescences are the only ones in the *Leptospermum* alliance that are more complex than a simple triad — their occurrence would seem to indicate that the ancestral uniflorescence form in the alliance was not dichasial.

Conflorescence development, with monads at several or many successive nodes, may involve a relatively unmodified, auxotelic, frondose R_z (Figs. 12a, b) as in section *Fabricia* in part, *L. firmum* Benth. (see 8.2, No. 36), and some species of section *Leptospermum*.

Further reduction (Fig. 12c) results in the proximal portion of the R_z being greatly shortened so that, even though it may retain a frondose region, most authors have described the flower(s) (usually one or two) as subsessile; the R_z may be anauxotelic or may grow on after flowering, sometimes to become the R_y of the next season's conflorescences. In Fig. 12d the phyllomes on the R_z are reduced to bracts (hypophylls); the numerous conflorescences, each reduced to one monad, are grouped in a superconflorescence, as in many species of section *Leptospermum*. The R_z 's are then so reduced that the flowers appear sessile on the R_y , the inconspicuous scarios-membranous perular bracts around their bases (concealing the abortive tip of the R_z) giving evidence of the extent of reduction and aggregation that has occurred.

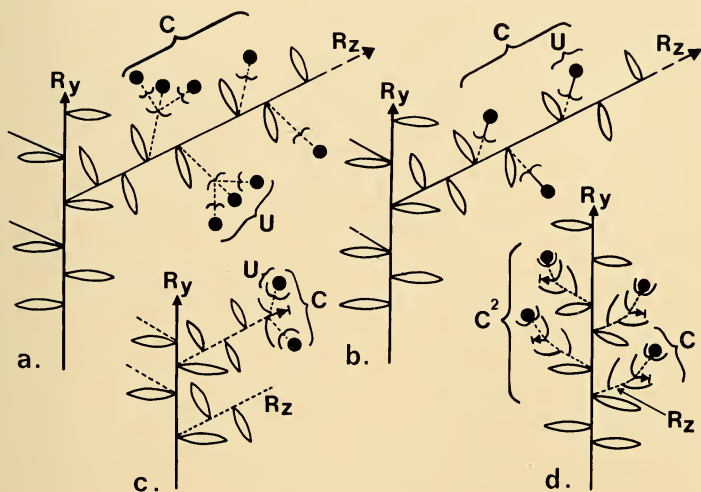


Fig. 12. Conflorescences and superconflorescences in *Leptospermum*. Non-elongated axes shown by broken lines.

- (a) Triad (very rare) and monad U's in relatively unspecialized conflorescence.
- (b) As (a) but U's regularly monads (anthopodia developed or not).
- (c) Conflorescence of several monads; R_z anauxotelic in the case illustrated (some otherwise similar cases are auxotelic) and frondose, but with the internodes not elongated. Such conflorescences often aggregated in superconflorescences.
- (d) Spiciform superconflorescence: the conflorescence axes as in (c) but bracteose.

8. SURVEY OF INFLORESCENCE CONDITIONS IN MYRTACEAE

8.1 Summary of inflorescence types in Myrtaceous genera

Table 3 presents a summary of the main inflorescence features of each generic taxon here recognized (see 2.2.3). These are arranged in the alliances, suballiances, and infra-alliances discussed above (2.2). Some supplementary information on the status and affinities of many of the genera is given below (8.2), together with additional information on inflorescence features.

TABLE 3
Inflorescence conditions in Myrtaceae
 (See key, p. 213)

1 Taxon	2 Terminal	Pan	Thy ^d	Metab	3 Bot ^d	Dich	Tri	Mon	4 Peduncle	5 Antho- podia	6 Meraxy- phylls	7 C	8 C'	9 R ₂ Fronduity	10 R ₂ Auxiliary	11 Access- ories	12 Phyllo- taxy	13 Note
A. LEPTOSPERMOIDEAE																		
A. 1. METROSIDEROS																		
ALLIANCE																		
A. 1. i. KANIA SUBALLIANCE																		
1 <i>Kania</i>	-	-	-	-	-	-	-	-	+	+	-	-	-	-	-	-	-	s
2 <i>Basia perma</i>	-	-	-	-	-	-	-	-	+	+	-	-	-	F	+	-	O	s
3 <i>Colizia (Moortia)</i> ¹	+/-	P	Th	Mb	B	D	Tr	M	NA/+	+/-	-	NA/-/+	-	F/FB	NA/+	-	O	i
4 <i>Lysicarpus</i>	-	-	-	-	-	-	Tr	-	+	+	-	-	-	Fr	+	-	O	s
A. 1. ii. METROSIDEROS																		
SUBALLIANCE																		
5 gen. aff. <i>Tritania</i> ("Parrot Creek")	+	-	Th	Mb	-	-	-	-	NA	+	-	NA	-	F	NA	+	O	s
6 <i>Tritania</i> s. str. (<i>T. nerifolia</i>)	-	P	-	Mb	-	D	Tr	-	+	+	-	-	-	F	+	-	O	si
7 <i>Mearnsia</i> s. strictiss. 8 gen. aff. <i>Mearnsia</i> ("Abatae")	+/-	P	Th	Mb	B	-	Tr	(M?)	+	+	+/-	NA/-/+	-	F/B	NA/+/-	-	O	s
9 gen. aff. <i>Mearnsia</i> ("Crystal")	-	-	Th	Mb	-	-	-	-	+	+	-	-	-	F	+	-	O	s
10 gen. aff. <i>Mearnsia</i> ("Inclus")	-	-	-	-	-	-	Tr*	-	+	+	+	+	-	Fr	+	-	O	si
11 gen. aff. <i>Mearnsia</i> ("Calyptroptala" s. str.)	-	-	-	-	-	-	Tr	(M)	+	+	-	-/+	-	Fr	+	-	O	s
12 <i>Tepuadia</i>	-	-	-	-	-	-	(Tr)	M	+	+	-	-	-	F	+	-	O	s
13 <i>Ballardia</i>	-	-	-	-	-	-	Tr	-	+	+	-	-	-	B	+	-	O	si
14 <i>Metrosideros</i> s. str. ("Carpolepis")	-	-	-	-	-	-	Tr	(M)	+	+/-	-	-/+	-/+	B	+/-	-	O	i
A. 1. iii. XANTHOSTEMON																		
SUBALLIANCE																		
15 <i>Xanthostemon</i> (incl. <i>Nazi</i> , <i>Freryga</i>)	-	P	-	Mb	B	-	Tr	M/M*	+	+	+/-	-/+	-	F/B	+/-	-	D/O	i
16 <i>Pleuracophyllum</i>	-	-	-	-	-	-	Tr	M	+	+	-	-	-	F/Fr	+	-	D	i
17 <i>Purpureostemon</i>	-	-	-	-	-	-	-	M	+	+	-	+	-	Fr	-	-	D	i

TABLE 3 — Continued

I Taxon	2		3			4	5	6	7	8	9	10	11	12	13					
	Terminal	Pan	Thyd	Metab	Bot ^d											Dich	Tri	Mon	Peduncle	Antho-
A.I. IV LOPHOSTEMON SUBALLIANCE																				
18 <i>Whiteodendron</i>	+?/-	P	-	Mb	-	-	-	NA?/+	+	NA?/+	F	NA?/+	+	D	i					
19 <i>Kjellbergodendron</i>	+?	P	Th	-?	-	-	-	NA?/+	+	-/+?	F/Pr?	NA?	+	D	i					
20 <i>Lindlayomyrtus</i>	-	P	-	Mb	B	-	-	+	+	-	F/Pr	-	+	D	i					
21 gen. nov. "R" (<i>Xanthostemon</i>)	-	P	-	-	-	-	-	+	+	-	F	+	+	O/D	i					
22 <i>pachybermus</i>	-	-	-	-	-	-	-	+	+	-	F	+	-	D	si					
23 <i>Tritanotopsis</i>	-	-	-	-	-	-	-	+	+	-	Fr	+	-	D	s					
25 gen. nov. "W" (<i>Tristania longedactis</i>)	-	-	-	-	-	-	-	+	+	-	F/Pr/B	+	+	D	s					
24 <i>Lophostemon</i>	-	-	-	-	-	-	-	+	+	-/+	F	+	-	D	s					
25 <i>Syncarpia</i>	-	-	-	-	-	-	-	+	+	-/+	F	+	-	O	si					
A.II HETEROPYXIS ALLIANCE																				
26 <i>Heteropyxis</i>	+/(+)	P	-	-	-	-	-	NA/(+?)	+	+/(+?) NA/(+?)	F/FB	NA/(+?)	+	D	i					
A.III BACKHOUSIA ALLIANCE																				
27 <i>Backhousia</i>	+/-	P	-	Mb	-	D	-	NA/+	+	NA/-	F/B	NA/+/-	+	O	i					
28 <i>Choricarpia</i>	-	P?	-	-	-	D	-	+	+	-/+	F/Pr	+	+	O	i					
A.IV EUCALYPTOPSIS ALLIANCE																				
29 <i>Eucalyptopsis</i>	+/-	P	-	Mb?	-	D	Tr	NA/+	-	NA/+	F/B	NA/-	+	O	si					
30 <i>Allosyncarpia</i>	-/(+)	-	-	-	-	-	Tr	+	+	-	B	-	-	O	si					
A.V EUCALYPTUS ALLIANCE																				
A.V.I ANGOPHORA SUBALLIANCE																				
31 <i>Artillastrum</i> (<i>Spermalepis</i> , <i>Myrtomeva</i> nom. illeg.)	-	-	-	-	-	D	Tr	-	+	-	F	+/(-)	-	O	s					
32 <i>Angophora</i>	+/-	-	Th	-	-	D	Tr	NA/+	+	NA/+	F/FB/Pr	NA/+/-	+	O	i					
33 "Blakella"	-	-	Th	Mb	-	-	-	+/-	+	-/+	F/B	+/-	-	O/do	i					
34 "Corymba"	+/-	-	Th	Mb?	-	D	Tr	NA/+	+	NA/+	F/FB/Pr	NA/+/-	(+)	O/do	i					

TABLE 3 — Continued

1	2	3	4	5	6	7	8	9	10	11	12	13						
Taxon	Terminal	Pan	Thy ^d	Metab	Bur ^d	Dich	Tri	Mon	Peduncle Antho- podia	Metasy- phylls	C ^c	Frondosity	R ₁	R ₂	Access- ories	Phyllo- taxy	Note	
A.V.ii SYMPHYOMYRTUS SUBALLIANCE																		
35 <i>Eucalyptus</i>	+/-	P	Th (Th)	Mb (Mb)	-	D	Tr	-	NA/+	-	NA/-	F/FB	NA/+/-	+			O/dO	i
36 <i>Symphomyrtus</i>	-	-	-	-	-	D	Tr	(M)	+ / (-)	-	-/+	F/FB/Fr	+/-	+			4O/(O)	i
37 " <i>Trochalepis</i> "	+	P	-	-	-	-	-	-	NA	-	NA	F	NA	+			dO/O	i
A.V.iii EUCALYPTUS s. str. SUBALLIANCE																		
38 "Gaultheria"	-	-	Th ²	-	-	D	-	-	+	-	-/+	F/FB	+	-			4O/(O)	i
39 " <i>Idiosperma</i> "	-	-	Th	-	-	D	(Tr)	-	+	-	-	F/Fr/B	+	-			dO	i
40 <i>Eucalyptus</i> s. str. ("Monocaulis")	-	-	-	-	-	D	-	-	+/-	-	-/+	F/FB	+ / (-)	+			4O/(O)	i
A.VI LEPTOSPERMUM ALLIANCE																		
A.VI.i LEPTOSPERMUM SUBALLIANCE																		
41 <i>Leptospermum</i>	-	-	-	-	-	-	(Tr/Tr*)	M	- / (+)	- / (+)	- / +	F/Fr/B	+ / -	-			D	si
42 <i>Agonis</i>	-	-	-	-	-	-	-	M	-	-	+	Fr	+ / (-)	-			D	s
43 <i>Kunzea</i>	-	-	-	-	-	-	-	M	-	-	-	Fr/(F)	+	-			D/(O)	s
44 <i>Singoa</i>	-	-	-	-	-	-	-	M	-	-	+	Fr	- / (+)	-			D	s
A.VI.ii CALOTHAMNUS SUBALLIANCE																		
A.VI.ii.a MELALEUCA INFRA- ALLIANCE																		
45 <i>Callistemon</i>	-	-	-	-	-	-	-	M	-	-	+	B/(F)	+	-			D	s
46 gen. aff. <i>Callistemon</i>	-	-	-	-	-	-	-	M	-	-	- / +	B	+	-			D	s
47 <i>Melaleuca</i>	-	-	-	-	-	-	Tr	M	-	-	+	Fr/B	+ / -	-			O/D	s
48 <i>Conothamnus</i>	-	-	-	-	-	-	Tr	M	-	-	+	Fr	+	-			O	i
49 <i>Lamarkia</i>	-	-	-	-	-	-	-	M	-	-	+	B	-	-			D	si
A.VI.ii.b CALOTHAMNUS INFRA-ALLIANCE																		
50 <i>Calothamnus</i>	-	-	-	-	-	-	Tr	-	-	-	+	F/Fr/B	+	-			D	s
51 <i>Bauhinia</i>	-	-	-	-	-	-	Tr	-	-	-	+	Fr	+	-			O	s
52 <i>Rugelia</i>	-	-	-	-	-	-	Tr	-	-	-	+	Fr	+	-			O	s
53 <i>Phymatocarpus</i>	-	-	-	-	-	-	Tr	-	-	-	+	Fr	+	-			O	s
54 <i>Eriocaulis</i>	-	-	-	-	-	-	-	M	-	-	+	B/Fr	+ / (-)	-			D	i

TABLE 3 — *Continued*

1 Taxon	2 Terminal	Pan	Thy ^d	Metab	Boi ^d	Dieh	Tri	Mon	4 Peduncle	5 Antho-	6 Meraxy-	7 C	8 C ²	9 Frondosity	10 K ₂ Autovecy	11 Access-	12 Phyllo-	13 Nore
B. III. CRYPTORHIZA ALLIANCE																		
109 <i>Macrotropus</i>	+	-	Th	Mb	B	D	Tr	M	NA	-	-	NA	-	B	NA	-	O	si
110 <i>Elpheroedax</i>	-	-	-	Mb	B	(D?)	Tr	M	+	+/-	-	-/+	-	F	+	+	O	si
111 <i>Campylopus</i> (incl. <i>andrus</i> , <i>Britton</i>)	-	-	-	-	-	-	-	-	+	+/-	-	-	-	F/Fr/B	+	+	O/O	si
112 <i>Poa</i>	-	-	-	-	-	-	-	M	+	+	-	-	-	F	+	-	O	s
113 <i>Leptocarpus</i>	-	-	-	-	-	-	-	M	+	-	-	-	-	F	+	-	O	s
114 <i>Cryptocarpus</i>	-	-	-	-	-	-	Tr?	M	+	-	-	-	-	F ₂	+	-	O	si
115 <i>Phyllocladus</i>	-	-	-	-	-	-	-	M	+	-	-	-/+	-	F/B	+/-	-	O	si
B. IV. OSBORNIANA ALLIANCE																		
116 <i>Osbornia</i>	+/-	-	-	-	-	-	Tr/Tr*	M/M*	-	-	+	NA/-	-	F	NA/+	-	O	i
B. V. ACMENA ALLIANCE																		
B. V.1. SYZYGIUM SUB-ALLIANCE																		
117 <i>Syzygium</i> (incl. <i>Caryophyllus</i> nom. rejic., <i>Jambosa</i> , <i>Pteris</i> , <i>Aphanomyrtus</i> , <i>Alphomomyrtus</i> , <i>Pseudosugenia</i> , <i>Tetraugenia</i>)	+ /(-)	P	-	Mb	B	-	Tr/Tr*	M	NA/(+)	+/-	+/-	NA/-	-	F/FB/B	NA/(+)	+	O/(dO?)	si
118 <i>Clastocladus</i> s. str.	+	P	-	Mb	-	-	Tr	M	NA	-	+/-	NA	-	F/B	NA	-	O	si
119 <i>Acacalyptus</i>	+	P	-	-	-	-	Tr?	M?	NA	+/-	+/-	NA	-	F	NA	-	O	s
120 <i>Cupressinac</i>	-	-	-	-	-	-	-	-	+	-?	-	-	-	F	?	-	O	s
B. V.2. ACMENA SUB-ALLIANCE																		
121 <i>Aceniasperma</i>	+	-	Th	Mb	B	-	(Tr)	(M)	NA	-	-	NA	-	B/(F)	NA	-	O	s
122 <i>Phacocladus</i>	+	P	-	Mb	B	-	-	-	NA	+/-	+/-	NA	-	F	NA	+	O	si
123 gen. nov. (= <i>Syzygium floribundum</i>)	+	P	-	-	-	-	-	-	NA	+/-	+/-	NA	-	F	NA	+	O	si
124 <i>Acenias</i> (incl. <i>Xenodictyon</i>)	+	P	-	Mb	B	-	-	-	NA	+/-	+/-	NA	-	F	NA	+	O	s

TABLE 3 — *Continued*

Key: Alternative states are shown +/-. Uncommon conditions are given in parenthesis. Some genera may include variants or derived conditions not recorded here.

Column 1: † Particular doubt about correct placement or recognition of taxon.

‡ Material of taxon not available for study; data from published sources recorded here where available.

- 2: Presence or absence of inflorescences terminal on the SGU.
 3: Inflorescence type. Referring to uniflorescences or to the whole inflorescence when the U/C distinction is inapplicable (when the whole inflorescence is terminal).

P = panicle
 Th = thyrsoïd (Us that resemble thyrsoids but have
 metaxyphylls are recorded as panicles).
 Mb = metabotryoid
 B = botryoid
 D = dichasium
 Tr = triad
 Tr* = metaxytriad
 M = monad
 M* = metaxymonad

- 4: Peduncle: Presence or absence recorded. Where terminal inflorescences are recorded (column 2) the main axes of the SGU's are anthotelic and the presence of a peduncle is non-applicable (NA).
 5: Anthopodia: Presence or absence recorded.
 6: Metaxyphylls: Presence or absence recorded.
 7: Degree of specialization of conflorescence: — = unspecialized; + = specialized either by aggregation or by condensation and marked reduction of component parts; +/- = a moderate degree of aggregation or a range from unspecialized to highly specialized.
 8: Degree of specialization of superconflorescence: — = unspecialized; + = specialized by aggregation and/or by condensation and marked reduction of component parts.
 9: Frondosity of K₂: F = frondose; B = bracteose; FB = frondobracteose; Fr = frondose except for reduced (bracteiform or caducous) phyllomes in the flowering region. In terminal inflorescences there is usually a sharp distinction between the frondose (proximal) and the bracteose inflorescence regions of the axis, but such cases are recorded as "Fr", rather than "Fr", since the bracteose region is more nearly equivalent to that within a uniflorescence than to an R₂ bearing uniflorescences laterally.
 10: Auxotely of K₂: recorded within blastotelic inflorescences only, NA in terminal inflorescences.
 11: Presence of either accessory Us or accessory axes within Us or within total inflorescence. A positive record indicates that accessories occur within the genus, but not necessarily within all species.
 12: Phyllotaxy of vegetative regions of adult plant. O = opposite (verticillate); dO = disjunct opposite; D = disperse.
 13: Notes: s = see text note (8.2) for supplementary information on systematic position, status, delimitation, or affinities. i = text note (8.2) on inflorescence features or phyllotaxy.

8.2 *Systematic and inflorescence information on particular taxa* (supplementary to Table 3)

A.1 *Metrosideros* alliance. We gratefully acknowledge the co-operation of Peter G. Wilson and John T. Waterhouse (University of New South Wales) in making available unpublished information on *Tristania* s. lat., *Xanthostemon* s. lat., and a number of allied genera. The recognition of segregate genera in these complexes is largely founded on the conclusions reached in their broadly-based comparative studies.

2. *Basisperma*. Although the inflorescence is dichasial, this resembles other genera of the suballiance in its basal placenta with erect anatropous ovules. The ovary is 2-locular (Foreman, 1978) but only one carpel develops to form the single-seeded fruit. Although the genus has previously been placed in the vicinity of the "*Tristania*" complex (i.e. the *Lophostemon* suballiance, rather than *Tristania* s. str), its gynoeceal structure indicates that it is more appropriately included in the *Kania* suballiance.

3. *Cloëzia*. Variably anthotelic or blastotelic, U/C distinction often inapplicable (see 5.3). So far as observed, dichasial branches are lateral (and acrotonic) or terminal on anthotelic SGU's and therefore form part of a terminal thyrsoid. Axes at times with some interpolated non-floriferous nodes. Recauscence and intranode development common; concaulescence occasional.

4. *Lysicarpus*. This monotypic genus, the only Australian representative of the suballiance, is particularly close to *Cloëzia*.

A.1.ii *Metrosideros* suballiance. Some of the interpretations, and occasionally the observations, of inflorescences given by Dawson (1970-76) for taxa 7-14 differ from those given here.

5. Gen. nov. "Parrot Creek". Assignment of this NE Queensland taxon to this suballiance is supported by (a) the large peltate placenta bearing anatropous ovules distally on the outer edge in several rows, and (b) the deep indentation of the ovary around the base of the style. The fascicled stamens, in which it differs from *Mearnsia*, are found in this suballiance also in *Tristania* s. str.

6. *Tristania* s. str. Monotypic: *T. neriifolia* (Sims) R. Br. Metabotryoids (a₁ with two nodes) or dichasia of 7-3 fls.

7-14. *Mearnsia* and allies. Dawson (1976) took an extremely broad view of *Metrosideros*, in which he recognized a subgenus *Mearnsia* (comprising genera 7-11 of our listing), as well as a subgenus each for genera 13 and 14. Curiously, he did not include *Tepualia*, which, as he observed earlier (Dawson, 1972e), is close to *Mearnsia*. On the basis of examination of material and from information presented in Dawson's series of papers, we consider generic status appropriate not only for *Metrosideros* subgen. *Carpolepis* Dawson (= *Ballardia* q.v.), but we regard his subgenus *Mearnsia* as comprising five groups of generic status. These correspond to Dawson's sections and two of his subsections. The Latin terminations of the sectional and subsectional names used by Dawson (1976) are inconsistent, and in some cases irregular, but they are used here for the time being.

7. *Mearnsia* s. strictiss. = *Metrosideros* subg. *Mearnsia* sect. *Mearnsia* sensu Dawson (1976). U/C distinction mostly inapplicable (see 5.3). Inflorescence terminal on frondose branch or on bracteose short shoot, or lateral on frondose branch (R₂). Sometimes unclear whether inflorescence is a botryoid with failure of apical flower or is a racemiform conflorescence.

8. Gen. aff. *Mearnsia* ("*Adnatae*") = *Metrosideros* subg. *Mearnsia* sect. *Adnatae*

Dawson. Median flowers often abortive except the most distal (see 6.2). Recaulcescence common.

9. Gen. aff. *Mearnsia* ("Crystalla") = *Metrosideros* subg. *Mearnsia* sect. *Crystalla* Dawson. The only African member of the *Metrosideros* alliance.

10. Gen. aff. *Mearnsia* ("Inclusis") = *Metrosideros* subg. *Mearnsia* sect. *Calyptropetalata* Dawson subsect. *Inclusis* Dawson. Since metaxyphylls are present, the apparent triads (metaxytriads) cannot represent reduced dichasia.

11. Gen. aff. *Mearnsia* ("Calyptropetalata" s. str.) = *Metrosideros* subg. *Mearnsia* sect. *Calyptropetalata* Dawson subsect. *Exsertis* Dawson.

13. *Ballardia* Montr. (1860) = *Metrosideros* subg. *Carpolepis* Dawson. *Ballardia* Montr. is later than *Ballardia* Cambess. (1829, now treated as a synonym of *Spergularia* in the Caryophyllaceae). The names are not identical and perhaps *Ballardia* Montr. need not be regarded as a later homonym, and consequently illegitimate, as has been done by Dawson (1976). If it is so regarded then it may be worth proposing for conservation. Leaves are commonly in whorls of three.

14. *Metrosideros* s. str. Rarely the R_2 is anthotelic, seen only and very occasionally in *M. tremuloides* (Heller) Rock, but the structures are otherwise similar to those in blastotelic conflorescences (in this case the U/C distinction breaking down). Dawson (1970b) reports dichasia rarely with >3 flowers, but we have not observed these. Table 3 records the common condition in the taxon rather than these exceptions.

15. *Xanthostemon*. Monads rarely with plurinodate a_1 (metaxymonads). Branching in larger U's often \pm subopposite or irregular, recaulescence common. Higher-order axes often reduced and flowers clustered. A diverse genus, but difficult to divide satisfactorily.

17. *Purpleostemon*. Dawson (1972a) illustrates a terminal botryoid, but the material available to us (at NSW and K) shows conflorescences consisting of dense aggregations of lateral monads. The disperse phyllotaxy of the vegetative branches is continued into the conflorescences. If terminal botryoids were present, one would expect them to show decussate or disjunct-opposite phyllotaxy as in those species of *Xanthostemon* that have many-flowered U's.

A.I.iv The *Lophostemon* suballiance, which is under study by Peter G. Wilson and J. T. Waterhouse, possibly needs division; as treated here, its members exhibit some considerable dissimilarities in reproductive and vegetative features, although some natural subgroups are evident within it.

18. *Whiteodendron*. U/C distinction not fully applicable, see 5.3. Frequently the central flowers of the lateral triads of the panicle fail to develop and these lateral triads are often accompanied by accessory triads or monads, giving a conformation of unusual aspect. Furthermore, there is often asymmetric development and recaulescence, combined at times with concaulescence of the two axes (one of them accessory) originating in the same axil. The phyllotaxy becomes more regularly opposite in the more distal parts of the flowering region.

19. *Kjellbergiodendron*. U/C distinction probably inapplicable (see 5.3). Branching within the inflorescence opposite or disjunct-opposite. Fruit fleshy, indehiscent; 1-seeded in contrast to *Whiteodendron*.

20. *Lindsayomyrtus* Hyland & van Steenis (1973). Phyllotaxy within the U largely disperse or disjunct-opposite, except at ultimate branchings.

21. Gen. nov. "R" (= *Xanthostemon pachyspermus* F. Muell. & F. M. Bail. = *Tristania pachysperma* (F. Muell & F. M. Bail.) W. D. Francis). The precise relationships of this genus are not clear at present. Inflorescence branching very irregular, disjunct-opposite. Recaulcescence frequent. Pherophylls absent at some branchings. Phyllotaxy partly disperse and partly opposite on vegetative regions of a single specimen.

22, 23, 24. *Tristaniopsis* (= *Tristania laurina* (Sm.) R. Br. and allies), gen. nov. "W" (= *T. longivalvis* F. Muell.), *Lophostemon* (= *Tristania conferta* R. Br. and allies). These have generally been included in *Tristania* s. lat., but are not closely allied to the type species (*T. neriifolia*), which is here regarded as constituting a monotypic genus of the *Metrosideros* suballiance. The New Caledonian species treated by Dawson (1977) are included in *Tristaniopsis*. Abortion of central flowers at some of the lower nodes is common in large dichasia of *Tristaniopsis*.

25. *Syncarpia*. All axes of the 7-flowered dichasia are condensed except for the proximal internode of the a_1 , resulting in a globose head of partially-fused flowers. Prophylls are developed only on the a_1 's and the a_2 's. Has some features in common with *Lophostemon*, but stamens not fascicled. *Choricarpia* (28) is not closely related, though it has been included in *Syncarpia* in the past.

26. *Heteropyxis*. Higher-order axes often reduced and flowers clustered. Branching often irregular or \pm disjunct-opposite; pherophylls not discernible at some branchings. Panicles frondobracteose and inflorescence limits not clearly defined. See 5.3.

27. *Backhousia*. U/C distinction non-applicable in some species (see 5.3). In dichasial species the median flowers at lower branchings are often suppressed and the higher-order axes (below the anthopodia) are usually very short, providing a near-parallel with *Eucalyptus*-alliance umbellasters.

28. *Choricarpia*. U: condensed globose dichasium or probably sometimes a condensed panicle. Small U's sometimes fully dichasial; those with more flowers have a_1 and/or a_2 plurinodate. All axes except proximal internode of a_1 are reduced. Often >1 accessory U.

29-30. *Eucalyptopsis* and *Allosyncarpia*. An undescribed species from the Atherton Tableland, north-east Queensland (*Hyland 6589*) resembles the New Guinean *Eucalyptopsis papuana* C. T. White in some features but the recently described and monotypic *Allosyncarpia* S. T. Blake (1977) of Arnhem Land, northern Australia, in others. Since this breaks down the sharpness of the differences given by Blake (1977), it tends to confirm our previously formed view that *Allosyncarpia* might well be included in *Eucalyptopsis*. The three species concerned share a generally similar and distinctive trichome type (2.2.3). Like many others in the family, the name *Allosyncarpia* is misleading, suggesting an affinity with a genus that is in fact not closely allied, despite the comparisons made by Blake. U/C distinction \pm inapplicable (see 5.3). Higher-order branch-axes not elongated; thus the flowers are in condensed dichasial umbellasters usually of 3-7 flowers (or sometimes more), with the perigynia of the flowers \pm fused. From the material available it is not clear whether >7 -flowered umbellasters are dichasial or metabotryoidal in structure. Disjunct-opposite branching sometimes common towards the base of the inflorescence/conflorescence. In *Allosyncarpia* the leaves usually in whorls of three, but this condition does not carry through into the umbellasters, which have the normal opposite arrangement of prophylls and branchings, so that the flowers are in triads.

A.V *Eucalyptus* alliance. Most of the nine taxa (27-35) within *Eucalyptus* s. lat. that are listed at generic level have previously been recognized at subgeneric level only

(Pryor and Johnson, 1971, and in press; Johnson, 1976), although Johnson (1976) considered that generic status could well be as appropriate as subgeneric. The current study has emphasized the distinctness of these taxa and the similarities of some of them to *Arillastrum*. They are circumscribed here as by Johnson (1976) and by Pryor and Johnson (in press). With the exception of *Angophora*, *Eudesmia*, *Symphomyrtus*, and *Eucalyptus* (here restricted) their names have not been published in generic rank, and are here treated as informal designations only. For reasons stated by Pryor and Johnson, the subgeneric names were deliberately published outside the framework of the International Code of Botanical Nomenclature.

Umbellasters (condensed dichasia or, less often, condensed metabotryoids) are a feature of the whole alliance; an umbellaster frequently represents a whole uniflorescence or, less often, a partial uniflorescence or part of a terminal inflorescence (see 5.2). Intranode elongation producing disjunct-opposite phyllotaxy is widespread but not universal. Within the umbellasters of *Symphomyrtus* (36) and *Eucalyptus* ("*Monocalyptus*", 40), the earlier branchings are dichasial, or at least opposite-decussate, but higher-order branching (above a_3) is sometimes pseudomonochasial, probably because of primordial crowding (Carr and Carr, 1959; Johnson, 1972, 1976). This may also be the case in some of the few species of *Eudesmia* and "*Gaubaea*" with >7 -flowered umbellasters, but (in some cases at least) the structure of such umbellasters appears to be metabotryoidal (or possibly even thyrsoidal in *Eudesmia* series *Miniatae*) in structure. Bracts (prophyllar pherophylls) are sometimes developed only at the lower branchings within the umbellaster, especially in *Eucalyptus* s. str. In some species, the prophylls of the a_1 are more or less fused into a calyptriform structure protecting the developing umbellaster. Like earlier authors, Johnson (1972, 1976), in his categorization of eucalypt inflorescences, assumed that the condensed dichasial unit (which he termed an "umbellaster") was fundamental. He took this as the unit inflorescence, and regarded aggregations of these as conflorescences (whether they were anthotelic, anauxotelic, or auxotelic). He pointed out some apparent departures from equivalence of all umbellasters and from dichasial form, and also the difference between determinate (anthotelic) and indeterminate (blastotelic) systems, but this scheme will not now stand in full. Necessary modifications are noted under individual generic groups. In referring to the basic inflorescence of Myrtaceae, Johnson (1972) used the incorrect phrase "thyrsoid, with dichasial branching". His meaning would have been correctly expressed as "a determinate (Trollian) panicle, with opposite-decussate branching".

31. *Arillastrum*. See Dawson (1970a). The listing by Shaw (1973) of *Arillastrum* as a synonym of *Stereocaryum* Burret (138) is in error. *Myrtomera* B. C. Stone (1962) was proposed as a new name for *Spermolepis* Brongn. & Gris non Rafin., but is illegitimate as a superfluous name, since it included the type (*S. gummifera* Brongn. & Gris. = *A. gummiferum* Panch. ex Baillon) of a name that should have been adopted (viz. *Arillastrum*). Dichasia of 7-3 flowers.

32. *Angophora*. U/C distinction not fully applicable (see 5.2), variable anthotelic, anauxotelic, or auxotelic development of major frondose axes. Terminal or lateral thyrsoids of umbellasters, or the umbellasters lateral on blastotelic R_z 's; when anthotelic the R_z sometimes with a single terminal flower flanked by two umbellasters. When blastotelic, C is thyrsiform. Johnson (1972, 1976) observed only the anauxotelic blastotelic cases, and his corymboid (" C_{1-4} ") conflorescence subtypes therefore represent only part of the flexible range in the *Angophora* suballiance.

33. "*Blakella*". In some species the whole thyrsoid or metabotryoid condensed

and \pm umbelliform. R₂ frondose or a bracteose brachyblast. The summary by Johnson (1972) requires correction: some species then thought to have thyriform conflorescences (Johnson's C₂, C₃ subtypes) in fact have anthotelic metabotryoids or thyrsoids. On the other hand, true anauxotelic conflorescences of condensed form, more or less corresponding to Johnson's C₄ subtype, do occur in such "*Blakella*" species as "*Eucalyptus grandifolia* R. Br. ex Benth.

34. "*Corymbia*". The above note for *Angophora* (32) also applies here, but the blastotelic condition is more common (constant in some species).

35. *Eudessmia*. Blastotelic with defined U's in most species but U/C distinction not applicable in "*Eucalyptus gamophylla* F. Muell. Main (primary) axis of SGU perhaps never anthotelic, and single terminal flowers (as distinct from terminal umbellasters) not observed on frondose branches. U's sometimes with plurinodate a, or, if only the peduncular (hypopodial) internode is elongated (i.e. apparent umbellasters), then with branching patterns of condensed metabotryoid form. In many cases U's reduced to 7-flowered or 3-flowered umbellastral condition, but it is uncertain whether a truly dichasial pattern exists in any umbellasters with >7 flowers (e.g. in the very condensed branching of the many-flowered U's of "*Eucalyptus phoenicea* F. Muell."). Johnson (1972) remarked on the "odd conditions" in *Eudessmia* and the need for further investigation. The position is now somewhat clearer, but more developmental study is needed.

36. *Symphyomyrtus*. U/C distinction applicable in all except one species. U = lateral umbellaster (condensed dichasium — or sometimes metabotryoid). The metabotryoid condition is found in some apparently quite advanced species, e.g. "*Eucalyptus crucis* Maiden. "*E. michaeliana* Blakely has thyrsoids with the terminal and two lateral dichasia condensed into separate umbellasters ("S₃" subtype of Johnson, 1972). Sometimes with intranodal elongation within umbellaster in section *Adnataria*. Accessories in certain sections only, e.g. part of section *Bisectaria*.

37. "*Telocalyptus*". Major axis of SGU anthotelic. The regularly anthotelic panicle (but with final branchings umbellastral) of this tropical group was first pointed out by Johnson (1972) and led to his (informal) naming of "*Telocalyptus*" (Johnson, 1976).

38. "*Gaubaea*". It is possible that the many-flowered umbellasters of "*Eucalyptus tenuipes* (Maiden & Blakely) Blakely & C. T. White are essentially thyrsoidal in structure, but dichasial umbellasters occur in "*E. curtisii* Blakely & C. T. White. Large branching auxotelic or anauxotelic (Johnson's "C₁" subtype) conflorescences of the latter species parallel those of blastotelic cases in the *Angophora* suballiance, but there are no anthotelic equivalents.

39. "*Idiogenes*". U/C distinction not applicable? U: thyrsoid with higher-order axes condensed to form 7-flowered dichasial umbellasters. U's lateral to frondose shoots, but the apparent thyrsoids are sometimes branched and it is uncertain whether the lower-order axes of the apparent thyrsoids are then anthotelic or blastotelic. Johnson (1972, 1976) recognized the anthotelic nature of the thyrsoids, but termed them "T₂ conflorescences", because of his concept of the umbellaster as the unit inflorescence (see note above under "*Eucalyptus* alliance").

40. *Eucalyptus* s. str. ("*Monocalyptus*"). Accessories in a few species only, e.g. part of series *Obliquae*. The umbellastral U's, in which all except the peripheral perophylls (bracts) are suppressed, appear to be dichasial so far as analysed (Carr and Carr, 1959; Johnson, 1972, 1976), often with reduction to pseudomonochasial branching at a₄ and beyond; but the thyrsoidal uniflorescences in "*Idiogenes*", and

perhaps "*Gaubaea*", suggest that the dichasium in *Eucalyptus* s. str. may be derived by shortening of a thyrsoid. Perhaps some trace of a plurinodate a_1 may yet be found.

41. *Leptospermum*. See 7.5. Preliminary consideration of the probable cladistic relationships of the sections with respect to allied genera suggests that they may be worthy of generic rank. Unspecialized C's occur in section *Fabricia*, part of section *Leptospermum*, and also in *L. firmum*, which apparently warrants equal status with the other sections. C²'s (with highly reduced C's) are well developed only in part of section *Leptospermum*. Section *Pericalymma* has well-developed C's but no C²'s.

Although highly condensed and with some bracts \pm displaced by growth pressures, the most developed U's, as to numbers of nodes, are the 3-flowered U's with an extra node (proximal or distal) on the a_1 or a_2 seen in *L. sp. aff. brachyandrum* (section *Leptospermum*). Triads without extra bracts also occur in that species, and rarely in *L. mjobergii* of section *Fabricia*.

C: racemiform or spiciform or reduced from these; unspecialized with U's at several successive nodes of unmodified frondose R_z , or of few monads crowded on a frondose or bracteose brachyblast, or reduced to one monad on a very short R_z . Variable as to auxotely of R_z , even within individuals in some species. C² (where developed): \pm racemiform or spiciform, with C's at several successive nodes. R_y frondose or with leaves reduced and/or caducous in flowering region. C² of spp. with single-monad C's may superficially greatly resemble simple spiciform C of a species such as *L. firmum*.

42-44. *Agonis*, *Kunzea*, *Sinoga*. Probably offshoots of the same line as *Leptospermum* sect. *Leptospermum*, but specialized in other directions.

A.VI.ii.a *Melaleuca* infra-alliance. See 7.3. C: spiciform or reduced to small dense clusters of flowers (monads) or to single monads (*Lamarchea*, and in a very few *Melaleuca* spp.). C² spiciform in a few species of *Melaleuca* that have bracteose R_z 's so short that the flowers appear sessile on the R_y .

46. aff. *Callistemon* (New Caledonia). Dawson (1978) illustrates triads in one species but our material of all four species shows only monads; the group appears to be an offshoot from *Melaleuca*, distinct from the Australian *Callistemon*.

49. *Lamarchea*. Apical bud of R_z usually not discernible but the numerous empty bracts (hypophylls) suggest extreme reduction and that the very short lateral axis bearing the flower is actually an R_z rather than an a_1 ; thus each flower represents a whole C.

A.V.ii.b *Calothamnus* infra-alliance. See 7.3. Differs from *Melaleuca* infra-alliance in the basifixed and more specialized anthers. C: spiciform; \pm secund in *Calothamnus* due to U's developing only in axils on one side of R_z and to leaves being commonly \pm reduced on floriferous side of flowering region.

54. *Eremaea*. Monad U's in axils of foliage leaves or of perular pherophylls. Flowers sometimes appearing terminal on frondose shoots because the R_z is often distorted around the base of the flower; the lateral position is usually more evident in fruit. Several U's sometimes occur at nearby nodes in a very loose C. Prophylls ("bracteoles") absent so far as seen, perhaps caducous very early.

55. *Baeckea*. The sections of *Baeckea*, and the allied genera, require reconsideration to determine the most appropriate generic disposition. U: usually 7-flowered (dichasia), 3-flowered, or 1-flowered, but rarely botryoids (*B. sp. aff. camphorata* R. Br.) indicating non-cymose ancestry. Higher-order axes of dichasia

are sometimes not elongated. The six sections (Bentham, 1867) show several different reduction series affecting the number of flowers and the elongation of peduncle and/or anthopodium.

57. *Scholtzia*. Recauscence common within the U's, recalling more primitive Leptospermoid genera.

59. *Hypocalymma*. See 7.4. C: mostly consisting of one or two pairs of U's on a bracteose short shoot, which is so condensed that the pairs of U's appear subsessile in leaf-axils of (frondose) R_y. C²: present in most species, spiciform but frondose.

A.VII.ii *Chamelaucium* suballiance. See 7.2. The distinctions between *Chamelaucium*, *Darwinia*, *Homoranthus*, *Rylstonea*, and *Verticordia* are unclear and require further study. *Homoranthus* and *Rylstonea* are both tentatively recognized here; at this stage there is perhaps no more evident reason to unite them under *Homoranthus* than to sink them under *Verticordia* or *Darwinia*, or to make other generic rearrangements in the complex. *Lhotzkya* is included within *Calytrix* in agreement with Court (1957). The original and apparently deliberate spelling "*Chamelaucium*" stands under the International Code of Botanical Nomenclature. It is fairly certainly derived from *camelaucum*, the mediaeval name of an ecclesiastical cap, in the derivation of which the Greek prefix *chamae-* plays no part. Consequently, the frequently seen "*Chamaelaucium*" should not be used.

C: racemiform, corymbiform, spiciform, or capituliform (the last in *Actinodium* with sterile "ray" U's). Some *Darwinia* spp. with large coloured leaves surrounding the C. Peduncles usually present, but often very short.

73-76. *Myrcia*, *Marlierea*, *Calyptranthes*, *Gomidesia*. In view of the considerable number of species with intermediate characters (McVaugh*, 1968), there seems no more reason (if as much) to recognize *Myrcia* and *Marlierea* as distinct from *Calyptranthes* than to segregate some of the distinctive species-groups currently included, for example, in *Syzygium*. *Gomidesia* seems to differ from *Myrcia* chiefly in an anther character that also tends to break down. The higher-order axes in all four genera are sometimes not elongated, the flowers then being in small dense clusters. Abortion of buds sometimes produces situations that are difficult to interpret and may perhaps involve anthotelic/blastotelic flexibility. (See 5.3.) In addition there are clear cases of flexibility in *Myrcia*. In *Marlierea* we have observed accessory branches only in *M. ferruginea* (Poir.) McVaugh, the sole species of *Krugia*, which was maintained by Kausel (1957b), but not by McVaugh (see also 9.1).

77. *Mitranthes* s. str. Here interpreted in the sense of McVaugh (1968: 381-2, 411). Our observations are taken from the lectotype species *M. ottonis* Berg.

78. *Nothomyrcia*. U/C distinction sometimes inapplicable. (See 5.3); monads occur in blastotelic cases, and are similar in position to the lateral flowers of botryoids in anthotelic cases.

79. *Myrceugenia*. Some massing of U's but this is by the presence of accessory U's, not by the formation of C's in the normal way. In *M. chrysocarpa* (Berg) Kausel, accessory flowering brachyblasts (extremely short) may persist on old wood, and may produce flowers (one or more monads) at a late stage when the primary lateral shoot arising at the same node is well developed and quite woody.

B.II. *Myrtus* alliance. Suballiances are not recognized here because of our present uncertainty as to the relationships of the many Old World genera. *Temu* (80)

*References in this section to McVaugh are to this paper unless otherwise specified.

was grouped by McVaugh with *Campomanesia*, *Paivaea*, and *Blepharocalyx* (112-114), which are here removed to the *Cryptorhiza* alliance, and with which *Temu* does not agree in its embryo characters. *Pseudocaryophyllus* (81) and *Pimenta* (82) constitute a group in McVaugh's treatment but, as he says, are presumably not very closely related. *Myrrhinium* (83), *Acca* (84), and *Feijoa* (85) follow in our listing, but McVaugh regarded them as of uncertain position among the "pimentoid genera" (equivalent to our *Myrtus* and *Cryptorhiza* alliances). Genera 86-94 constitute McVaugh's group "*Psidium* and related genera" (*Mosiera* and *Corynemyrtus* being included by him in the synonymy of *Myrtus*), except that *Marlieriopsis* (109) is here removed to the *Cryptorhiza* alliance. Since we have as yet been unable to determine the affinities of various Western Pacific genera (96-108) sufficiently to refer them either to particular American subgroups or to distinguish groupings amongst themselves, they are here all listed after the American taxa and *Myrtus* s. str. (95). It does not follow that they necessarily constitute a coherent group separate from those recognized by McVaugh in the New World. Recognition of segregate genera may have been a little excessive in this alliance and a comprehensive review is desirable.

80. *Temu*. The name *Temu* Berg would be illegitimate if regarded as an orthographic variant, and therefore a later homonym, of *Temus* Molina, but we doubt the necessity of this interpretation of the Code. Though regarded by McVaugh as perhaps doubtfully distinct from *Blepharocalyx* (110), *Temu* is reported to have a "pimentoid" embryo (i.e. the common type in the *Myrtus* alliance), unlike *Blepharocalyx*.

81. *Pseudocaryophyllus*. The occurrence in one species (*P. crenatus* Legrand) of terminal inflorescences (see 5.3) is apparently unique in the American members of the *Myrtus* alliance, but compare the Old World *Descaspermum* (96).

83. *Myrrhinium*. Dichasia (∞ -3 fls), or panicles and metabotryoids (a, with 2-3 nodes). Often ramiflorous with U's crowded on bracteose brachyblasts. An isolated genus.

85. *Feijoa*. Included by McVaugh in *Acca*, with some degree of reservation. Flowering region bracteose or with reduced but herbaceous leaves (frondulose).

86. *Calycolpus*. Monads usually on bracteose brachyblasts, but occasionally also in leaf axils. Anthopodia short when present.

87. *Mosiera*. This name is tentatively used here for most of the American species that have generally been referred to *Myrtus* (95) by recent authors. McVaugh did not formally recognize *Mosiera*, but he gave evidence that it has no particularly close affinity with the Mediterranean *Myrtus communis* L. and its vicariant *M. nivellii* Battand. & Trab. of the Saharan mountains, to which two species *Myrtus* is here restricted.

88. *Psidium*. *Epsyzygium* Suessenguth & Ludwig (in Suessenguth, 1950), from Hawaii, seems to have no connection with *Syzygium* and to correspond in placentation and other features with species of *Psidium*. Supra-axillary monads (an example of concaulescence), mentioned in the protologue as unique in the family, are in fact found at times in *Psidium*. Species of that genus are naturalized in various islands of the Pacific. Kausel (1957b), also presumably from the description, tentatively referred *Epsyzygium* to his "Myrtoideae" (= *Myrtus* alliance).

89. *Psidiopsis*. Monotypic genus tentatively recognized. Included by McVaugh in *Psidium* (88), but it seems to stand well apart from any species of that genus in its markedly appendaged calyx-lobes and is reported by Niedenzu (1898) to differ also in

its basifixed anthers. Transferred to *Calycolpus* (86) by Burret (1941b) without discussion, but it seems equally out of place there.

90. *Corynemyrtus*. Provisionally treated as a synonym of *Myrtus* by McVaugh, but it seems no closer to *M. communis* than do other groups of this general affinity. Information from Kiaerskou (1893). Anthopodia when present very short. Possibly not distinct from *Psidium* (88) (see addendum).

91. *Amomyrtella*. The only specimen seen under this name (*Venturi* 9595 at K) does not agree with Kausel's description and figure, and is presumably misidentified. It has frondose shoots with axillary triads, rather than the short racemiform C's described by Kausel (1956).

95. *Myrtus* s. str. See note 87.

96. *Decaspermum*. Some species with well-defined paniculate U's or reduced types (metabotryoids to monads), others with flexible development of axes (see 5.1) including anthotelic frondose branches (but not anthotelic primary axes of SGU).

98. *Archirhodomyrtus*. Dr A. J. Scott (pers. comm.) proposes to transfer the eastern Australian *Rhodomyrtus beckleri* (F. Muell.) L. S. Smith to *Archirhodomyrtus*, previously thought to be endemic in New Caledonia. We agree with this disposition.

99. *Rhodomyrtus*. Recauscence occasional. R₂ sometimes a bracteose brachyblast. Metaxyphylls present in branched U's but absent in monads. The inclusion of *Psidiomyrtus* is in agreement with Burret (1941a). Bentham (1869) suggested that *Macropsidium* might be referable to *Rhodomyrtus*, on the basis that the 4-locular ovary with uniseriate ovules (as described by Blume, 1850) "may be in fact a 2-celled ovary divided by longitudinal spurious dissepiments". It is very tentatively included here in the absence of observation or further information; the flowers are described as sessile, axillary, and fascicled.

100. *Octamyrtus*. Very close to *Rhodomyrtus*, seemingly with floral specialization to ornithophily. Sometimes with extra pair (s) of bracts on a₁.

101. *Rhodamnia*. Metaxyphylls as in *Rhodomyrtus* (99).

109. *Marlieriopsis*. Unplaced by McVaugh, and its position here is tentative; we have not been able to check the embryo type. Flowering SGU's are thyrsoids or metabotryoids without any proximal frondose portion. (See 5.3).

110. *Blepharocalyx*. 7-flowered dichasia and 7-flowered botryoids occur in supposedly conspecific material of *B. salicifolius* (Kunth) Berg.

111. *Campomanesia*. It appears that *Britoa* is most reasonably included here (see, e.g., Rotman, 1976). *Acrandra*, apparently differing only in the appendaged anthers, is also tentatively included (see McVaugh). All species that we examined have monads, but *Acrandra* is reported to have triads (Niedenzu, 1898), and Mattos (1967) reports inflorescences of up to seven flowers in *Campomanesia* subgenus *Britoa*.

112. *Paivaea* is provisionally included in this alliance because of its similarity to *Campomanesia* (111), although it was not listed by Kausel in his Cryptorhizoideae. Fruits have neither been seen by us nor described in the literature. *Paivaea* may be no more nor less distinct than other taxa currently treated as subgenera of *Campomanesia*.

113. *Legrandia*. Affinity somewhat dubious; placed by McVaugh in the vicinity

of the "eugenioid genera", but regarded by Kausel (1956) as a member of his Cryptorhizoideae on the basis of embryo structure.

114. *Cryptorhiza*. Although Kausel (1956) lays great stress on the embryo character of this genus (see 2.2.1), McVaugh appears to suggest that it may belong with *Myrcianthes* (126); unless the embryo was misdescribed, this is difficult to accept. We have seen only monads, but triads are reported by Urban (*vide* McVaugh).

116. *Osbornia*. Apparent "triads" at least sometimes bear 2 pairs of minute extra bracts on the a_1 (above the node bearing the side flowers of the metaxytriad). Triads (or metaxytriads) and monads may both occupy either terminal or lateral positions on frondose branches.

B.V *Acmena* alliance. This Old World and Pacific alliance is distinguished largely on the basis of the predominantly terminal inflorescence, the consistent absence of "standard" Myrtaceous hairs, the evident affinities among the genera in wood anatomy (Ingle and Dadswell, 1953), and characteristic floral anatomy (Schmid, 1972a, b, c). As in the *Eugenia* alliance, thick but separate cotyledons appear to be the basic condition but a distinctive modification (of single or multiple origin?) is found in the *Acmena* suballiance (Merrill and Perry, 1938; Henderson, 1949; Kausel 1957; Hartley and Craven, 1977; J. T. Waterhouse, personal communication; and our own observations). Although the cotyledons are described as completely fused in some taxa, the degree of fusion varies in the *Acmena* suballiance and in some genera the cotyledons are largely or completely free — although closely interlocked.

117. *Syzygium*. (See 5.3.). Inflorescences in *Syzygium* are terminal on major frondose shoots of SGU's or on very short brachyblasts arising from old wood (ramiflorous or cauliflorous), or (rarely) are lateral uniflorescences on a blastotelic R_z (e.g. *S. coolminianum*). When ramiflorous, the SGU's proceed directly to flowering without a proximal frondose region. Some species have (a) frequent suppression of median flowers, (b) higher-order axes not elongated and flowers clustered, or (c) extra empty hypsophylls on the a_1 or a_2 (mostly in the more reduced inflorescences).

Syzygium here includes the small groups *Pareugenia*, *Aphanomyrtus* (in agreement respectively with Perry, 1950, and Perry *vide* Schmid, 1972c), and *Tetraeugenia* (see below), as well as *Jambosa* and *Caryophyllus*; it is in need of thorough review as a whole. Schmid (1972c), on the basis of a comparative study of floral anatomy, takes a somewhat broader view, including *Cleistocalyx* (115) and *Acicalyptus* (116), which are tentatively maintained here but are certainly very close to *Syzygium*.

Some species-groups within *Syzygium* may perhaps be as distinct as some of the three genera which follow it.

We have seen no material of "*Eugenia*" *flosculifera* Henderson, which is included by Henderson (1949) in "section *Syzygium*", but with the remark that "it should perhaps be placed in a new section of the genus". He gives a description of its distinctive embryo type with completely fused cotyledons, forming "a hollow ball when fully ripe", and of its unusually few stamens. It apparently has both terminal and axillary panicles.

Henderson's sections of *Eugenia* s. latiss. tend to be equivalent to groups treated as genera here and by Merrill and Perry. Henderson (1949) says of his section *Fissicalyx*, comprising two Malayan species, that "these plants might be better placed in a new genus". This view is based on the insertion of the stamens on the inner surface

of the perigynium, which extends above the disc. The cotyledons appear to be as in *Syzygium*. The flowers are described as sessile, solitary, and terminal, or occasionally in pairs at the ends of the branches.

The small group of Malasian spp. sometimes distinguished as *Aphanomyrtus* (incl. *Pseudoeugenia*; see Merrill, 1937) is unusual in *Syzygium* in its few stamens. It is doubtless significant, as Schmid suggests, that the monocyclic vascularization that he reports is associated with small flower-size. In facies and inflorescence these species fall within the general range of *Syzygium*. The monotypic *Tetraeugenia* (no material seen) was maintained with some lack of conviction by Merrill (1950), and also has small flowers with monocyclic vasculature (Schmid, 1972c); it would presumably also fall within *Syzygium* as treated here.

Some *Syzygium* species of the New Hebrides, New Guinea, and Fiji have very large flowers and leaves, and in those respects tend to resemble *Cupheanthus* (120). In these species the monads, or occasionally triads, are often borne ramiflorously, constituting SGU's.

Although most *Syzygium* species are glabrous, several New Guinea species possess a dense indumentum of multicellular "non-standard" hairs (2.2.2).

The leaves of *Syzygium alternifolium* (Wight) Walp., as illustrated by Wight (1840-3), but of which we have not seen specimens, appear to be disjunct-opposite or possibly spiral in phyllotaxy.

118. *Cleistocalyx*. Here excluding *Acicalyptus* (119). Often ramiflorous, as in *Syzygium*.

119. *Acicalyptus*. Commonly included in *Cleistocalyx* (Merrill and Perry, 1939), but appears to be a separate development from the *Syzygium* complex. Differences in leaf venation and in flowers give the two genera a different aspect, and there seems little practical difficulty in separating them. Differences in floral anatomy are reported by Schmid (1972b); he regards *Cleistocalyx* and *Acicalyptus* as probably best treated as sections of *Syzygium* but in any case not appropriately grouped together in a single segregate genus, a view apparently supported by Perry in 1970 (Schmid, 1972b).

120. *Cupheanthus*. Some inflorescence information from Seemann (1865: 76). Phyllotaxy opposite or ternate. Remarkably large-flowered and large-leaved. Relationships need clarification; we have seen only fragmentary material.

121. *Acmenosperma*. The single species is highly variable. Often included in *Syzygium*, but it has a very distinctive embryo (Kausel, 1957; Henderson, 1949: 8).

123. Gen. nov. (= *Syzygium floribundum* F. Muell.). Mr J. T. Waterhouse has drawn our attention to distinctive features of this species, which we regard as generically separate. In common with other members of the *Acmena* suballiance, it has a funicular mass ramifying through the cotyledons and has cryptocotylar germination. It resembles *Acmena* spp. in having all the ovules attached near the top of the ovary, but is similar to *Acmenosperma* and *Piliocalyx* in its less specialized anthers. The placentation is axile in all four genera, but there is much distortion of position during the development of the single seed. The funiculus appears to enter the seed of "*S. floribundum*" near the base of the fruit; the point of entry is apical in *Acmenosperma*, *Acmena*, and *Piliocalyx* (Kausel, 1957b). The panicles are frondobracteose, and the limits of the inflorescence are unclear.

Acmenosperma and gen. nov. (123) may seem to combine the characters of *Syzygium* and *Acmena*, since they lack the specialized divergent anther-loculi of *Acmena* but possess embryos with specializations broadly of the *Acmena* type. To us, especially in view of the differences in embryological detail noted above, and the

importance of embryo characters generally in the family, this is no justification for uniting these four genera. Such lumping would obscure differences and lead logically to treating as one clumsy genus the whole of a large assemblage that is of equivalent status to other multigeneric alliances (in effect, tribes) in the family. Rather, it would be worth while to study *Syzygium* itself, with cladistic principles critically in mind, in order to elucidate the relationships within it and with allied genera. This could well result in some dismemberment of the diverse and unwieldy *Syzygium*.

124. *Acmena*. See under 123. Including *Xenodendron*; see Merrill and Perry (1938).

B.VI *Eugenia* alliance. Includes members with \pm fused cotyledons ("eugenoid" embryo-type) and others with free bean-like cotyledons ("plinioid" embryo-type). These are referred to separate groups by Kausel and by Melchior (1964) (2.2.1), but, like McVaugh, we are impressed by strong cross-resemblances in other characters and retain these predominantly American genera in a single group. However, we cannot agree with McVaugh's comment (1968: 366) that the plinioid "condition may have developed secondarily from some eugenoid type" or that "the pseudomonocotyledonous embryo . . . represents a very old specialization" on the ground given that "it is found in both Old and New Worlds". Rather, undifferentiated or fused-cotyledon embryo-types would appear to be the more specialized, and may have arisen in several lines within the *Eugenia* alliance, as well as almost certainly separately in the *Acmena* alliance (in so far as the cotyledons are truly fused and not merely interlocked in the *Acmena* suballiance, q.v.).

We have taken a wide range of recorded and observed features into account and, though no linear arrangement can be satisfactory, have attempted to place genera near their apparent relatives. Plinioid embryos are found in 125 (but cotyledons thin), 126, 128-130, 132-137, and in some Old World spp. of 140. Eugenioid embryos (some with incomplete fusion of cots.) occur in 127, 131, 138-140, 142? and 143-144. Dubious cases and others requiring comment are mentioned under the individual genera. The only reported case of phanerocotylar germination in the alliance is in *Luma* (125), which has planoconvex but thin cotyledons.

125. *Luma*. We agree with McVaugh that this does not fit in the *Myrcia* alliance, where it was placed by Kausel (1957b). Nevertheless, as McVaugh says, it stands apart from other genera in the *Eugenia* alliance, though showing some features in common with *Myrcianthes* (126). We have not observed botryoids and do not know whether the occasional "short axillary bracteate racemes" reported by McVaugh are U's or C's.

127. *Pseudomyrcianthes*. Synonymized under *Myrcianthes* (126) by McVaugh, but placed amongst eugenoid genera by Kausel (1956), although with indication that the cotyledon fusion is not complete. Here placed near *Myrcianthes* on the basis of their resemblance in almost all features (but see addendum).

128. *Acreugenia*. Information from Kausel (1956). Included in *Myrcianthes* (126) by McVaugh. Material seen at K under the name of the type species, *A. pungens* (Berg) Kausel, differs greatly in inflorescence and "bracteoles" from Kausel's description and figure; it is presumably misidentified although it has sharply pungent leaf-tips, as described for *Acreugenia*, a very unusual feature in the Myrtoideae.

131. *Myrciaria*. Despite its eugenoid embryo, this genus agrees in most characters with *Paramyrciaria* (132), which in turn shows resemblance to "*Pliniopsis*" (133) and to *Siphoneugenia* (134). R_2 is sometimes a bracteose brachyblast. So far as seen, metaxephylls are present except in the case of monads. This accords with the regular occurrence of connate "bracteoles", since the ultimate hypsophyll pair on each axis

(being closely connate) leaves no room for the emergence of axillary axes, whereas the non-connate hypsophylls at lower nodes normally subtend lateral axes. Thus on a uninodate axis (as of a monad or the lateral axes of a triad or a botryoid) the prophylls are themselves "bracteoles", whilst on a plurinodate axis the non-prophyllar "bracteoles" are metaxyphylls by definition. For descriptive purposes, the designation "bracteoles" is in this instance more convenient than the "prophyll-metaxyphyll" terminology used for wider comparisons. The case illustrates how the fixing of a presumably adaptive stereotyped condition in one portion of a morphological system (in this case the ultimate bracts) can affect the developmental possibilities of other portions (axillary shoots).

132. *Paramyrciaria*. A monotypic genus possibly closely related to *Myrciaria* (131), but separated by Kausel (1967) on the basis of its distinct cotyledons. Metaxyphylls present both in single-flowered U's (metaxymonads) and below median flowers of 3-flowered U's (metaxytriads), corresponding with the occurrence of connate "bracteoles" as in *Myrciaria*. Kausel (1967: 340) stated that *Paramyrciaria* has 2-flowered racemes with the terminal bud inactive; it would appear that he had observed damaged or incompletely developed U's.

133. "*Pliniopsis*". = *Plinia* subgen. *Pliniopsis* Kausel = the greater part of *Myrciaria* sect. *Cauliflorae* Berg. Transferred provisionally ("vorläufig") by Kausel (1956) to *Plinia* because of its wholly free cotyledons (cf. undifferentiated embryo of *Myrciaria*). It differs, however, from *Plinia* s. str. (137) in inflorescence and in the absence of a well-defined radicle in the embryo, and seems out of place in that genus as well as in *Myrciaria* (131); see also McVaugh (1968: 388). U's commonly with one or more proximal pairs of empty bracts (often perules) on the a_1 , or several U's arising from a very short brachyblast.

134. *Siphoneugena*. Including *Myrciariopsis*, see Kausel (1967). Also see above under 131. Metaxyphylls present in branched U's but absent in monads. Note the spelling: "*Siphoneugenia*" is a common error.

135. Gen. aff. *Siphoneugena*, = "*Mitranthes*" sensu Legrand non Berg, see McVaugh (1968: 391). Possibly not distinct from *Siphoneugena*. Metaxyphylls as in 134.

136. *Pilothecium*. McVaugh expresses some doubt about the recognition of this as an independent genus, but gives no indication of where it might be included. We have examined only the lectotype species. The recording of dichasia, metabotryoids, triads, and monads is from Kausel (1962); we observed only thyrsoids. The inflorescences do not support the sinking of the genus in *Eugenia* by Legrand (1975) (see addendum). There is some flexibility in the development of the laterals (see 5.3). Primary axes of the SGU are blastotelic in the limited material seen.

137. *Plinia* s. str., excluding "*Pliniopsis*" (133). See McVaugh for the many complexities in typifying and delimiting this genus. *Plinia* and *Calycorectes* (138) greatly resemble each other despite differences in embryo type and ovule number. A careful comparative study of other reproductive and vegetative characters in this and other members of the alliance may indicate whether there has been parallel or convergent evolution of embryo types or of other features. Often ramiflorous; C's very short, few-flowered, spiciform or racemiform, possibly sometimes aggregated into C²'s. The well-developed paniculate U's of *P. ekmaniana* Urb. are unusual and are not included in Table 3, since the generic position of this and other West Indian species needs reconsideration.

138. *Calycorectes*. See note 137. Short (5-flowered) botryoids are reported in *C.*

sellowianus Berg (Martius, 1857, pl. 34). *C. pohlianus* (Berg) Kiaersk., illustrated in Martius (1857, pl. 35, as "*Schizocalyx pohlianus a panicularis*") and represented at K by *Glaziou 9435*, is a species of *Syzygium* (*S. jambos*?), presumably cultivated.

139. *Hexachlamys*. Accepted with some doubt by McVaugh, and certainly close to *Eugenia* (140); but, as pointed out by Legrand (1950, 1961) and Kausel (1967), it differs in the hardened endocarp (true or perigynial?), as well as in the characters mentioned by McVaugh.

140. *Eugenia*. *Stenocalyx* is here included in *Eugenia*, as by McVaugh (1968) and Schmid (1972c); so is *Jossinia* (as extended by Merrill, 1950, consisting of the Old World species), an inclusion also advocated by Schmid. Some Old World species included in *Jossinia* have separate cotyledons (e.g. *E. oraria* Guill., *E. indica* Wight), whereas in others the cotyledons are completely or partially fused. Presumably the sometimes separate cotyledons led Kausel (1957b) to recognize *Jossinia* and assign it to his Plinioideae.

Myrtopsis O. Hoffm. (non *Myrtopsis* Engl., nom. conserv., Rutaceae) — type species *Eugenia malangensis* (Hoffm.) Engl. — and *Chloromyrtus* are included following Amshoff (1958), although *E. klaineana* (Pierre) Engl. (*Chloromyrtus klaineana*) is reported to be entirely glabrous, not the usual condition in *Eugenia*. Several African *Eugenia* spp. have evolved an unusual habit, with \pm herbaceous stems arising from a woody subtterranean stock; this habit is found in members of various families growing on the Kalahari sands (White, 1977), and is also facultative in one subspecies of *Syzygium guineense* (Willd.) DC.

C²: considerable development in some species; i.e. aggregations of racemiform C's, each R₂ being a bracteose short shoot. Sometimes ramiflorous or cauliflorous (see 7.1). Some specimens referred to *Eugenia* have inflorescences (panicles, botryoids, or dichasia) discordant with those of the great majority of species; these may be misidentified material or may represent species which should be segregated or transferred elsewhere; they are not covered in the tabulation.

141. *Meteoromyrtus*. Only the rather fragmentary original collection has been seen. In the absence of fruits, the affinity of this little-known and apparently monotypic Indian genus is uncertain, but its aspect is reminiscent of *Eugenia* (140), from which it appears to differ only in the pendulous ovules attached near the top of the placenta (whence the generic name). There is no evident reason to refer it to the *Myrtus* alliance, as was tentatively done by Kausel (1957b).

142. *Stereocaryum*. "*Schizocalyx*" sensu Brongn. & Gris non auct. = "*Calycorectes*" sensu Guillaumin non Berg. New Caledonian, in contrast to the South and Central American *Calycorectes*. The thick, hard endocarp (true or perigynial?) is unusual in the family, but cf. *Hexachlamys* (139).

143-144. *Calyptrogenia* and *Hottea*. Affinity doubtful; moreover, McVaugh considers that *Calyptrogenia* may not be distinct from *Hottea*. Here tentatively placed in the *Eugenia* alliance on the basis of the apparently \pm connate cotyledons. R₂ in *Hottea* is a very short bracteose shoot bearing a single monad in the few specimens examined; the R₃ is frondose. The non-Haitian material examined under the name *Calyptrogenia* is diverse and its identity is doubtful; the tabulation covers only the type species, *C. ekmanii* (Urb.) Burret from Haiti, which shows only monads.

9. FLOWERS, FRUITS AND INFLORESCENCES — FUNCTIONAL ASPECTS

9.1 Modifications of floral structure

The floral structure of ancestral Myrtaceae appears to have been pre-adaptive for

a number of parallel or convergent modifications, repeated separately in several or many evolutionary lines. Notable among these are calyprate perianth structures and modifications of the androecium.

Calyx-lobes that are wholly or partly fused but that split more or less irregularly at anthesis are a feature of *Marlierea* spp., *Calypttranthes* spp., *Psidiopsis*, *Marlieriopsis*, *Plinia*, *Calycorectes*, and *Hottea*. Less often, one enlarged segment of the calyx may be calyptriform as in *Marlierea* sp. (= *Krugia*) and *Calypttranthes* spp. In part of *Syzygium* the perianth segments cohere to form a cap, which falls as a whole. Fully-developed calyptras have been associated in seven alliances, and repeatedly within some of them; they are usually associated with conspicuous stamens. Examples are *Pleurocalyptus*, *Eucalyptopsis* (type species), *Eucalyptus* and most allies, *Calypttranthes* spp., *Mitranthes*, *Psidium* spp., *Cleistocalyx*, *Acicalyptus*, *Piliocalyx*, gen. aff. *Siphoneugena*, and *Calyptrogenia*.

Most often the calyptra (in *Eucalyptus* s. lat. usually called an "operculum") is calycine, but the *Eucalyptus* alliance shows several independent developments (Pryor and Johnson, 1971; Johnson, 1972, 1976): (1) sepals free, calyptra corolline (e.g. most of *Eudesia* sect. *Quadraria*, "*Gaubaea*"; these in different suballiances); (2) calyptra single and probably calycine in nature, the corolla being absent (*Eucalyptus* s. str.); (3) calyptra calycine, petals \pm free but falling with calyptra (spp. of "*Corymbia*" sect. *Rufaria*, J. B. Williams, personal communication); (4) calyptra of joint calycine and corolline nature from a fused ring-meristem (*Eudesia* sect. *Apicaria*, sect. *Quadraria* (in part)); (5) separate calycine and corolline calyptas, usually with the former being shed first but in a few species both falling together ("*Blakella*", "*Corymbia*" sect. *Ochraria*; most of *Symphyomyrtus*; two separate suballiances represented); (6) conditions to some extent between (1) and (5) (a few spp. of *Symphyomyrtus*; "*Telocalyptus*"; "*Idiogenes*").

The petals of genera aff. *Mearnsia* ("*Calyptropetala*" and "*Inclusis*") are free but coherent and fall as a cap. Fused or coherent "bracteoles" (prophylls) may closely simulate floral calyptas, as in *Calytrix*, *Calythroopsis*, *Chamelaucium*, *Pileanthus*, and *Verticordia*.

Fascicled stamens are common in many alliances of the Leptospermoideae, being particularly obvious in *Whiteodendron*, *Tristaniopsis*, genus "R" (21), *Lophostemon*, genus "W" (23), *Melaleuca*, *Conothamnus*, *Lamarchea*, *Calothamnus*, *Beaufortia*, *Phymatocarpus*, and *Regelia*, but rather less so in *Basisperma*, genus aff. *Tristania* (5), *Tristania* s. str., *Kjellbergiodendron*, *Lindsayomyrtus*, *Eudesia* spp., and *Eremaea*. Mayr (1969) observes that in *Myrtus* s. str. and *Syzygium* ("*Eugenia myrtifolia*"), as well as in the fasciculate-stamened *Melaleuca*, the early stages of floral development show five (or four), initially epipetalous, primordial protuberances upon which the individual staminal primordia later develop in centripetal succession, even where this condition is not apparent in mature flowers. This, rather than an androecial ring-meristem, is probably the basic condition in the family, and some fasciculation of filaments would seem to be a primitive feature, though actual staminal phalanges are lacking in developed flowers of Myrtoideae and in many Leptospermoideae.

Pollen release from the anther-loculi is generally by longitudinal, though sometimes divergent, dehiscence slits, but is by apical slits or pores in *Symphyomyrtus* sect. *Bisectaria* series *Foecundae* and sect. *Adnataria*, the *Calothamnus* infra-alliance (in contrast with the *Melaleuca* infra-alliance), and the *Chamelaucium* suballiance (with oily rather than dry pollen), while in most species of *Eucalyptus* s. str. the two

slits are confluent at the top. *Gomidesia*, of the *Myrcia* alliance, is marked by anthers with two sets of pollen-sacs, at different levels, that open (apparently) extrorsely and introrsely respectively.

Stamens in non-fasciculate, multiseriate to pauciseriate arrangements are characteristic of many genera. When relatively few, they may even show an apparently secondary fasciculate arrangement opposite the sepals, rather than in the general antepetalous position; this condition characterizes *Astartea*. Lower stamen numbers, equal to or twice the petal number, occur in *Heteropyxis* (with unisexual flowers), *Baeckea* spp., *Syzygium* spp. (those species previously referred to *Aphanomyrtus* and *Tetraeugenia*), and in the *Chamelaucium* alliance. It seems clear that such numbers represent derived conditions.

Some other prominent variants of external floral structure are as follows:

Fusion of the perigynia of several flowers into a compact head, which develops into a compound fruit (see 6.5). Such conditions have evolved independently in *Syncarpia*, *Choricarpia subargentea*, *Symphomyrtus lehmannii*, and the *Eucalyptopsis* alliance (to various extents in the three known species, see 8.2).

Change in number of perianth parts: 5-merismy of perianth, as of androecial group-primordia, appears primitive but reduction to 4-merismy is common, while increase is also occasionally found, as in *Octamyrtus* (to 8-merous) and *Hexachlamys* (4-7-merous). (In *Osbornia* the apparent 8-merismy is false: the calyx and corolla are scarcely distinguishable, with their parts simulating a single whorl.)

Zygomorphy: a very rare condition in Myrtaceae but shown (to varying extents) by species of *Calothamnus*, and perhaps functionally associated with the one-sided development of the spiciform conflorescence therein.

Differences in flower shape: broad, saucer-shaped flowers are common (e.g. in *Lindsayomyrtus*, *Lophostemon*, *Leptospermum*, *Baeckea*, *Pileanthus*, and many Myrtoideae) but prolongation of the perigynium above the ovary may result in tubular flowers (e.g. in *Calytrix*, *Darwinia*, *Cupheanthus*, and *Siphoneugena*). Erect and elongated red petals in *Octamyrtus* produce quasi-tubular flowers apparently adapted to bird-pollination. Erect sepals and petals characterize *Homalocalyx*. In some species of *Chamelaucium* erect petals are combined with an extended perigynium, whereas others have broad, shallow flowers.

Quite often, the fruits of particular Myrtaceae genera are regarded as wholly inferior, and less frequently others are described as superior, but in fact no member of the Myrtaceae has completely epigynous or hypogynous flowers (in contrast to the excluded *Psiloxylon*, see 2.2.3). Nevertheless, this perigynous family shows wide variation in the degree to which the top or sides of the ovary, and subsequently of the fruit, are free of the perigynium, as well as in the prolongation or expansion (e.g. in *Paivaea*) of that organ above the ovary or fruit. The fruit may be almost entirely enclosed by the perigynium, especially in indehiscent cases such as the Myrtoideae or the *Chamelaucium* suballiance. Capsular fruits dehiscence loculicidally above the perigynial attachment, but the valves vary from being deeply enclosed (e.g. in "*Corymbia*" species) below the perigynium rim to constituting almost the whole of the apparently almost "superior" fruit in the mature state (e.g. in *Basisperma*, *Xanthostemon*, *Whiteodendron*, *Lindsayomyrtus*, and some others of the *Metrosideros* alliance, as well as *Heteropyxis*); the latter is perhaps a primitive condition, though produced to varying extents by differential post-floral growth. A censer-mechanism of seed shedding is achieved in various groups (e.g. in many species of the *Eucalyptus* alliance) by the combination of top-opening capsular fruits with corymbiform inflorescences or conflorescences. The fenestrate fruits of *Mearnsia* s. str.

are remarkably modified to release the seeds partly through collapsed areas (between the main vascular strands) in the sides of the capsule and of the thin-walled perigynium (Dawson, 1970b, 1976).

Reduction in carpel number is common, yielding 3-locular, 2-locular, or rarely 1-locular ovaries; increase is less so, but occurs (for example) in some *Symphyomyrtus* and *Eucalyptus* s. str. and in *Leptospermum* sect. *Fabricia*. Internally, there are major changes in floral vasculature, placentation, ovular orientation, and embryological features, as well as in the form and anatomy of seeds. The *Eucalyptopsis* and *Eucalyptus* alliances show a differentiation between functional ovules and ovulodes; the latter lack embryo-sacs but presumably perform some function in seed dispersal. Many capsule-bearing groups (e.g. *Leptospermum* and its allies) regularly produce sterile seeds (formed from "normal" ovules) as well as fertile seeds, and sometimes (e.g. *Eucalyptus* alliance) such sterile seeds are produced in addition to ovulodes.

Duration of flower and fruit development exhibits marked differences, of more or less obvious adaptive value. The flower-buds of *Darwinia* spp., for example, mature over a few months, and the fruits, with the perigynium little changed from the flowering condition, mature in a few weeks. In tropical members of the *Eucalyptus* alliance (especially "*Blakella*" and "*Corymbia*") the development of flowers and fruits is completed in less than a year. By contrast, the development of flower buds in many species of *Eucalyptus* s. str. takes up to two years, and fruit maturation extends over six to nine months. The fruits may then remain on the plant for some years before seed release, a feature associated with fire-prone habitats (Pryor and Johnson, in press), and shown also by many woody-fruited members of the *Leptospermum* alliance.

9.2 Adaptive syndromes

Just as the inflorescence must effectively present the flowers for pollination, so must its later stage, the infructescence, bear the fruits suitably for seed dispersal. For a species to survive, the shapes, sizes, and functions of its floral structures and fruits must be adaptively co-ordinated with the sizes and relationships of the parts of the inflorescence, which are in turn constrained by its basic structural plan.

Pollination of Myrtaceae may be by insects, birds or, in some cases, gliding or non-flying mammals (Rourke and Wiens, 1977, and references therein), and possibly by bats as well, though we know of no evidence of the last. Wind-pollination has been reported (Pryor, 1976) as a rare condition in *Symphyomyrtus* sp. ("*Eucalyptus tereticornis* Sm."). Breeding systems (including compatibility relationships) have been studied in *Eucalyptus* s. lat. (e.g. Pryor, 1976), while a few species of *Darwinia* (Briggs, 1964), although closely related to outcrossing species, show regular self-pollination before anthesis.

Investigations of reproductive biology have been limited to a few genera, but an association between red flower-colour and ornithophily appears to be established and probably applies in the brilliant brush-blossoms of certain species of *Metrosideros*, *Mearnsia* s. str., *Purpureostemon*, *Melaleuca*, *Callistemon*, *Calothamnus*, *Beaufortia*, *Feijoa*, *Myrrhinium* (filaments very long, dark red, but relatively few), and a minority of the species of *Xanthostemon*, "*Corymbia*", *Eudesmia*, *Symphyomyrtus*, *Melaleuca*, and *Syzygium*. The cream-coloured brush-blossoms of the majority of the *Eucalyptus* alliance and of *Syzygium* are also visited by birds, and indeed birds may be among the visitors to flowers of many genera with moderately long and fairly numerous stamens.

Ornithophilous specialization has arisen separately in a number of lines, and may be found throughout almost the whole ecological range of the family, in rainforests, woodlands, heaths, and probably even in the Australian eremaea (in *Lamarckia*).

Small flowers, presumably insect-pollinated, with conspicuous petals, also occur through the whole ecological range but are particularly common in scleromorphic heaths and scrubs on infertile soils (Johnson and Briggs, in press). In such shrubby communities, it is common for the flowers to be variously massed in cymes or superconflourescences (e.g. *Leptospermum* spp., *Agonis*, *Baeckea* spp., *Calytrix*, *Calythopsis*, *Micromyrtus*, *Thryptomene*, *Homalocalyx*, *Wehllia*). *Rylstonea* has small but rather conspicuous cymes of pendulous flowers. Functional aggregations or large panicles are found in some Myrtaceae of forests and woodlands also (e.g. *Kania*, *Xanthostemon* spp., *Backhousia*, *Choricarpia*, *Allosyncarpia*, spp. of *Myrcia* and its allies, *Temu*, *Pimenta*, *Xanthomyrtus*, *Marlieriopsis*, spp. of *Syzygium* and its allies, *Myrcianthes*, and *Pseudanmomis*). It is notable, however, that in mesomorphic or only moderately scleromorphic species of the undergrowth or understorey of the less sclerophyllous communities the situation is often rather different. There one finds a higher proportion than among the more specialized scleromorphs of small to medium-sized, or occasionally quite large, flowers with approximately equally conspicuous (or inconspicuous) corolla and androecium, often in monads and triads that are not massed (e.g. *Cloëzia* spp., *Myrceugenia*, *Psidium* spp., *Ugni*, *Myrteola*, *Myrtus* s. str., *Rhodamnia*, *Archirhodomyrtus*, *Austromyrtus* spp., *Lophomyrtus*, *Uromyrtus*, *Neomyrtus*, *Myrtastrum*, *Myrtella*, *Pilidiostigma*, *Blepharocalyx* spp., *Campomanesia*, *Luma*, *Reichea*, *Eugenia* spp., and *Stereocaryum*).

Various organs provide the most conspicuous structures of the flower, as in the following examples (which also indicate colours and common inflorescence conditions). Where conflourescence or superconflourescence structure is usual and well-developed, this is also indicated (P = panicle, Th = thyrsoid, Mb = metabotryoid, B = botryoid, Tr = triad, M = monad, -C = conflourescences commonly specialized, -C² = superconflourescences commonly specialized, ± = present in some members only). Table 3 should be consulted for a more complete listing of inflorescence conditions in these genera. The examples are not exhaustive.

Most conspicuous structure:

Perigynium: red: *Symphyomyrtus* spp. e.g. *S. sp.* (= "*Eucalyptus*" *forrestiana* Diels (Tr)); *Balaustion* sp. (M).

Calyx-segments: white, pink, red, purple, or yellow, and lacinate or fimbriate: *Verticordia* (M - C - ±C²).

Calyx-segments, petals, style, and extended perigynium: white, yellow, or pink, and often combined with reddish "bracteoles" (prophylls): *Homoranthus* (M - ±C). *Rylstonea* (M - C).

Petals: white or cream (only a few examples listed): *Heteropyxis* (P), *Sinoga* (M - C), *Marlieriopsis* (Th, Mb); white and pink in different species: *Leptospermum* (M - C - ±C²), *Baeckea* (D, Tr, M), *Calytrix* spp. (M - C), *Chamaelucium* (M - ±C - ±C²), *Eugenia* (M - C - ±C²); pink: *Wehllia* sp. (M - C), *Pileanthus* sp. (M - C - ±C²); red: *Balaustion* sp. (M), *Octamyrtus* (M), *Fenzlia* (M); purple: *Calytrix* spp. (M - C); yellow: *Leptospermum* (sect. *Fabricia*) sp. (M - C), *Hypocalymna* spp. (M - C²), *Wehllia* sp. (M - C).

Petal and staminal filaments about equal (only a few examples listed): white or cream: *Lysicarpus* (Tr), *Lophostemon* (D, Tr - ±C), *Myrcia* (P, Mb, B, Tr, M),

Psidium (Tr, M — \pm C), *Ugni* (M — \pm C), *Myrtus* s. str. (M); yellow: *Xanthomyrtus* (Tr, M); white or pink: *Rhodomyrtus* (Tr, M — \pm C).

Staminal filaments: white or cream: most species of all genera of *Eucalyptus* alliance (Th, Mb, D etc. — \pm C), *Calyptrothanas* (P, B, Tr, M etc.); white or pink: "*Calytropetalum*" (Tr — \pm C); white and red in different spp.: *Metrosideros* s. str. (Tr — C), *Mearnsia* s. str. (P, Th, Mb, B, Tr — \pm C), "*Corymbia*" (Th, D, Tr — \pm C), *Kunzea* spp. (M — C), *Melaleuca* spp. (Tr, M — C — \pm C²), *Callistemon* (M — C), *Syzygium* (P, Mb, B, Tr, M); red: gen. aff. *Callistemon* (in part) (M — C), *Calothamnus* (Tr — C), *Eremaea* spp. (M — C); red and green in the same or different spp.: *Symphomyrtus* spp. (*S. lehmannii* green) (D — \pm C), *Melaleuca* spp. (Tr, M — C), *Callistemon* (M — C), *Beaufortia* (Tr — C); pink: "*Corymbia*" spp. (Th, D, Tr — \pm C), *Symphomyrtus* spp. (D — \pm C), *Melaleuca* spp. (Tr, M — C — C²), *Syzygium* spp. (P etc.); dark red or purple: *Purpureostemon* (M — C), *Melaleuca* spp. (Tr, M — C — C²), *Phymatocarpus* (Tr — C), *Regelia* spp. (Tr — C), *Myrrhinium* (P, D); orange: *Eudessmia* spp. (Mb, D — \pm C), *Eremaea* spp. (M — C); yellow: *Xanthostemon* spp. (P, Mb, B, Tr, M — \pm C), *Conothamnus* (Tr — C).

Involucral "bracts": red, pink, purple, or yellow: *Darwinia* spp. (M — C, pseudanthia).

Sterile "ray" monads: white or pink: *Actinodium* (M — C, pseudanthia).

The foregoing sample of conditions in particular genera is incomplete and not randomly selected, but it demonstrates the variety of flower types and colours that occurs in each of the inflorescence categories.

The presentation of the flowers is affected by the position and orientation of the inflorescence and the relative elongation of axes, in addition to the basic inflorescence structure. Ramiflory and cauliflory may be partly associated with the support of large fleshy fruits but, more importantly, these conditions involve a shift of the flowers and fruits from the periphery of the foliage to the interior of the crown. This doubtless involves pollinators and seed-dispersal agents that live under the canopy. Most inflorescences are held more or less erect or spreading, but the conflorescences of *Rylstonea* and most of the pseudanthial conflorescences of *Darwinia* spp. are nodding, as are uniflorescences in many species of *Symphomyrtus* and some of the large flowers of cauliflorous or ramiflorous species (e.g. of *Syzygium*). The flowers of *Balaustion pulcherrimum* Hook., and of some *Darwinia* spp., are probably visited by ground-feeding rather than perching birds. Corymbiform massing of flowers is common in the short, broad thyrsoids of *Angophora* spp., "*Corymbia*" spp., and "*Gaubaea*" sp. ("*Eucalyptus curtisii* Blakely & White), and also in the panicles of *Syzygium* spp., as well as in the very differently constructed conflorescences or superconflorescences of monads exhibited by *Pileanthus* and *Verticordia*.

It would seem that primitive Myrtaceae had partly superior capsular fruits that were not particularly woody, as indeed is still the case in many genera of the *Metrosideros* alliance and in *Heteropyxis*. In Myrtoideae the fruits came to be wholly surrounded by the perigynium, which became fleshy, in association with zoochory. Large size and/or reduction in seed number are common secondary developments. In many Leptospermoideae also, the fruits became largely enclosed in the perigynium, but for the most part remained capsular with free loculicidal valves at the top. In habitats subject to fire and periodic drought, the perigynium has become thickly woody, protecting the seeds from heat and desiccation. In a few cases (e.g.

Lindsayomyrtus) there are quite large oligospermous fruits, developed almost entirely from the free part of the ovary. A striking contrast in fruit size and perigynial thickening is found within *Symphomyrtus*: one may compare "*Eucalyptus*" *microtheca* F. Muell. and "*E.*" *macrocarpa* Hook., respectively with fruit diameters of 3-4 mm and c. 90 mm and found in virtually fire-free and fire-prone situations; seed-size in these differs greatly too, and factors other than fire are also involved. Woody thickening is largely confined to the perigynium; where part or all of the capsule is superior that portion is seldom very woody, exceptions being the thickened valves in a few species of *Symphomyrtus* and *Eucalyptus* s. str.

Succulent fruits characterize the Myrtoideae but have also evolved as a rare condition in three other lines (*Kjellbergiodendron*, *Kunzea pomifera* F. Muell., and *Leptospermum semibaccatum* Cheel), whilst in the mangrove genus *Osbornia* the fruits appear to have lost the usual succulence of the Myrtoid perigynium, while remaining indehiscent. In this last case, animal dispersal has presumably been replaced by floating on the water. In the *Backhousia* alliance and the *Chamelaucium* suballiance the fruits have become indehiscent and few or one-seeded, but have remained small and without a markedly succulent perigynium. The whole fruit functions as a disseminule in these cases. The various methods of dispersal are yet to be studied in detail. In *Backhousia* spp. the persistent calyx retards the fall of the fruits, which twirl through the air. In many of the *Chamelaucium* alliance the whole perianth persists on the shed fruit. Fruits advertise their presence, presumably to birds or to primates with colour-vision, by red, orange, yellow, and blue coloration of the outer layer of the fruiting perigynium (pseudo-exocarp).

Several inflorescence modifications, which must have evolved repeatedly in various separate groups, are frequently associated with the support of large fruits, and sometimes large flowers. Such modifications are reductions in branching and in overall flower number, and the shortening or thickening of axes. Where the fruits persist for several years before seed-release, even small fruits require adequate support on perennial axes, as in the conflorescences and superconflorescences of sessile or subsessile flowers in some *Leptospermum* species and in the *Calothamnus* suballiance generally.

Biogeographic considerations have been omitted from this discussion (a brief account of the phytogeography of Myrtaceae is given by Johnson and Briggs, in press), but the occurrence of similar adaptive features and syndromes in taxonomically widely separated groups is matched by their occurrence in geographically remote regions.

10. CONCLUSION

To us, as to most investigators of the Myrtaceae, the family — as here constituted — appears to be a very coherent one. Although its two subfamilies may correspond with a natural division within it, their more primitive members would not have been very dissimilar, and it may indeed be that the *Eucalyptopsis* and *Eucalyptus* alliances together diverged very early from the rest of the Leptospermoideae, even before the clear separation of the latter from the Myrtoideae. Within its general morphological framework, the family shows great diversity in environmental adaptations, vegetative features, inflorescences, flowers, and fruits.

The numerous stamens, produced in phalanges by *dédoublement*, appear to have been pre-adaptive for the evolution of brush-blossoms, which in the less specialized cases may be facultatively bird-pollinated, but in the more advanced cases are often

tightly adapted to pollination by long-billed nectar-eating birds. Attraction of pollinators by massing of flowers has presumably been a major factor in conflorescence and superconflorescence specialization, though this must have followed a reduction (presumably under different selective conditions) of many-flowered uniflorescences. The adaptive value of perigynium thickening in the fruits (fleshy in zoochorous Myrtoideae, woody in fire-prone habitats in which usually only Leptospermoideae have been able to succeed) has doubtless sometimes been involved in reductions of the degree of branching of inflorescences. Factors promoting increase or decrease in the number of flowers in the functional floral grouping seem often to have acted together, or in sequence, to achieve a new balance — a somewhat similar presentation of flowers, achieved by a different structural plan. The widespread, but spatially and temporally discontinuous, incidence of such adaptational factors has led to many parallel or convergent trends at various levels of evolutionary divergence.

Because of this very extensive parallelism, inflorescences cannot be used, either alone or as predominating features, in determining affinities and satisfactory suprageneric groupings. They are, however, useful in characterizing and distinguishing certain groups, and in understanding relationships of species and genera within alliances. They may also provide a valuable check when considering trends in other features: do the postulated affinities and phylogeny involve associated changes in inflorescences that are improbable on general biological grounds, or discordant with patterns found elsewhere in the family?

Superficial characterizations of inflorescences or comparisons between distantly related Myrtaceous groups are likely to be misleading. Effective comparison calls for a clear determination of equivalence, in the light of correspondences in the family as a whole.

Inflorescences in Myrtaceae, like other organs and as in other families studied in some detail, illustrate the channelling of evolutionary possibilities imposed by genetically determined patterns of development and by stages in evolutionary change that have already been attained. Riedl (1977) discusses the positive and negative feedback cycles involved in such channelling, in systems-analytical terms and with reference to epigenetic control. The stabilization of uniflorescence-conflorescence patterns, while allowing further change *within* this framework, can be seen in this light.

We believe that the scheme of relationships embodied in the systematic framework presented here approaches an understanding of Myrtacean phylogeny more closely than do previous systems. Nevertheless, much more comparative investigation is needed, of chemistry as well as morphology and anatomy. Studies of development in a wide range of genera and of the putatively related families are necessary for more thorough comparison and evaluation of trends in androecia, gynoecia, ovules, embryos, and such vegetative features as trichomes.

As the relationships thus become better known, the evolutionary history may be elucidated in the light of phytogeography, fossil evidence (very meagre and unpromising at present), and past dispersal opportunities, as well as co-evolution of pollinators, fruit-dispersal agents, phytophagous insects, and fungal and microbial pathogens. Concurrently, the study of inflorescence form on a firm comparative basis should contribute to a general understanding of the evolution and biology of the family. In turn, the adaptive reasons for, and sequences in, evolutionary changes in inflorescences themselves should become clearer.

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ADDENDUM

Since completion of the text, we have seen the paper by Legrand (1975) in which he discusses *Pilothecium*, to some extent redefining it and reducing it to subgeneric rank under *Eugenia*. He indicates that there is considerable variation in inflorescences within and amongst the species; his descriptions do not permit us to interpret the inflorescences fully in terms of the criteria used in this paper, but some of them appear to be less reduced than is the rule in *Eugenia*. It might therefore be best to retain *Pilothecium* until the whole *Eugenia* complex is more thoroughly revised. Legrand points out that *Pseudomyrcianthes* as to its type species "*Eugenia pyriformis*", appears to be a perfectly representative *Pilothecium*; it should therefore be deleted from the genera tentatively recognized herein.

Legrand criticizes Kausel's separation of plinioid and eugenioid groups, pointing out the variability of embryo conditions amongst closely related species and genera; this is in general agreement with the standpoint that we have adopted. He recognizes the significance of the differences between the *Syzygium* and *Eugenia* groups, where a complex of characters is involved. He makes no mention of the cryptorhizoid embryo-type, which does seem to be distinctive though it is not clearly associated with a complex of other characters.

Legrand also points out that *Corynemyrtus* was referred by Burret (1941a) to the synonymy of *Psidium*; we had overlooked this point, which needs further checking.

APPENDIX I. THE RELEVANCE OF TROLL'S SYSTEM OF INFLORESCENCE TYPOLOGY

i. *General*

As mentioned above (3), the contribution of Wilhelm Troll is outstanding in its clarification and systematization of inflorescence structures. Troll's great work *Die Infloreszenzen* was intended to consist of nine major sections. Only three of these have been published (Troll, 1964, 1969), in one and a half "Bänder", together making up two books of over 1,200 pages. In contrast to the simple and clear style of his earlier introduction to plant morphology (Troll, 1954, 1957), the treatise on inflorescences is written in so intricate and complex a style that it is very difficult for non-German-speakers to comprehend in detail. Consequently it has been neglected or only imperfectly understood by most English-language botanists. The brief exposition by Weberling (1965) should have remedied this to some extent, but one must study Troll in detail and absorb his way of thinking as illustrated by many examples and discussions, in order to grasp fully his typological approach and the application of his theory. Even this is inadequate for a full understanding, owing to the non-publication of the late parts of his monograph, dealing for instance with polytelic synflorescences, inflorescence conditions in woody plants, proliferating synflorescences (auxotely in our terminology), and the inflorescences of monocotyledons.

The effort required to study Troll's inflorescence work is rewarded by a greatly increased understanding of inflorescences and the spatial relationships of shoot, leaf, and flower organs (irrespective of one's acceptance of all his premises), and demonstrates how inadequate, and indeed vapid, were the attempts by such English-language authors as Rickett (1944, 1955) to describe and classify inflorescences.

Nevertheless, several of his concepts, including a number of the most fundamental, are incompatible with certain aspects of the inflorescences we have studied. These aspects are sometimes mentioned here with particular reference to Myrtaceae, but they are of general relevance in developing logical systems of inflorescence analysis.

Although he indicated his intention to deal with woody plants in future volumes, it is clear that Troll's system of inflorescence typology was developed from study of annual dicotyledonous herbs, chiefly of the North Temperate Zone.

He does include examples from perennial herbs (but chiefly geophytes etc. with annual above-ground parts) and, more casually, woody plants (but especially those of marked seasonal growth as familiar in European woods and gardens), as well as a few from monocotyledons, but the difficulties that arise in those cases are not explicitly faced in his published volumes.

Troll's concepts of the *Unterbau* (the substructure, i.e. the branching or unbranched vegetative zone proximal to the flowering region) and of the *synflorescence* both have connotations of a system of growth that reaches its culmination in flowering. (It is possibly symptomatic that the continuation of vegetative growth after flowering by the axis of an inflorescence — auxotely in our terminology — is termed "Prolifikation", which may suggest that a perennial condition for a flowering axis is considered somewhat aberrant.)

The concept of the *Hauptfloreszenz* (i.e. main florescence — not main inflorescence as translated by Carolin, 1967), appears to have been conceived in relation to the single main flowering stem of a polytelic herbaceous plant. Although the term may be applied elsewhere, it does not carry the same significance in arborescent species with numerous inflorescences.

Troll's typological "theory" does not necessarily imply a system of causal explanation or of temporal sequence, though he does mix in such ideas in some of his comments through his book. The approach depends on the setting-up of conceptual archetypes from which other arrangements can be considered derived, in the sense that one can derive one geometrical arrangement from another by changing the numbers, lengths, or (within stricter limits) positions of component elements, while preserving a certain set of relationships amongst them (the structural plan, or *Bauplan*). Having decided on the *Bauplan*, the "theory" and the terminology are to a considerable degree inflexible, and the whole structure can thus topple if the choice of *Bauplan* basic to it is shown to be ill-founded. We fear that, in the framework of evolutionary reality, Troll's system (or any other typological one) must indeed collapse for just this reason, despite the continued value and validity of much of his analysis if it is divorced from his theory-bound terminology.

Twice, Troll seems to have been unfortunate in beginning from the wrong point: (1) the consequences of his initial concentration on hapaxanthic herbs are mentioned above, and have been the subject of criticism by Carolin (1967); (2) the concept of the *main florescence* (*Hauptfloreszenz*, HF), with its more or less associated ideas of the *basal internode* (*Grundinternodium*), *terminal internode* (*Endinternodium*), *paracladia*, *synflorescence*, and *enrichment zone*, seems to have begun with a consideration of indeterminate, racemose forms (blastotelic-anauxotelic in our terminology, polytelic in Troll's), leading to his equating the single terminal flower (*Terminalblüte*, E) on the lowest-order (main) axis of a monotelic (anthotelic) synflorescence to the HF of a polytelic synflorescence. This concept is manifestly unworkable when applied to cases where within-group transitions are observable between otherwise comparable inflorescences ending respectively in a flower or an indeterminate bud. Since it is part of the essence of his approach, its unacceptability has been a major factor leading to partial or total rejection of Troll's system by ourselves, as well as by Carolin (1967) and Stauffer (1963).

These two authors each advanced some alternative definitions, using some of Troll's terms; we cannot recommend Carolin's redefinitions of main florescence (also termed by him "the inflorescence itself"), synflorescence, and enrichment-zone, for they so alter Troll's concepts that confusion is inevitable if the same terms are used. Moreover, though less typological than Troll's, these redefinitions are inadequate to distinguish many common situations; for example, Carolin's definition of a synflorescence would in many cases lump Myrtaceous uniflorescences and conflorescences into a single class.

Stauffer, writing before Troll's main exposition of his system, put forward criticisms that still appear largely valid and have not been answered in Troll's subsequently published work. Like Carolin and ourselves, he points out in particular the correspondence in general structure between anthotelic and blastotelic forms in certain taxa, and defines paracladia (repetition branches) differently from Troll, stressing the sequence of flower development and of anthesis (largely ignored by Troll — and fortunately not presenting any evident problem in the Myrtaceae!). More generally, Stauffer emphasizes the difficulties in setting up a general theory of inflorescences on deductive bases, and the necessity of working from the facts of nature and not from preconceived ideas. This is tantamount to a rejection of the typological approach, a rejection with which we agree.

Typology amounts to the selection of particular sets of relations between structures as models to which observed cases are referred by certain more or less defined procedures of conceptual (in the present case usually essentially geometric)

“derivation”. Unless such a system is based on actual temporal derivation (evolution) in nature, illuminated by ontogeny, the starting points and the “allowable” conceptual derivations are primarily governed by a general conception of a “norm” and by the simplicity of the process of subsequent derivation therefrom. If they are found not to fit in with phylogenetic relationships (which are generally, but not unreasonably, *inferred*), or even with relationships resulting from some other and perhaps more tractable typological approach, the system is in serious trouble, because its terminology is fixed and dependent on the original arbitrary or idealistic assumptions.

For these reasons, it is desirable to reduce the typological element (one cannot eliminate it since it is implicit in language and probably in thought) and to employ a descriptive, relatively theory-free, system for general classification of structures like inflorescences, which vary in many directions and in which it is difficult to determine evolutionary homology over the wide domain of angiospermous orders. Special terminologies, or special-purpose definitions, carrying more implication of homology, can then be introduced when required for use over smaller domains, with their limitations clearly indicated.

Variables in inflorescences are several: topology, metric relations (including allometric relations between organs of the same or different kinds), developmental sequence, and so on, and we hope to set these out elsewhere, together with an arrangement of the more useful of Troll's and other well-known descriptive terms for inflorescence types and components, as considered in relation to these variables. Some such acceptable terms, as used in this paper, are defined above (3) or in Appendix II.

ii. *Some particular concepts and terms*

In matching synflorescence structure between his polytelic and monotelic cases, Troll (1964: 150–151), as we have seen, equates (in a “purely formal” sense, to be sure) the racemose or thyrisc (not thyrsoïd) *Hauptfloreszenz* (HF, main florescence) of the former with the single *Endblüte* (E, terminal flower) of the latter. In keeping with this, he matches the *Grundinternodium* (GJ, basal internode) of the HF (i.e. the first internode above the most distal paracladium) with the *Endinternodium* (EJ, terminal internode) of the E (i.e., in our terminology, the anthopodium of the terminal flower), on the ground that below this EJ one finds the most distal paracladium. In each case the region bearing paracladia is known as the *Bereicherungszone* (BZ, enrichment zone, the “field of enrichment” of Weberling, 1965). As already stated, we reject this formal correspondence and the terminology based upon it, as inconsistent with the actual situation in many inflorescences (though it can be applied well enough without contradiction within some taxa, large or small). Stauffer (1963) rejects it in Troll's interpretation, but does accept the paracladium (or *Bereicherungszachse* = enrichment axis) concept in a modified sense, making allowance for the undoubted fact that *repetition of structural plan* of the HF (the essence of the paracladium concept) must, in some groups, be assessed in terms not only of branching geometry, but also of order of flower initiation and/or maturation. Thulin (1975) makes a similar point.

Carolin (1967: 25) discusses this question also, distinguishing “morphological” from “physiological” (flowering-order) definitions of the BZ: we do not agree with his view that, whilst the latter may assist “in determining intra plant relationships”, it will not do so (as the “morphologically” defined BZ will) “in determining taxonomic relationships” (for which we read “inferred phylogenetic relationships” if it is to have any substantive meaning). We have found no need for any of the above concepts in

analysing Myrtaceous inflorescences, and some of them would lead only to confusion and misinterpretation; still, the notions of enrichment zones and paracladial repetition (as an aspect of "serial homology") are of use, *descriptively*, in certain families with other patterns of inflorescence comparability.

Polytely (many-endedness) and *monotely* (one-endedness), as concepts, reflect Troll's emphasis on the facts that in the former the first axes to end in flowers are all of the second order ("biaxial systems") and that each ultimate unit of repeating structure (the HF and the paracladia) has *many* flowers. In the monotelic case, an axis of the first order ends in a flower (the E) and the *ultimate* paracladia (in his sense, not necessarily in Stauffer's!) all consist of *single* flowers also. Thus these terms are theory-bound, and consequently will not do to replace *indeterminate* (*open*) or *determinate* (*closed*). Stauffer considers *open* (*offen*) and *closed* (*geschlossen*) to be adequate terms, but since these and *determinate* or *indeterminate* are words of wide application in other senses, and since so-called "open" ("indeterminate") shoots may in fact be quite determined (anauxotelic) in their growth possibilities, we find *blastotelic* (comprising anauxotelic and auxotelic) and *anthotelic* (3.1.1) and the corresponding nouns in *-tely* usefully unequivocal, and propose them for general use in a *descriptive, theory-free* sense.

While rejecting elements of Troll's terminology, we should also note the limitations of some of the terms we have adopted. *Uniflorescence* and *conflorescence* cannot be taken as phylogenetically-based terms, implying a particular degree of aggregation. The flexibility of the anthotelic/blastotelic condition, as in Myrtaceae, precludes this, except within limited fields of affinity or among relatively similar inflorescences. Notwithstanding these problems, we consider such terms useful, and indeed necessary to express equivalences and evolutionary trends of the types postulated here. Used over a wide field they are descriptive only; within a narrower field they probably do apply to phylogenetically homologous structures, but this must be evaluated in each case. Since Troll stresses the *Unterbau* as part of his synflorescence system, some limit is required lest the incorporation of the linking proximal axes should result in the whole crown of a flowering tree being taken as a single synflorescence — scarcely a useful interpretation. We reject the synflorescence concept, yet some problem remains here. To provide a frame of reference for specifying the relative positions of nearby axes, we define (2.2) the SEASONAL GROWTH UNIT (SGU). Axes with similar relative positions within the SGU show regularities in the potential for florigenous or vegetative development, and it appears that further study of such patterns is warranted in the Myrtaceae, and doubtless in other families.

We have retained the term *prophyll* (*Vorblatt*), as used by Troll; the prophylls being the first two foliar organs (only one in monocotyledons) on a vegetative or reproductive branch. Although it is dubious whether there is any essential difference between prophylls and later phyllomes (and prophylls are absent from flower-stalks in some families), nevertheless in many groups (including Myrtaceae) the prophyllar node is usually retained on all branches, though more distal nodes are often lost by curtailment of the growth or termination in a flower. Every superficial axillary bud has at least its prophylls, though of course these may not be developed in cryptic buds, which are merely meristematic patches hidden in the cortex (e.g. epicormic buds of eucalypts etc.). Where a panicle terminates a frondose axis, the prophylls on the main axis (a_1) are separated from the terminal flower by many nodes and are sometimes leaf-like in form. On the other hand, the prophylls of higher-order axes within the panicle would be "bracteoles" associated with individual flowers and very different

from foliage leaves in their development. Usually (in Myrtaceae and many other anthotelic families) the side flowers are "bracteolate" (bracteoles = prophylls), but central flowers are often "ebracteolate" (lack metaxyphylls) except when they are solitary (i.e. in true monads, where again the prophylls are the "bracteoles").

Related to the prophyll concept is that of the *basipodia* (Troll, 1964: 194 ff.), comprising the *hypopodium*, *mesopodium*, and *epipodium*. These are respectively the internodes below, between, and above the prophylls (the mesopodium is absent if the prophylls are opposite or if there is only one prophyll). Taking the flower as the reference point we introduce the term *anthopodium* (3.4); on an axis with only the prophyllar node(s) this corresponds with the epipodium but there is no connection between the concepts as such.

Troll introduces several useful terms in German form only, whereas in other cases he gives equivalents for international usage. We have adopted the Greek-based translation *pherophyll* in place of *Tragblatt* (Troll uses *Deckblatt* also in much the same sense), referring to subtending foliar organs. Similarly, *metaxyphyll* is used in place of *Zwischenblatt* (see 3.5).

APPENDIX II. DEFINITION OF TERMS

Terms newly introduced are given in capitals; many of these are discussed above (3.1-3.5). Well-known and unequivocal terms (e.g. *axis*, *node*) are not listed. T: term (or German equivalent) used by Troll (1954, 1957, 1964, 1969) but not necessarily originated by him. Bracketed terms [] are not accepted in our analysis, although the concepts to which they refer are sometimes accepted under other terms. Corresponding nouns indicated: (n); adjectives: (adj.); more or less the same as: \approx . N.B. In definitions, the term *inflorescence* is usually to be understood as including *partial inflorescence* and also *uniflorescence* (or part thereof). The symbols after certain terms refer strictly to use in the present paper.

a_1 — The main or primary axis of a uniflorescence (anthotelic in Myrtaceae). In the case of an anthotelic inflorescence terminating a main shoot, $a_1 = R_2$ (q.v.), and its use is therefore avoided.

a_2 — A second-order axis of a uniflorescence (anthotelic in Myrtaceae).

$a_3 \dots n$ — A third (. . . nth) order axis of a uniflorescence (anthotelic in Myrtaceae).

Accessory (T) — Used of an additional axis, inflorescence, or bud above or below the main axillary axis subtended by a particular pherophyll (Fig. 5).

Acrodromous — Used of leaf venation type in which two or more primary or strongly developed secondary veins run in convergent arches toward the leaf apex (the arches not recurved at the base). In *basal acrodromous* venation the acrodromous veins originate at the base of the leaf lamina (Hickey, 1973).

Acrotonic (T) — Producing lateral flowers or flowering branches mainly in the upper part of the season's growth. Sometimes also used to describe the form of a branching system in which the lateral branches are more extensively developed in the upper part. (Cf. *basitonic*, *mesotonic*, *pantotonic*.)

ANAUXOTELIC (n. ANAUXOTELY) — Applied to inflorescences, to parts of inflorescences, or to axes, that are blastotelic (not ending in a flower) but in which growth does not continue beyond the flowering region (cf. *auxotelic*). From Greek: the end not growing.

ANTHOPODIUM — The internode between a flower and the most distal node of the axis that it terminates. [*Pedicel*] is sometimes used for this internode, but is often employed to include also the penultimate and even lower internode(s); it is therefore avoided here. From Greek: flower-foot. (See Appendix I, i.)

ANTHOTELIC (n. ANTHOTELY) — Ending in a flower or in an aborted but distinctly floral bud; applied to inflorescences, parts of inflorescences, and axes; \approx [*determinate*], [*closed*], or [*monotelic*], but without the theoretical connotations of the last term (cf. *blastotelic*). (See 3.1.)

AUXOTELIC (n. AUXOTELY) — Applied to blastotelic inflorescences, to parts of inflorescences, or to axes, that continue growth beyond the flowering region (cf. *anauxotelic*). From Greek: the end growing. (See 3.1.)

Axonoscopic (T) — Used of an accessory axis (or bud) situated above the primary axillary axis arising at the same node (cf. *phylloscopic*). From Greek: looking toward the stem.

[*Basal internode*] — = [Grundinternodium, GJ] (T). See Appendix I.

Basitonic (T) — Producing lateral flowers or flowering branches mainly towards the base of the season's growth. Sometimes also used to describe the form of a branching system in which the lateral branches are more extensively developed toward the base. (Cf. *acrotonic*, *mesotonic*, *pentotonic*.)

Bauplan (T) — Structural plan; conceived in typology as the basis in terms of which a set of other forms can be interpreted; e.g. panicles elaborated to various extents (including their reduced derivatives) share a common *Bauplan*.

[*Biaxial*] (T) — See Appendix I.

BLASTOTELIC (n. BLASTOTELY) — Not ending in a flower, i.e. ending in a non-floral bud; applied to inflorescences, parts of inflorescences, or axes; \approx [*indeterminate*] or [*polytelic*], but without the theoretical connotations of the latter term. (Cf. *anthotelic*; embraces *auxotelic* and *anauxotelic*, see 3.1.) From Greek: ending in a bud or sprout.

Botryoid (T) (adj. *botryoidal*; symbol: B) — An anthotelic inflorescence with multinodate main axis and unbranched lateral axes that have prophyllar nodes only (uninodate in Myrtaceae) or that consist of an anthopodium only. Embraces raceme-like (n. *EUBOTRYOID*), spike-like (n. *stachyoid*), umbel-like (n. *sciadioid*), and other variants. (Cf. *botryum* (incl. *raceme*), which differs in being blastotelic.) (Fig. 7c.) As with other terms designating inflorescence types, *botryoid* is applied either to a whole inflorescence or, within an inflorescence, to a portion possessing structure of the relevant type. Thus, some of the branches of a panicle may themselves be appropriately termed botryoids, whereas others may be paniculate (although less ramified than the total panicle of which they form a part).

Botryum (T) (pl. *botrya*; adj. *BOTRYINE*) — A simple blastotelic inflorescence in which the primary axis bears lateral flowers (provided with prophylls or not). Used by Troll collectively for "simple" inflorescences, viz. racemes, spikes, (blastotelic) umbels etc.

Brachyblast (adj. *brachyblastic*) — A blastotelic shoot of limited growth (=

short shoot), usually with densely crowded nodes. Sometimes used also for early stages of growth of temporarily brachyblastic shoots that grow on only after flowering.

Bract — A much-reduced leaf; commonly associated with inflorescence structures (then = *hypsophyll*, q.v.) or with resting buds (then = *perule*, q.v.). An ambiguous term in common usage; we do not equate *bract* with *pherophyll* (q.v.), since *pherophylls* may be bracteose or frondose.

Bracteole — An empty phyllome at the ultimate (or also penultimate in dispersephyllotactic cases) node of an axis terminating in a flower. Use of this term is generally avoided here (see 3.5).

Bracteose (T) — Of a shoot: bearing bract-like foliar organs (cf. *frondose*, *frondo-bracteose*, *frondulose*); of a phyllome: having the reduced nature of a bract (q.v.).

Brochidodromous — Leaf venation type in which the secondary veins are joined together in a series of prominent arches and do not extend to the margin (Hickey, 1973).

Cauliflory (adj. *cauliflorous*) — Condition in which (non-frondose) inflorescences are produced from resting buds on well-developed trunks or major limbs. (Cf. *ramiflory*.)

Concaulescence (T) — Fusion (partial or complete) of an axis with an axis of lower order (e.g. fusion of a lateral axis to the main axis). Involved in cases of "supra-axillary" branching. (Cf. *recaulescence*.)

Conflorescence (symbol: C) — A floriferous branch system in which the main axis bears uniflorescences, but itself qualitatively different in structure from the uniflorescences. The main axis (R_2) of the conflorescence is blastotelic, but in Myrtaceae the uniflorescence axes are anthotelic (cf. *superconflorescence*, see 3.3). (Term used by Johnson, 1972, 1976; Johnson and Briggs, 1975; but more precisely defined here). *Conflorescence* refers to an entirely different concept from that of [*coflorescence*] as used by Troll.

In inflorescences of Myrtaceous type a conflorescence may result phylogenetically from (i) the aggregation of previously separated inflorescences by reduction of intervening axes, or from (ii) a change to blastotelic in the main axis of a ramified inflorescence (through anthotelic/blastotelic flexibility), which may partition it into a number of separate uniflorescences, each equivalent to only a lateral part of the original inflorescence; these uniflorescences would then together constitute a conflorescence (see 6.1).

Where comparison with related groups reveals that a highly reduced structure that does not show two levels of organization (e.g. an apparent monad, borne on a minute R_2) is derived by reduction of a conflorescence, the latter concept is extended to cover the reduced derivative.

Corymb (adj. *corymbose*) — A *botryum* (blastotelic) in which, by differential elongation of the lateral axes, the flowers come to lie more or less in one plane, orthogonal to the main axis. Troll's usage for an anthotelic (paniculate) inflorescence of this form is rejected, on grounds of consistency; likewise we cannot accept his use of [*corymboid*] for another anthotelic (thyrsoidal) arrangement. It would be logical to use *corymboid* for a botryoid of corymb-like form. The compound cases may be called *corymbiform panicles*, *corymbiform thyrsoids*, etc.

Corymbiform — Having the form of, or resembling, a corymb.

Cryptocotylar — Of germination or seedlings in which the cotyledons remain within the seed-coat. (\approx [*hypogeal*] but the reference point is the seed-coat rather than soil level.)

Cyme (adj. *cymose*; T, in part) — An inflorescence in which the main and all of the subsequent axes are pronodate and each is terminated by a flower; i.e. an anthotelic inflorescence with strictly sympodial branching. Troll's use of *cymoid* for a whole inflorescence with such a structure is a consequence of his system of typological derivation; he rejects *cyme* but applies *cymose* to partial inflorescences of this form. Whereas, following Troll's usual but not universal practice, we adopt *-oid* as a termination for many anthotelic inflorescence forms, we except *cyme* and *panicle* where the basic terms refer to anthotelic cases.

Dichasium (T) (adj. *dichasial*; symbol: D) — A *cymose* inflorescence with opposite or disjunct-opposite lateral branches produced on both sides of the main axis and subsequent axes. (Cf. *monochasium*, *pseudomonochasium*). All axes pronodate (in fact uninodate, though occasionally \pm disjunct), except the highest-order axes, which may (not normally in Myrtaceae) consist of a single internode (i.e. the *anthopodium*). Rickett (1955) restricts the unqualified term *dichasium* to what we (and Troll) call a *triad* (q.v.); we reject this restriction as unnecessary and because a triad can also represent a reduced botryoid (see 6.2 (i)).

DISJUNCT-OPPOSITE PHYLLOTAXY — A variant of opposite (and decussate) phyllotaxy in which the two phyllomes at a node are separated by elongation of the nodal region (i.e. by an *intranode*), often giving the appearance of "alternate" leaf arrangement but readily distinguished by decussate, not spiral, sequence.

Disperse phyllotaxy (T) — Non-opposite (non-*verticillate*) phyllotaxy; including strictly alternate (i.e. distichous) and spiral (helical) phyllotaxy.

[*Enrichment Zone* = *Bereicherungszone*, BZ] (T) — See Appendix I.

Epipodium (T) — The internode immediately distal to the prophylls. (Cf. *hypopodium*, *mesopodium*.)

EUBOTRYOID — a *botryoid* (q.v.) in which the flowers are stalked.

[*Florescence*] (T) — Term used by Troll (1964, 1969) in combination with prefixes for various components of the [*synflorescence*]. Not adopted here, but see Appendix I.

Frondobracteose (T) — With foliar organs showing a gradual acropetal transition from foliage leaves to bracts (i.e. to *hypsophylls*). (Fig. 4.)

Frondose (T) — Of a shoot: bearing leaf-like (expanded) foliar organs (cf. *bracteose*); of a phyllome: having the nature of an expanded leaf, not reduced.

Frondulose (T) — With reduced but still leaf-like foliar organs.

Hapaxanthly (T) (adj. *hapaxanthic*) — Condition of producing only a single flowering during the life of the individual plant, as in annual herbs and in certain palms etc. From Greek: once flowering.

[*Hauptfloreszenz*, HF] (T) — See Appendix I, = [*main florescence*].

Hypopodium (T) — Lowest internode on a shoot, proximal to (lower) prophyll. (Cf. *epipodium*, *mesopodium*.)

Hypotagma (R) — See under *Unterbau*.

HYP SOPHYLL — Reduced phyllome (bract) associated with the inflorescence

region; may or may not be a *pherophyll* (q.v.) also. From Greek: high leaf = *Hochblatt* of Troll. The rare and imprecise meaning of "the bract of an inflorescence" is rejected.

Inflorescence (T) — Originally referred to the process of coming into flower, but now a general term for the flower-bearing system of a plant, and more particularly for portions of such systems separated from each other by vegetative portions of the plant. A useful term if deliberately kept rather imprecise. (In its more restricted sense, \approx *Blütenstand* of German authors.)

Infructescence — As for *inflorescence* but applied to fruit-bearing stage.

Intranode — An elongation of the nodal region in *disjunct-opposite phyllotaxy* (q.v.).

[*Main florescence*] — See Appendix I; = [*Hauptfloreszenz*, HF].

Median flower — A flower (on an anthotelic axis) that is flanked by axes or by other flowers (Fig. 3.; cf. *side flower*). The term can be extended to disperse-phyllotactic systems such as monochasia, where there is only one proximate flanking unit.

Mesopodium (T) — Internode between two prophylls in cases of disperse phyllotaxy, probably also applied by Troll to the prophyllar intranode in cases of disjunct-opposite phyllotaxy. (Cf. *epipodium*, *hypopodium*).

Mesotonic (T) — Producing lateral flowers or flowering branches mainly in the middle portion of the season's growth. Sometimes also used to describe a branching system with more extensive development of laterals in the median part (cf. *acrotonic*, *basitonic*, *pantotonic*).

METABOTRYOID (adj. *metabotryoidal*; symbol: Mb) — Anthotelic inflorescence with multinodate main axis that bears pronodate laterals branched only to one further order (i.e. with lateral dichasial triads or, in monochasial systems, with 2-flowered laterals). Differs from a *botryoid* in its branched laterals and from a *thyrsoid* in having laterals branched only to the first degree; derivable by reduction of either a panicle or a thyrsoid. From Greek: changed botryoid. (See 3.2, Figs. 2c, 7b)

METAXYMONAD (symbol: M*) — Plurinodate monad; i.e. an inflorescence resembling a monad but with one or more non-branching nodes on the axis in addition to the prophyllar node(s) (a "monad with metaxyphylls", Fig. 7h).

METAXYPHYLL — On an anthotelic axis, a phyllome (usually a *hypsophyll*) that is empty (except sometimes for an abortive axillary bud) and situated between the ultimate pherophyll(s) (or the prophylls) and the flower. From Greek: middle leaf or between leaf, = *Zwischenblatt* of Troll. Occurring in pairs, if present, in the opposite-decussate systems of Myrtaceae. (See 3.6, Fig. 3.)

METAXYTRIAD (symbol: Tr*) — Plurinodate triad; i.e. an inflorescence resembling a triad but with one or more non-branching nodes on its primary axis distal to the prophylls (a "triad with metaxyphylls", Fig. 7g).

Monad (T) (adj. *monadic*; symbol: M) — An inflorescence (or uniflorescence) consisting of a solitary flower together with its axis and the prophylls (if any) of that axis.

Monochasium (adj. *monochasial*) (\approx *Wickel*, *Schraubel*, etc. of Troll) — A *cymose* inflorescence in which an axis of any order (except the last) produces a single lateral branch. Includes various subtypes (*cincinnus*, *bostryx*, etc., not relevant here).

(Cf. *dichasium*, *pseudomonochasium*.) All axes pronodate except the highest-order one, which may consist of an anthopodium only. Includes cases where 2 prophyllar nodes are present but only one bears a branch, hence not the most precise of terms.

[*Monotelic*] (T) ([n. *monotely*]) — Troll's term for inflorescences in which the primary and other axes end in flowers (cf. [*polytelic*, *uniaxial*, *determinate*, *closed*], *anthotelic*). Not accepted here (see Appendix I).

Multinodate — Of an axis with nodes distal to the prophyllar node(s). Includes *plurinodate*. (Cf. *pronodate*, *uninodate*.)

Panicle (T) (adj. *paniculate*; symbol: P) — An anthotelic inflorescence in which (i) the main and at least some of the lateral axes have nodes distal to the prophyllar node(s), and (ii) the lateral branch systems are not themselves thyrsoids (or aggregates of thyrsoids). This is equivalent to Troll's concept of the *Rispe* (syn. *panicula*). Condition (ii) excludes complex thyrsoids (["complex determinate thyrses"] or ["heterocladic thyrses"]) in the terminology of Troll (1964, 1969). In practice this means that the critical distinction is that in the *panicle* each multinodate lateral branch (of whatever order) must *either* itself bear single flowers at two (or more) successive nodes (i.e. be botryoidal in the distal position at least) *or* ultimately bear branches that show this condition, whereas in the *complex thyrsoid* no axes have such botryoidal portions. This distinction is rather artificial since it depends on the notion that a triad is cymose but a monad is not. Although most of the inflorescences or uniflorescences recorded in Table 3 as panicles fulfil the conditions of Troll's definition, it is possible that some of them may be definable as complex thyrsoids — all gradations from panicle to thyrsoid occur in Myrtaceae and the distinction is not of much importance here. (The common English-language usage of "panicle" for branched blastotelic systems is rejected in favour of the German usage of Troll's more precise system; most of the blastotelic "panicles" are *dibotrya* or *pleiobotrya*, as those terms are used by Troll (1964) and endorsed here.)

PANTOTONIC — Producing lateral flowers or flowering branches \pm equally throughout the nodes of the season's growth (cf. *acrotonic*, *basitonic*, *mesotonic*). From Greek: all extended.

[*Paracladium*] (T) ([pl. *paracladia*, adj. *paracladial*]) — Term applied (Troll, 1964, 1969; but used earlier and in somewhat varying senses by other authors) to lateral branches of a synflorescence that repeat the structure of the main florescence of that system (3 [*enrichment branch*, *Bereicherungssachse*] of Stauffer, 1963, but see Appendix I for discussion of some difference of concept). Not employed in our analysis of Myrtaceae.

Partial inflorescence (T) — A portion of an inflorescence, particularly a part sufficiently ramified to show the same structural plan as the inflorescence as a whole.

[*Pedicel*] — Not used here because of vague and inconsistent application. Much the same applies to the German [*Blütenstiel*] (or to [*flower-stalk*]). (See *anthopodium* and Appendix I, ii.)

Peduncle — A rather unsatisfactory term, retained here for the present to designate the proximal internode (*hypopodium*) of the uniflorescence axis (a_1) when appreciably elongated. Regarded here as non-applicable in inflorescences that terminate (or themselves constitute) SGU's (i.e. where $R_2 = a_1$ and a uniflorescence cannot be distinguished). Thus restricted, it covers only one aspect of the traditional range of meaning, which is too vague to employ in precise analysis. One of the meanings given in most glossaries, i.e. the stalk of a "solitary flower", is particularly incompatible with the use of [*pedicel*] for almost entirely comparable cases,

depending solely on the frondose or bracteose nature of the pherophylls.

Perigynium — A cup or tube around the ovary (whether considered to be phylogenetically derived from receptacular tissue or from “fusion” of the outer floral whorls), bearing the outer floral organs at or near its distal edge and sometimes extending upwards or outwards beyond the ovary. In Myrtaceae the perigynium is usually fused to part or all of the ovary wall, but is often readily separable from it. This neutral and descriptive term is preferred to [*hypanthium*], which suggests an organ beneath the flower, and to the often confusing [*floral tube*].

Perulate — Of a bud or axis: furnished with perules (cf. *perular* = “of the nature of a perule”).

Perule (adj. *perular*) — A phyllome modified as a protective scale of a resting bud.

Phanerocotylar — Of germination or seedlings in which the cotyledons emerge from the seed-coat; \approx [*epigeal*], but the emphasis is not on elevation of the cotyledons above the soil surface.

PHEROPHYLL — A subtending foliar organ. From Greek: bearing-leaf (= *Tragblatt* (alternatively *Deckblatt*) of Troll). (Fig. 3.)

Phyllome — A leaf or modified leaf; inclusive term for leaves, perules, “bracts”, hypsophylls, pherophylls, etc. In the present context not used for floral organs, though these may be phyllopic in origin. The older usage for “an assemblage of leaves” is virtually obsolete.

Phylloscopic (T) — Of an accessory axis, inflorescence, or bud situated between the subtending leaf and the chief axillary axis arising at the same node, i.e. below the chief axillary axis (Fig. 5, cf. *axonoscopic*). From Greek: looking toward the leaf.

Plurinodate — Applied to a multinodate axis with only one or few nodes distal to the prophyllar nodes. A term of convenience when indicating the general low number of additional nodes (cf. *pronodate*, *uninodate*, *multinodate*).

[*Polytelic*] (T) (n. [*polytely*]) — Troll's term for inflorescence condition in which the primary axis does not end in a flower but bears flowers laterally, and in which any multinodate higher-order axes (*paracladia*) repeat this pattern. \approx [*biaxial*, *indeterminate*, *open*], *blastotelic*. Not accepted here (see Appendix II).

PRONODATE — Of an axis bearing no nodes beyond the (one or two) prophyllar nodes (in Myrtaceous uniflorescences such an axis is usually actually uninodate). From Latin: before knotted, referring to the first nodes.

Prophyll (T) — In dicotyledons: one of the first two leaves on a branch axis of any order; in monocotyledons: the (single) first leaf on a branch axis. Not usually applied to the cotyledons, though in a sense homologous with them.

Prophyllar node — A node that bears the prophyll(s); the proximal one or two nodes on a branch. In opposite-decussate cases there are two prophylls but a single prophyllar node.

PSEUDOMONOCHASIAM — A laterally depleted dichasium, i.e. a cymose inflorescence with essentially opposite-decussate phyllotaxy in which only one flowering axis develops at each node (see 8.2, No. 40).

Pseudosciadium (T) — An umbelliform cyme. (See *umbellaster* and cf. *sciadioid*.)

R_x — The branch from which the R_y arises. Commonly an axis bearing super-

conflorescences, or the main axis in certain extremely complex aggregations.

R_y — The branch from which the R_z arises; a branch of penultimate order (excluding axes within the uniflorescence). Commonly the main axis of a superconflorescence. (See 3.4.)

R_z — The branch from which the a_1 arises, an axis that bears uniflorescences; commonly the main axis of a conflorescence. (See 3.4.) The R indicates *ramus* (= *branch*); the subscripts run backwards from that of the highest order (z) existing at the time when the relevant uniflorescences are produced laterally to it.

Raceme (adj. *racemose*) — A *botryum* in which the flowers are stalked, in contrast to a *spike* (with sessile flowers).

Racemiform — Having the form of a raceme. Applied herein to conflorescences of this form in which the main axis grows on either before, during, or after flowering, as well as to anauxotelic cases.

Ramiflory (adj. *ramiflorous*) — Condition in which (non-frondose) inflorescences are produced from resting buds on woody branches formed in previous, but recent, seasons. (Cf. *cauliflory*.)

Recaulescence (T) — Adnation (partial or complete) of an axis to its perophyll, or a condition interpreted as such; usually seen as "bracts carried out on to the branch that they should subtend". *Recaulescence* and *concaulescence* (q.v.) are examples of *metatopy* (T).

Sciadoid (T) — An umbelliform botryoid. (Cf. *pseudosciadium*, *umbel*, *umbellaster*.)

Sciadium (T) — (= *umbel*, q.v.)

SEASONAL GROWTH UNIT (symbol: SGU) — A shoot, or branched system of shoots, arising in one season (terminally or laterally) from an axis formed in a previous growing season. (See 3.1.)

Short shoot — A blastotelic shoot of limited growth (= *brachyblast*, q.v.)

Side flower — A flower flanking the median flower of a triad (the triad may be a grouping within a larger dichasium or within a paniculate system). (= *Seitenblüte* of Troll) (Fig. 3a).

Spike (T) (adj. *spicate*, see also *spiciform*) — A *botryum* bearing sessile lateral flowers: of \pm elongated form as a whole (in contrast to the broadened axis of a *capitulum*) but the internodes not necessarily elongated.

Spiciform — Having the form of, or resembling, a spike. Herein applied to conflorescences in which the main axis grows on either before, during, or after flowering, as well as to anauxotelic cases.

SUPERCONFLORESCENCE (symbol: C²) — A compound inflorescence of second or higher order; a functional inflorescence-system consisting of several or many conflorescences. (See 3.3, Figs. 8-12.)

[*Synflorescence*] (T) — Trollian term for system comprising a main florescence or terminal flower, together with paracladia. Not used in our analysis. (See Appendix I, i.)

Thyrse (T, as to his ["polytelic thyrses"] only) (adj. *thyrsic*) — A blastotelic inflorescence with a multinodate main axis that bears lateral cymes (commonly lateral dichasia). (Fig. 2a.)

Thyriform — Having the form of a thyrse. Herein applied to confluences in which the main axis may grow on, as well as to auxotelic cases.

THYRSOID (adj. THYRSOIDAL; symbol: Th) — An anthotelic inflorescence with a multinodate main axis that bears lateral cymes of order of branching > 1 (in Myrtaceae commonly lateral dichasia of > 3 flowers). Differs from a metabotryoid in its repeatedly branched lateral cymes, and from a thyrse in its anthotelic main axis (see 3.2, Fig. 2b); (= [“*monotelic thyrse*”] of Troll). The adjective “thyrsoid” is eschewed here (and replaced by *thyrsoidal*), since it has been used for *thyrisc* (= *thyrisch* of Troll) and even more vaguely. To our knowledge, the present is the first defined usage of *thyrsoid* as a noun comparable with *botryoid*, etc. For *complex thyrsoid* see under *panicle*.

Triad (T) (adj. *triadic*; symbol: Tr) — A three-flowered inflorescence of dichasial form (Fig. 7i). Here interpreted strictly, to exclude *metaxytriad* (q.v.). Triads may be phylogenetically derived from botryoids as well as from dichasia.

Umbel (U) (= *sciadium*, adj. *umbellate*, *sciadic*, see also *umbelliform*) — Here interpreted strictly as a blastotelic inflorescence of botryine structure, but with the nodes crowded so that the flowers or flower-stalks arise almost from one point. (Cf. *pseudosciadium*, *sciadioid*, *umbellaster*.)

Umbellaster (adj. *umbellastral*) — An anthotelic umbelliform grouping of flowers (with or without anthopodia or hypopodia), which may be derived from condensation of a cyme (dichasial, partly pseudomonochasial, or monochasial), of a thyrsoid, or of a metabotryoid. (Cf. *pseudosciadium*, which is included under *umbellaster* but is always cymose.) When introduced by Johnson (1972, 1976), the non-cymose nature of some eucalypt umbellasters was not recognized.

Umbelliform — Having the form of, or resembling, an umbel.

[*Uniaxial*] (T) — See Appendix I.

Uniflorescence (symbol: U) — A unit inflorescence forming part of a confluence (see 3.2). Term originated by Johnson and Briggs (see Johnson, 1976) in the sense of “unit inflorescence”. As now defined, it is not completely equivalent to that concept as applied to members of the *Eucalyptus* alliance by Carr and Carr (1959) or by Johnson (1972, 1976) (see 5.2, 8.2); [*unit inflorescence*] as used by Johnson and Briggs (1975), embodies a generally similar concept (see 3.3), but is applied in the blastotelic family Proteaceae.

Uninodate — Of a pronodate axis with only one node. The presence of an *intranode* (q.v.) does not prevent an axis being regarded as uninodate, but in dicotyledons with non-decussate phyllotaxy a pronodate axis is generally binodate.

Unterbau (T) — Structure of vegetative parts of plant below (proximal to) floriferous regions (of synflorescence) (Troll, 1964, 1969). Although not employed herein, an international term would be useful since *substructure* and *infrastructure* are used in other senses; *hypotagma* (from Greek: understructure) was proposed for this purpose by Troll (1964).

Verticillate phyllotaxy (T) — Leaf arrangement with two or more leaves at each node; includes *opposite*, and also *whorled* (i.e. *ternate* and higher-numbered) phyllotaxies.

APPENDIX III — INDEX OF GENERIC NAMES IN MYRTACEAE

For each generic taxon the serial number (Table 3) is followed by a coding indicating subfamily (1 letter abbreviation), alliance (2 letters) and suballiances (3 letters). Intra-alliance placement of members of the *Calothamnus* suballiance is given in Table 3. Synonyms are in italics but include only names mentioned in this paper.

SUBFAMILIES: L = Leptospermoideae, M = Myrtoideae.

ALLIANCES: Ac = *Acmena*, Bh = *Backhousia*, Ch = *Chamelaucium*, Cr = *Cryptorhiza*, Ec = *Eucalyptus*, Eg = *Eugenia*, Eo = *Eucalyptopsis*, He = *Heteropyxis*, Le = *Leptospermum*, Mc = *Myrcia*, Me = *Metrosideros*, Mt = *Myrtus*, Os = *Osbornia*.

SUBALLIANCES: Acm = *Acmena*, Ang = *Angophora*, Bae = *Baeckea*, Cal = *Calothamnus*, Cha = *Chamelaucium*, Euc = *Eucalyptus*, Kan = *Kania*, Lep = *Leptospermum*, Lop = *Lophostemon*, Met = *Metrosideros*, Sym = *Symphomyrtus*, Syz = *Syzygium*.

Acca s. str.	84	M.Mt	210	220					
Acicalyptus	119	M.Ac.Syz	174	192	211	223	224	228	
Acmena	124	M.Ac.Acm	171	192	211	224	225		
<i>Gen. aff. Acmena</i> (<i>Syzygium floribundum</i>)	123	M.Ac.Acm	192	211	224				
Acmenosperma	121	M.Ac.Acm	192	211	224				
<i>Acrandra</i> = <i>Campomanesia</i>	(111)	(M.Cr)	211	222					
Acroegenia	128	M.Eg	174	184	212	225			
Actinodium	72	L.Ch.Cha	198	201	202	209	220	233	
"Adnatae" (<i>gen. aff. Mearnsia</i>)	8	L.Me.Met	195	206	214				
Agonis	42	L.Le.Lep	208	219	231				
Allosyncarpia	30	L.Eo	170	172	174	184	191	197	198
			207	216	231				
Amomyrtella	91	M.Mt	210	222					
Amomyrtus	92	M.Mt	210						
Angophora	32	L.Ec.Ang	172	184	185	189	190	207	217
			232						
<i>Aphanomyrtus</i> = <i>Syzygium</i>	(117)	(M.Ac.Syz)	210	223	224	229			
Archirhodomyrtus	98	M.Mt	210	222	231				
Arillastrum	31	L.Ec.Ang	168	172	184	189	207	217	
<i>Aspidogenia</i> = <i>Reichea</i>	(129)	(M.Eg)	212						
Astartea	56	L.Ch.Bae	209	229					
[<i>Aulacocarpus</i> = <i>Mouriri</i> , <i>Melastomataceae</i>]	—	—	175						
Austromyrtus	97	M.Mt	210	231					
Backhousia	27	L.Bh	170	191	195	198	207	216	231
			233						
Baeckea	55	L.Ch.Bae	168	170	173	197	209	219	229
			231						
Balaustion	58	L.Ch.Bae	173	209	231				
Ballardia	13	L.Me.Met	197	206	214	215			
Basisperma	2	L.Me.Kan	167	206	214	228	229		
Beaufortia	51	L.Le.Cal	208	228	230	232			
"Blakella"	33	L.Ec.Ang	172	184	189	207	217	218	228
Blepharocalyx	110	M.Cr	171	195	211	221	222	231	
<i>Britoa</i> = <i>Campomanesia</i>	(111)	(M.Cr)	171	211	222				
Callistemon	45	L.Le.Cal	202	203	208	219	230	232	
<i>Gen. aff. Callistemon</i>	46	L.Le.Cal	202	208	219	232			
Calothamnus	50	L.Le.Cal	170	202	203	208	219	228	229
			230	232					
Calycolpus	86	M.Mt	210	221	222				
Calycorectes	138	M.Eg	212	226	227	228			
Calyptranthes	75	M.Mc	184	192	209	220	228	232	
Calyptrogenia	143	M.Eg	212	227	228				

"Calyptropetala" (<i>gen. aff. Mearnsia</i>)	11	L. Me. Met	206	215	228	232			
Calythropsis	61	L. Ch. Cha	209	228	231				
Calytrix	60	L. Ch. Cha	201	209	220	228	229	231	
Campomanesia	111	M. Cr	171	172	194	211	221	222	231
" <i>Carpolepis</i> " = <i>Ballardia</i>	(13)	(L. Me. Met)	206	214	215				
<i>Caryophyllus</i> = <i>Syzygium</i>	(117)	(M. Ac. Syz)	211	223					
Chamelaucium	67	L. Ch. Cha	184	201	209	220	228	229	231
<i>Chloromyrtus</i> = <i>Eugenia</i>	(140)	(M. Eg)	212	227					
Choricarpia	28	L. Bh	168	170	198	207	216	229	231
Cleistocalyx s. str.	118	M. Ac. Syz	192	211	223	224	228		
Cloëzia	3	L. Me. Kan	191	206	214	231			
Conothamnus	48	L. Le. Cal	208	228	232				
" <i>Corymbia</i> "	34	L. Ec. Ang	172	183	184	189	207	218	228
			229	230	233				
Corynemyrtus	90	M. Mt	174	210	221	222	235		
Cryptorhiza	114	M. Cr	171	174	211	223			
" <i>Crystalla</i> " (<i>gen. aff. Mearnsia</i>)	9	L. Me. Met	168	206	215				
Cupheanthus	120	M. Ac. Syz	184	192	197	211	224	229	
Darwinia	68	L. Ch. Cha	170	183	184	201	209	220	229
			230	232					
Decaspermum	96	M. Mt	184	187	188	193	210	222	
<i>Episzygium</i> = ? <i>Psidium</i>	(88)	(M. Mt)	210	221					
Eremaea	54	L. Le. Cal	202	208	219	228	232		
Eucalyptopsis	29	L. Eo	170	172	191	198	207	216	228
			229						
Eucalyptus s. str.	40	L. Ec. Euc	170	172	173	174	182	183	184
			185	197	208	217	218	219	228
			230	233					
Eudesmia	35	L. Ec. Sym	173	183	185	189	195	208	217
			218	228	230	232			
Eugenia	140	M. Eg	165	169	172	182	183	193	194
			199	200	212	226	227	231	235
" <i>Eugeniomyrtus</i> " = ?	—	—	171						
" <i>Exsertis</i> " = " <i>Calyptropetala</i> " s. str.	(11)	(L. Me. Met)	215						
(<i>Fabricia</i> — See <i>Leptospermum</i>)	(41)	(L. Le. Lep)	203	204	219	230	231		
Feijoa	85	M. Mt	170	174	210	221	230		
Fenzlia	107	M. Mt	210	231					
(" <i>Firmum</i> " — See <i>Leptospermum</i>)	(41)	(L. Le. Lep)	204	219					
<i>Fremya</i> = <i>Xanthostemon</i>	(15)	(L. Me. Xan)	206						
[<i>Fropiera</i> = <i>Psiloxylon</i> , <i>Psiloxylaceae</i>]	—	—							
" <i>Gaubaea</i> "	38	L. Ec. Euc	173	183	208	217	218	228	232
Gomidesia	76	M. Mc	192	209	220	229			
Heteropyxis	26	L. He	167	170	174	184	191	198	207
			216	229	231	232			
Hexachlamys	139	M. Eg	183	212	227	229			
Homalocalyx	62	L. Ch. Cha	209	229	231				
Homoranthus	69	L. Ch. Cha	174	209	220	231			
Hottea	144	M. Eg	174	212	227	228			
Hypocalymma	59	L. Ch. Bac	173	202	203	204	209	220	231
" <i>Idiogenes</i> "	39	L. Ec. Euc	173	208	218	228			
" <i>Inclusis</i> " — (<i>gen. aff. Mearnsia</i>)	10	L. Me. Met	206	215	228				
<i>Jambosa</i> = <i>Syzygium</i>	(117)	(M. Ac. Syz)	211	223					
<i>Jossinia</i> = <i>Eugenia</i>	(140)	(M. Eg)	212	227					
Kania	1	L. Me. Kan	167	170	174	206	231		
Kjellbergiodendron	19	L. Me. Lop	168	191	207	215	228	233	
<i>Krugia</i> = <i>Marlierea</i>	(74)	(M. Mc)	220	228					

Kunzea	43	L. Le. Lep	208	219	232	233				
Lamarchea	49	L. Le. Cal	202	208	219	228	231			
Legrandia	113	M. Cr	171	211	222					
Leptospermum	41	L. Le. Lep	178	184	198	203	204	205	208	
			219	229	230	231	233			
<i>Lhotzkya</i> = <i>Calytrix</i>	(60)	(L. Ch. Cha)	209	220						
Lindsayomyrtus	20	L. Me. Lop	207	215	228	229	233			
Lophomyrtus	103	M. Mt	210	231						
Lophostemon	24	L. Me. Lop	198	207	216	229	231			
Luma	125	M. Eg	212	225	231					
Lysicarpus	4	L. Me. Kan	206	214	231					
<i>Macropsidium</i> = ? <i>Rhodomyrtus</i>	(99)	(M. Mt)	210	222						
Marlierea	74	M. Mc	192	209	220	228				
Marlieriopsis	109	M. Cr	171	192	211	221	222	228	231	
Mearnsia s. strictiss.	7	L. Me. Met	183	184	191	206	214	229	230	
			232							
Melaleuca	47	L. Le. Cal	184	198	202	203	208	219	228	
			230	232						
Meteoromyrtus	141	M. Eg	169	174	212	227				
Metrosideros s. str.	14	L. Me. Met	174	183	184	191	206	215	230	
Micromyrtus	66	L. Ch. Cha	201	209	231					
Mitranthes s. str.	77	M. Mc	209	220	228					
<i>Mitropsidium</i> = <i>Psidium</i>	(88)	(M. Mt)	210							
" <i>Monocalyptus</i> " = <i>Eucalyptus</i> s. str.	(40)	(L. Ec. Euc)	208	217	218					
<i>Mooria</i> = <i>Cloëzia</i>	(3)	(L. Me. Kan)	206							
Mosiera	87	M. Mt	174	210	221					
<i>Myrceugenella</i> = <i>Luma</i>	(125)	(M. Eg)	212							
Myrceugenia	79	M. Mc	209	220	231					
Myrcia	73	M. Mc	192	209	220	231				
Myrcianthes	126	M. Eg	172	194	212	223	225	231		
Myrciaria	131	M. Eg	212	225	226					
<i>Myrciariopsis</i> = <i>Siphoneugena</i>	(134)	(M. Eg)	212	226						
Myrrhinium	83	M. Mt	195	210	221	230	232			
Myrtastrum	105	M. Mt	210	231						
Myrtella	108	M. Mt	174	210	231					
Myrteola	93	M. Mt	210	231						
<i>Myrtomera</i> = <i>Arillastrum</i>	(31)	(L. Ec. Ang)	207	217						
<i>Myrtopsis</i> O. Hoffm. non Engl. = <i>Eugenia</i>	(140)	(M. Eg)	212	227						
Myrtus s. str.	95	M. Mt	169	210	221	222	228	231	232	
<i>Nani</i> = <i>Xanthostemon</i>	(15)	(L. Me. Xan)	198	206						
Neomyrtus	106	M. Mt	210	231						
Nothomyrcia	78	M. Mc	192	209	220					
Octamyrtus	100	M. Mt	210	222	229	231				
<i>Orthostemon</i> = <i>Feijoa</i>	(85)	(M. Mt)	170							
Osbornia	116	M. Os	167	170	192	211	223	229	233	
Paivaea	112	M. Cr	171	211	221	222	229			
Paramyrciaria	132	M. Eg	174	212	225	226				
<i>Paramitranthes</i> = <i>Siphoneugena</i>	(134)	(M. Eg)	212							
<i>Pareugenia</i> = <i>Syzygium</i>	(117)	(M. Ac. Syz)	211	223						
(<i>Pericalymna</i> — See <i>Leptospermum</i>)	(41)	(L. Le. Lep)	219							
<i>Phyllocalyx</i> = <i>Eugenia</i>	(140)	(M. Eg)	212							
Phymatocarpus	53	L. Le. Cal	208	228	232					
Pileanthus	64	L. Ch. Cha	169	172	173	198	201	209	228	
			229	231	232					
Piliostigma	115	M. Cr	169	171	211	231				
Piliocalyx	122	M. Ac. Acm	192	211	224	228				
Pilothecium	136	M. Eg	172	174	193	195	212	226	235	
Pimenta	82	M. Mt	170	197	210	221	231			

[Platyspermatum — genus <i>incertae sedis</i> not Myrtaceae]	—	—	173	175					
Pleurocalyptus	16	L. Me. Xan	170	206	228				
Plinia s. str.	137	M. Eg	212	226	228				
"Pliniopsis"	133	M. Eg	174	212	225	226			
Pseudanamomis	130	M. Eg	212	231					
Pseudocaryophyllus	81	M. Mt	192	210	221				
<i>Pseudoeugenia</i> = <i>Syzygium</i>	(117)	(M. Ac. Syz)	211	224					
Pseudomyrcianthes	127	M. Eg	174	212	225	235			
<i>Psidiomyrtus</i> = <i>Rhodomyrtus</i>	(99)	(M. Mt)	210	222					
Psidiopsis	89	M. Mt	174	210	221	228			
Psidium	88	M. Mt	170	210	221	222	231	232	235
[<i>Psiloxylon</i> , <i>Psiloxylaceae</i>]	—	—	163	175	181	229			
Purpureostemon	17	L. Me. Xan	206	215	230	232			
<i>Gen. nov.</i> "R"	21	L. Me. Lop	207	216	228				
Regelia	52	L. Le. Cal.	208	228	232				
Reichea	129	M. Eg	212	231					
Rhodammia	101	M. Mt	184	210	222	231			
Rhodomyrtus	99	M. Mt	210	222	232				
Rylstonea	70	L. Ch. Cha	174	209	220	231	232		
<i>Saffordiella</i> = <i>Myrtella</i>	(108)	(M. Mt)	211						
" <i>Schizocalyx</i> " auct. = <i>Stereocaryum</i>	(142)	(M. Eg)	227						
Scholtzia	57	L. Ch. Bae	209	220					
Sinoga	44	L. Le. Lep	208	219	231				
Siphoneugena	134	M. Eg	212	225	226	229			
<i>Gen. aff.</i> <i>Siphoneugena</i>	135	M. Eg	212	226	228				
<i>Spermolepis</i> = <i>Arillastrum</i>	(31)	(L. Ec. Ang)	207	217					
<i>Stenocalyx</i> = <i>Eugenia</i>	(140)	(M. Eg)	193	212	227				
Stereocaryum	142	M. Eg	169	212	217	227	231		
Symphomyrtus	36	L. Ec. Sym	173	184	198	208	217	218	228
			229	230	231	232	233		
Syncarpia	25	L. Me. Lop	170	183	198	207	216	229	
Syzygium	117	M. Ac. Syz	169	171	173	184	187	192	193
			195	198	211	220	223	224	225
			227	228	230	231	232	235	
"Telocalyptus"	37	L. Ec. Sym	173	184	187	192	197	208	218
			228						
Temu	80	M. Mt	210	220	221	231			
Tepualia	12	L. Me. Met	168	206	214				
<i>Tetraeugenia</i> = <i>Syzygium</i>	(117)	(M. Ac. Syz)	211	223	224	229			
Thryptomene	65	L. Ch. Cha	201	209	231				
Tristania s. str.	6	L. Me. Met	206	214	216	230			
<i>Gen. aff.</i> <i>Tristania</i> ("Parrot Creek")	5	L. Me. Met	206	214	228				
Tristaniopsis	22	L. Me. Lop	183	207	216	228			
Ugni	94	M. Mt	210	231	232				
Uromyrtus	104	M. Mt	210	231					
Verticordia	71	L. Ch. Cha	198	201	209	220	228	231	232
<i>Gen. nov.</i> "W"	23	L. Me. Lop	207	216	228				
Wehlia	63	L. Ch. Cha	209	231					
Whiteodendron	18	L. Me. Lop	191	207	214	228	229		
Xanthomyrtus	102	M. Mt	210	230	231	232			
Xanthostemon	15	L. Me. Xan	184	198	206	215	229	231	232
<i>Xenodendron</i> = <i>Acmena</i>	(124)	(M. Ac. Acn)	212	225					

References

- AMSHOFF, G. J. H., 1958. — Notes on Myrtaceae VII. Myrtaceae of French Equatorial Africa. *Acta Bot. Neerl.*, 7: 53-58.
- BAMBER, R. K., 1962. — The anatomy of the barks of Leptospermoideae. *Aust. J. Bot.*, 10: 25-54.
- BEHNKE, H. D., 1975. — The bases of angiosperm phylogeny: ultrastructure. *Ann. Mo. Bot. Gard.*, 62: 647-663.
- BENTHAM, G., 1865. — Myrtaceae. In, Bentham, G. and Hooker, J. D., *Genera Plantarum*. London: Reeve.
- , 1867 (1866). — *Flora Australiensis*, 3. London: Reeve.
- , 1869. — Notes on Myrtaceae. *J. Linn. Soc. London, Bot.*, 10: 101-166.
- BERG, O., 1855-56. — Revisio Myrtacearum Americae hucusque cognitarum s. Klotzschii "Flora Americae aequinoctialis" exhibens Myrtaceae. *Linnaea*, 27: 1-472.
- BEUSEKOM-OSINGA, R. J. VAN, 1977. — Crypteroniaceae. *Flora Malesiana*, 1 (8): 187-205.
- , and BEUSEKOM, C. F. VAN, 1975. — Delimitation and subdivision of the Crypteroniaceae (Myrtales). *Blumea*, 22: 255-266.
- BLAKE, S. T., 1977. — *Allosyncarpia ternata*, a new genus and species of Myrtaceae subfamily Leptospermoideae from northern Australia. *Austrobaileya*, 1: 43-46.
- BLUME, C. L., 1850 (1849). — *Museum Botanicum Lugduno-Batavum*, 1 (6). Leiden: Brill.
- BRIGGS, B. G., 1964. — The control of interspecific hybridization in *Darwinia*. *Evolution*, 18: 292-303.
- BURRET, M., 1941a. — Myrtaceen-Studien. *Notizbl. Bot. Gart. Mus. Berl.*, 15: 479-550.
- , 1941b. — Myrtaceenstudien. II. *Reprint Nov. Spec. Regni Veg.*, 50: 50-60.
- CANDOLLE, A. P. DE, 1828. — *Prodromus Systematis Naturalis Regni Vegetabilis*, 3. Paris: Treuttel and Wurtz.
- CARLQUIST, S., and DEBUHR, L., 1977. — Wood anatomy of Penaeaceae (Myrtales): comparative, phylogenetic, and ecological implications. *J. Linn. Soc. London, Bot.*, 75: 211-227.
- CAROLIN, R., 1967. — The concept of the inflorescence in the Order Campanulales. (Presidential Address). *Proc. Linn. Soc. N.S.W.*, 92: 7-26.
- CARR, D. J. and CARR, S. G. M., 1959. — Developmental morphology of the floral organs of *Eucalyptus*. I. The inflorescence. *Aust. J. Bot.*, 7: 109-141.
- CARR, S. G. M. and CARR, D. J., 1966. — Cotyledonary stipules in the Myrtaceae. *Nature*, 210: 185-186.
- , 1970. — Oil glands and ducts in *Eucalyptus* L'Hérit. II. Development and structure of oil glands in the embryo. *Aust. J. Bot.*, 18: 191-212.
- , and MILKOVITS, L., 1970. — Oil glands and ducts in *Eucalyptus* L'Hérit. III. The flowers of series *Corymbosae* (Benth.). Maiden. *Aust. J. Bot.*, 18: 313-333.
- CORNER, E. J. H., 1976. — *The Seeds of Dicotyledons*, 2 vols. Cambridge: Cambridge University Press.
- COURT, A. B., 1957. — Changes in the nomenclature of some Victorian dicotyledons. *Victorian Nat.*, 73: 173-176.
- CROIZAT, L., 1960 (1961). — *Principia Botanica*, 1b. Caracas: L. Croizat.
- CRONQUIST, A., 1968. — *The Evolution and Classification of Flowering Plants*. London: Nelson.
- DAHLGREN, R., and RAO, V. S., 1969. — A study of the family Geissolomataceae. *Bot. Notiser*, 122: 207-227.
- DAWSON, J. W., 1968a. — An analysis of flowers and fruits in New Zealand *Metrosideros*. *N.Z. J. Bot.*, 6: 43-55.
- , 1968b. — The vegetative buds of the New Zealand species of *Metrosideros*. *N.Z. J. Bot.*, 6: 240-242.
- , 1970a. — Pacific capsular Myrtaceae 1. Reproductive morphology of *Arillastrum gummiferum* Panch. ex Baillon (New Caledonia). *Blumea*, 18: 431-440.
- , 1970b. — Pacific capsular Myrtaceae 2. The *Metrosideros* complex: *M. collina* group. *Blumea*, 18: 441-445.
- , 1970c. — Pacific capsular Myrtaceae 3. The *Metrosideros* complex: *Mearnsia halconensis* group and *Metrosideros diffusa* group. *Blumea*, 18: 447-452.
- , 1972a. — Pacific capsular Myrtaceae 4. The *Metrosideros* complex: *Xanthostemon*, *Nani*, *Pleurocalyptus*, *Purpureostemon*. *Blumea*, 20: 315-322.
- , 1972b. — Pacific capsular Myrtaceae 5. The *Metrosideros* complex: *M. elegans* group. *Blumea*, 20: 323-326.
- , 1972c. — Pacific capsular Myrtaceae 6. The *Metrosideros* complex: *M. perforata* and the *M. operculata* group. *Blumea*, 20: 327-329.
- , 1972d. — Pacific capsular Myrtaceae 7. *Mooria*. *Blumea*, 20: 331-334.
- , 1972e. — Pacific capsular Myrtaceae 8. *Tepualia*. *Blumea*, 20: 335-337.
- , 1974. — Pacific capsular Myrtaceae 9. The *Metrosideros* complex: *M. queenslandica* group. *Blumea*, 22: 151-153.

- , 1975. — Capsular Myrtaceae 10. The *Metrosideros* complex: *M. angustifolia* (South Africa). *Blumea*, 22: 295-297.
- , 1976. — Pacific capsular Myrtaceae 11. Redefinition of *Metrosideros* Banks ex Gaertn. and definition of infrageneric categories. *Blumea*, 23: 7-11.
- , 1977. — Pacific capsular Myrtaceae 12. *Tristania* (New Caledonia). *Blumea*, 23: 337-340.
- , 1978. — Pacific capsular Myrtaceae 13. *Melaleuca* and *Callistemon* (New Caledonia). *Blumea*, 24: 119-122.
- ERDTMAN, G., 1952. — *Pollen Morphology and Plant Taxonomy. Angiosperms*. Stockholm: Almqvist Wiksell.
- EYDE, R. H., 1975. — The bases of angiosperm phylogeny: floral anatomy. *Ann. Mo. Bot. Gard.*, 62: 521-537.
- FAIRBROTHERS, D. E., MABRY, J. J., SCOGIN, R. L., and TURNER, B. L., 1975. — The bases of angiosperm phylogeny: chemotaxonomy. *Ann. Mo. Bot. Gard.*, 62: 765-800.
- FERNANDES, A., 1971. — Contribution à la connaissance du genre *Heteropyxis* Harv. *Mitt. Bot. St. Samml. München*, 10: 207-234.
- FOREMAN, D. B., 1978. — Notes on *Basisperma lanceolata* C. T. White (Myrtaceae). *Brunonia*, 1: 95-101.
- GUILLAUMIN, A., 1950. — Plantae neocaledonicae a C. Skottsberg a. 1949 lectae. *Acta Horti Gotob.*, 18: 247-265.
- HARTLEY, T. G. and CRAVEN, L. A., 1977. — A revision of the Papuanian species of *Acmena* (Myrtaceae). *J. Arnold Arb. Harv. Univ.*, 58: 325-342.
- HEGNAUER, R., 1964-73. — *Chemotaxonomie der Pflanzen*, 3-6. Basel and Stuttgart: Birkhauser.
- HENDERSON, M. R., 1949. — The genus *Eugenia* (Myrtaceae) in Malaya. *Gard. Bull., Singapore*, 12: 1-293.
- HICKEY, L., 1973. — Classification of the architecture of dicotyledonous leaves. *Am. J. Bot.*, 60: 17-33.
- , and WOLFE, J. A., 1975. — The bases of angiosperm phylogeny: vegetative morphology. *Ann. Mo. Bot. Gard.*, 62: 538-589.
- HOLMGREN, P. K., and KEUKEN, W., 1974. — Index Herbariorum. Pt I. *The Herbaria of the World*, Sixth edition. Utrecht: Oosthoek, Scheltema, and Holkema.
- HUTCHINSON, J., 1959. — *The Families of Flowering Plants. I. Dicotyledons*. Second edition. Oxford: Clarendon Press.
- HYLAND, B. P. M., and VAN STEENIS, C. G. G. J., 1973. — The generic identity of *Xanthostemon brachyanthus* C. T. White: *Lindsayomyrtus* novum genus (Myrtaceae). *Blumea*, 21: 189-192.
- INGLE, H. D., and DADSWELL, H. E., 1953. — The anatomy of timbers of the south-west Pacific area. III Myrtaceae. *Aust. J. Bot.*, 1: 353-401.
- JACOBS, M. R., 1955. — *Growth Habits of the Eucalypts*. Canberra: Commonwealth of Australia Forestry and Timber Bureau.
- JOHNSON, L. A. S., 1972. — Evolution and classification in *Eucalyptus* (Presidential Address). *PROC. LINN. SOC. N.S.W.*, 97: 11-29.
- , 1976. — Problems of species and genera in *Eucalyptus* (Myrtaceae). *Plant Syst. Evol.*, 125: 155-167.
- , and BLAXELL, D. F. (in press). — New taxa and combinations in *Eucalyptus* — 4. *Telopea*, 1.
- , and BRIGGS, B. G., 1975. — On the Proteaceae — the evolution and classification of a southern family. *J. Linn. Soc., London, Bot.*, 70: 83-182.
- , (in press). — Three old southern families — Myrtaceae, Proteaceae, and Restionaceae In, Keast, A. (ed.), *Biogeography and Ecology of Australia*, 1. The Hague: Junk.
- KAUSEL, E., 1956. — Beitrag zur Systematik der Myrtaceen. *Ark. Bot., Ser. 2*, 3: 491-516.
- , 1957a. — Beitrag zur Systematik der Myrtaceen. II. *Ark. Bot., Ser. 2*, 3: 607-611.
- , 1957b. — Myrtaceae. In, Angely, J., *Catálogo e Estatística dos Gêneros Botânicos Fanerogâmicos*, 28: 1-4. Curitiba: Instituto Paranaense de Botânica.
- , 1962. — Zur Systematik von *Pilotheicum* Kiärskou. *Ark. Bot., Ser. 2*, 4: 401-405.
- , 1967 (1966). — Lista de las Mirtáceas y Leptospermáceas argentinas. *Lilloa*, 32: 323-368.
- KIAERSKOU, H., 1893. — Enumeratio Myrtacearum brasiliensium. In, Warming, E. (ed.), *Symbolarum ad Floram Brasiliæ Centralis Cognoscendam*, 39: 1-200. Copenhagen: Gjellerup.
- KUBITZKI, K., 1969. — Chemosystematische Betrachtungen zur Grossgliederung der Dicotylen. *Taxon*, 18: 360-368.
- LEGRAND, [C.] D., 1950. — Contribuciones mirtológicas argentinas. *Darwiniana*, 9: 280-305.
- , 1961. — Mirtáceas del Estado de Santa Catarina (Brasil). *Sellowia*, 13: 265-363.
- , 1975. — Sobre *Pilotheicum* (Kiaersk.) Kaus. *Bradea*, 2: 33-40.
- MCVAUGH, R., 1956a. — Tropical American Myrtaceae. Notes on generic concepts and descriptions of previously unrecognized species. *Fieldiana, Bot.*, 29: 143-228.
- , 1956b. — Tropical American Myrtaceae II. Notes on generic concepts and descriptions of previously unrecognized species. *Fieldiana, Bot.*, 29: 391-532.
- , 1968. — The genera of American Myrtaceae — an interim report. *Taxon*, 17: 354-418.

- MARTIUS, C. F. P. DE [VON], 1857. — *Flora Brasiliensis. Enumeratio Plantarum in Brasilia*. 14 (1). Leipzig: Fleischer.
- MATTOIS, J. R., 1967. — *Britoa* (Berg) Mattos, sub-gènere de *Campomanesia* Ruiz et Pav. *Loefgrenia*, 26: 1-72.
- MAYR, B., 1969. — Ontogenetische Studien an Myrtales-Blüten. *Bot. Jahrb. Syst. Pflanzengesch. Pflanzengeogr.*, 89: 210-271.
- MELCHIOR, H., 1964. — Myrtales. In, Engler, A. (ed.) *Syllabus der Pflanzenfamilien*. II: 345-366. Berlin: Borntraeger.
- MERRILL, E. D., 1937. — *Aphanomyrtus* Miquel and *Pseudoeugenia* Scortechini. *Blumea*, Suppl. I: 107-111.
- , 1950. — Readjustments in the nomenclature of Philippine *Eugenia* species. *Philipp. J. Sci.*, 79: 351-424.
- , and PERRY, L. M., 1937. — Reinstatement and revision of *Cleistocalyx* Blume (including *Acicalyptus* A. Gray), a valid genus of the Myrtaceae. *J. Arnold Arbor. Harv. Univ.*, 18: 322-343.
- , 1938. — A synopsis of *Acmena* DC., a valid genus of the Myrtaceae. *J. Arnold Arbor. Harv. Univ.*, 19: 1-20.
- , 1939. — The Myrtaceous genus *Syzygium* Gaertner in Borneo. *Mem. Am. Acad. Arts Sci.*, 18: 135-202.
- METCALFE, C. R., and CHALK, L., 1950. — *Anatomy of the Dicotyledons*. 2 vols. Oxford: Clarendon Press.
- MÚJICA, M. B., and CUTLER, D. F., 1974. — Taxonomic implications of anatomical studies on the *Oliniaceae*. *Kew Bull.*, 29: 93-123.
- MULLER, J., 1975. — Note on the pollen morphology of Crypteroniaceae s.l. *Blumea*, 22: 275-294.
- NIEDENZU, F., 1898. — Myrtaceae. In, Engler, A., and Prantl, K., *Die natürlichen Pflanzenfamilien*. 3 (7): 57-105. Leipzig: Engelmann.
- ORCHARD, A. E., 1975. — Taxonomic revisions in the family Haloragaceae I. The genera *Haloragis*, *Haloragodendron*, *Glichrocaryon*, *Meziella* and *Gonocarpus*. *Bull. Auckland Inst. Mus.*, 10: 1-299.
- PERRY, L. M., 1950. — Notes on some Myrtaceae of Fiji. *J. Arnold Arbor. Harv. Univ.*, 31: 350-371.
- PETIT, L.-A., 1908. — *Recherches sur la Structure Anatomique du Fruit et de la Graine des Myrtacées*. [Thesis, Université de Paris.] Lons-le-Saunier: Lucien Declume.
- PRYOR, L. D., 1976. — *The Biology of Eucalypts*. London: Edward Arnold.
- , and JOHNSON, L. A. S., 1971. — *A Classification of the Eucalypts*. Canberra: Australian National University Press.
- , (in press). — *Eucalyptus*, the universal Australian. In, Keast, A., (ed.), *Biogeography and Ecology of Australia*, 1. The Hague: Junk.
- PULLE, A. A., 1952. — *Compendium van de Terminologie, Nomenclatuur en Systematiek der Zaadplanten*. Third edition. Utrecht: A. Oosthoek.
- RAO, V. S., and DAHLGREN, R., 1969. — The floral anatomy and relationships of Oliniaceae. *Bot. Notiser*, 122: 160-171.
- RICKETT, H. W., 1944. — The classification of inflorescences. *Bot. Rev.*, 10: 187-231.
- , 1955. — Materials for a dictionary of botanical terms — III. Inflorescences. *Bull. Torrey Bot. Club*, 82: 419-445.
- RIEDL, R., 1977. — A systems-analytical approach to macro-evolutionary phenomena. *Q. Rev. Biol.*, 52: 351-370.
- ROTMAN, A. D., 1976. — Revisión del género *Campomanesia* en la Argentina (Myrtaceae). *Darwiniana*, 20: 327-340.
- ROURKE, J., and WIENS, D., 1977. — Convergent floral evolution in South African and Australian Proteaceae and its possible bearing on pollination by non-flying mammals. *Ann. Mo. Bot. Gard.* 64: 1-17.
- SCHMID, R., 1972a. — A resolution of the *Eugenia-Syzygium* controversy (Myrtaceae). *Am. J. Bot.*, 59: 423-436.
- , 1972b. — Floral anatomy of Myrtaceae. II. *Eugenia*. *J. Arnold Arbor. Harv. Univ.*, 53: 336-363.
- , 1972c. — Floral anatomy of Myrtaceae. I. *Syzygium*. *Bot. Jahrb. Syst. Pflanzengesch., Pflanzengeogr.* 92: 433-489.
- SEEMANN, B., 1865. — *Flora Vitiensis*. London: Reeve.
- SHAW, H. K. A., 1973. — *A Dictionary of the Flowering Plants and Ferns*, by J. C. Willis. Eighth edition. Cambridge: Cambridge University Press.
- SMITH-WHITE S., 1950. — Cytological studies in the Myrtaceae. iii. Cytology and phylogeny of the Chamelaucioideae. *Proc. Linn. Soc., N.S.W.*, 75: 99-121.
- , 1954. — Cytological studies in the Myrtaceae. iv. The subtribe Euchamaelaucinae. *Proc. Linn. Soc. N.S.W.*, 79: 21-28.
- , 1959. — Cytological evolution in the Australian flora. *Cold Spring Harbor Symp. Quant. Biol.*, 24: 273-289.

- STAFLEU, F. A., and COWAN, R. S., 1976. *Taxonomic Literature*. Second edition. 1: A-G. Utrecht: Bohn, Scheltema and Holkema.
- STAUFFER, H. U., 1963. — Gestaltwandel bei Blütenständen von Dicotyledonen. *Bot. Jahrb. Syst. Pflanzengesch., Pflanzengeogr.*, 82: 216-251.
- STEBBINS, G. L., 1974. — *Flowering Plants: Evolution above the Species Level*. Cambridge, Mass.: Belknap Press, Harvard University Press.
- STERN, W. L., and BRIZICKY, G. K., 1958. — The comparative anatomy and taxonomy of *Heteropyxis*. *Bull. Torrey Bot. Club*, 85: 111-123.
- STONE, B. C., 1962. — *Myrtomera*, a new generic name for *Spermolepis* Brongn. and Gris (Myrtaceae). *Pac. Sci.*, 16: 241.
- SUESSENGUTH, K., 1950. — *Amaranthaceae, Asclepiadaceae, Combretaceae, Geraniaceae, Meliaceae, Myrtaceae, Rhamnaceae, Rubiaceae*. *Mitt. Bot. StSamml., München*. 1: 1-23.
- (TAKHTADZHAN, A. L.), 1970. — *Proiskhozhdeniye i Rasseleniye Tsvetkhovykh Rasteniy*. Oliver and Boyd.
- (TAKHTADZHAN, A. L.), 1970. — *Proiskhozhdeniye i Rasseleniye Tsvetkhovykh Rasteniy*. Leningrad: Izdatel'stvo "Nauka".
- THONNER, F., 1915. — *The Flowering Plants of Africa*. London: Dulau.
- THORNE, R. F., 1976. — A phylogenetic classification of the Angiospermae. *Evol. Biol.*, 9: 35-106.
- THULIN, M., 1975. — The genus *Wahlenbergia* s. lat. (Campanulaceae) in tropical Africa and Madagascar. *Symb. Bot. Ups.*, 21: 1-223.
- TROLL, W., 1954. — *Praktische Einführung in die Pflanzenmorphologie*. 1. *Der Vegetative Aufbau*. Jena: Gustav Fischer.
- , 1957. — *Praktische Einführung in die Pflanzenmorphologie*. 2. *Die Blühende Pflanze*. Jena: Gustav Fischer.
- , 1964. — *Die Infloreszenzen. Typologie und Stellung im Aufbau des Vegetationskörpers*, 1. I *Deskriptive Morphologie der Infloreszenzen*; II *Typologie der Infloreszenzen*. Jena: Gustav Fischer.
- , 1969. — *Die Infloreszenzen. Typologie und Stellung im Aufbau des Vegetationskörpers*, 2. III *Monotele Synfloreszenzen*. Jena: Gustav Fischer.
- UPHOF, J. C. T., 1962. — *Plant Hairs. Handbuch der Pflanzenanatomie* IV (5). Berlin: Borntraeger.
- VLIET, G. J. C. M. VAN, 1976. — Wood anatomy of the Rhizophoraceae. *Leiden Bot. Ser.*, 3: 20-75.
- , and BAAS, P., 1975. — Comparative anatomy of the Crypteroniaceae sensu lato. *Blumea*, 22: 173-195.
- WALKER, J. W., and DOYLE, J. A., 1975. — The bases of angiosperm phylogeny: palynology. *Ann. Mo. Bot. Gard.*, 62: 664-723.
- WEBERLING, F., 1956. — Untersuchungen über rudimentäre Stipeln bei den Myrtales. *Flora*, 143: 201-218.
- , 1958. — Über das Vorkommen rudimentärer Stipeln bei den Lecythidaceae (s.l.) und Sonneratiaceae. *Flora*, 145: 72-77.
- , 1960. — Weitere Untersuchungen über das Vorkommen rudimentärer Stipeln bei den Myrtales (Combretaceae, Melastomataceae). *Flora*, 149: 189-205.
- , 1963. — Ein Beitrag zur systematischen Stellung der Geissolomataceae, Penaeaceae und Oliniaceae sowie der Gattung *Heteropyxis* (Myrtaceae). *Bot. Jahrb. Syst. Pflanzengesch. Pflanzengeogr.*, 82: 119-128.
- , 1965. — Typology of inflorescences. *J. Linn. Soc. London, Bot.*, 59: 215-221.
- , 1966. — Additional notes on the Myrtaceous affinity of *Kania eugenioides* Schltr. *Kew Bull.*, 20: 517-520.
- WHITE, C. T., 1951. — Some noteworthy Myrtaceae from the Moluccas, New Guinea, and the Solomon Islands. *J. Arnold Arbor. Harv. Univ.*, 32: 139-149.
- WHITE, F., 1977. — The underground forests of Africa: a preliminary review. *Gard. Bull., Singapore*, 29: 57-71.
- WIGHT, R., 1840-43. — *Icones Plantarum Indiae Orientalis, or Figures of Indian Plants*, 2. Madras: R. Wight.
- WILSON, K. A., 1957. — A taxonomic study of the genus *Eugenia* (Myrtaceae) in Hawaii. *Pac. Sci.*, 11: 161-180.
- WUNDERLICH, R., 1971. — Die systematische Stellung von *Theligonum*. *Oesterr. Bot. Z.*, 118: 329-394.
- YOUNG, D. J., and WATSON, L., 1970. — The classification of dicotyledons: a study of the upper levels of the hierarchy. *Aust. J. Bot.*, 18: 387-433.