
Inflorescence Morphology, Heterochrony, and Phylogeny in the Mimosoid Tribes Ingeae and Acacieae (Leguminosae: Mimosoideae)

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**Inflorescence Morphology, Heterochrony, and Phylogeny
in the Mimosoid Tribes Ingeae and Acacieae
(Leguminosae: Mimosoideae)**

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I. Abstract

In earlier work (Grimes, 1992) on inflorescence morphology in the mimosoid tribes Ingeae and Acacieae I proposed that differences in inflorescence morphology result from three properties: the organization of components of the inflorescence and their relative positions; the hierarchical arrangement of the axes of the inflorescence and the position they assume in total tree architecture; and the heterochronic development of components of the inflorescence. Further work shows that the first two properties are better stated in terms of heterochrony; namely, that the organization of components of the inflorescence differs due to differences in timing of the development of organ systems and that the hierarchy of axes likewise differs due to heterochronic changes. Neither de novo origin of organs or organ systems nor suppression or loss of organs or organ systems accounts for the diversity in form. Observed heterochronic differences in the inflorescence structure may be divided into three

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types: spatial differences in the relationship between the unit inflorescence and the subtending leaf (hysteranthly); differences in the time of formation and/or the duration of whole axes; and changes in development pathways, leading to shoot dimorphism. These heterochronies are used as characters in a cladistic analysis, and it is shown that although some are homoplasious, many provide synapomorphies of clades of exemplars representing genera in the Ingeae and Acacieae.

Zusammenfassung

In einer früheren Arbeit (Grimes, 1992) über die Morphologie von Infloreszenzen in den mimosoiden Triben Ingeae und Acacieae wurde vorgeschlagen, dass die Unterschiede in der Morphologie der Infloreszenzen auf drei Eigenschaften zurückzuführen sind. Erstens unterscheiden sich die Infloreszenzen hinsichtlich der Organisation ihrer Bestandteile und deren relativen Lage zueinander. Zweitens unterscheiden sie sich hinsichtlich der hierarchischen Anordnung der Infloreszenzachsen und deren Position in der gesamten Baumarchitektur. Und drittens unterscheiden sich die Infloreszenzen hinsichtlich der heterochronischen Entwicklung ihrer einzelnen Bestandteile. Weitere Untersuchungen zeigen, dass die beiden ersten Eigenschaften besser im Sinne der Heterochronie verstanden werden können, und zwar dahingehend, dass die Organisation der Infloreszenzbestandteile durch Unterschiede in der relativen zeitlichen Entwicklung einzelner Organsysteme begründet ist, und dass die Hierarchie der Achsen in gleicher Weise auf heterochronische Veränderungen zurückzuführen ist. Weder ein *de novo* Ursprung einzelner Organe oder ganzer Organsysteme noch die Suppression oder der Verlust von Organen oder Organsystemen ist verantwortlich für die Vielfalt der Formen. Die beobachteten heterochronischen Unterschiede in der Struktur der Infloreszenzen können in drei Typen unterteilt werden. Erstens gibt es Unterschiede in der Beziehung hinsichtlich des Zeitpunktes der Ausbildung zwischen der Einzelinfloreszenz und dem darunterliegenden Tragblatt (Hysteranthie). Zweitens kann es Unterschiede hinsichtlich des Zeitpunktes der Ausbildung und/oder der Dauer ganzer Achsen geben. Und letztlich können heterochronische Veränderungen in ganzen Entwicklungsabläufen zum Dimorphismus zwischen Langtrieben und Kurztrieben führen. Diese Heterochronien werden als Eigenschaften in einer kladistischen Analyse verwendet, und es wird gezeigt, dass während einige homoplasisch sind, viele jedoch Synapomorphien von Kladen darstellen, die aus Gattungen der Ingeae und Acacieae bestehen.

II. Introduction

Within the tribes Ingeae and Acacieae (Fabaceae, Mimosoideae) is a diverse array of inflorescence morphologies. Nonetheless, all of these types are variations on a common theme: This theme is a series of metamers, each of which possesses one to several unit inflorescences. The unit inflorescence is always an axillary, blastotelic, pedunculate, capitulate or spicate raceme. I proposed that the different morphologies of the inflorescences are the result of three properties (Grimes, 1992). First, the inflorescences may differ in the organization of components of the inflorescence and their relative positions. For instance, peduncles may form at the oldest first-formed (i.e., proximal) nodes of any shoot, with leafy nodes at the younger, distal nodes, or peduncles may form only at the younger nodes. Second, inflorescences may differ in the hierarchical arrangement of the axes of the inflorescence and the position they assume in total tree architecture. For example, peduncles may form only on ephemeral branches that do not become integrated into total tree architecture, or they may form only on primary branches

integrated into total tree architecture. Finally, inflorescences may differ in heterochronic development of components of the inflorescences. So, peduncles at the distal (or proximal) nodes may be subtended by a fully formed leaf, or they may occur at efoliate nodes or nodes at which development of the leaf has been suppressed.

In evaluating these properties it is important at the outset to distinguish processes that may lead to structural modification of organs or organ systems. All structural modifications may result from one of three basic processes: *de novo* origin of novel organs; loss of organs; or heterochronic (including allometric) changes in the development of organs. It is also important to point out that loss of an organ is a structural change (loss of genetic material) that must in practice be distinguished from suppression of an organ, which can be seen as a heterochronic change (cf. Tucker, 1989).

Evaluation of the inflorescence structure of ingoid Mimosoideae reveals that no *de novo* origin of novel structures has taken place: the components of all inflorescences are the same. Loss of organ systems is more difficult to evaluate, but it appears that, at most, suppression of organs or parts of developmental pathways has occurred. For instance, the various kinds of leaf hysteranthly occur because development of the leaf primordia is either delayed or suppressed. Other examples in which developmental pathways may be suppressed will be mentioned in various places in this article. What has become apparent since my 1992 article is that heterochronic changes have a more profound influence on inflorescence structure than that implied by the three listed properties and that many hierarchical and organizational differences may be a result of heterochronic differences. For example, the distinction between peduncles that form at the oldest or youngest nodes of a branch, which is a change in the organization of components of the inflorescence (the first property of Grimes, 1992), is also a heterochronic one: that is, the time of formation of some organs differs from that of others during growth of the branch.

The objectives of this article, then, are two. First, various modifications of the inflorescence in tribe Ingeae will be described, then evaluated in the context of heterochrony. Second, the modifications will be examined in the context of a cladogram of exemplar species of tribes Ingeae and Acacieae in order to place them in a phylogenetic context. We may then evaluate the phylogenetic information provided by the observed differences: How many are homoplastic and how many synapomorphic? It will then also be possible to polarize the various character-state changes.

III. Terminology

"Heterochrony" in the broad sense is change in the relative time of appearance and/or rate of development for characters already present in the ancestor (Gould, 1977). The nomenclature of heterochrony has become detailed (e.g., Alberch et al., 1979; McKinney, 1988; McNamara, 1986), but in this article the simple definition provided by Gould (1977) will suffice. Some authors (e.g., Alberch, 1980; Gould, 1977; Stanley, 1975, 1989) have suggested that morphological changes during evolution may occur as a result of heterochrony, and Tucker (1989) has argued that heterochrony, specifically organ suppression, has been an important factor in floral evolution of the Leguminosae. It might be noted that most of the heterochronic changes discussed in this article are probably allometric; that is, rates of growth of one organ system change relative to those of another. However, descriptive developmental studies of inflorescences (as opposed to flowers) are few (e.g., Grimes, 1996), and the possibility of differences in onset or offset of growth (i.e., predisplacement, postdisplacement, hypermorphosis, progenesis *sensu* McKinney & McNamara, 1991) cannot be ruled out.

Grimes (1992) introduced terminology that will be followed here, and the following discussion, slightly modified, is taken directly from that work. The approach to describing inflorescence morphology was in the context of metamerism, or of repeating units of plant growth. The idea is that all plants conform to patterns of growth through the production of repeating units and that the particular pattern of growth is determined by the arrangement, duration, and modification of the repeating units. The repeating units may, in turn, be organized in a hierarchical system. So, for instance, generative cells constitute the meristem, which produces metamers, which together make up modules.

The metamer is defined as the internode, upper node, attached leaf, and axillary bud(s) (Barlow, 1989), and metamerism (White, 1984) is the serial repetition of metamers within or along an organism. The metamers, whether identical or modified inter se, are homologous in structure. The same meristem may produce metamers of different composition; that is, parts may be modified (e.g., a leaf may be modified into a tendril), but their repetitive nature remains the same.

Metamers, in their various modifications, are organized into repeating units, and these determine the aspect and organization of the shoot system. These repeating units have properties different from those of their constituent metamers, and their arrangement determines the aspect of the whole plant. One such repeating unit is the module, a term with imprecise and/or conflicting definitions (see Grimes, 1992). Other terms applied to suprametameric units of growth are "submodule" (Barlow, 1989) and "seasonal growth unit" (SGU) (Briggs & Johnson, 1979), but a deficiency of both of these concepts is their dependence on seasonal phenomena: many tropical trees exhibit no seasonally related growth (Holttum, 1953; Koriba, 1958).

All of these concepts—module, submodule, and SGU—have a more serious deficiency: the repeating sequences of metamers may be different at different places on a shoot, or on different shoots, and the sequences themselves may be organized into sequences. When, and at what level, is one sequence comparable to another?

A definition that allows for comparison among all types of shoots must account for the different variables contributing to their growth: that growth is repetitive; that the repetitive patterns are often independent of external phenomena; that plants are constructed from metamers that may be dissimilar from other metamers on the same axis and from metamers on different axes or plants; and that metamers may be organized into sequences of different orders. In order to establish a hierarchy of sequences I proposed the term "repeating growth unit" (RGU), defined as the smallest, complete, repeating sequence of metamers produced by a meristem (Grimes, 1992). As an example, the RGU of *Abarema jupunba* (Willd.) Britton & Killip in Figure 1 consists of some number of sterile metamers with leaves followed by some number of fertile metamers with leaves and unit inflorescences.

Any sequence of metamers within a RGU that does not include all possible sequences in that RGU is a subsequence (SS). So, in Figure 1, on the shoot with three leafy metamers followed by three floriferous ones, the sequences of leafy and floriferous metamers each would constitute a subsequence. Any branch system arising from a sylleptic bud is a subunit. Subunits may or may not repeat the same sequence of metamers as is found on the main axis of the RGU. This distinction is important in postulating homology of subunits and, therefore, of RGUs.

The concept of RGU now permits a more precise definition of "module": the series or sequence of RGUs produced by a single apical meristem. All prior definitions of module are subsumed in this one, though that of Jones (1985) is indistinguishable in practice, without changing the meaning of any of them. With this definition, "module" may now be used to refer to either determinate or indeterminate axes and will allow comparisons between them.

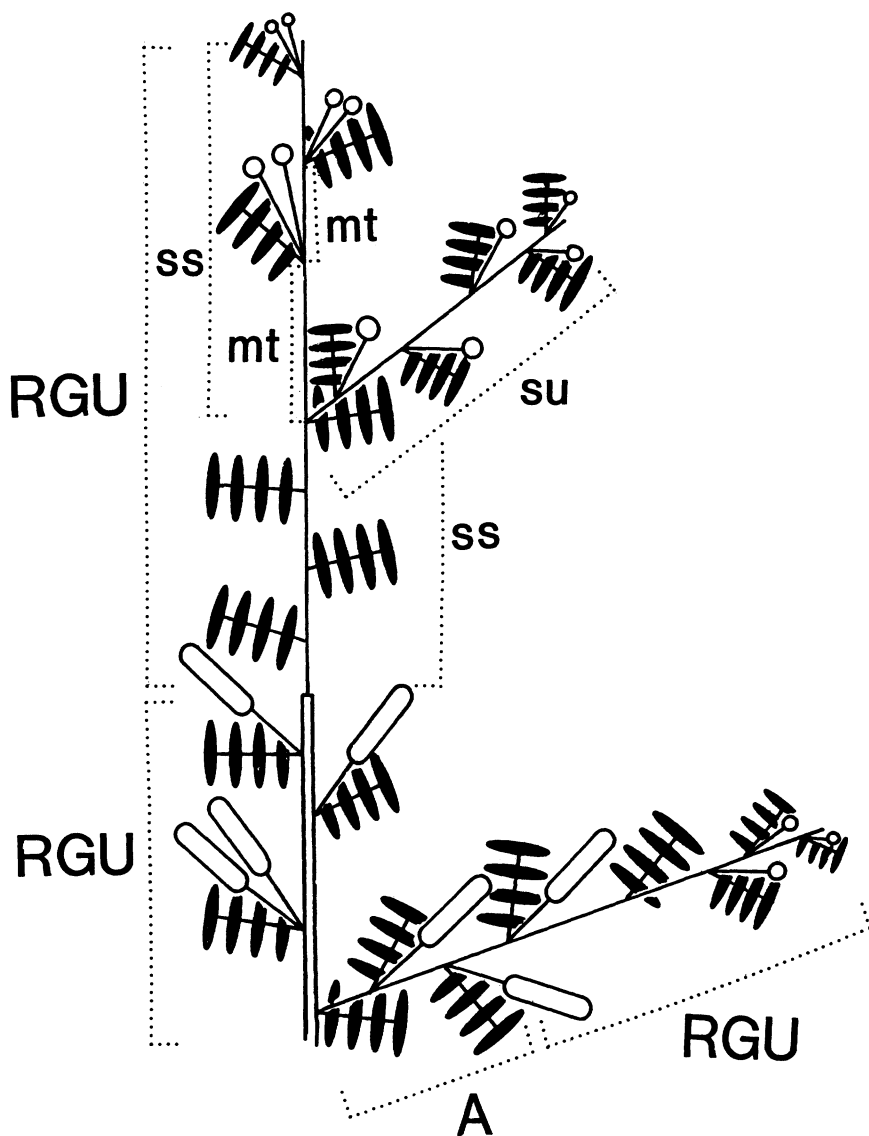


Fig. 1. An inflorescence in *Abarema jupunba* (Willd.) Britton & Killip, illustrating the concepts of metamer, Repeating Growth Unit (RGU), and associated terms. A metamer (mt) is the internode, node, leaf, and associated axillary bud(s). An RGU is defined as the smallest repeating complete sequence of metamers on a shoot. The hollow stem represents the penultimate RGU. A subsequence of metamers, or a sequence that does not include all possible sequences of the RGU, is indicated by "ss." Any sylleptic branches are subunits (su). The terminal RGU here is made of a subsequence of three vegetative metamers, a subsequence of metamers with axillary inflorescences, and a subunitary branch. "A" was a sylleptic branch of the penultimate RGU and is a subunit that formed the base of a new branch system of RGUs.

The complete hierarchy on a shoot, then, is cell–meristem–metamer–subsequence¹–[+ subunits]–subsequence¹⁺ⁿ–[+ subunits]–RGU–module. This definition is free from temporal constraints, it will allow metamers to exhibit great modification, and it will enable comparisons to be made among sequences.

For every given species, then, one can define the RGU in terms of the kinds of metamers produced by the meristem and by the sequence in which they are produced. The exact number of metamers, or the number of any particular kind, may be variable, and in some years in which plants may not bloom fertile metamers may be lacking altogether. The precise numbers of kinds is not important, merely the generalized pattern of kinds produced. For instance, in *Abarema* no fertile metamers with suppressed leaves have ever been seen to be the first kind produced by an RGU. Although in *Chloroleucon* (Fig. 2) the RGU consists of some number of fertile, leafless metamers or some number of fertile, leafy metamers, followed by some number of sterile metamers, it has never been observed that within any given RGU the sterile metamers are produced before the fertile ones.

The terms “sytleptic buds” and “proleptic buds” were given special definition in Grimes (1992) and are used in that sense here. As far as is known in mimosoid legumes, at least one bud is formed at every node concomitant with, or slightly after, formation of the leaf primordium. Sytleptic buds are those buds that continue development while the RGU on which they are formed is still completing development itself: that is, before the complete sequence of metamers has been produced. Proleptic buds, in contrast, are those that form but that delay development until after the RGU on which they sit has completed development: that is, development is delayed somewhat. These definitions, then, propose some sort of heterochronic difference between the two types of buds.

IV. Observed Differences in Inflorescences

For ease of presentation the observed heterochronic differences in inflorescence structure may be divided into three major types: observed heterochronic differences in the relationship between the unit inflorescence(s) and the subtending leaf (leaf hysteresis); observed differences in the time of formation and/or duration of whole axes; and dimorphic axes or shoots, in which is one RGU may have metamers modified differently from those of other RGUs.

In my earlier article (Grimes, 1992) I recognized that some morphological differences resulted from apparent heterochronic changes in the development or relationship of the unit inflorescence and the subtending leaf. Four recognized differences are summarized in Figure 3. When leaf primordia and inflorescence primordia form and develop at the same time they may be termed “coeval” (Fig. 3A). Because genera are polymorphic for coeval development (i.e., not all species exhibit coeval development; some show late- or early-suppressed hysteresis) of unit inflorescences and subtending leaves, coeval development is not included in the cladistic analysis discussed here. In other taxa allometric changes are seen: leaf primordia and inflorescence primordia form at the same time, but development of the leaf primordia is changed. In some taxa the leaf primordia and inflorescence primordia form at the same time, but development of the leaf primordium is delayed (but not suppressed) relative to the subtended unit inflorescence. This type, called “developmental hysteresis” (Fig. 3B) (Grimes, 1995), is included in the cladistic data set as character 19. In other taxa development of the leaf primordia may be suppressed; that is, the primordia form but never develop into leaves. Called “spatial hysteresis” (Grimes, 1995), this is character 16 in the data set. The terms “spatial hysteresis” and “developmental hysteresis” were used to reflect a difference in how heterochronic development is expressed. Spatial hysteresis implies that heterochronic

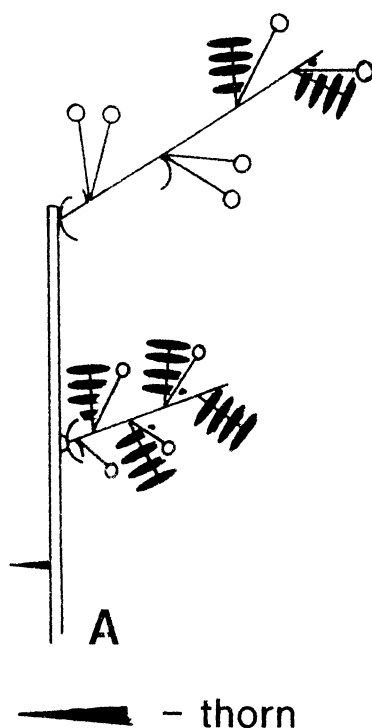


Fig. 2. A inflorescence in *Chloroleucon*. As in Fig. 1, the hollow stem represents the penultimate RGU. The new RGUs consist of some number of fertile metamers with or without subtending leaves, often followed by some number of sterile metamers.

development of the leaves subtending peduncles takes place only along some (either the distal or proximal) of the nodes of the subsequence or fertile metamers and that some are fully suppressed. Developmental hysteresis implies that all leaves subtending peduncles of all nodes of the subsequence of fertile metamers exhibit delayed development relative to development of the subtended peduncle, but none is fully suppressed.

Spatial hysteresis may in turn be divided into two types. In the first, the fertile metamers are acrotonic, or produced at the terminal, younger, nodes of the RGU. The leaf primordia of the youngest, most terminal nodes of these compound inflorescences are suppressed, leading to what Barneby and Grimes (1996, 1997) referred to as a terminal, efoliate pseudoraceme of capitula (or spikes). Labeled “late-suppressed hysteresis” (Fig. 3C), this is included as character 18 in the data set. In the second type, the fertile metamers are the first produced of any RGU, or basitonic in disposition, and the leaves at the oldest, most proximal of these may be suppressed relative to the subtended unit inflorescence. This “early-suppressed hysteresis” (Fig. 3D) is character 17 in the data set.

Heterochrony was assumed to be the cause of the four above-mentioned differences, with no empirical study to determine whether structural modification of any metamers might account for the differences. Since then I conducted a developmental study of the branch apices of some mimosoid legumes (Grimes, 1996). Included were species exhibiting coeval development (e.g., *Ebenopsis ebano* (Berlandier) Barneby & Grimes), early-suppressed hysteresis

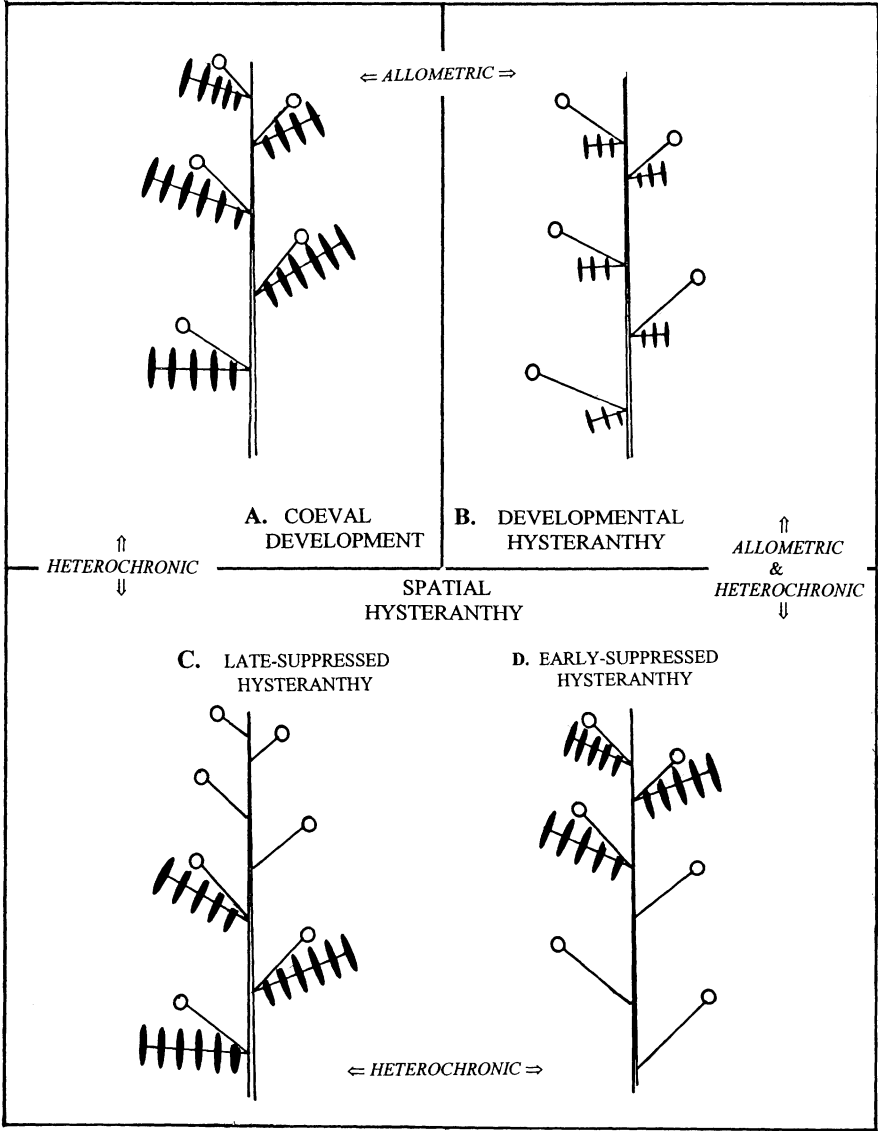
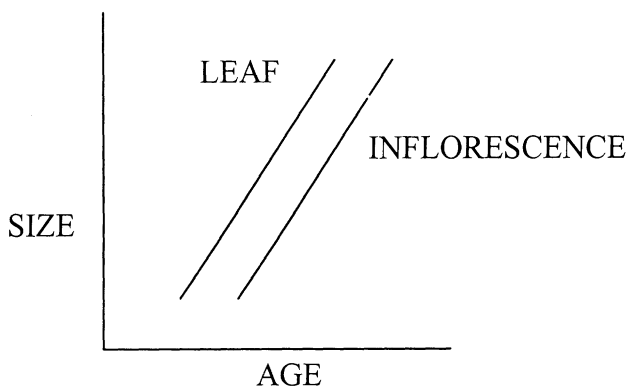


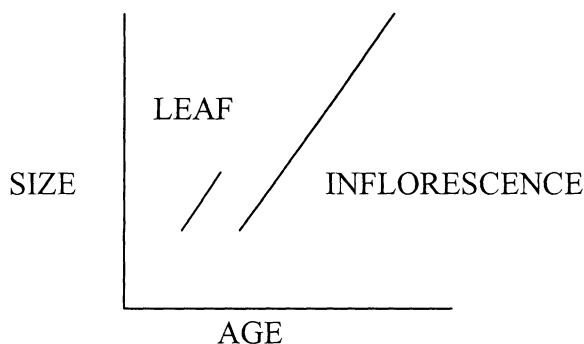
Fig. 3. Heterochronic differences in development of unit inflorescence and the subtending leaf. The three boxes represent the three main types of development: coeval, developmental hysteresis, and spatial hysteresis. Spatial hysteresis is of two types, late suppressed and early suppressed. The italicized captions represent the kind of difference between the major types. So, for instance, the difference between coeval development and developmental hysteresis is an allometric one; that between coeval development and spatial hysteresis is heterochronic in the strict sense.

thy (e.g., *Lysiloma microphyllum* Benth.), and late-suppressed hysteranthly (*Zapoteca tetragona* (Willd.) H. M. Hern.). In all the species studied it was found that inflorescence buds form in the nodes of leaf primordia: there is no suppression or loss. Differences seen then result from the time of formation of floral buds and the rate of development of the leaf—a heterochronic difference.

More specifically, the difference between developmental and spatial hysteranthly illustrates a difference between a heterochronic change (s.str.) and an allometric change. Spatial hysteranthly involves differences in developmental timing at two levels: within the developmental pathway of the leaf itself, and within the developmental pathway of the RGU. It also involves two different organ systems, the leaves and the unit inflorescences. Coeval development of the leaf and the subtended unit inflorescence may be simply modeled: formation of leaf primordium \Rightarrow development and differentiation \Rightarrow leaf. So may that of the unit inflorescence: formation of inflorescence bud \Rightarrow growth and differentiation \Rightarrow unit inflorescence. The relative growth of the leaf and the unit inflorescence may likewise be modeled:

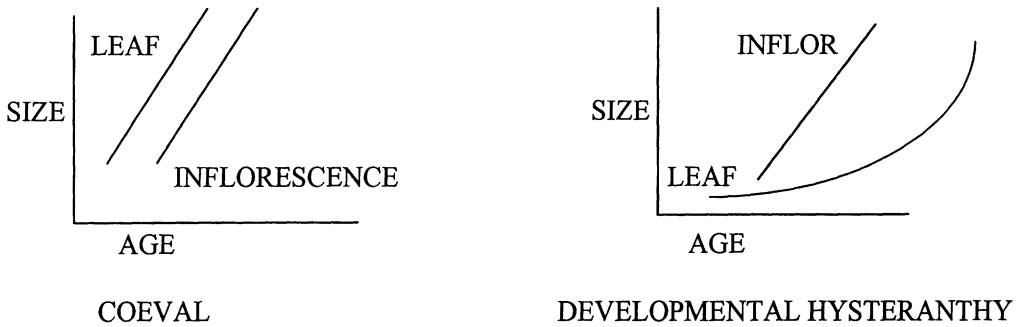


However, in the case of spatial hysteranthly the developmental pathway is changed: formation of leaf primordium \Rightarrow suppression, or cessation of growth.



Heterochronic differences, then, are effected in the developmental pathway of the leaf itself. It must be stated at this point that no polarity between these heterochronic differences is yet implied. It should be noted (cf. McKinney & McNamara, 1991) that this is a case of progenesis, or early offset of growth (heterochrony), not a matter of rate of growth (allometry). The unit inflorescence and the subtending leaf primordium form at the same time in both coeval and suppressed hysternathy, but the duration of growth of the leaf primordium is changed.

In contrast, the difference between developmental hysternathy and coeval development of leaf primordia and inflorescence primordia is one of allometry, or change in rate of growth. The developmental pathway of both remains the same: formation of leaf primordium \Rightarrow development and differentiation \Rightarrow leaf; and formation of inflorescence bud \Rightarrow growth and differentiation \Rightarrow unit inflorescence. However, the growth curves are different and may be modeled:



But heterochronic differences are also effected in the development of the RGU. In early-suppressed hysternathy the formation of the primordia of the unit inflorescence is precocious in terms of age of the RGU relative to the time of formation in late-suppressed hysternathy. In other words, the developmental pathway of unit inflorescences is turned on early in the development of the RGU, as is the suppression of development of the leaf primordia. The opposite situation is found in late-suppressed hysternathy.

The second set of observed structural and/or heterochronic differences concerns the whole axis of the RGU (i.e., a branch) and reflects combinations of heterochronic changes in three attributes of the RGU. Figure 4 diagrammatically summarizes the combinations of these features that are known in Ingeae and Acacieae. First, branches (or inflorescences) may develop sylleptically (as subunits) or proleptically (as new RGUs) from axillary buds. This is the major division in the diagram not because it is believed to be the most fundamental or important but because it is the only difference universally expressed in the group. Second, branches may be either ephemeral (abscising after fruit), or persistent. As both of these latter types may arise proleptically or sylleptically, they form columns under each major heading. Third, either branches may be both vegetative and reproductive or some RGUs may produce axillary subunits of ephemeral, strictly reproductive branch systems. Again, these types may develop in either sylleptic or proleptic systems; these are the rows in the diagram. None of these conditions is correlated exclusively with any of the others; for instance, ephemeral branches may develop either proleptically or sylleptically, and they may be either strictly reproductive or at once vegetative and reproductive.

Finally, some observed differences in inflorescence structure involve shoot dimorphism: axes on one branch, RGU, or subunit have metamers modified differently from metamers on other branches or RGUs. A simple example of these is brachyblasts, or short shoots. These oc-

PROLEPTIC SYSTEMS 5(1)			SYLLEPTIC SYSTEMS 5(0)	
EPHEMERAL BRANCHES	PERSISTENT BRANCHES		10(0) EPHEMERAL BRANCHES	10(1) PERSISTENT BRANCHES
D <i>Chloroleucon</i> alliance 12(1)		VEGETATIVE AND REPRODUCTIVE		B <i>Abarema</i> alliance 9(1)
C <i>Pithecellobium</i> 13(1) E (?) The <i>Inga</i> alliance (ramiflory, cauliflory) 14(1), 15(1)		SEPARATE REPRODUCTIVE	A <i>Albizia</i> , <i>Enterolobium</i> , Others 6(0)	
	Universal	STRICTLY VEGETATIVE		C <i>Pithecellobium</i> 8(1)

Fig. 4. Summary of the combinations of temporal differences found in tribe Ingeae. Specifically, the differences include whether branches arise proleptically or sylleptically; whether they are at once vegetative and reproductive or strictly vegetative or strictly reproductive; and whether they are ephemeral or persistent. The words above the boxes refer to columns, the words between the boxes apply to rows. So *Albizia*, for instance, has sylleptic, ephemeral, separate reproductive branches. All members of the tribe have proleptic vegetative branches. The numbers with the words indicate the character and state of the character for the columns and boxes.

cur in axils on long shoots and are different in that elongation of the internode is suppressed. These structural and/or heterochronic differences will be described in some detail below.

Vegetative branching—that is, origin of branches that persist as part of the “architecture” of the tree—may arise either proleptically or both sylleptically and proleptically. This is the major division between the two groups in Figure 4, and it is illustrated in Figure 5. The condition in which vegetative branching is sylleptic is not common in either tribe. It is found in the *Abarema*, *Balizia*, and *Hydrochorea*, where the branches are at once vegetative and reproductive (Fig. 4, box A). *Pithecellobium*, too, has sylleptically developing, persistent branches, but these are apparently strictly vegetative (Fig. 4, box B). This condition of sylleptically developing branches that are integrated into the architecture of the tree is included as character 7 in the cladistic data set; the difference between kinds of vegetative branching, whether reproductive or at once reproductive and vegetative, are characters 8 and 9 in the data set.

Some plants have strictly reproductive sylleptic branches, referred to as annual, axillary, strictly reproductive branch systems in my 1995 analysis (Grimes, 1995). These are branches that form and develop concurrent with the RGU on which they form but that are strictly reproductive and abscise after fruiting. This condition is seen in relatives of *Albizia* and in several other groups, and it is illustrated in Figure 6 (cf. Fig. 4, boxes C & E) and included in the data set as character 6. Species of *Zygia* may have similar branches that develop on cauliflorous knots on old wood: these will be discussed further below.

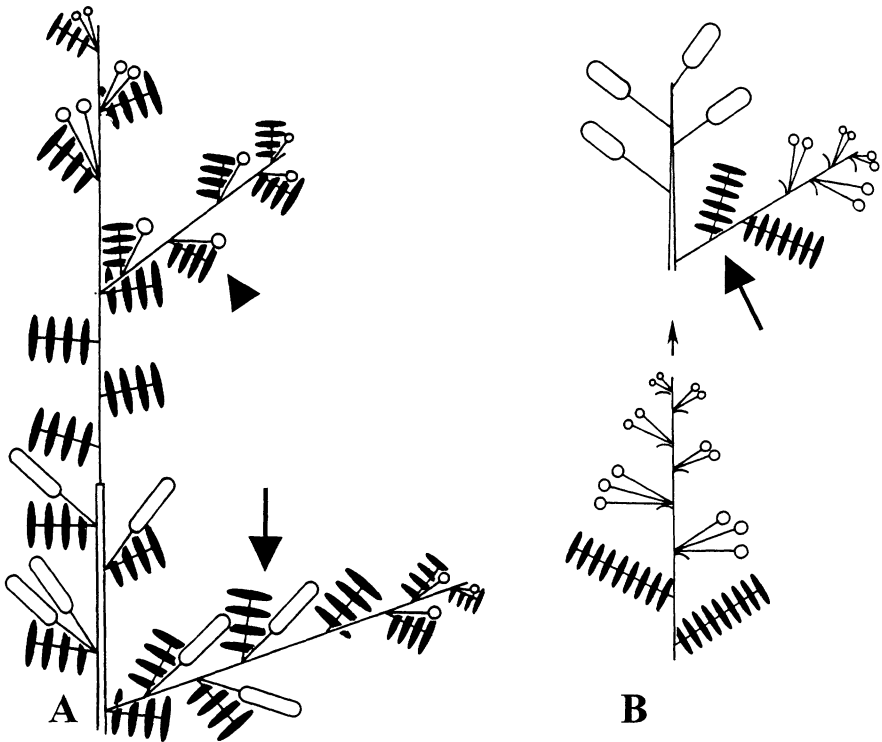


Fig. 5. Two types of vegetative branching patterns. In **A** the vegetative branches arise sylleptically. The arrow is pointing to a branch that was a subunit (syллеptically developing branch) of the penultimate RGU and that is continuing to grow as a new RGU. The arrowhead points to a syллеptically developing branch, a subunit, of the current RGU. The major axis is auxotelic ("indeterminate"), meaning that the meristem continues to produce RGUs for some time. In **B** the lower branch is the penultimate RGU. In the upper branch the penultimate RGU was anauxotelic ("determinate"), meaning that the meristem died. The arrow points to the current RGU, which has arisen proleptically on the penultimate RGU.

In contrast, in *Pithecellobium*, similar annual, axillary, strictly reproductive branch systems arise proleptically (Fig. 4, box D). This is included in the data set as character 13. These branches are ephemeral, but, as in the syллеptic systems, other branches that develop proleptically may be persistent. Likewise, as in syллеptic systems, branches that arise proleptically may be strictly reproductive or at once vegetative and reproductive. The separate reproductive branch systems of *Albizia* and *Enterolobium*—that is, syллеptic branches—are subunits (not RGUs); those of *Pithecellobium*, which develop proleptically, arise as RGUs not subordinate to a contemporaneous branch.

Not all ephemeral branches are strictly reproductive and syллеptic. For instance, species of *Chloroleucon* and related genera may have some proleptically developing, at once vegetative and reproductive branches that are ephemeral. This is illustrated in Figure 7, is represented in Box E of Figure 4, and is included in the data set as character 12. These branches develop from buds that remain dormant for some period, then flower and abscise from the branch; they do not form part of the vegetative architecture of the tree. *Chloroleucon* and its relatives are also unusual in the Ingeae in that there appears to be some degree of preformation of the shoots.

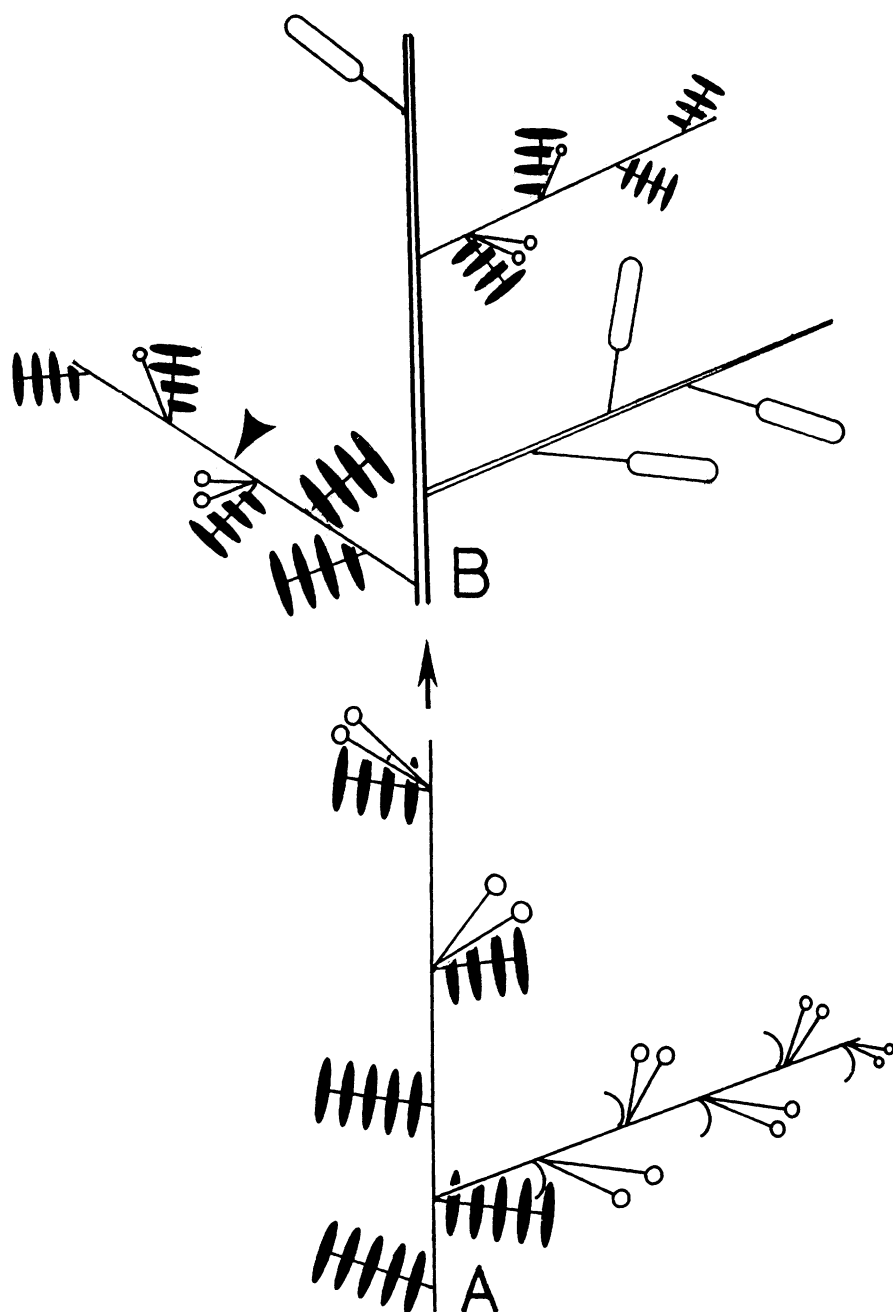


Fig. 6. Inflorescence morphology in some species in tribe Ingeae. The penultimate RGU is seen in **A**, with an axillary, sylleptically developing, strictly reproductive branch. The current RGU is seen in **B** (arrowhead); the penultimate axillary, strictly reproductive branch does not continue to grow and will abscise after the fruit has fallen. Likewise, that meristem of the penultimate RGU is anauxotelic ("determinate").

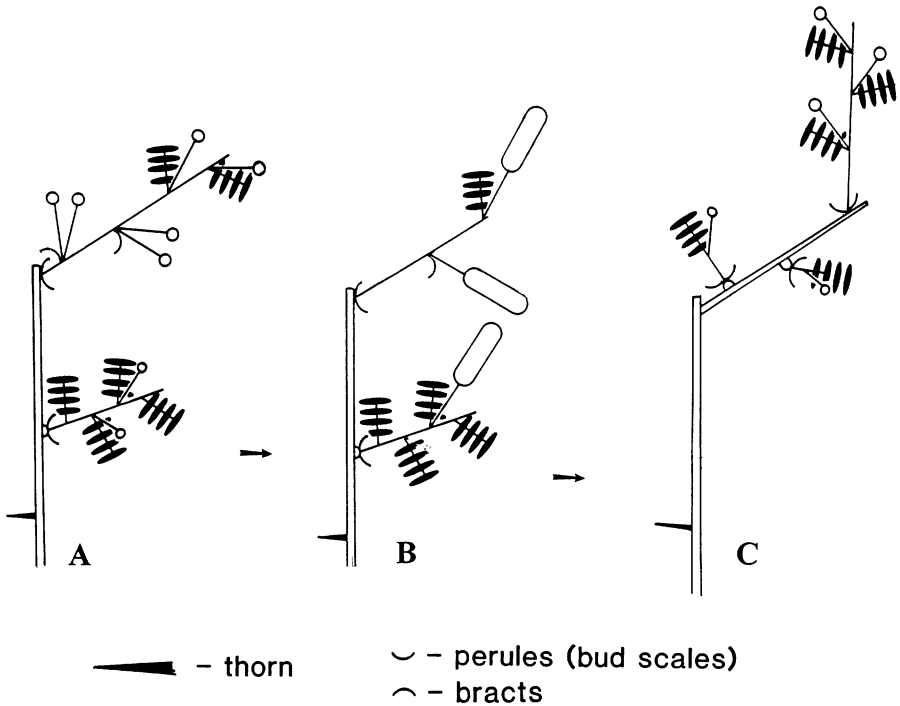


Fig. 7. Ephemeral branches in *Chloroleucon* and its relatives. **A.** The penultimate RGU is the hollow stem. Two new RGUs are developing: The lower is from a proleptically developing bud and exhibits some coeval development of the leaves and unit inflorescences; the upper is also from a proleptically developing bud and exhibits early-suppressed hysteranthly. **B.** Some unit inflorescences have formed fruit. **C.** After flowering and fruiting the lower branch has abscised; the upper has become integrated into the architecture of the plant.

Genera in the *Chloroleucon* alliance also apparently exhibit some degree of shoot preformation (sensu Brown & Sommer, 1992), which is character 4 in the data set; that is, many of the metamers with associated unit inflorescences form at the end of growth of the current RGU, have some period of dormancy in a perulate bud, and then extend during formation of the next RGU. This situation is also found in some species of *Acacia* subgenus *Phyllodineae* (e.g., *Acacia suaveolens* Willd. and *A. iteaphylla* F. Muell. ex Benthham).

Two other kinds of shoot dimorphism are also found in tribe Ingeae, both of which may result from heterochronic changes. For instance, *Zygia* was mentioned above as a genus that possesses annual, axillary, strictly reproductive branches. These, like the branches in *Albizia* and relatives, flower, set fruit, and then abscise. However, instead of arising on vegetative RGUs, they arise from meristems that repeatedly form these strictly reproductive branches and that are separated from the vegetative RGUs (character 15 in the data set). This is a heterochronic difference if timing of developmental steps is changed. For example, if cauliflory arises from a bud that has been formed in a leaf axil but remains dormant for some time and is buried in wood (preventitious sensu Fink, 1983), it is a heterochronic change in that a period of dormancy has been inserted into a developmental pathway. If, in contrast, cauliflory arises through the formation of adventitious

buds, the difference is not heterochronic. Because no developmental studies on cauliflory in Ingeae have been done, it is not known which case obtains in Ingeae.

Another kind of shoot dimorphism is the possession of long and short shoots in species of *Ebenopsis* and its allies and in some species of *Acacia*. This is character 10 in the data set (not shown in Fig. 4). In this case brachyblasts form in the leaf axils, with some or all formation of the unit inflorescences taking place on these short shoots. This difference may be viewed as heterochronic in that part of a developmental pathway, in this case elongation of an internode, is deleted or suppressed.

Some taxa have inflorescences that are "simple"; that is, they consist only of unit inflorescences distributed at leafy nodes along the main axis of the branch. No subunits are present, no sylleptically developing branches are produced, and no kind of morphological or heterochronic elaboration is exhibited. Species with these types of inflorescences are distributed among several genera of Ingeae and Acacieae. Because this condition is different from that of the outgroup, it is included as character 20 in the data set.

V. Phylogenetic Analysis

The data set used in the phylogenetic analysis is modified from one I published earlier (Grimes, 1995). I have made a fair number of changes or corrections, though, so the characters are listed in their entirety. The major differences in the data set used here and that of the 1995 analysis include filling in missing data, adding a few more taxa, and more detailed description of heterochronies. The taxa and characters are listed in Appendix 1; the data set is reproduced in Appendix 2.

The matrix was constructed using *Dada* (Nixon, 1995) and run in *Nona* (Goloboff, 1993), using the "mult*" option, followed by "max*". Random addition sequences were run 35 times, holding 35 trees at each replication. Strict consensus trees were generated by *Hennig86* (Farris, 1988). The trees were examined using *Clados* (Nixon, 1994). All characters were unordered in the analysis.

VI. Results and Discussion

Analysis of the data set resulted in 24 trees of 366 steps with a CI of 0.29 and an RI of 0.64. A strict consensus tree is shown in Figure 8. The numerous alternate trees result from unresolved relationships among some basal members of the tribes and include many exemplars of *Albizia* ("Genera incertae sedis" in Barneby & Grimes, 1996) and some exemplars of the Old World genera *Wallaceodendron*, *Archidendron*, and *Serianthes*. As pointed out by Barneby and Grimes (1996), resolution of the relationships of these groups depends on taxonomic study of African and Asian members of *Albizia*. Cladistic analysis of the Old World genera would also be useful. The terminal branches of the cladogram are well resolved, however, and include, for the most part, those genera discussed by Barneby and Grimes (1996, 1997), as well as some exemplars of *Acacia*.

After discussion of the heterochronies, general results of this analysis will be compared with those of the 1995 analysis. One of the 336 cladograms was arbitrarily chosen to show the distribution of characters in the following discussion.

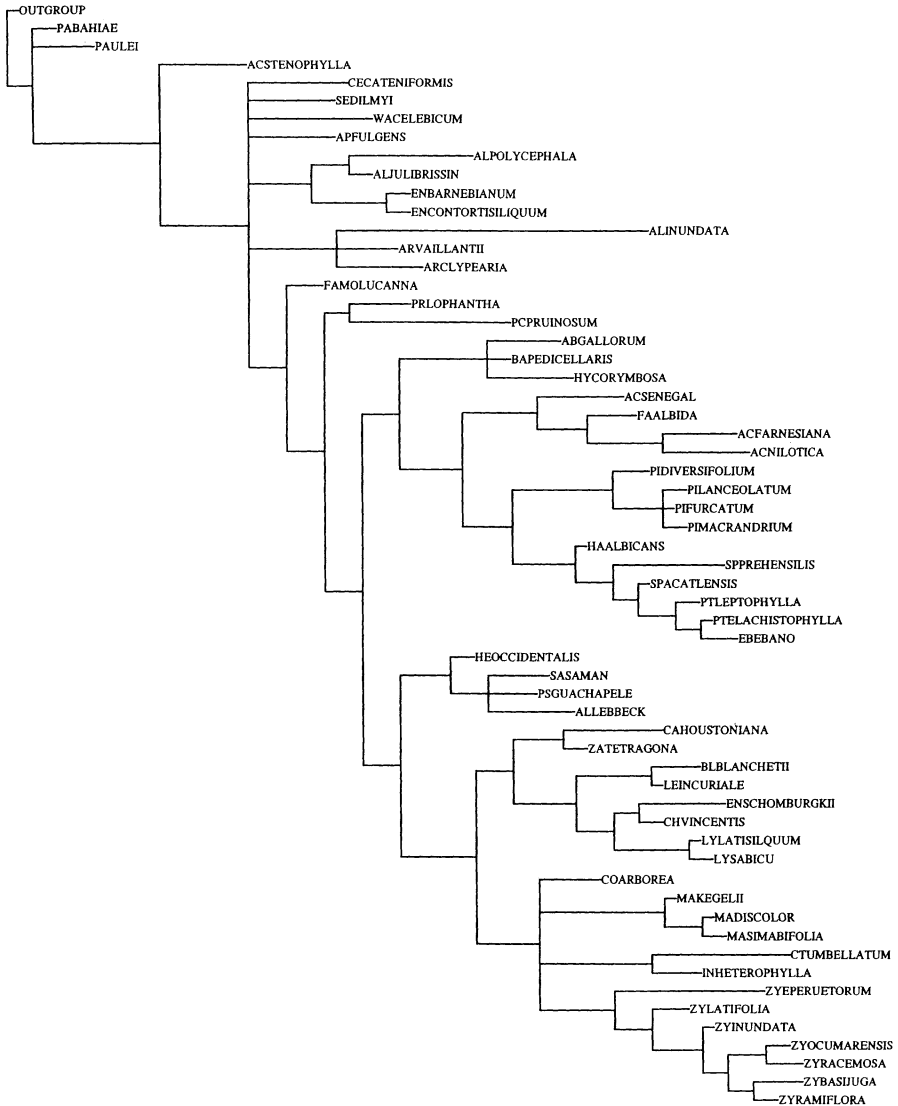


Fig. 8. A strict consensus tree of 336 equally parsimonious trees. The first two letters of the terminals represent the following genera, followed by the specific epithet. AB = *Abarema*; AC = *Acacia*; AL = *Albizia*; AP = *Archidendropsis*; AR = *Archidendron*; BA = *Balizia*; BL = *Blanchetiodendron*; CA = *Calliandra*; CE = *Cedrelinga*; CH = *Chloroleucon*; CO = *Cojoba*; CT = *Cathormion*; EB = *Ebenopsis*; EN = *Enterolobium*; FA = *Faidherbia*; FL = *Falcataria*; HA = *Havardia*; HE = *Hesperalbizia*; HY = *Hydrochorea*; IN = *Inga*; LE = *Leucochloron*; LY = *Lysiloma*; MA = *Macrosamanea*; PA = *Parkia*; PC = *Pararchidendron*; PI = *Pithecellobium*; PR = *Paraserianthes*; PS = *Pseudosamanea*; PT = *Painteria*; SA = *Samanea*; SE = *Serianthes*; SP = *Sphinga*; WA = *Wallaceodendron*; ZA = *Zapoteca*; ZY = *Zygia*.

A. DISTRIBUTION OF HETEROCHRONIES

All of the heterochronic changes involving the unit inflorescence and the subtending leaf are homoplasious (Fig. 9). Late-suppressed hysteranthly (char. 18) is the condition in both members of the sister group (and in some Mimoseae). The derived state arises five times, with two reversals to the plesiomorphic condition. Likewise, developmental hysteranthly (char. 19) is homoplasious, the derived state arising three times. If accelerated transformation were used, developmental hysteranthly would be definitive of a clade including *Samanea*, *Hydrochorea*, and *Hesperalbizia* (the *Samanea* alliance), with one reversal, but also arising in *Hydrochorea*, a member of the *Abarema* alliance.

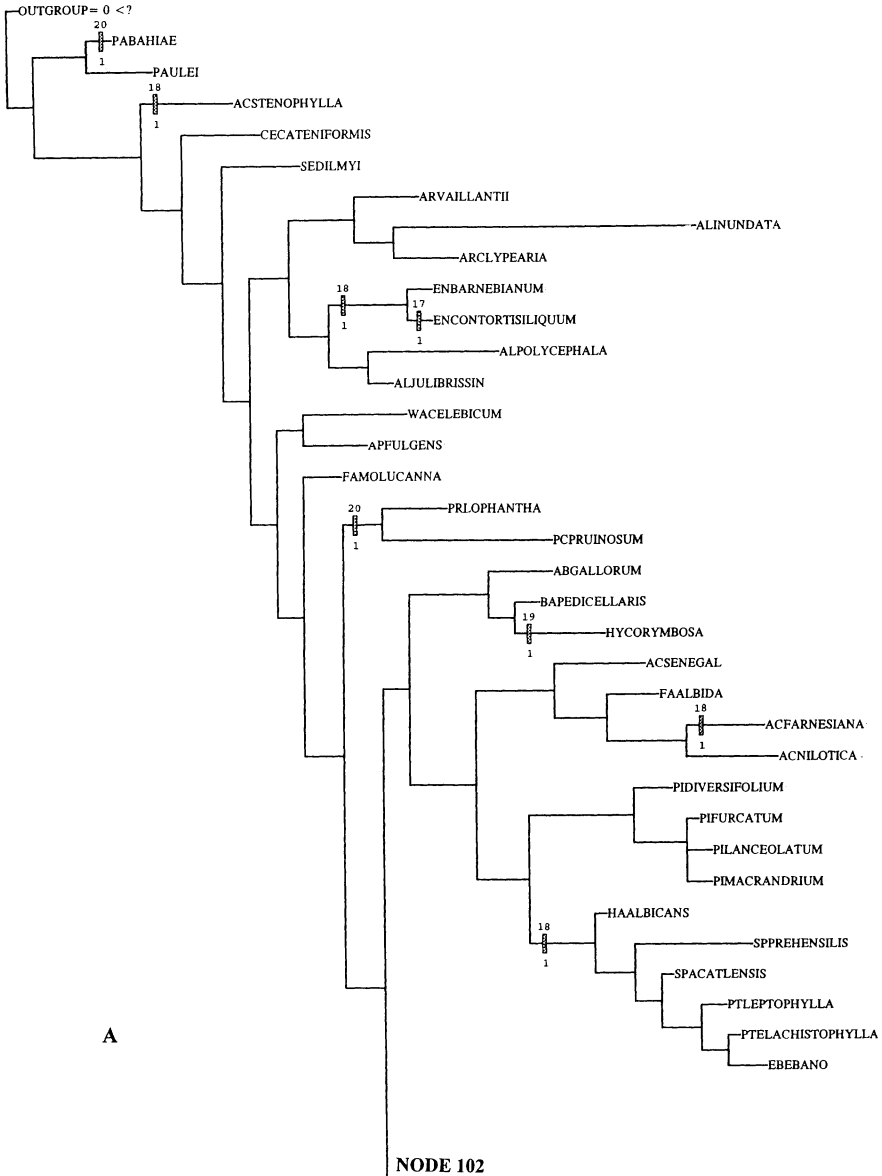
The condition of early-suppressed hysteranthly (char. 17) is also homoplasious, arising twice: it is descriptive of the *Chloroleucon* alliance but is also known in *Enterolobium contortisiliquum*. The distribution of taxa that have simple inflorescences (char. 20) is also plotted on Fig. 9. Again, simple inflorescences are those that have no sylleptic branching, no modification in duration of branches, and no shoot dimorphism: the inflorescence consists entirely of unit inflorescences (singly, paired, or fasciculate) distributed along nodes of the axis of the RGU. This character arises four times, indicating that it is probably a nonhomologous derived state due to loss or suppression of character states (i.e., organs) from different ancestral types.

Of the heterochronic changes involving the branch buds, vegetative branching that is strictly proleptic (char. 5(0)) is the condition in *Parkia*. The derived state, in which branching is sylleptic as well as proleptic (char. 5(1)) arises six times and reverses once. It is not plotted. Although sylleptically developing branches is the character state in the outgroup, the sylleptic branches there are the annual, axillary, strictly reproductive branches (char. 6(0)); a major clade includes those taxa that have other kinds of sylleptic branches (Fig. 10, char. 7(1)). The *Abarema* alliance is characterized by sylleptically developing long shoots that are at once vegetative and reproductive, as well as persistent (char. 9(1)). The *Pithecellobium* alliance is characterized by sylleptically developing short shoots that are strictly vegetative at first (char. 8(1)), though inflorescences may develop on them proleptically (char. 13) (cf. the discussion of *Ebenopsis ebano* in Grimes, 1996).

Another clade possesses short shoots (Fig. 10, char. 10(1)), which are here considered a heterochronic phenomenon in that part of the developmental pathway—specifically, elongation of internodes—has been suppressed. At this time the definition of this character is arbitrary. The short shoots do not look alike. Detailed studies of the short shoots in these taxa is required to determine how many kinds exist.

An additional condition reflecting heterochronic changes in the branch systems has to do with whether the branches are ephemeral or persistent; these differences are independent of whether the branches are vegetative and reproductive or strictly reproductive. One type of ephemeral branch—annual, axillary, strictly reproductive—has already been discussed. Another type of ephemeral branch is the proleptic, at once vegetative and reproductive, branch (char. 12). This character is a synapomorphy of the *Chloroleucon* alliance, with a reversal in *Enterolobium schomburgkii* (Fig. 11). Possession of preformed shoots, or possession of shoots that are nearly fully formed, yet undeveloped and contained in perulate buds (char. 4(1)), is also a synapomorphy of this clade.

Cauliflory and ramiflory are considered to comprise two characters. First, both types of inflorescences require that some form of meristem persist in the leaf axils (char. 14). In the case of ramiflory these meristems produce inflorescences early, sometimes contemporaneous with the leaf. In the case of cauliflory, presumably the meristems are buried in wood and become active after some longer period. In this case vegetative and reproductive growth occur on to-



tally different axes (char. 15). The persistent meristems are a synapomorphy of the *Inga* alliance (Fig. 11), with a reversal in *Inga* and *Cathormion*. The separation of vegetative and reproductive growth (char. 15), fully expressed cauliflory, is a synapomorphy of the genus *Zygia* (Fig. 11).

In Figure 12 I attempt in one diagram to polarize the character-state changes of the heterochronies. The basal condition is that in which vegetative branching is proleptic (chars. 5(0) and 7(0)), and taxa possess annual, axillary, strictly reproductive branches (char. 6(0)). From

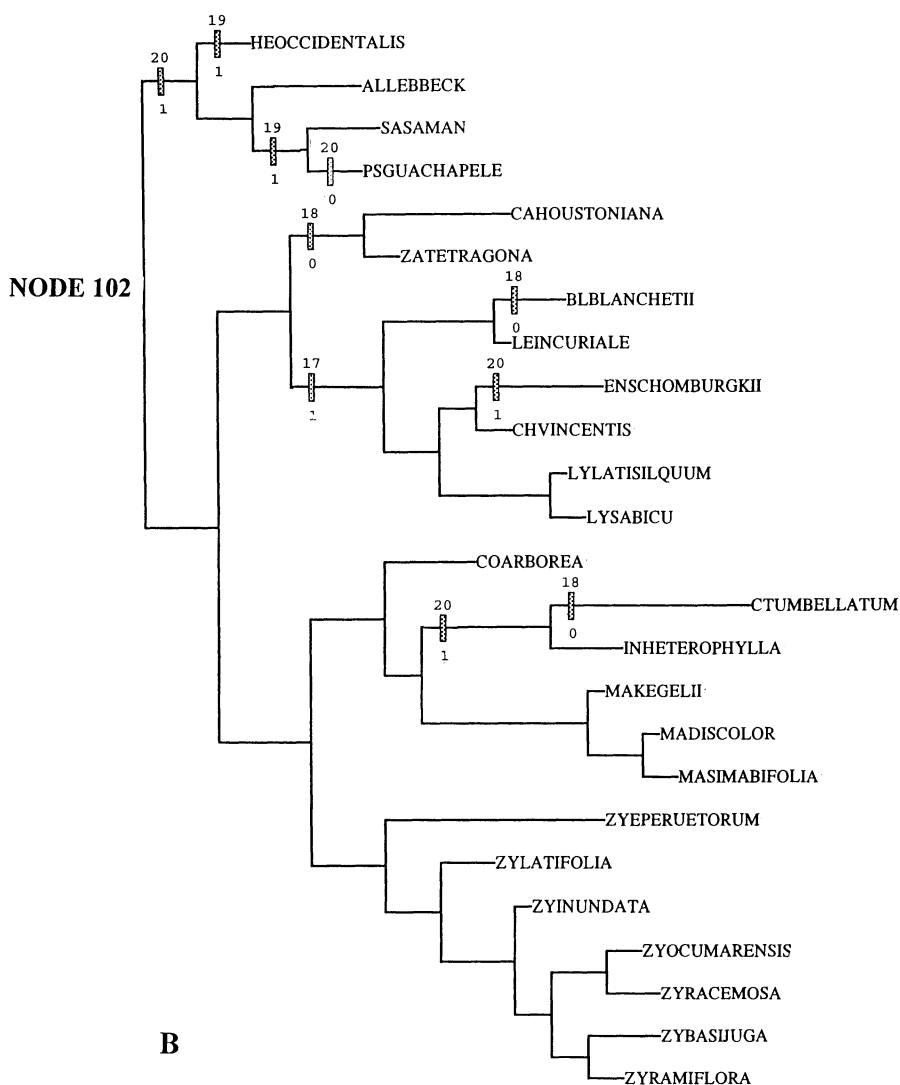


Fig. 9A and B. An arbitrarily chosen tree from the 24 equally parsimonious trees, showing the distribution of the various forms of leaf hysteranthly, and of simple inflorescences. Early-suppressed hysteranthly (char. 17), late-suppressed hysteranthly (char. 18), and developmental hysteranthly (char. 19) are all homoplasious. Character 20(1) is simple inflorescence.

this condition the four major suites or syndromes of characters have been derived, as well the "simple inflorescence." The homoplastic condition of simple inflorescences being shown by "20*" on the diagram. In the clade including the *Abarema* alliance and *Pithecellobium*, vegetative branching becomes sylleptic (char. 5(1)), and annual, axillary, strictly reproductive branches are lost or suppressed (char. 6(1)). Sylleptic vegetative branching (char. 7(1)) is of two kinds: the *Abarema* alliance has sylleptic, persistent branches that are both reproductive

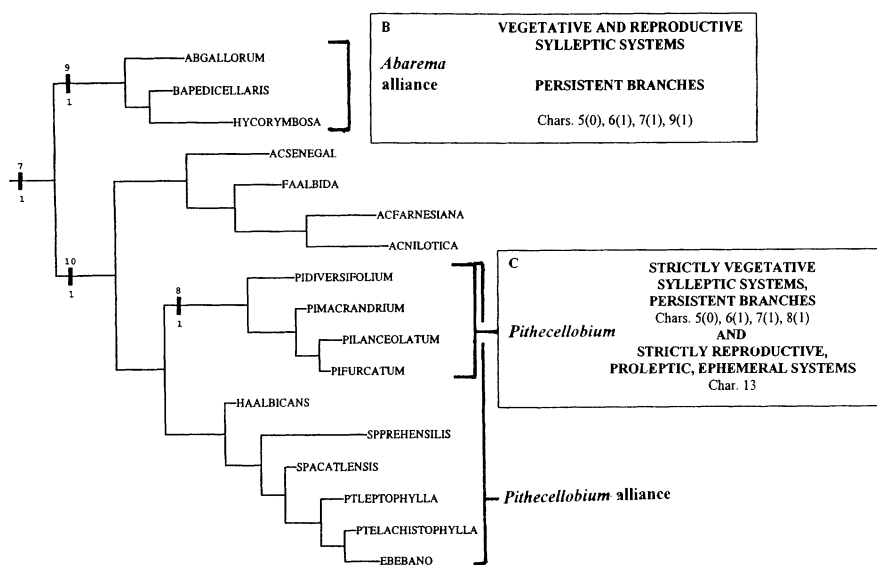


Fig. 10. A portion of the tree, showing the distribution of various heterochronies. See the text for discussion. The alliances recognized by Barneby and Grimes (1996) are indicated for comparison. The boxes showing the distribution of characters taken from Fig. 4 are appended to the side of the cladogram.

and vegetative (char. 9(1)), whereas *Pithecellobium* has sylleptic, persistent branches that are strictly vegetative (char. 8(1)); the strictly reproductive branches in *Pithecellobium* arise proleptically (char. 13(1)).

The two other major syndromes likewise arise from the primitive suite or syndrome. Again, annual, axillary, strictly reproductive branches are lost or suppressed (char. 6(1)), as are any sylleptic branches (char. 7(2)). The *Chloroleucon* alliance is characterized by proleptically developing, at once vegetative and reproductive, ephemeral branches (char. 12(1)). The *Inga* alliance is characterized by persistent, axillary, reproductive meristems (char. 14(1)), and *Zygia* also by true cauliflory; that is, separation of vegetative and reproductive branching (char. 15(1)).

B. COMPARISON WITH THE PREVIOUS ANALYSIS

In comparison with the results of my 1995 analysis, *Acacia* remains polyphyletic. *Acacia stenophylla*, representing the Australian Phyllodinae, is sister to the remainder of the Ingeae + Acacieae; the remaining exemplars of Acacieae (ACSENEGAL, ACFARNESIANA, ACNILOTICA) are nested in the Ingeae between the *Abarema* and *Pithecellobium* alliances. The monotypic *Faidherbia*, sometimes included in *Acacia* and sometimes in Ingeae, is a member of the clade including the other exemplars of Acacieae. Even though detailed monographic work on *Acacia* awaits completion, these results are credible. In terms of growth and inflorescence structure, and to some degree pollen structure, these exemplars of Acacieae (ACSENEGAL, ACFARNESIANA, ACNILOTICA) are much more similar to American Ingeae in the *Pithecellobium* alliance than they are to the phyllodinous Australian acacias, in this analysis represented only by *Acacia stenophylla*.

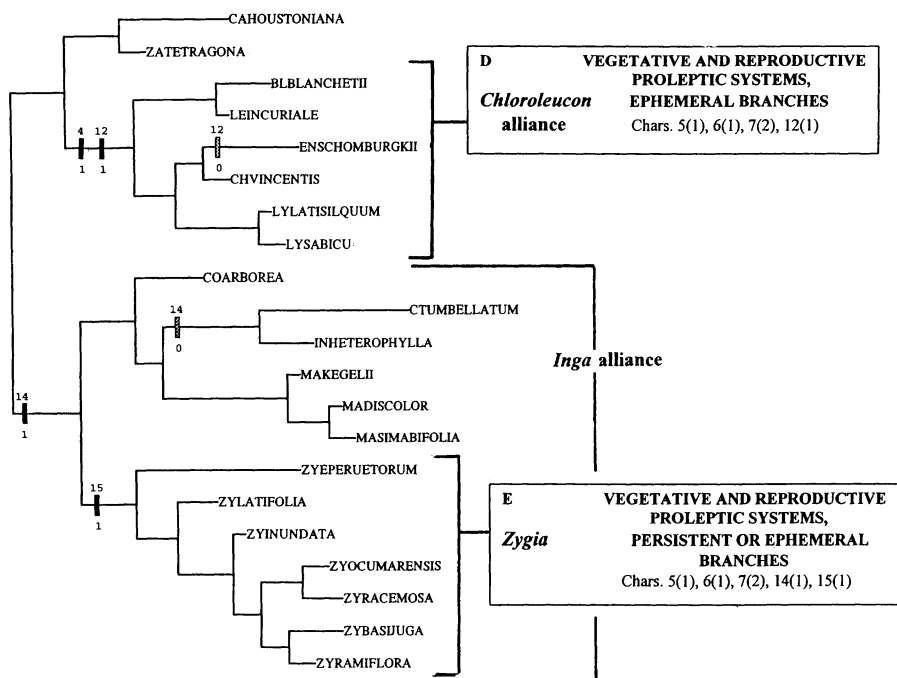


Fig. 11. A portion of the tree, showing the distribution of various heterochronies. See the text for discussion.

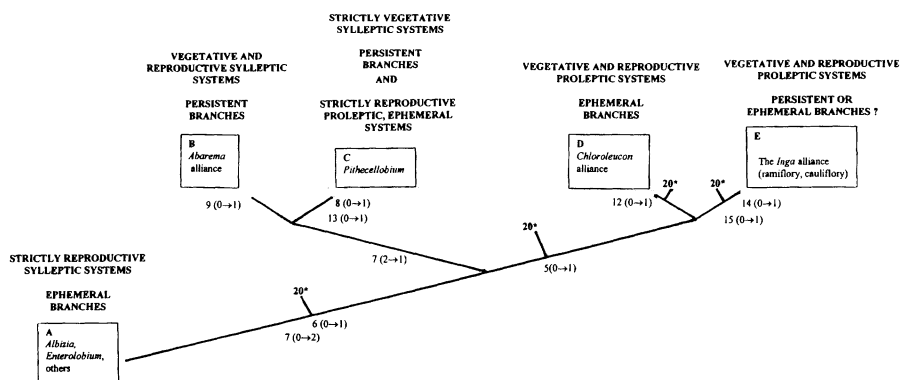


Fig. 12. Polarity of some of the character-state changes of the heterochronies discussed in the text.

Paraserianthes sensu Nielsen (1981) remains polyphyletic; the nomenclatural changes reflecting this were made by Barneby and Grimes (1986), who transferred *Paraserianthes falcata* (L.) I. Nielsen to *Falcataria moluccana* (Miq.) Barneby & Grimes.

The monophyletic "alliances" of Grimes (1995) and Barneby and Grimes (1996) remain for the most part the same. The *Inga* alliance remains a monophyletic group characterized by

persistent axillary reproductive meristems (ramiflory). This clade now includes *Cathormion umbellatum*. *Inga heterophylla*, the exemplar used here, does not have persistent axillary meristems (char. 14), though these do occur in other species of *Inga*.

The taxa included in the *Abarema* alliance (the genera *Abarema*, *Hydrochorea*, and *Balizia*) are the same, but the relationships among the three are unresolved. A species-level cladistic analysis of these three genera is presented in Barneby and Grimes (1996), with *Abarema* the most derived of the three genera.

The *Samanea* alliance still includes the genera *Hesperalbizia*, *Samanea*, and *Pseudosamanea*, but now it also includes *Albizia lebbbeck*, which is strikingly similar in appearance to *Samanea saman*.

The *Pithecellobium* alliance remains a monophyletic group, with the topology exactly the same. Likewise, *Macrosamanea* and *Cojoba*, both subjects of species-level analyses (Barneby & Grimes 1996, 1997, respectively) remain part of the *Inga* alliance. The *Chloroleucon* alliance now includes *Lysiloma*, poorly studied at the time of my 1995 analysis. Likewise, *Blanchetiodendron*, in 1995 basal to the *Chloroleucon* alliance, is now included in the clade. *Enterolobium* sect. *Robrichia* Barneby & Grimes (ENSCHOMBURGKII) is a member of the same clade. Two other exemplars of *Enterolobium* (ENBARNEBIANUM, ENCONTORTOSILIQUUM) appear at the base of the cladogram, indicating that *Enterolobium* may be polyphyletic. Although the fruits of all species of *Enterolobium* are remarkably similar, such fruits are also found outside *Enterolobium*, and, furthermore, they differ in some technical characters.

VII. Conclusions

Of the three properties listed by Grimes (1995) as being responsible for inflorescence morphology, two—the organization of components of the inflorescence and their relative positions, and the hierarchical arrangement of axes of the inflorescences and the position they assume in total tree architecture—may restated in terms of heterochronies. That is, heterochronic or allometric changes in the development of leaves, axillary branches, and associated organ systems are responsible for differences in the organization of components of the inflorescence and the position they assume in total tree architecture and for differences in the hierarchical arrangement of the axes of the inflorescences.

For the most part the heterochronies involving the leaves and axillary peduncle are homoplasious and are at best descriptive of some of the clades and alliances recognized by Grimes (1995) and Barneby and Grimes (1996).

In contrast, heterochronies involving branch duration, timing of development of the branches, and their nature (reproductive or vegetative + reproductive) provide synapomorphies of large clades of mimosoid legumes in tribe Ingeae + Acacieae. It is apparent that heterochrony has played a large role in the diversification of inflorescence morphologies in mimosoid legumes and that many of these changes are diagnostic of large groups of species and genera. No differences in inflorescence structure attributable to de novo origin of organs were found. However, many organs or organ systems appear to have been lost or suppressed. True loss—that is, deletion of genetic information—is not a heterochronic phenomenon. However, suppression of genetic information—e.g., a developmental pathway—is a heterochronic phenomenon. In conclusion, the vast majority of differences found in the inflorescence structure of the Ingoid mimosoids can be explained by heterochronic or allometric changes in the development of components. Although the kinds of heterochronic changes are not many, in different combinations they have produced an array of inflorescence structures,

structures that have not been readily amenable to description using classical, typological nomenclature.

It is apparent that heterochrony is a widespread phenomenon in the morphological diversification of members of tribes Ingeae and Acacieae. Many of the defined characters, such as those of leaf hysterothecy, are homoplasious but nonetheless may still be important factors in speciation. Other heterochronic characters, however, are synapomorphies of large clades and provide evidence that heterochrony may be an important macroevolutionary process in the Mimosoideae.

The importance of heterochronic changes in morphological diversification in mimosoid legumes has been understated, and it merits further study.

VIII. Acknowledgments

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X. Appendix 1: Taxa and Characters Used in the Phylogenetic Analysis

TAXA

The following taxa have been added to the data set since 1995:

1. An idealized outgroup was created representing tribe Mimoseae. *Parkia* is used as the sister group to the Ingeae + Acacieae, but since it is polymorphic for many of the characters used in the analysis, it was not used to root the tree. Rather, an idealized outgroup was created scored only for those characters that distinguish *Parkia* and Ingeae + Acacieae from the Mimoseae.
2. *Parkia*, the sister group to Ingeae + Acacieae, was divided into two taxa to reflect difference in inflorescence morphology. PABAHIAE (*Parkia bahiae*) has inflorescences similar to those of the *Samanea* alliance; PAULEI (*Parkia ulei*) has inflorescences similar to those of some South American species of *Albizia*.
3. CAUMBELLATUM (*Cathormion umbellatum* (Vahl) Kostermans), variously transferred to either *Albizia* or *Pithecellobium*, has been erroneously described (e.g., Kostermans, 1954) as having stipular spines. In reality, the plants possess sterile lignescent stipules, like those known in *Chloroleucon* (Barneby & Grimes, 1996).
4. ALPOLYCEPHALA (*Albizia polycephala* (Benth.) Killip) and ALBINUNDATA (*Albizia inundata* (Mart.) Barneby & Grimes) have been added as other representatives of *Albizia*, which is not a monophyletic genus. They differ inter se and from other species currently assigned to *Albizia* by characters of the inflorescence, pollen, and fruit.
5. *Archidendron clypearia* (Jack.) I. Nielsen, ARCHCLYPEARIA, has been added because it differs from *Archidendron vaillantii* in several states.
6. *Abarema gallorum* Barneby & Grimes, ABGALLORUM, replaces a generalized taxon of *Abarema* because it is one of the most primitive members of the genus (cf. Barneby & Grimes, 1996: 22).
7. *Sphinga prehensilis* (C. Wright) Barneby & Grimes, SPPREHENSILIS, replaces *Pithecellobium platylobum* (PPLATYLOBA) as the exemplar for the genus.
8. *Painteria leptophylla* (DC) Barneby & Grimes, PNLEPTOPHYLLA, replaces a generalized *Painteria*.
9. *Leucochloron incuriale* (Vell.) Barneby & Grimes, LEUCINCURIALE, is a name change for *Pithecellobium incuriale* (Vell.) Benth.
10. *Albizia occidentalis*, ALOCCID (Grimes, 1995) has been transferred to *Hesperalbizia* (Barneby & Grimes, 1996). The new name, HEOCCIDENTALE, is used here.

CHARACTERS

The characters used in the analysis reported in this article are listed below. The number of any character used in the 1995 data set is included in parentheses. Characters and character states are not discussed unless they are new or modified. They are numbered according to the conventions of Hennig86.

- 0 (1). Stamens: 0 = 5–10; 1 = reduplicated.
- 1 (2). Stamens: 0 = free at base; 1 = united into a tube.
- 2 (18). Meristems: 0 = not covered by leaf petiole; 1 = covered by leaf petiole. The meristems in Ingeae and Acacieae are covered (“protected”) in various ways (Grimes, 1996). This is one of the morphologies completely surveyed for the tribe.

3 (new). Phylotaxy: 0 = spiral; 1 = distichous. It has been noted that these states vary within the tribe (Barneby, 1998; Grimes, 1996).

Characters 6–10 either are modified from characters 4–6 in the 1995 data set or are completely new, and they pertain to the variables shown in Figure 4.

4 (19). Shoots: 0 = not preformed; 1 = preformed. Grimes (1996) pointed out that several taxa were incorrectly scored for this character in the 1995 article. The mistakes have been corrected.

5 (5). Branching: 0 = sylleptic and proleptic; 1 = proleptic only.

6 (25). Annual, axillary, strictly reproductive branch systems: 0 = present; 1 = lacking.

The following three characters require some explanation. The outgroup possesses sylleptic branches of the kind immediately preceding. Other taxa may have different types of sylleptic branches, or sylleptic branches may be lacking altogether. Character 7 reflects this, whereas characters 8 and 9 refer to different kinds of sylleptic branches.

7 (new). Sylleptic branches: 0 = strictly reproductive; 1 = vegetative; 2 = lacking. The outgroup and many members of the ingroup have these ephemeral branches.

8 (new). Sylleptic branches: 0 = not as follows; 1 = strictly vegetative.

9 (new). Sylleptic branches: 0 = not as follows; 1 = vegetative and reproductive.

10 (9). Short shoots (brachyblasts): 0 = lacking; 1 = present.

11 (new). Sylleptic branches: 0 = ephemeral; 1 = persistent; 2 = lacking.

12 (new). Vegetative and reproductive proleptic branches: 0 = all persistent; 1 = some ephemeral.

13 (new). Proleptic branches: 0 = all persistent; 1 = some branches strictly reproductive and ephemeral.

14 (24). Persistent axillary meristems: 0 = absent; 1 = present.

15 (new). Reproductive growth: 0 = with vegetative; 1 = separate from vegetative on cauliflorous knots.

16 (10). Spatial hysteresis: 0 = present; 1 = absent.

17 (12). Hysteresis: 0 = not early suppressed; 1 = early suppressed.

18 (11). Hysteresis: 0 = not late suppressed; 1 = late suppressed.

19 (13). Hysteresis: 0 = not developmental; 1 = developmental.

20. Inflorescences: 0 = elaborated; 1 = simple.

21 (new). Meristems: 0 = not covered with spines; 1 = covered with stipular spines. Some, but not all, of the ingoid taxa with stipular spines show precocious development of these spines (Grimes, unpub. data). That is, the stipules reach mature size before the associated leaf does. The cluster of precociously developed spines thus covers the growing meristems. Different from this character, the meristem may be covered by precociously developing stipules, as in *Lysiloma microphyllum* Benth (Grimes, 1996), or by the petiole of the leaves themselves, which grow over and cover the meristem, as in *Abarema*, *Albizia*, and many other mimosoid legumes. The alternate characters remain incompletely surveyed and are not included in the data set.

22 (16). Stipules: 0 = not modified into spines; 1 = modified into spines.

23 (17). Perulate buds: 0 = lacking; 1 = present.

24 (new). Leaves: 0 = bipinnate; 1 = pinnate. In the 1995 analysis, this character state, "pinnate leaves," was autapomorphic for *Inga*. *Archidenron clypearia*, included herein, also has pinnate leaves, as do all members of genus *Inga*, *Calliandra hymenaeodes* (Persoon)

Bentham, and *Cojoba rufescens* (Bentham) Britton & Rose. The latter two species are not included in the analysis.

- 25 (20). Petiolar nectaries: 0 = present; 1 = lacking.
- 26 (21). Venation: 0 = pinnate; 1 = palmate; 2 = pinnate-palmate.
- 27 (22). Paravenal mesophyll: 0 = absent; 1 = nonextended; 2 = extended. This is based on unpublished data. See Kevekedes et al. (1988) for definitions and discussion.
- 28 (23). Leaflets: 0 = opposite; 1 = alternate.
- 29 (26). Peduncles: 0 = ephemeral; 1 = modified into persistent thorns.
- 30 (27). Inflorescence: 0 = with a functionally terminal flower; 1 = without a functionally terminal flower.
- 31 (28). Flowers: 0 = monomorphic; 1 = dimorphic.
- 32 (29). Flowers: 0 = hermaphrodite; 1 = andromonoecious.
- 33 (30). Peripheral flowers: 0 = symmetrical; 1 = falcate along the longitudinal axis.
- 34 (31). Intrastaminal disc: 0 = not in all flowers; 1 = in all flowers.
- 35 (32). Bracts: 0 = unmodified; 1 = dimorphic, one kind nectariferous.
- 36 (33). Anthers: 0 = longer than broad; 1 = broader than long.
- 37 (34). Stemonozone: 0 = absent; 1 = present.
- 38 (35). Stigma: 0 = poriform; 1 = enlarged, discoid, funnellform.
- 39 (new). Polyad disposition: 0 = various; 1 = ingoid. The latter is an informal designation for use here. In *Parkia* the polyads are arranged in a linear series in the anther theca. In all Ingeae the polyads are arranged eight per theca, with four abutting each side of the sac, each individual one internally abutting a polyad facing the opposite side.
- 40 (new). Polyad shape: 0 = round; 1 = symmetrically flattened. In the outgroup the polyads form spheres of monads. In Ingeae all polyads are flattened, forming a lenslike polyad two monads thick.
- 41 (36). Pollen: 0 = lacking internal pores; 1 = with proximal internal pores.
- 42 (37). Pollen: 0 = homomorphic; 1 = thicker on the central grains; 2 = thicker and more sculptured on the central grains. In the 1995 analysis this was scored as a two-state character. Following the summary of Guinet and Grimes (1997), the character is divided into three states in this analysis.
- 43 (42). Polyad: 0 = symmetrical on both faces; 1 = exhibiting inner-outer polyad dissymmetry (Guinet & Grimes, 1997; Guinet & Hernández, 1989). In this condition, the central grains of a polyad facing the outside of the anther sac, nearest to the pollen mother cells, are more distinctly ornate and their tectum is thicker than are those of the central grains facing the inside of the pollen sac.
- 44 (38). Supplementary pores: 0 = not faced by fours; 1 = faced by fours.
- 45 (new). Apertures: 0 = not porate; 1 = porate.
- 46 (new). Apertures: 0 = not extraporate; 1 = extraporate.
- 47 (new). Apertures: 0 = colporate; 1 = not colporate.

The preceding three characters are taken from Guinet (1981). They were not used in the 1995 analysis because they were homogeneous for the taxa then included.

- 48 (39). Equatorial apertures: 0 = absent; 1 = present, colporate; 2 = present, porate.
- 49 (41). Aperture clusters: 0 = by threes and fours; 1 = by twos and threes.
- 50 (43). Areoles: 0 = absent; 1 = present.
- 51 (44). Sculpturing: 0 = not reticulate; 1 = reticulate.
- 52 (45). Tectum: 0 = imperforate; 1 = perforate.

- 53 (46). Channels: 0 = isometric; 1 = nonisometric.
 54 (47). Columellae: 0 = columellate; 1 = granular.
 55 (48). Polyad number: 0 = sixteen; 1 = eight; 2 = twenty-four or more.
 56 (50). Areolate tectum: 0 = not as follows; 1 = restricted to central grains.
 57 (new). Ovary: 0 = sessile; 1 = on a gynophore.

Most of the new characters below have been taken from Gunn (1984) and checked against herbarium specimens.

- 58 (51). Fruit: 0 = not follicular; 1 = follicular along ventral suture.
 59 (new). Fruit: 0 = dehiscent; 1 = indehiscent.
 60 (new). Pod: 0 = not follicular; 1 = follicular along dorsal suture.
 61 (52). Pod: 0 = not dehiscent along both sutures; 1 = dehiscent along both sutures.
 62 (53). Pod: 0 = not elastically dehiscent; 1 = elastically dehiscent from the apex.
 63 (54). Valves: 0 = plane; 1 = twisting after dehiscence.
 64 (new). Valves: 0 = not withering after dehiscence; 1 = withering after dehiscence.
 65 (55). Pod: 0 = not follicular; 1 = follicular, septate, and resinous inside.
 66 (56). Pod: 0 = not lomentiform; 1 = lomentiform.
 67 (57). Pod: 0 = not septate; 1 = septate, the septae not separating between the valves.
 68 (new). Valves: 0 = contiguous with replum; 1 = separating from replum.
 69 (58). Pod: 0 = not septate; 1 = septate, the septae separating from opposite septa at dehiscence.
 70 (59). Endocarp: 0 = not breaking between seeds; 1 = contiguous, but breaking between the seeds and coherent.
 71 (new). Valves: 0 = tan or brown internally; 1 = internally red or orange.
 72 (60). Valves: 0 = externally brown or tan; 1 = externally red.
 73 (new). Mesocarp: 0 = not mealy; 1 = mealy.
 74 (57). Endocarp: 0 = contiguous; 1 = forming packets around seeds.
 75 (new). Endocarp: 0 = adherent to mesocarp; 1 = becoming free from mesocarp.
 76 (61). Seeds: 0 = abscising from funicle; 1 = persistent on funicle.
 77 (new). Seeds: 0 = longitudinal; 1 = oblique; 2 = transverse.
 78 (new). Seeds: 0 = discrete; 1 = overlapping.
 79 (new). Aril: 0 = absent; 1 = present. The aril is scored as one state in this analysis, though Maumont (1993) has demonstrated two types. The distribution of the two different types is as yet incompletely known.
 80 (63). Pleurogram: 0 = present; 1 = absent.
 81 (65). Internal hourglass cells: 0 = absent; 1 = present.
 82 (66). External hourglass cells: 0 = absent; 1 = present.
 83 (67). Mucilage on seeds: 0 = lacking; 1 = present.
 84 (68). Seed coat: 0 = brown to black; 1 = translucent; 2 = translucent/bicolored.
 85 (69). Seed coat: 0 = margin nerveless; 1 = girdled with submarginal nerve.
 86 (70). Seed coat: 0 = not winged; 1 = winged.
 87 (new). Seed coat: 0 = papery or hard; 1 = grapeskinlike.
 88 (new). Seed coat: 0 = confluent with embryo; 1 = loose around embryo.
 89 (new, taken from Maumont, 1993). Resinoid tissue: 0 = lacking; 1 = present.
 90 (new). Endosperm: 0 = absent; 1 = present.
 91 (71). Septate fibers: 0 = absent; 1 = present.
 92 (72). Confluent parenchyma: 0 = absent; 1 = present; 2 = abundant paratracheal.

- 93 (73). Rays: 0 = uniseriate; 1 = uniseriate to biseriate; biseriate to pluriseriate.
94 (74). Crystal fibers: 0 = absent; 1 = in single chains; 2 = biseriate crystal chains.
95 (75). Germination: 0 = epigeal; 1 = hypogeal.

XI. Appendix 2: Data Set Used in the Cladistic Analysis

	0	5	10	15	20	25	30	35
OUTGROUP	00????	?????0	?????0	0?????	??????	??????	??????	?0?0?0
PABAHIAE	00000	00000	00000	00000	10000	00000	00100	000?1
PAULEI	00000	11200	02000	00000	00000	00000	00100	000?1
CTUMBELLATUM	11??0	11200	02000	0000?	10000	00201	0100?	000?2
ACSENEGAL	11100	11100	11?00	00000	01100	02200	10000	01102
ACFARNESIANA	11100	01100	11000	01010	01100	02100	00000	01002
ACNILOTICA	11100	11100	11000	00000	01100	01000	00000	01002
ACSTENOPHYLLA	10?00	00000	00000	0?010	00000	????0	000?0	01002
FAALBIDA	11100	01100	11000	00000	01100	02100	10000	01102
LYLATISILQUUM	11011	11200	02100	00110	00010	02000	00000	0?102
LYSABICU	11011	11200	02100	00110	00010	02200	00000	0?102
ALPOLYCEPHALA	11100	00000	00000	00000	00000	02000	01000	00102
ALINUNDATA	11100	00000	00000	00000	00000	02000	10000	00102
ENSCHOMBURGKII	11011	11200	02000	00110	10010	02000	01000	00102
SASAMAN	11100	11200	02000	01011	10000	01000	01000	00102
CECATENIFORMIS	11100	00000	00000	00000	00000	02200	00000	00102
ARVAILLANTII	11100	00000	00000	00000	00000	01100	00?0?	?0102
ARCLYPEARIA	11100	00000	00000	00000	00001	01000	0000?	00102
CAHOUSTONIANA	11010	?1?00	02?00	00000	00000	12200	00100	00112
ZATETRAGONA	11010	11200	02000	00000	00000	12200	0000?	001?2
ABGALLORUM	11100	01101	01000	00000	00000	01?00	01000	00102
BAPEDICELLARIS	11100	01101	01000	00000	00000	01000	01000	00102
HYCORYMBOSA	11100	01101	01000	01001	00000	01000	01000	00102
ENBARNEBIANUM	11100	00000	00000	01010	00000	02000	00000	00102
ENCONTORTISILQUUM	11100	00000	00000	00110	00000	02000	00000	00102
MADISCOLOR	11010	11200	02001	01010	00000	00000	00000	10102
MASIMABIFOLIA	11010	11200	02001	01010	00000	00100	00000	10102
MAKEGELII	11010	11200	02001	01010	00000	00200	00000	00102
ZYBASIJUGA	11010	11200	02001	10010	00000	01100	00010	00102
COARBOREA	11010	11200	02001	00010	00000	00200	00000	00102
ZYRAMIFLORA	11010	11200	02001	10010	00000	01100	10011	00102
ZYEPUETORUM	11010	11200	02001	10010	00000	01?00	10010	00102
ZYINUNDATA	11010	11200	02001	10010	00000	01?00	?0011	00102
ZYOCUMARENSIS	11010	11200	02001	10010	00000	01000	00001	00102
ZYRACEMOSA	11010	11200	02001	10010	00000	00?00	00010	00102
ZYLATIFOLIA	11010	11200	02001	10010	00000	?0000	?0011	00102
INHETEROPHYLLA	11?10	11200	02000	00010	10001	01?00	00000	00?02
HAALBICANS	11000	0?100	12000	00010	01100	011?0	?0000	00102
SPPREHENSILIS	11000	01100	12000	01010	01100	01200	00000	00102
SPACATLENSIS	11000	01100	12000	01010	01100	01200	00000	00102
PTELACHISTOPHYLLA	11000	01100	12000	01010	01100	02000	00000	00102
PTLEPTOPHYLLA	11000	01100	12000	01010	01100	02200	00000	00102
PSGUACHAPELE	11100	11200	02000	01011	00000	01000	01000	00102
EBEBANO	11000	0110?	12000	01010	01100	02000	00000	00102
ALJULIBRISSIN	11100	00000	00000	00000	00000	00000	01000	00102
SEDILMYI	11?00	00000	00000	00000	00000	00010	10000	00102
FAMOLUCANNA	11100	01000	00000	00000	00000	02200	00000	00102
PIDIVERSIFOLIUM	11000	01110	11010	00000	01100	01100	00000	00102
PILANCEOLATUM	11000	01110	11010	00000	01100	01100	10000	00102
PIFURCATUM	11000	01110	11010	00000	01100	01100	10000	00102
PIMACRANDRIUM	11000	01110	11010	00000	01100	01100	10000	00102
ALLEBBECK	11100	11200	02000	01010	10000	00000	01000	00102
HEOCCIDENTALIS	11100	11200	02000	01011	10000	01100	00000	00102
BLBLANCHETII	11011	11200	02100	00100	00010	02?00	01000	00102
LEINCURIALE	11011	11200	02100	00110	00010	02200	00000	00102
CHVINCENTIS	11011	11200	02100	00110	00010	02001	0?000	00102
PRLOPHANTHA	11100	01200	02000	00000	10000	02000	10000	00102
WACELEBICUM	11100	00000	00000	00000	00000	01000	00000	00102
APFULGENS	11100	00000	00000	00000	00000	01000	10000	00102
PCPRUINOSUM	11100	11200	02000	00000	10000	01010	00000	00102

40	45	50	55	60	65	70	75	80	85	90	95
??0??	?????	?????	?????	?????	?????	?????	?????	?????	?????	?????	?
00000	10101	1?10?	20000	00000	00000	00000	00?00	10?10	0000?	0????	0
00000	10101	1?10?	20000	00000	00000	00000	00?00	10?10	0000?	0????	0
11101	??1?0	10?01	01011	00000	11000	10010	00000	00??0	0000?	01??0	?
11101	10100	00??1	01100	01000	00000	000?0	00200	1?1?0	00000	0????	?
11201	??1??	10100	?1101	00000	00000	000?0	00200	10000	00000	00001	?
11200	00001	00100	?1001	00000	00000	00000	00?00	10?00	00000	0????	?
11201	1110?	10001	?10?0	0?000	00000	00000	00001	10110	00000	0????	?
11200	10100	10101	00001	00000	00000	00000	00200	10110	00000	1????	?
11211	10100	10101	01000	00000	00010	00000	00200	10100	00000	?????	?
11211	10100	10101	01000	00000	00010	00000	00200	10100	0000?	?????	?
11101	11001	10101	0?000	01000	01000	00000	00100	10100	01000	01121	0
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11001	10100	10001	21001	00000	00100	00000	00200	10100	00000	00021	0
11001	10100	10101	20001	00000	00000	00010	00200	10110	00000	00011	0
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11001	10100	10111	01000	10000	00001	0?010	00200	00100	00000	00201	1
11001	111?0	10101	0101?	10010	00000	0?010	01200	00100	000?0	00201	1
10001	10100	00100	11000	01100	00000	00000	00?00	10100	00000	0022?	?
11101	10100	10101	01000	01100	00000	00000	00200	10100	00000	00???	?
11211	10100	10101	01000	01010	00000	01000	01200	?0112	00001	00011	0
11211	10100	10101	01000	00000	00000	00000	00200	10112	00001	00011	0
11211	10100	10101	01000	00000	01000	10001	00200	1?100	00001	00011	0
11001	10100	10001	??001	00?00	00100	00010	00200	10100	00?00	00021	0
11001	10100	10001	??001	00?00	00100	00010	00200	10100	00?00	00021	0
11001	10100	10101	20000	01000	00000	00000	00210	00100	10010	01101	?
11001	10100	10101	20000	01000	00000	00000	00210	00100	10010	01101	?
11001	10100	10101	20000	01000	00000	00000	00210	00100	10010	01101	?
11201	10100	10001	20010	00000	00000	00010	00200	00100	10010	0????	?
11201	10100	10101	01000	01001	00000	00100	01000	00100	00000	00111	?
11201	10100	10001	01010	00000	00000	00010	00200	00100	10010	0????	?
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11201	10100	10001	0?010	01000	00000	00010	00200	00100	10010	0????	?
11201	10100	10001	01010	00000	10001	00010	00200	00100	10010	0????	?
11201	10100	10001	01010	00000	10001	00010	00200	00100	10010	00111	0
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11001	10100	10101	01000	01000	00000	00000	00200	111?0	00000	1101?	?
11011	010?1	01001	01000	01000	00000	00000	00200	111?0	00000	110??	?
11101	10100	10101	01000	01000	00000	00000	00200	111?0	00000	110??	?
11101	10100	10101	01000	01000	00000	00000	00200	101?0	00000	11???	?
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11001	10100	10101	21010	00000	00000	00000	00200	10110	00000	00011	?
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11001	10100	10?01	0?000	01000	00000	00000	00200	10100	00000	00021	0
11001	10100	101?1	01001	00000	00101	00000	00200	10110	000?0	00?02	0
11001	10100	10101	?1000	01000	00000	00000	00?00	10110	00000	00??2	0
11001	10100	10101	01000	01010	0000?	01100	01001	001?0	00000	01011	1
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11001	10100	10101	01010	00010	00000	?1000	00001	001?0	00000	01???	?
11001	10100	10101	01010	00010	00000	?0000	00001	001?0	00000	01???	?
11?01	10100	10101	0?010	00000	00000	00000	00200	10100	00000	10021	0
11001	10100	10101	01000	01000	00000	00000	00200	10110	00000	00???	?
11001	10100	10101	0?000	01000	00000	00000	00200	00111	11100	00???	?
11001	10100	10101	??0?0	0?000	00000	00000	00200	001?1	11100	00???	?
11001	10100	10001	??0?0	0?0?0	0000?	00000	00200	10100	00000	000??	?
11001	10100	10001	01000	01000	00000	00000	00200	10110	00000	10?02	0
11001	10100	10111	01001	01000	00000	10011	10200	11110	000?0	00012	?
11001	10100	10111	?0000	01000	00000	01000	00200	101?0	010?0	00002	0
11001	10100	10111	01111	11111	00000	01000	00200	10110	000?0	00000	?