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Steps Toward the Natural System of the Dicotyledons

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STEPS TOWARD THE NATURAL SYSTEM OF THE DICOTYLEDONS: VEGETATIVE ANATOMY[1]

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ABSTRACT

The value of vegetative anatomy in phylogenetic analysis is documented. Examples of the use of vegetative anatomy at different taxonomic levels show the continuing role of the anatomical method in building a more natural system of classification of the dicotyledons. The importance of correlating wood and leaf anatomical features with ecological and floristic preferences of taxa is emphasized. Caution is required in basing phylogenetic interpretations upon similarities and differences in xylem structure. The transition from scalariform to simple perforation plates is the only aspect of vessel element evolution that is not potentially reversible and all phylogenetic analyses must reflect this important principle. Some groups outside the Magnoliidae (Annoniflorae) possess very primitive xylems and can be used as evidence to support a pattern of multiple early radiations of the dicotyledons, as well as the increased awareness of a lack of clear subclass definition. The application of anatomical characters in cladistic analysis is reviewed, and the need to utilize strictly homologous features, to provide accurate scoring of character states, and to give proper interpretations to character state transformations is emphasized.

Key words: Cladistics, classification, dicotyledons, wood anatomy, xylem.

INTRODUCTION

It has been just over ten years since I reviewed the major characters of vegetative anatomy that provide a basis for the study of angiosperm phylogeny at the higher taxonomic levels, and how these characters relate to contemporary systems of classification (Dickison 1975). At that time the guiding principles of systematic anatomical study were discussed and numerous examples were cited of the modern application and interpretation of anatomical evidence in forming a more natural system of the angiosperms. This paper was followed by the excellent reviews of Stern (1978) and Puri (1978), in which the value of the anatomical method in phylogenetic analysis was further documented. More recently, the initial two volumes of the second edition of the "Anatomy of the Dicotyledons" (Metcalfe and Chalk 1979, 1983) have also added a wealth of valuable new synthesis. Critical examination of vegetative anatomy of dicotyledons, including the secondary xylem, leaf anatomy, young stem structure, and nodal anatomy continues to reveal previously undescribed structural conditions and provides an extra measure of confidence for the independent resolution of systematic problems, particularly by helping place systematically difficult taxa, evaluating the taxonomic homogeneity and naturalness of taxonomic units, such as families and orders, and strengthening alliances not otherwise firmly established. It is less likely that vegetative anatomy will now result in fundamental changes in the current major synthesis of dicot classification.

This contribution calls attention to a few important observations, conclusions, and interpretational advances, as well as providing selective examples at different taxonomic levels of the continuing role of vegetative anatomy in building a more

natural system of the dicotyledons. No attempt is made to present an extensive survey of the recent anatomical literature. With the ever increasing use of phylogenetic (cladistic) systematic approaches, I will also devote space to a brief discussion of guidelines, as well as potential pitfalls, in the application of anatomical data in cladistics.

TRENDS OF XYLEM EVOLUTION

Undoubtedly more has been written about the evolutionary trends in the secondary xylem and the value of wood structure in understanding the phylogeny and classification of dicotyledons than any other tissue or part of the vegetative plant body. It is widely appreciated that the frequently presented major trends of xylem evolution have been a useful guide to understanding dicotyledonous evolution (Metcalfe and Chalk 1950; Carlquist 1961; Dickison 1975; Stern 1978). The validity of these trends has been further strengthened by samplings of fossil woods, from geologically older to younger floras. Those from the Tertiary of India, for example, show a gradual increase in the percentage of specimens with advanced features (Bande and Prakash 1984).

Recent years have witnessed a renewed awareness among plant anatomists of the importance of correlating wood (and leaf) anatomical characters with plant habit and the ecological and floristic preferences of taxa (Baas 1973; Carlquist 1975, 1988; van der Graaff and Baas 1974; Rury and Dickison 1984). Advances in the field of ecological wood anatomy, or ecophyletic wood anatomy as it has been termed by my former student, P. M. Rury, have resulted from critical comparison of correlations between climatic variables and various wood anatomical characters of all woody members of a taxon. This ecological and functional approach to the study of plant structure is leading to a new synthesis, and has contributed in a significant way to a more complete understanding of the diverse, structurally adaptive trends of specialization within the xylem. Baas and Miller (1985), have stressed, however, that the functional and evolutionary explanation of this variation awaits experimental clarification and remains a matter of considerable debate (see Baas 1976). Rury and Dickison (1984) noted many relationships between xylem and leaf anatomy, and were of the opinion that considerations of the possible ecophysiological significance and adaptive value of diverse xylem structures among woody taxa are unwise in the absence of leaf structural comparisons of the species under study. Excellent, extensive reviews on the general subject of ecological wood anatomy have been provided by Baas (1976, 1982, 1986a) and Carlquist (1975, 1980, 1985a, 1988). One result of these studies has been a more refined use of wood anatomical evidence for systematic purposes.

Although virtually all aspects of xylem structure are now known to be influenced in either a qualitative or quantitative manner by ecological conditions, I will restrict my comments to the vessel element. The well-accepted trend among conducting elements from primitive tracheids to vessel elements has been extensively documented and described. This transition has been claimed to be among the most reliable tools known in the study of phylogeny because it has long been believed to be largely unidirectional and irreversible (Bailey 1957).

Among the important fundamental conclusions that have resulted from numerous recent investigations and syntheses of classical wood anatomical studies is the hypothesis that comparatively long, evolutionarily primitive, yet wide,

vessel elements are of adaptive value in mesic habitats (Carlquist 1975). A number of trends of specialization related to vessel element morphology and abundance can be recognized that are directly related to changes in plant habitat and habit, as well as latitude and altitude of provenance (Fig. 1). Bailey (1957), among others, had previously pointed out that in certain specialized cases, such as lianas, vessel members may become quite transformed as a result of the climbing habit, and do not, therefore, indicate true phylogenetic advancement. Ayensu and Stern (1964) also encountered similar modification and stressed that habit-related anatomical modification may be superimposed upon phylogenetic advancement, and that the separation of these facets is often difficult. These now well-established evolutionarily divergent trends are clearly the result of complex interrelationships between the ecology and aspects of plant morphology. In many diverse groups of dicotyledons, however, features such as vessel element length, tangential diameter, wall thickness, and frequency are known to be under the strong control of the single ecological factor of water availability. The recent recognition of trends toward the increased differentiation of, and specialization in, fibers and vessel elements are especially evident among related species occupying different habitats, where wood anatomical specializations often increase progressively along a decreasing moisture gradient. Thus, wood anatomy is readily influenced by the environment, and woods are commonly interpreted as showing various degrees of structural mesomorphy or xeromorphy.

It has become clearer, accordingly, that although the major classical phylogenetic trends in vessel element evolution remain largely valid for dicotyledons as-a-whole, many of the individual character transformations, such as long to short and comparatively narrow to wide elements, are now known to be potentially reversible to a considerable extent within certain taxonomic groups (Baas 1973, 1986a; Carlquist 1980). In fact, the transition from scalariform perforation plates with many bars to scalariform few barred to ultimately transverse simple perforations is, as far as is known, the only aspect in vessel element advancement for which there is no documented evidence of reversibility. Although Baas (1982) finds the arguments in favor of the irreversibility of perforation plates unconvincing, to date an example of a reversion from simple to scalariform has never been described and doubtless has a low probability of occurring.

It must once again be reemphasized, therefore, that caution be used in basing phylogenetic interpretations regarding relationships and classification upon similarities and differences in xylem structure, particularly those founded upon statistical differences among wood conducting cell size and frequency. Furthermore, unlike most other character state transformations the irreversibility of perforation plate type must be given extra emphasis in cladistic analyses of woody families. It is never possible to derive a taxon with scalariform perforation plates from one with simple plates since no reversals are allowable in this character. All cladograms must reflect this basic principle.

RECENT APPLICATIONS OF WOOD ANATOMY TO THE NATURAL SYSTEM OF DICOTYLEDONS

Xylem anatomy, for the most part, has been found to correlate generally with other lines of evidence in supporting the major phylogenetic conclusions of contemporary phylogenists such as Cronquist, Dahlgren, Takhtajan, and Thorne,

whereby Magnolialian plants are accorded a basal position in the classification system (Dickison 1975; Stern 1978). However, the large Cronquist and Takhtajan subclasses of dicotyledons are anatomically typically very diverse (Dickison loc. cit.). I have pointed out previously that even though the subclass Magnoliidae contains several wood anatomically very primitive families, many magnolialian taxa are structurally moderately advanced to advanced, a fact recently reiterated by Carlquist (1982). Since the Hamamelidae, Dilleniidae, and Rosidae include some comparatively very unspecialized members, according to the well-established tenets of secondary xylem evolution they could only have had a derivation from ancestors resembling the least advanced representatives of the magnolialian complex.

Gottwald (1977) reemphasized the very unspecialized structure of the woods in some primitive groups outside the Magnoliales. In his opinion there is no compelling evidence to support the belief that all dicotyledons diverged from a single basal magnolialian stock, and proposed an early separation of the dicotyledons into at least two major phyletic groups, both of which contain structurally very primitive extant members. A somewhat similar concept has also been presented by Carlquist (1982), who pointed to the quite primitive wood structure in the hamamelid-rosoid complex (incl. Pittosporales, woody Saxifragales) and suggested that the magnolialian (anonalean, lauralean) radiation was perhaps not the only early radiation of primitive angiosperms. Within the Dilleniidae, exceedingly primitive woods, along with other indices of low advancement, are found in such families as Dilleniaceae and Theaceae, further reinforcing the idea of multiple early lines of radiation among primitive dicotyledons, and that the Magnoliidae should not be envisioned as a unified basal group structurally more primitive than all derivatives.

Some modern systems of classification have emphasized a strong connection between woody rosoids, such as Cunoniaceae, Brunelliaceae, etc., and the Fagaceae and Hamamelidaceae (Dahlgren 1977). Such a relationship is indicated by general aspects of morphology and anatomy as well as floral morphology (Dickison 1989), and perhaps leaf venation and tooth morphology (Hickey and Wolfe 1975). Doyle and Donoghue (1987) have emphasized the occurrence within the Hamamelidae of both triporate and tricolpate pollen groups. This distinction is perhaps indicative of the fact that the Hamamelidae are probably polyphyletic, with the triporate Amentiferae actually being rosids (Doyle and Donoghue loc. cit.). Wood anatomy provides no direct evidence in support of, or against, such merging of subclass lines, other than the presence of very primitive woods among members of both groups. It is of interest to note, however, that the relatively uncommon condition of split-lateral nodal leaf traces occurs in both Cunoniaceae and the hamamelidalean genus *Myrothamnus,* although it is unclear whether this feature is phylogenetically significant.

The primitive Cunoniaceae are central to the idea of more closely linking or uniting the rosids and Hamamelidae, and although it falls outside the primary focus of this paper, a consideration of whether the apetalous or petaliferous condition is primitive in the Cunoniaceae is paramount. Petals are uniformly present in some genera, uniformly absent in other genera, and in certain instances, present or absent in different species of the same genus (e.g., *Ceratopetalum*). Most contemporary system makers, such as Thorne (1976) and Cronquist (1981), have
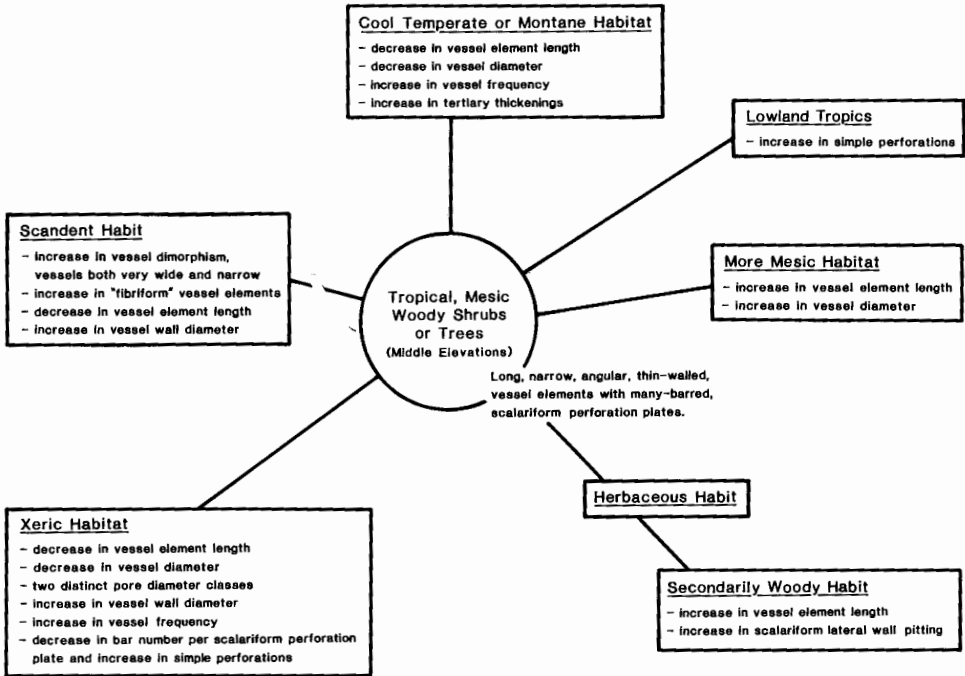
Fig. 1.   Major ecophyletic trends of vessel element specialization.

assumed that the ancestral cunoniaceous plant bore flowers with petals. Ehrendorfer (1977) and Ehrendorfer, Morawetz, and Dawe (1984), however, have argued in favor of the position that petals are a derived feature. Cuatrecasas (1970) was also of the opinion that apetally is ancestral in *Brunellia*. Not only are petals absent in the two primitively apocarpous cunoniaceous genera *Acsmithia* and *Spiraeanthemum*, but both Brunelliaceae and Davidsoniaceae are also apetalous. The xylem of the above two genera has remained at a very low level of advancement, representing the primitive condition in the Cunoniaceae. Ehrendorfer et al. (1984) suggested that petals arose from stamens in petaliferous Cunoniaceae and that this is supported by petal position, form, and the fact that both petals and stamens are one-trace structures. In my opinion the available evidence favors the interpretation that petals probably represent a primitive character state in the Cunoniaceae. A small, primitively petaliferous, apocarpic flower with a stable, intermediate number of parts can be envisioned as an ancestral condition for many Rosidae and Hamamelidae (see Dickison 1989).

Within the Rosales, Thorne (1976) recognized three closely allied suborders, the Rosineae, Saxifragineae, and Cunoniineae. The Cunoniineae, comprising the families Cunoniaceae, Davidsoniaceae, Brunelliaceae, Eucryphiaceae, Staphyleaceae, and Corynocarpaceae, have been the focus of my research for several years. It has become widely accepted on a mostly phenetic basis that the Cunoniaceae, Eucryphiaceae, Davidsoniaceae, and Brunelliaceae form a natural assemblage, although the distinctness of the families is still uncertain and some merging of groups may ultimately prove the best treatment. Although the rather variable anatomy generally supports this association, it must be emphasized that the shared

wood features, as in many other woody Saxifragales, are mostly primitive character states, or symplesiomorphies. Xylem anatomy of the more primitive genera of the Cunoniaceae reinforces the basal position of the family within the rosalean complex, despite the fact that the Cunoniaceae are unusually diverse both morphologically and anatomically, representing quite different levels of advancement (Dickison 1980a).

The small, monogeneric, Southwest Pacific family Corynocarpaceae is a notable exception to the primitive xylem syndrome of this grouping, possessing a very specialized wood structure with moderately short vessel elements having exclusively simple perforation plates that are distributed as solitary elements or in multiples and irregular clusters. Intervascular pitting is mainly alternate. Imperforate tracheary elements are essentially libriform fibers of very short length with a tendency toward storied arrangement. Axial parenchyma is storied and occurs predominantly in broad bands between five and ten cells wide with also some vasicentric distribution (Patel 1975). The most natural placement of the Corynocarpaceae in the general system still awaits determination.

Views on the affinities of the Staphyleaceae are in the process of change, with most contemporary phylogenists convinced that the family has more in common with the Saxifragales-Cunoniales rather than the more traditional alignment with Sapindales. Floral morphology and vascularization strongly supports the close relationship of this family with the woody saxifragalean complex (Dickison 1986). Pollen morphology (Dickison 1987a), the primitive wood anatomy (Carlquist and Hoekman 1985), as well as leaf and nodal anatomy are totally consistent with this view. Foliar features that are widespread in both groups include a uniseriate palisade mesophyll, druse crystals, simple, unicellular and multicellular trichomes, midrib with a single arc-shaped bundle and subdermal collenchyma, and hydathodal marginal teeth vascularized by a major central vein accompanied by a pair of connivent lateral veins. In addition, domatia of similar structure occur in both groups. The generalized trilacunar, three-trace node as seen in some Staphyleaceae predominates in saxifragalean-cunonialean plants, although more complex patterns commonly occur (Dickison 1987b).

Modern wood anatomical researches are no longer restricted to only the truly arborescent, or economically valuable, members of a group, but tend to be comprehensive in nature including all gradations of shrubby taxa as well as lianas and trees. As a result, a more refined and wider knowledge of wood characters and their distributional patterns within dicotyledons as-a-whole is accumulating, and how these patterns reflect natural relationships. Features once thought to be largely sporadically occurring divergent trends of specialization are, in some cases, now being used to circumscribe major groups. An excellent example from contemporary anatomical research is the recognition that the constant combined occurrence of vestured pits and included phloem, both rather uncommon derived features, can now be used to characterize the core families of woody Myrtales, comprising Combretaceae, Lythraceae, Melastomataceae (including Crypteroniaceae), Myrtaceae, Oliniaceae, Onagraceae, Penaeaceae, Punicaceae, Psiloxylaceae, and Sonneratiaceae (van Vliet and Baas 1984). Van Vliet and Baas summarized their broadly based survey of the Myrtales, by noting that the shared possession of these two characters is strong evidence in favor of treating the Thymelaeaceae in the Myrtales, and not near Euphorbiales or Malvales in the

Dilleniidae as advocated by Takhtajan (1980), Dahlgren (1980, 1981), and Thorne (1981, 1983). The lack of internal phloem and vestured pits, coupled with other vegetative and reproductive features, are equally forceful reasons to remove families such as the Lecythidaceae and Rhizophoraceae from the core Myrtales as has been done by Thorne (1976) and Cronquist (1968).

Careful investigation of the structural variation among vestured pits at the SEM level enabled van Vliet (1978, 1979) to recognize two major types of vesturing that can be used to distinguish subfamilies of the Combretaceae. Carlquist (1985b) reported the presence of rayless wood in *Viviania,* and remarked that this feature, while infrequent in dicotyledons generally, is present in all of the geranioid groups and can be used to strengthen the affinities of these taxa.

COMMENTS ON THE APPLICATION OF ANATOMICAL
CHARACTERS TO CLADISTIC ANALYSIS

Recent years have seen the widespread use of cladistic methods in phylogenetic analysis. As discussed by Bremer and Wanntorp (1978), Wiley (1981), and others, this approach uses nested patterns of shared derived character states and the principle of parsimony to provide a logical and repeatable method for constructing hypotheses and analyzing phylogenetic relationships among taxa. It appears desirable to briefly discuss this methodology in relation to anatomical data in view of the growing interest and debate that these procedures and philosophies have aroused.

In addition to the recognition of strictly monophyletic taxa, an essential prerequisite for the reconstruction of phylogenetic relationships is critical character analysis. Thoughtful analysis of characters is perhaps the most useful aspect of the cladistic procedure. Character analysis encompasses the accurate interpretation of character homology, correct assignment of character states to taxa, and valid hypotheses of character state polarity and transformation in the case of multiple state characters. A basic assumption in character analysis is that the characters being compared are homologous, i.e., share a common ancestry or origin. Even though the need to use strictly homologous anatomical characters was emphasized by Young and Richardson (1982), in an earlier cladistic study of primitive angiosperms Young (1981) failed in his attempt to demonstrate convincingly that the absence of vessels in extant woody dicotyledons is in all instances a derived feature because, in part, of questionable hypotheses of homology among the characters used.

The assessment of homology among anatomical features often requires careful study. Superficially similar mature stomatal types can arise by different developmental pathways and thus may not be homologous (Rasmussen 1981). The importance of examining stomate ontogeny in determining homologies has been strongly emphasized by Baranova (1987) and clearly outlined by Abu-Asab and Cantino (1987) in their fine study of the phylogenetic implications of leaf anatomy in the subtribe Melittidinae of the Labiatae. The recognition of new stomatotypes based on adult structure, such as the recently described laterocytic condition (Hartog and Baas 1978; Baranova 1983), in groups that had previously been characterized by other stomatal types, can readily lead to the dubious assumption that all stomates belonging to such newly recognized categories are homologous.

It is important to make the distinction, furthermore, between general (diag-nostic) characters that enable one taxon to be separated and distinguished from another, or that may imply a phenetic relationship among taxa, and those char-acters that can be used phylogenetically. For example, in a study of the Staphy-leaceae I have found that mature stomatal pattern can be used to distinguish the two subfamilies recognized by Pax (1893). The subfamily Staphyleoideae, con-taining *Euscaphis, Staphylea,* and *Turpinia,* has anisocytic mature stomata (sensu Metcalfe and Chalk 1950), whereas the subfamily Tapiscioideae, consisting of *Huertea* and *Tapiscia,* is distinguished by a paracytic stomatotype. Although systematically useful, there is no implication that one condition represents a lower evolutionary level than the other.

Scalariform intervessel pitting is another character state that can have various origins, and it would clearly be a mistake to regard all scalariform pits as com-parable. In some species scalariform pitting clearly represents an ancestral con-dition. Carlquist (1962), however, has shown that in a few plants, particularly secondarily woody forms, scalariform pitting results from the extension of primary xylem features into the secondary xylem (paedomorphosis or juvenilism). In a few members of the Melastomataceae, van Vliet (1981) described a situation in which scalariform pitting may very well have evolved from an alternate pitting pattern. In yet other taxa, such as the arborescent cunoniaceous genus *Cerato-petalum,* the origin and interpretation of the distinctive narrow, scalariform in-tervessel pits is unclear (Dickison 1980*a*). Another example is provided by ves-tured pits that can define an entire order, like Myrtales, as well as unrelated families such as Leguminosae and Rubiaceae. Miller (1977) and Baas and Werker (1981) even observed that vestured pits can be variable at the species level in Boragi-naceae and Cistaceae.

Anatomical characters often exist in multistate conditions within the taxonomic unit under study, and thus it is not only necessary to identify the primitive or plesiomorphic state, but to accurately code the variable character in a manner that reflects the most probable evolutionary pathways, or morphocline, for the derived conditions. The establishment of morphoclines that are an accurate rep-resentation of evolutionary specialization is sometimes not only difficult but im-possible. If a terminal taxon has variable states for the given character, the gen-erally safe procedure is to score the taxon as having the primitive state of the variable character, even if only a single species of the taxon still retains the primitive condition. For example, the nodal structure of the Cunoniaceae is un-usually diverse (Dickison 1980*b*), although the generalized trilacunar, three-trace node predominates and is considered the basic pattern in the family. It is hy-pothesized that the multilacunar condition evolved by amplification in the number of independent lateral traces; whereas the unilacunar node resulted from reduction. The evolutionary transition from opposite to whorled leaves has also been ac-companied by the formation of more specialized split-lateral nodes, that un-doubtedly have arisen more than once in the family. The New Caledonian genus *Pancheria* is particularly variable in nodal structure, but in a cladistic study should be scored as having the plesiomorphic state since trilacunar, three-trace nodes with independent lateral traces occur in at least one species. To score the genus otherwise would imply that the ancestor of *Pancheria* was also variable in nodal anatomy, which is unlikely.

Clearly, the accurate scoring of character states is dependent upon careful and standardized methods of data accumulation and a complete knowledge of the total range of structural variation as derived from comprehensive study of all members of a taxon. Wheeler (1986), for example, has pointed out inconsistencies among workers in the methods of counting numbers of vessels per unit area and percentages of solitary vessels in preparing wood descriptions. Often the primitive, or derived, state of an anatomical character is restricted to uncommon or geo-graphically isolated members of a taxon and therefore, phylogenies based on few species are suspect. It is also important to remember that coding can be directly influenced by the current status of character state definition. The recent debate relating to the terminology of wood imperforate elements is a good case in point (Carlquist 1986a; Baas 1986b). As is well known, woods of dicotyledons show the evolutionary trend from tracheids to fiber-tracheids with bordered pits to advanced libriform fibers with simple pits. However, since this is an evolutionary trend, all stages in the reduction in pit size and number and eventual elimination of the tracheid pit border are observable in extant woods. The distinction between the two cell types is therefore often unclear. The question then becomes, exactly when in practical terms should an element be referred to as a libriform fiber as opposed to a fiber-tracheid. Without outlining various proposals, it is obvious that in a cladistic analysis it would be significant whether a taxon was coded as possessing one cell type or the other. Similar terminology questions exist with references to vestures and warts (Ohtani, Meylan, and Butterfield 1984) and wood rays.

I emphasized in my 1975 paper that comparative vegetative anatomy will continue to play a central role in formulating phylogenetic hypotheses and in the construction of a more natural system of dicotyledons. Completions of more broadly based studies, clearer understandings of character state variation, and a renewed appreciation of the necessity of correlating anatomical diversity with the ecological and floristic preferences of taxa have led to a more refined approach toward utilizing anatomical evidence in solving systematic problems. Baas (1982) was absolutely correct in pointing out that temptations to use small differences in wood structure and elsewhere in attempts to produce cladograms may increase as efforts are made to reconstruct phylogenies. I. W. Bailey warned us nearly forty years ago, however, that such misuse of anatomical data will certainly lead to incorrect or dubious conclusions.

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FOOTNOTE

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