A VIEW OF THE CURRENT STATUS OF COMPARATIVE WOOD ANATOMY

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Abstract. The primary objective of this contribution is to present a view of how and to what extent comparative systematic wood anatomy has changed over the past fifty years and what research priorities should be for the future. Wood anatomy has resolved itself into a series of subdisciplines, each of which deals with particular questions. Thus, wood anatomical study has passed successively from a consideration of wood data based upon well-defined and largely unchallenged principles to a more flexible view of wood evolution based on structure-function relationships at the cellular level and the establishment of correlations between anatomy and ecology. The questions and phenomena to be investigated are so complex and variable that, in many cases, they can be analyzed only through the active cooperation of a group of experts.

Key words: Aristolochiaceae, cladistics, systematics, wood anatomy.

Resumen. El objetivo de esta contribución es presentar un punto de vista de cómo y en qué medida los estudios en anatomía sistemática de la madera han cambiado en los últimos cincuenta años y qué prioridades de investigación deberán de seguirse en el futuro. La anatomía de la madera se ha diversificado en una serie de subdisciplinas, cada una con preguntas particulares. Por lo tanto, el estudio de la anatomía de la madera pasó de ser una fuente de datos bien definida y con principios incuestionables a una disciplina más flexible sobre la interpretación de la evolución de los caracteres de la madera basada en la relación estructura-función a nivel celular y en el establecimiento de correlaciones entre anatomía y ecología. Las preguntas y fenómenos por investigar son tan complejos y variables que en muchos casos, éstos podrán ser analizados sólo a través de la cooperación activa de grupos de expertos.

Palabras clave: Aristolochiaceae, cladística, sistemática, anatomía de la madera.

This contribution concerns itself with the long tradition of comparative wood anatomy and presents a personal view on the present status of the discipline. Since its inception comparative wood anatomical research has undergone different stages of development. Following the establishment of the basic sequences of wood characters evolution in the 1930's and 1940's anatomists concerned themselves primarily with describing and comparing the more readily available and most economically important tree species. My own career in plant anatomy began in the early to mid-1960's. At the time the major trends in wood evolution established by Bailey, Frost, Kribs and others were generally agreed upon. Through the analysis of large volumes of descriptive data, the discipline

succeeded in establishing many valid correlations between character states and in defining primitive and advanced conditions. A number of important trends of structural specialization were outlined. Unfortunately, many studies appeared in which the taxa under investigation were aligned evolutionarily or assigned to a particular evolutionary level or position on the basis of the possession of a minor wood anatomical features or combination of variable features whose functional and ecological significance were largely unknown. Too often, wood anatomical data were interpreted by well-meaning but anatomically naive individuals who intentionally overvalued or undervalued wood features and, as a result, presented inaccurate or weakly founded hypotheses of relationships. Wood

anatomy has subsequently witnessed a significant change in a number of fundamental concepts and in some instances methodologies. The discipline has passed successively from a period of rigidly interpreting structural variation upon supposedly well-defined and largely unchallenged principles, to the present time of more flexible interpretations of wood structure following correlations between development, ecology, and plant habit, as well as considerations of structure-function relationships at the cellular level.

The current awareness among plant anatomists of the importance of relating wood characters with plant habit and the ecological and floristic preferences of taxa has led to a more refined approach to the study of wood anatomy and its applications to understanding the evolutionary relationships of extant dicotyledons. This ecological and functional approach to the study of plant structure has contributed in a significant way to less firmly fixed patterns of thought and a more complete understanding of the diverse, structurally adaptive trends of specialization within the xylem.

Character analysis

In addition to the need to recognize strictly monophyletic taxa and to compare homologous characters, the application of wood anatomical characters to cladistic analysis has led to an even greater need for a more complete understanding of structural diversity and precision in character analysis. It is the wood anatomists responsibility to provide systematic botanists with a reliable and accurate data base, properly scored character states, and carefully considered interpretations of characters state transformations. 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. As I emphasized in an earlier contribution (Dickison, 1989), the coding of character states for phylogenetic purposes can also be directly influenced by the current status of character state definition. As is well known, woods of dicotyledons show the evolutionary trend from tracheids with bordered pits to advanced libriform fibers with simple pits. Since this is an evolutionary trend, all stages in the reduction in pit size and number and eventual elimination of the pit border are observable in extant dicots. 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 libriform fiber as opposed to a tracheid or fiber-tracheid. Since in a cladistic

analysis it would be significant whether a taxon was coded as possessing one cell type or the other, reliable and accurate observations coupled with clear character state terminology is paramount. The recent list of microscopic features for hardwood identification (IAWA Committee, 1989) is a valuable tool in this regard. The IAWA Committee appointed to work on the list, however, pointed out that the list is not complete and does not encompass all structural patterns encountered in dicots.

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 continuing efforts are made to reconstruct phylogenies. This has already been evidenced in some studies. Furthermore, Herendeen (1996) has emphasized that quantitative anatomical features, that play such an important role in wood descriptions, present special problems for cladistic analysis. Since wood cell size is often highly variable and shows continuous variation in mean measurements, discrete quantitative character states may not be definable, and attempts to classify the variation into well-defined character states are often suspect (IAWA Committee, 1989). As a result, quantitative characters, that have assumed major importance in clarifying aspects of wood evolution, may not be usable, or become usable only with caution, in a cladistic study.

Divergent taxa

The importance of examining all members of a taxon before making phylogenetic inferences, especially the seemingly least divergent or most divergent members of a group, is well illustrated by the Aristolochiaceae. The Aristolochiaceae are a sizable family of primarily tropical vines and herbs. In North America the family is represented by *Aristolochia*, the Dutchman's pipe vine, and *Asarum*, the wild-ginger. The largest genus *Aristolochia* is apetalous, with a highly specialized, bilaterally symmetrical, gamosepalous, petaloid calyx, inferior ovary, and lianous habit, offers few clues to family relationships (Thorne, 1963). On the other hand, the unfamiliar, rare, monotypic, phylogenetic relict from China, *Saruma henryi* Oliv., provides important phylogenetic information. *Saruma* has attracted much attention as a primitive component of the Aristolochiaceae because, unlike all other members of the family, its actinomorphic flowers possess conspicuous petals and the gynoeceum is composed of multiple carpels that show extensive freedom and that mature into a follicular fruit, and the occurrence of pollen grains of a primitive monosulcate type (Dickison, 1992).

In contrast to the unspecialized floral features, it is of considerable interest that the xylem anatomy of *Saruma* has recently been shown to be rather specialized and to illustrate a distinct and previously unreported trend of specialization in the family (Dickson, 1996). All Aristolochiaceae with the exception of *Saruma* possess exclusively tall, multiseriate xylem rays composed of predominantly upright cells. *Saruma* is of interest because the mature xylem is rayless, illustrating a distinct shift toward raylessness in the family. Furthermore, traditional axial parenchyma is absent in *Saruma*. Instead, the ground tissue is composed totally of a living, fibrous, intermediate cell type that is elongated but comparatively short, has tapered ends, along with lignified walls and very reduced borders.

The inclusion of the rare genus *Saruma* in a discussion of the xylem anatomy and phylogeny of the Aristolochiaceae is critical in that it provides clues relating to the paths of structural specialization and ancestry not evident in other members of the family. Although, the undifferentiated secondary xylem of *Saruma* shows the existence of tall, multiseriate rays, in fully differentiated xylem the rays are lost as the erect ray cells become transformed into more elongate, lignified cells resembling other elements of the ground tissue. The xylem of *Saruma* indicates that the genus may well have been derived from a plant having some cambial activity and possessing a typical aristolochiacean wood anatomy containing wide, tall rays.

Reversibility of wood anatomical characters

Despite the obvious importance of wood anatomical data in the formulation of systematic and phylogenetic hypotheses, wood anatomists have often been extremely modest in making claims as to the evolutionary significance of their data, and as to its utility for clarifying and solidifying systematic conclusions. As a result, wood anatomy has not always assumed its rightful role in modern phylogenetic studies. A question of considerable current importance in this regard is to what extent and under what circumstances the major trends in wood character evolution are reversible? Of special interest is the validity of the long held belief that the trend from primitive tracheids to vessel elements is irreversible (Bailey, 1957). The small number of genera of living woody dicotyledons that are devoid of vessels have been generally regarded to be primitively vesselless, that is, they had vesselless ancestors and continue to exist in the primitive state today. In recent years the assertion of irreversibility of several major trends in wood evolution, especially the vessel element, have been challenged (Dahlgren

and Bremer, 1985; Donoghue and Doyle, 1989; Doyle and Donoghue, 1993; Loconte and Stevenson, 1991). Carlquist (1983, 1987, 1996) summarized arguments against this suggestion and the multiple loss of vessels in extant dicotyledons. The most recent contributions questioning the premise of the irreversibility of vessel element evolution have been presented by Baas and Wheeler (1996) and Herendeen (1996). In these investigations previous assumptions of vessel element irreversibility were tested by mapping selected wood features onto previously published cladograms of the Magnoliidae and "lower" Hamamelididae. The results purportedly show that many wood characters are homoplasious, and that the vesselless condition in a number of woody families is a derived feature. The principal argument in favor of this conclusion is that it is most parsimonious in these branching diagrams to assume a secondary loss of vessels in these groups.

In my view this conclusion is contrary to a basic foundation of evolutionary wood anatomy. The evolutionary trends in vessel element evolution were conceived entirely independently of the various systems of classification and phylogenetic trees showing hypotheses of relationships of dicotyledons. This approach avoided circular arguments based upon assumptions regarding the primitive or specialized character states of extant angiosperms. Therefore, interpretations that vessellessness is primitive is based solely upon wood structural differences of the representative taxa, and entirely without reference to putative specializations within suites of other character states. This is what makes the vessel element evolution story so phylogenetically significant. For wood anatomists to forget this basic foundation of evolutionary wood anatomy would be a mistake.

As pointed out by Endress (1997) in his discussion of floral evolution, key innovations in morphology and anatomy are novel characters that, once acquired, do not disappear again but become stabilized in the group where they originated. They are successful traits that have resulted in physiological and structural improvements and lead to evolutionary radiations. The development of vessel elements and other wood specializations represent key structural innovations that were of such magnitude that they became an integral feature of nearly all angiosperms. Although the size and abundance of vessel elements are known to be ecologically variable within certain taxonomic groups, the transition from imperforate tracheids to perforate vessel elements with scalariform perforation plates is, as far as documented structural evidence shows, irreversible.

During the process of differentiation cells undergo determination, during which there is a commit-

ment of a particular course of development. As a result, undifferentiated cells assume new identities and become transformed into specialized cells. A cell can be regarded to be determined if it has undergone a self-perpetuating change in character state and irreversibly commits itself to a specialized course of development. Vessel elements become determined during their differentiation because they irreversibly enter a differentiation pathway that leads to a breakdown of the perforation plate membrane, thus becoming dead, perforate elements. Determination is a complex and poorly understood, genetically based process by which the structural and physiological characterization of cells become fixed to a specific and stable fate. The chance that such a developmental pathway could be reversed in the case of vessel elements would appear very small.

When using wood characters in phylogenetic analyses and in the construction of cladograms I would argue that the major trends in structural specialization are powerful tools that should be utilized as premier evidences in the data base. Wood anatomy can be used as an independent test of systematic hypothesis. In my view, hypotheses of relationships that are not consistent with the established trends of wood evolution should be seriously questioned.

Research priorities

I would now like to briefly outline a few directions in which future research and attention could be profitably directed. Wood anatomist need to continue to pursue innovative research programs across as broad an academic front as possible. The often fixed boundaries between comparative wood anatomy and other disciplines are rapidly breaking down and diversified new techniques are being applied. The study of wood anatomy is now a truly interdisciplinary field and properly trained individuals are a paramount necessity for complex research undertakings involving evolutionary, functional, and ecological aspects of the subject. Although contemporary wood anatomical research requires that individuals receive increasingly broad training, few individuals have the knowledge and expertise to successfully combine the descriptive and experimental disciplines of anatomy, physiology, and ecology. Anatomists must continue to secure more extensive information of a descriptive nature while at the same time through empirical methods endeavor to extend the discipline to other fields. The questions and phenomena to be investigated in the area of comparative wood anatomy are so complex and variable that, in many cases, they can be analyzed accurately and thoroughly only through the active cooperation

of a group of experts. Only as a result of such collaboration will wood anatomy move to a new level of understanding and become fully integrated with other fields. As a case in point one only needs to point to ecological wood anatomical studies. Most of the wood samples currently in xylaria and that are being collected today contain only a bare minimum of accompanying ecological data relating to the source plant. Little is generally known of the soil conditions under which the plant grew and precise rainfall data is usually unavailable. Careful field work between ecologists and anatomist is essential in order to accumulate the types of data that are now required. In order for this interesting and important aspect of wood research to advance, considerably more refined and detailed ecological data are required. The same can also be said for structure-function relationships within the wood. The relationship between wood and leaf morphology, and anatomy and physiology continues to receive scant attention. In most cases advances will not be made to solve highly complex problems without the willing and active cooperation between anatomists, ecologists, and physiologists.

There are still characters whose occurrences have not been reliably compiled, codified, and analyzed in dicotyledons. Not only are characters and character states unknown for many taxa, but the role of a number of characters in the vital activities of the plant is obscure. A possible role of axial wood parenchyma in water conduction has recently been hypothesized (Canny, 1995, 1997), although what advantages the many varied parenchyma distributional patterns confer on individuals are very unclear. We must also not lose sight of the fact that available data still do not provide a thoroughly reliable basis for arranging the diversified patterns of wood parenchyma into a single linear series of increasing specialization (Bailey, 1957). Various wood parenchyma patterns clearly evolved multiple times along different transformation pathways.

I have the suspicion that the occurrences of living wood fibers may be under represented in the literature. I would urge comparative anatomists to utilize more liquid-preserved woods in their studies. The increasing use of the scanning electron microscope has detected features in taxa where they were not previously observed. Vestured pits are sometimes only visible with the SEM and the recent reports of partially intact pit membranes in vessel element perforation plates are good examples of the advantages of SEM. There continues to be an under representation of shrubs and subshrubs in wood collections and, as a result, anatomical descriptions. As discussed earlier, the value of examining uncommon or habit-diver-

gent taxa in evolutionary and systematic studies has been well documented. Intensive and sustained research efforts are required to produce descriptive wood anatomical inventories in poorly studied geographic areas of the world, such as Mexico.

Wood anatomists occupy a unique position in regard to their potential to contribute to solutions to major questions of phylogeny and issues of structure and function. Owing to the highly specialized nature of this work, there is a continuing need for individuals trained in and conversant in wood anatomy. Research institutions must not overlook the need for pursuing investigators in this area and should allocate resources and facilities for training younger workers.

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