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COMMENTARY: TYPOLOGY, HOMOLOGY, AND HOMOPLASY IN COMPARATIVE WOOD ANATOMY

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SUMMARY

Comparative wood anatomy consists of two main efforts: wood identification and evolutionary studies. Evolutionary studies can be divided into two main areas: systematic wood anatomy and ecological wood anatomy. The goal of wood identification is the association of a name with a sample; that of systematic wood anatomy is the discovery of the nested hierarchy of synapomorphies that characterize the phylogeny of the woody plants; the main thrust of ecological wood anatomy has been to identify structure-function relationships that have evolved repeatedly across clades. Wood anatomical characters can be divided into three types: typological, homologous, and homoplasious. Wood identification can and should use all three types; systematic wood anatomy must focus on homologies; homologies may be of interest to ecological wood anatomy, but homoplasies have been its principal focus. The use of typological characters developed for wood identification can produce misleading results in studies of evolutionary wood anatomy and must be avoided. Robust phylogenies are important for discovering wood anatomical homologies and homoplasies; also important is the need to make explicit, testable hypotheses, and to identify the type of causation (ultimate or proximate) that is of interest for a given study.

Key words: Ecological wood anatomy, homology, homoplasy, synapomorphy, systematics, typology, wood anatomy, wood identification.

Wood is a rich source of information regarding systematics and adaptive evolution. Nevertheless, wood anatomical characters are not used in such studies as often as they could be. I suggest that some traditional features of comparative wood anatomy are to blame, one of the most important being the use of typological wood identification characters inappropriately applied to evolutionary studies. The major branches of comparative wood anatomy (Fig. 1) have, or should have, differing goals and methods. These different aims require the use of different types of characters. The goal of wood identification is to assign a name to a wood sample (Wheeler & Baas 1998). Typological, homologous, and homoplasious characters are all potentially useful for identification. Evolutionary studies are those that attempt to reconstruct some aspect of the evolutionary process, and can be divided into two main groups: systematic and ecological (Fig. 1). Systematic studies associate characters with nodes of the phylo-

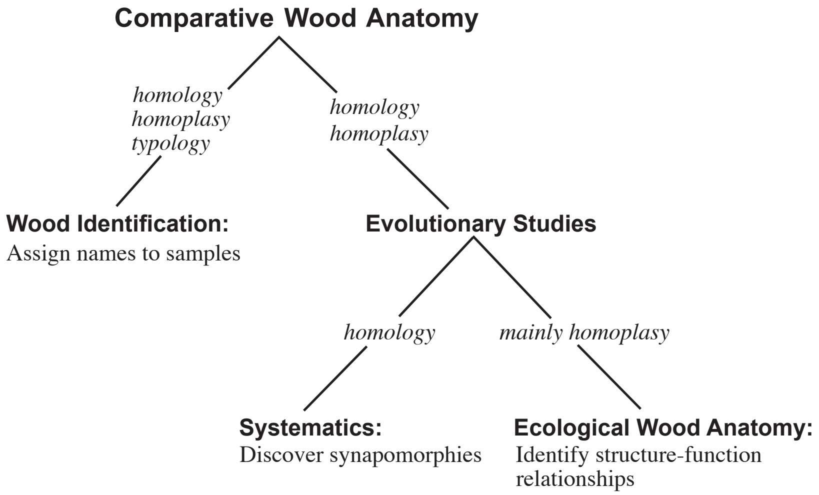

Fig. 1. The divisions of comparative wood anatomy (bold letters) and the kinds of character relations that characterize each field (italics). The main goals of these fields are given below their names.

genetic hierarchy, and thus homologies are the focus. Homologies may be of interest for ecological wood anatomy, but more often homoplasious characters are examined. Characters appropriate for evolutionary studies can be used for wood identification, but many wood identification characters cannot be applied to evolutionary studies. I review the types of characters appropriate for each field and offer some specific suggestions, paying particular attention to the use of well-supported phylogenies as frameworks for the interpretation of wood anatomical data.

Typology, homology, and homoplasy

Typology is the manifestation of Platonic essentialism in evolutionary biology (Hull 1965). Wood anatomists do not explicitly seek the unchanging Platonic essence underlying variation in wood cells, but nevertheless routinely work with characters that are essentialistic. Such an approach elevates a single feature or an arbitrary suite of features (analogous to the Platonic essence) above all others as the basis for grouping taxa. For example, the Linnean system of plant classification is essentialistic because groupings are based on stamen number regardless of any other characteristics. Typological wood anatomical characters have two particularly common expressions: 1) Arbitrary divisions of biological continua; and 2) A "garbage can" effect that lumps many phenomena together as one based on a single key feature. As discussed in more detail in following sections, such characters may be very useful for wood identification but cannot be applied to studies of evolutionary wood anatomy. This is because using arbitrary characters to group taxa will result in groupings that are also arbitrary, that is, they will not reflect biological processes that are independent of human imagination (examples are given in the next paragraph). The alternative for studies of evolutionary wood anatomy is to look for similarity produced by biological processes. Two such processes account for the majority of similarity among taxa: common descent and similar evolutionary responses to similar selection pressures. The categories of characters that correspond to these processes are homology and homoplasy, and the groupings of taxa that they imply are assumed to reflect processes independent of human imagination.

Note the way groupings of taxa based on typological characters do not reflect biological processes:

1) Arbitrary divisions of continua. The continuous variation in many characters can be arbitrarily divided into discrete categories to facilitate wood identification (e.g. IAWA Committee 1989). For example, the lines between "growth rings distinct" vs. "indistinct or absent" or "fiber pits < 3 µm" vs. "fiber pits > 3 µm" are arbitrary because the lines could just as well be drawn in other places, e.g. "earlywood vessel area 4× the area of latewood vessels or greater" vs. "less differentiation among vessels", or "fiber pits < 3.5 µm" vs. "fiber pits > 3.5 µm". To the extent that these distinctions are arbitrary, the groupings of taxa based on them will also be arbitrary. Take the extreme example of a grouping of all the woody taxa with distinct growth rings. This group is not related by common descent or even a group of functionally similar species, with southern beeches from Patagonia being grouped with spurges from Somalia. This example may be exaggerated, but arbitrary characters nevertheless may confound phylogenetic analyses even at the interspecific level in similar if more subtle ways.
2) The "garbage can" effect. The IAWA list character "woods with odors" would put in one group all woods with any noticeable odor, from the sweet-smelling *Cedrela* and *Bursera* to sour *Forchhammeria* and *Gyrocarpus*. This grouping of taxa is based on the key feature of "odor". These odors are surely based on very real secondary compounds, so why is this grouping artificial? Again, this grouping certainly does not reflect common descent and cannot be considered to represent similar responses to similar selection pressures because the odors and compounds that produce them are so different. The growth ring character mentioned above also may qualify as a garbage can character. For example, the group "growth rings indistinct or absent" may in many cases mix functionally very different phenomena, e.g. placing one taxon with the ontogenetic capacity to produce growth rings (albeit slight) in the same category as a taxon that lacks this capacity. Ecological behavior and capacity to respond to selection might be expected to be very different in these different taxa.

Problems with the use of arbitrary characters have been famously examined in the evolutionary literature dealing with adaptation. Lewontin (1978) charged many studies of adaptation with arbitrary atomizations of the environment into "problems" for organisms to "solve" with equally arbitrary characters. Larson and Losos (1996) suggest a solution: homologies are non-arbitrary characters that are assumed to have independence beyond human imagination. We can avoid the use of typological characters by using specific methods devised for recognizing homologies. These methods are discussed below.

However, before attempting to discover homologies, it is necessary to decide what is meant by "homology". This is necessary because different concepts of homology have been developed for different research programs. Brigandt (2003), for example, shows that comparative/evolutionary biology, molecular biology, and developmental evolutionary biology each have their own distinctive suites of homology concepts. So many concepts have been developed because each one is designed to result in different kinds of information to answer different kinds of questions. Using the incorrect homology concept will result in inappropriate information for the question at hand.

The types of homology that wood anatomists most commonly deal with are *taxic* and *transformational*. Taxic homology is the sense that is synonymous with synapomorphy (Patterson 1982). One of the most important attributes of synapomorphies is that they are inseparable from a specification of a level of the phylogenetic hierarchy (a clade). Assertions such as "simple perforation plates are a synapomorphy" or "laticifers are homologous" are meaningless by themselves. However, "simple perforation plates are a synapomorphy of the two-taxon clade in Fig. 2" or "axially oriented laticifers characterize Moraceae" specify unique groups of the phylogenetic hierarchy.

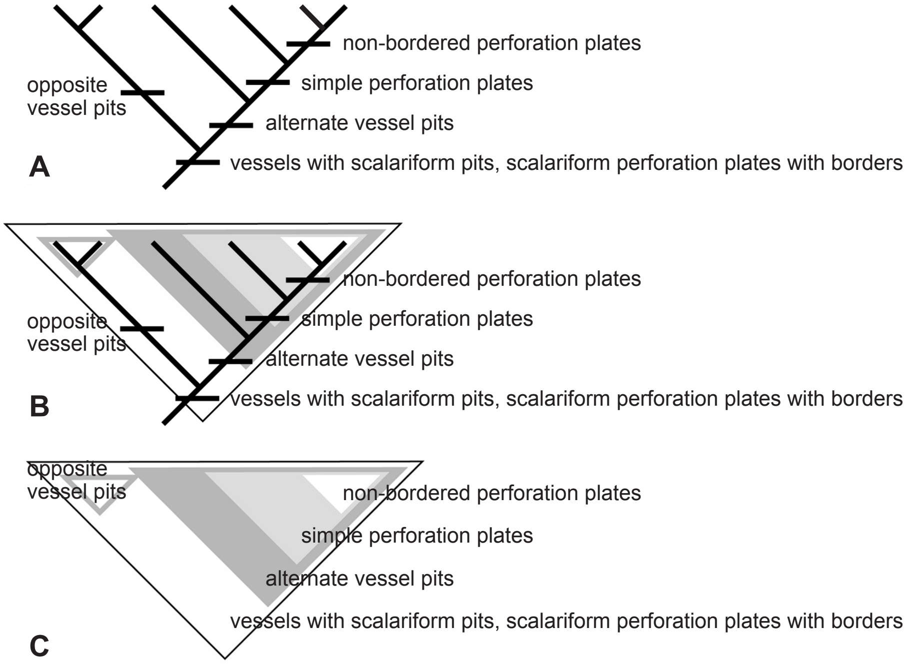

Fig. 2. A phylogenetic tree represents a nested hierarchy of synapomorphies (taxic homologies). – A: The distribution of synapomorphies is often indicated on phylogenetic trees with bars below the nodes. In this tree, all of the species have vessels. The four taxa of the right-hand clade all have elements with alternate vessel pits. Those in the left-hand clade all have elements with opposite pits. The three-taxon clade has elements with alternate pits and simple perforations. The two-taxon clade at extreme right has elements with alternate pits, and simple perforations that are non-bordered. – B: To illustrate this nesting more graphically, in addition to bars representing synapomorphies, each group of taxa sharing a synapomorphy has been outlined. – C: The nested pattern of the distribution of synapomorphies is even more obvious when only the triangles are presented in a Venn diagram. Systematic wood anatomy must strive to discover such nested patterns of character variation.

Although taxic homology is the most appropriate type to use when searching for synapomorphies, the type that probably corresponds most closely to many workers' intuitive sense of homology is called transformational homology. Transformational homology is the correspondence of one structure to another within the same individual or in another organism. In contrast to taxic homology, these statements do not require specification of a level of the phylogenetic hierarchy to have meaning (Patterson 1982; Carine & Scotland 1999). Assertions of transformational homology include "petals are homologous to leaves" or "vessel elements are derived from tracheids". This is the perspective that has prevailed in classical plant morphology (cf. Sattler & Rutishauer 1997; Kaplan 2001). Studies of transformational homology in wood include investigation of the changes in ray shape between taxa (Barghoorn 1941) and documentation of the ontogenetic differences between vessel elements and vasicentric tracheids (Olson *et al*. 2003). Because they do not specify groupings, statements of transformational homology do not specify synapomorphies. Because these different concepts of homology answer different questions, workers must consciously select the appropriate concept. For the remainder of this discussion, I will use "homology" in its taxic sense, as a synonym of synapomorphy.

Much remains to be learned about homology. For example, it is not clear how one structure can be "the same" as another within and between taxa nor what causes the persistence of these parts over time (see for example Wagner 2001; Schwenk 2001; Schwenk &Wagner 2001). Nevertheless, useful operational criteria exist for recognizing taxic homologies as currently conceived. Taxic homologies are discovered by formulating and testing explicit hypotheses (Rieppel & Kearney 2002). An example of an approach for recognizing synapomorphies is provided by the three criteria of Patterson (1982; built upon by workers such as De Pinna 1991, and Scotland 2000): 1) *Similarity*. The features postulated to be taxic homologies are assessed for similarity in features such as structure, function, development, and location (Stevens 1984; Rieppel & Kearney 2002). 2) *Conjunction*. If it is hypothesized that vessel elements with scalariform perforation plates are a synapomorphy of taxon A and simple perforation plates are a synapomorphy of taxon B, the implication is that these cell types are derived from a common ancestor that diverged in a mutually exclusive manner to give rise to these differing structures in the taxa in question (Fig. 3). We would reject our hypothesis that scalariform perforation plates characterize clade A and simple ones clade B if we were to find both types of perforation plates in either taxon. The conjunction criterion helps diagnose whether or not the correct level of the phylogenetic hierarchy is being studied, with failure of the test often indicating that one of the hypothesized synapomorphies may be a synapomorphy at a more inclusive phylogenetic level or a homoplasy recurrent in several taxa at low phylogenetic levels. For example, finding some taxa with scalariform perforation plates in taxon B in Figure 3 could indicate that, instead of being a synapomorphy of clade A, scalariform perforation plates are a synapomorphy of the A+B clade (see also De Pinna 1991). 3) *Congruence*. This concept is one of the most crucial in phylogenetic systematics. The tree of life consists of clades nested within clades. By definition, each clade is characterized by synapomorphies (Fig. 2 & 3). If a taxon has one synapomorphy, it is bound to have others.

Therefore, the best confirmation that a given characteristic is a synapomorphy is the finding that other synapomorphies also characterize the group under study. These tests can be applied at any level of the phylogenetic hierarchy. Moving down in the tree in Figure 3 to the A+B node, we can now search for synapomorphies of this clade, a candidate being the presence of perforation plates.

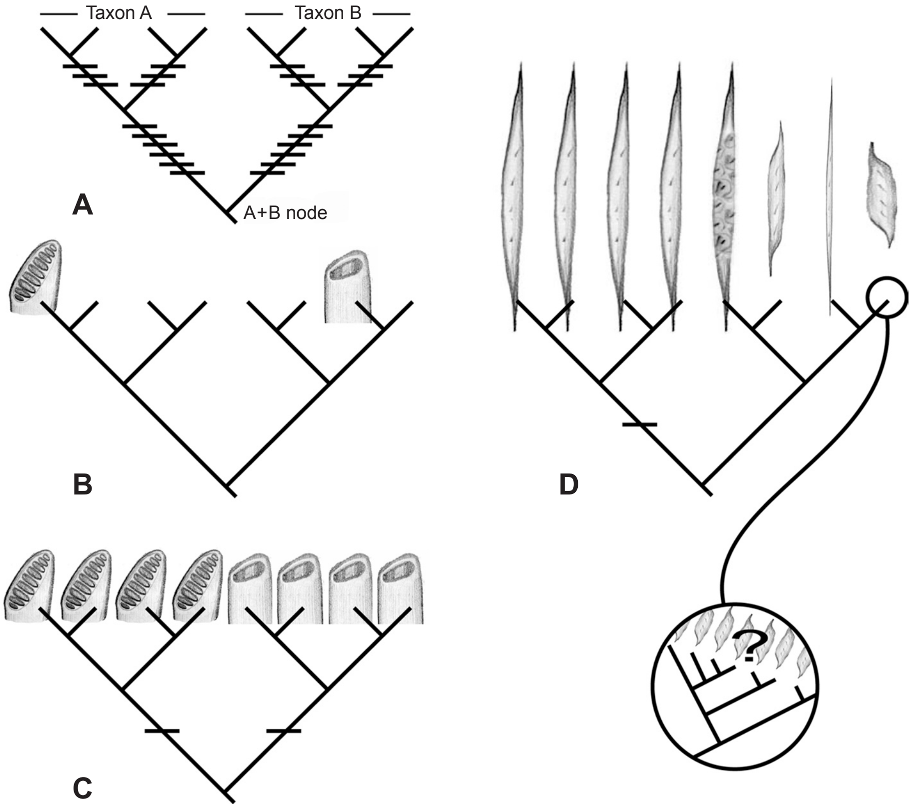

Fig. 3. Congruence and the use of phylogenies to discover anatomical synapomorphies. – A: Well-supported imaginary phylogeny with numerous synapomorphies (horizontal lines). – B: The phylogenetic distribution of known anatomical variation is assessed and hypotheses of homology generated. In this case, one taxon in clade A is known to have scalariform perforation plates, whereas one from clade B is known to have simple ones. Perhaps each perforation type is synapomorphic for its respective clade. – C: Anatomical variation is studied further and hypotheses of homology are tested, e.g. using the methodology described in the text. In this case we confirm our hypothesis and conclude that scalariform perforation plates are a synapomorphy of clade A and simple plates are a synapomorphy of clade B. – D: To find more synapomorphies of the left-hand clade, or to continue looking for one for the right-hand clade, continue with other characters. In this case, the fiber types on the right are neither similar nor congruent with the phylogeny and so are not considered a synapomorphy of clade B. On the other hand, libriform fibers are likely a synapomorphy of clade A. Characters not synapomorphic at this level of the phylogenetic hierarchy may be synapomorphic at other levels, e.g. parenchyma-like fibers may be a synapomorphy of the clade represented by the extreme right-hand taxon.

Another useful set of criteria was proposed by Wagner (1989). Although they were intended to guide research on the origin and maintenance of homologies and not for recognizing synapomorphies, his three criteria are nevertheless an excellent complement to those of Patterson. Wagner (1989) suggested that homologies should exhibit the properties of conservation, individuality, and uniqueness. *Conservation* is manifested in the observed similarity that allows us to recognize a structure as the "same" across taxa. *Individuality* is the property of a homology to develop in a semiautonomous manner within an organism. A leaf or a vessel element, though integrated in the function of the whole organism, are units to some extent ontogenetically distinct from the rest of the plant and would seem to satisfy this criterion. Note that some perfectly acceptable taxic homologies, e.g. lost structures, do not show individuality and would not be considered homologies under Wagner's criteria. Finally, *uniqueness* is simply the observation that homologies occur sufficiently rarely that they characterize the members of unique clades, that is, are synapomorphies. Therefore, any characteristic satisfying the criteria of homology *sensu* Wagner should also be a taxic homology.

Homoplasies are the result of similar responses to similar selection pressures, resulting in similar structure-function relationships in different taxa. Homoplasies can result from parallelism, convergence, or evolutionary reversal. Parallelisms can be difficult to distinguish from synapomorphies, because ancestors start with the same character state that changes in parallel and independently in related lineages, resulting in similar structures in the descendent taxa. Parallelism is often taken as indication of the kinds of developmental predispositions to certain kinds of change that are present in a taxon (i.e. constraint, Gould 2002). Convergences are similarities, usually in distantly related taxa, that result from evolutionary changes that began with different character states in the ancestral taxa. Finally, reversals are cases in which a character changes to its previous state. Reversals are not necessarily the same as loss of a character, which in many cases may be a taxic homology, e.g. in a group with highly parenchymatized xylem, lack of paratracheal axial parenchyma is a synapomorphy of the red-flowered clade of *Moringa* (Olson 2002a). The same method for discovering homologies will also reveal homoplasies. Such characteristics appear to be homologues but are incongruent with true synapomorphies (Patterson 1982; Fig. 4).

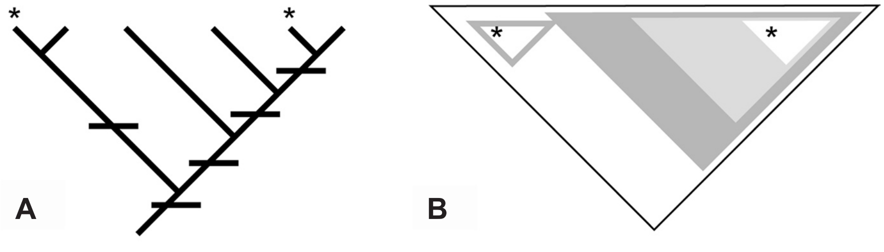

Fig. 4. Incongruence reveals homoplasy. – A: Starting with the same imaginary tree as in Fig. 2, we identify the distribution of the character * (e.g. vestured pits, simple perforation plates, etc.). – B: The group of species with character * is not congruent with the pattern of nesting of the other characters. If this character passes other homology criteria, such as similarity and conjunction, then we have identified a feature that has evolved through convergence, parallelism, or reversal – a homoplasy.

The three categories of characters can thus be identified by the way in which they reflect biological processes. Typological characters will reflect them not at all. Homologies reflect similarity that is the result of descent from the same common ancestor, whereas homoplasies are similarities that reflect similar evolutionary solutions to similar environmental challenges. The following three sections examine each of the three branches of comparative wood anatomy and discuss the character types appropriate to each.

Characters for wood identification

Explicitly typological groupings are often used in comparative wood anatomy. For example, the variety of rays were classed by Kribs into "Types" (Kribs 1935). Some of these ray types may be genuinely similar between taxa, and thus represent homoplasies, but others almost certainly are highly artificial. Ray type is an example of a garbage can character, because it places many different taxa in the same group (e.g. "taxa with Heterogeneous Type II rays") on the basis of a single character elevated above all others (e.g. cell shape). Nevertheless, typological groupings are often extremely useful for wood identification. IAWA Committee (1989) contains numerous arbitrary categories, for example "scalariform perforation plates with ≤ 10 bars"; "intervessel pits small, 4–7 µm in diameter"; "Vessels with mean tangential diameter 100–200 µm"; "≥ 100 vessels/mm^2". All of these groupings are arbitrary divisions of biological continua that may greatly facilitate the identification of a wood sample.

In addition to typological characters, homologous and homoplasious characters may also be of great utility. For example, tile cells have long been known to be a synapomorphy of what is now known as Malvaceae s.l., and aid in recognizing many members of this group. Likewise, characters that are likely homoplasious may be of great utility. For example, the key of Fahn *et al.* (1986) includes a section that groups all species with "included phloem". This group includes species from six families from four orders of basal and core eudicots (Table 1). Examining this table or the distribution of this character on a cladogram readily shows that it is homoplasious. Thus, any character from any source that aids in the association of a name with a given sample may be employed for wood identification. Indeed, the limitation to any one category of character types in the election of characteristics for wood identification should be actively avoided.

Table 1. Families and clade memberships of eudicots with "included phloem" from the wood identification key of Fahn *et al.* (1986).

Major clade	Ranunculales	Caryophyllales + Dilleniales		Eurosids II		Euasterids I
Order	Ranunculales	Caryophyllales		Brassicales		Lamiales
Family	Menispermaceae	Amaranthaceae	Nyctaginaceae	Brassicaceae	Salvadoraceae	Acanthaceae

Characters for systematic wood anatomy

Mayr (1965) and Hull (1965) noted that identification schemes and systematics are distinct efforts that are nevertheless often confused. In systematic wood anatomy, it is difficult to avoid typological characters that would be more appropriate for wood identification than systematics. For example, the following characters are arbitrary divisions of continua: "frequency of solitary vessels > 60 %" vs. "frequency of solitary vessels

< 60 %" (Malécot *et al*. 2004); "predominant xylem cell type axial parenchyma" vs. "predominant xylem cell type libriform fibers" (Olson 2002a); "small trees 6–20 m tall" vs. "large trees more than 20 m tall" (Slik & Van Welzen 2001).

Typological characters can be avoided and homologous and homoplasious characters identified by formulating and testing explicit hypotheses of homology. For example, casual review of Caricaceae and Moringaceae showed that both had hollowings in the pith. Therefore, I hypothesized that pith hollowings might be a synapomorphy of the Caricaceae + Moringaceae clade (Olson 2002b) and tested this notion using the criteria of Patterson (1982). This character was apparently congruent with molecular phylogenies at the generic and family levels and so met the congruence criterion. Anatomical study showed that hollow piths in Caricaceae involve cell death in a wide swath of pith, with no secretion into the resulting space, whereas the pith hollowings of Moringaceae originate as schizogenous gum ducts. Therefore, I rejected the notion that hollow piths in Caricaceae were similar to those of sister taxon Moringaceae, and thus pith hollowings are not a synapomorphy of the Caricaceae + Moringaceae clade (Olson 2002b).

The most powerful tools currently available to comparative wood systematists are robust phylogeny reconstructions. Every advantage should be taken of these phylogenies to direct explicit searches for the nested hierarchical pattern of anatomical character variation. One of the most crucial concepts in systematics is that of congruence, because a true homology will co-occur with others (Patterson 1982). For example, the nodes in a molecular phylogeny represent a nested hierarchy of molecular synapomorphies (Fig. 3A). The search for a wood anatomical synapomorphy can be started with clades that are well supported by molecular data (i.e. have several molecular synapomorphies). The task is then to find anatomical characteristics that are found only in the members of a certain clade. Having found features congruent with a clade, then homology testing proceeds, e.g. by evaluation of the similarity and conjunction criteria of Patterson (1982). An admirable effort is that of Stevens (2001 onwards), which attempts to document morphological and other synapomorphies for all of the major nodes of the angiosperm phylogeny.

Typologies commonly enter systematic wood anatomy via wood identification — The rest of this section illustrates ways in which typological approaches of wood identification can be inappropriately applied to systematics. Examples include the use of standardized lists such as IAWA Committee (1989), the use of quantitative characters, and the equation of synapomorphy with homogeneity of character states. All of these situations can be avoided by basing systematic wood anatomy on explicit searches for homologies.

The standardized lists on which wood descriptions are based, such as IAWA Committee (1989) include features with high probabilities of being found in any given sample. In contrast, a synapomorphy in its strictest sense is presumed to have arisen only once in the history of life and therefore can be used to diagnose the descendents of a single common ancestor. The IAWA list would be cumbersome to the point of being useless if it were filled with features unique to each clade (assuming these were known). Thus it is not surprising that very few of the features on the list represent synapomorphies that characterize major clades, tile cells being perhaps the noteworthiest exception.

As a result, anatomists basing their searches for synapomorphies only on lists such as IAWA Committee (1989) or similar characters will rarely find them, especially at high phylogenetic levels.

The IAWA list is also unlikely to yield synapomorphies because many of the characters on the list are quantitative. The use of quantitative characters in phylogeny reconstruction is a major conceptual challenge, because all of the approaches proposed to date result in typological characters for at least three reasons:

1) *The choice of character state delimitation method is arbitrary.* Variation between species in quantitative characters can be depicted as frequency distributions (Fig. 5). Sometimes this variation is overlapping, as among species 1–3 and 4–6 in Figure 5, and sometimes it is non-overlapping, as between these species groups. Statistically defensible methods have been proposed for dividing such variation into states (e.g. Goldman 1988; Thiele 1993; Wiens 2001). However, there does not appear to be any biological reason to select one over the other (Stevens 1991; see also Bookstein 1994). As a result, the approaches proposed to date result in arbitrary characters because the choice of method is arbitrary.
2) *Quantitative characters are highly essentialistic*. Like all essentialistic characters, quantitative characters group taxa based on a single key feature and disregard other information. With respect to quantitative characters, it is the dimensional measurement that is the key feature. Information from various characteristics is used to decide which features are to be compared (e.g. vessel elements in taxon A are identified based on perforations, incorporation into vessels, etc., and are compared with vessel elements in taxon B). However, when the similar/not similar decision is made, it is based only on the dimensional measurement. A taxon is placed in category A if its dimension is within one range, and B if the dimensions are within another; no other information is taken into account. This practice is essentialistic because the quantitative data behave as essences that take precedence over any other information. Qualitative characters have their own problems (e.g. see Hawkins 2000), but when properly conceived escape from the extreme essentialism of quantitative characters because assessments of similarity are based on multiple features (structure, function, location, etc.) rather than being decided exclusively by a comparison between two sets of measurements.
3) *Quantitative characters are vulnerable to being "garbage can" characters*. It is easy to group truly non-similar entities together when using quantitative characters. For example, two vessel elements of the same length, one with tails, scalariform perforation plates and pits, and the other lacking tails and having simple perforations and alternate pits would be coded as having the same states, when they are likely functionally and phylogenetically very different.

Applying the tests of homology cited above serves to illustrate the problems mentioned here. Imagine two taxa, one with vessel-vessel pits of 5.5 μm mean diameter and the other with pits of 6 μm mean diameter. Are these features similar in the sense of Patterson (1982)? Although the question is entirely statistically accessible, it is nevertheless for the moment insoluble. This is because if we accept only identical frequency distributions as identical character states (e.g. method 3 in Fig. 5), then we will never find a state with

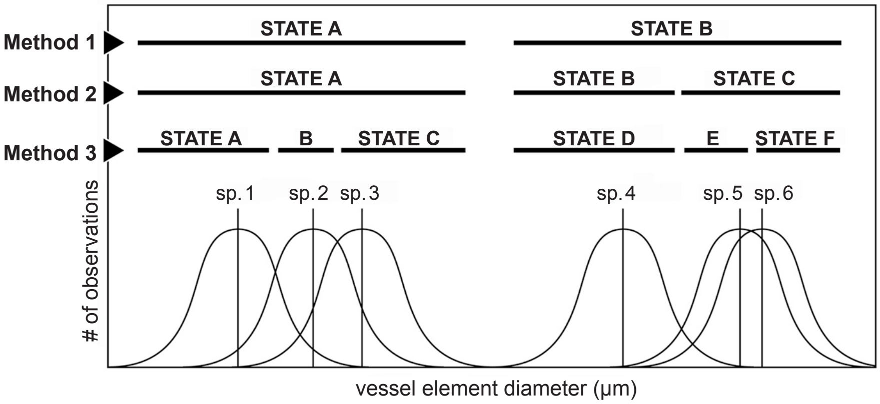

Fig. 5. Graph of frequencies of vessel diameters for six species and the identification of character states. None of the species have identical means, though some are close, e.g. spp. 5 and 6. Different criteria for dividing quantitative variation between taxa into states would divide this distribution into states in different ways. Method 1 places the species into two groups whose frequency distributions do not overlap (A and B). Other methods, such as method 2, might divide the variation into three states: A (spp. 1–3), B. (sp. 4), and C (spp. 5, 6), or into six states (method 3).

more than one taxon (in addition to being highly essentialistic). On the other hand, as mentioned above, the choice of more inclusive statistical approaches that delimit states with more than one taxon is an arbitrary one (e.g. methods 1, 2 in Fig. 5).

If quantitative characters are to be avoided as characters for cladistic phylogeny reconstruction, what can be done in a systematic context with the large number of quantitative data that wood anatomists regularly collect? I suggest that at present the best that can be done is to note variation that is congruent with other characters as hypotheses for potential synapomorphies. For example, recent molecular phylogeny reconstructions show the Frankeniaceae + Tamaricaceae + Plumbaginaceae + Polygonaceae clade within Caryophyllales s.l. to be well supported (Cuénod *et al*. 2002; Gaskin *et al*. 2004). Members of all of these families have conspicuously tiny vessel lateral wall pits, a feature not shared with other Caryophyllales (Olson *et al*. 2003). This characteristic thus meets both the congruence and conjunction criteria of Patterson (1982). For reasons cited above, it awaits confirmation via a convincing application of the similarity criterion.

Another instance of the transfer of essentialistic wood identification criteria to systematics is exemplified by Baas *et al*. (2000), who compared the “homogeneity” of wood anatomy in selected orders pre-and post-APG (1998). Homogeneity was defined by the authors as uniformity of structure, e.g. all of Gentianales *sensu* APG have simple perforation plates and non-vestured pits whereas under previous non-molecular classifications they were less homogeneous because some members also had scalariform perforations and non-vestured pits. Although this paper is couched in systematic terms, uniformity of structure within a group is of principal interest in wood identification (e.g. if a sample has structure X it must be taxon Y). Homogeneity is less of interest in systematics because it is not always equivalent to synapomorphy. This is because synapomorphies are not necessarily possessed in the same state by all members of a

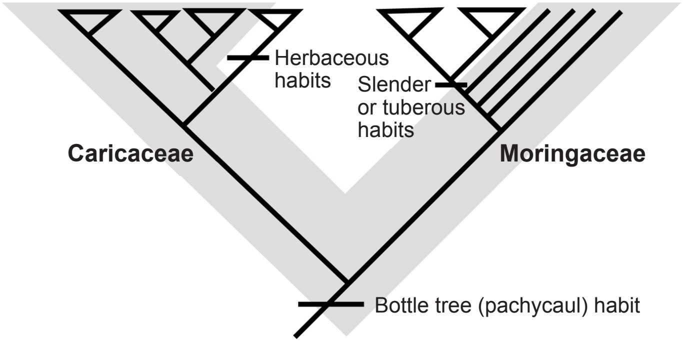

Fig. 6. Non-"homogeneity" of a synapomorphy. The phylogenetic distribution of the pachycaul life form in the Caricaceae + Moringaceae clade is shown in gray. It is a derived feature within Brassicales, and a likely synapomorphy of the two-family clade, though it is only present in the basal members of the clade.

clade. In Figure 3C, all of the members of clade A have scalariform perforation plates, and all of the members of clade B have simple plates. In such a case, each state is both uniform and a synapomorphy of its clade. A more complicated situation is illustrated by the real life example of the bottle tree life form as a synapomorphy of the Caricaceae + Moringaceae clade (Fig. 6). Bloated pachycaul stems with thick fibrous bark and highly parenchymatized xylem are found in both families, and are unique in Brassicales. The pachycaul life form thus appears to be a synapomorphy of the two-family clade. However, the life form is present only in the basal members of each family (Olson 2002b), showing that characters that are not uniform in their states throughout a clade may still be considered synapomorphies of that clade.

In summary, systematic wood anatomy is the directed effort to discover anatomical synapomorphies for each node of the phylogeny of woody plants. To avoid typological and homoplasious characters, this search must employ explicit hypotheses of taxic homology (synapomorphy). Such studies should specify the criteria used to test these hypotheses, basing the search for synapomorphies on thorough study of the group of interest rather than the typological approaches embodied in many of the tools of wood identification.

Characters for ecological wood anatomy

Synapomorphies may reflect structure-function relationships, but by definition they are restricted to single clades. Traditionally, ecological wood anatomy has taken a broader perspective, often using floras of entire regions, and has sought anatomical correlations with environmental variation across clades (e.g. Carlquist & Hoekman 1985; Alves & Angyalossy-Alfonso 2000). Features that are restricted to clades are therefore usually excluded from such studies. There is no reason, however, that study of the adaptive significance of clade-specific characters cannot be highly ecologically informative. Studies of functional wood anatomy (e.g. Hacke & Sperry 2001; Sperry & Hacke 2004) focus on smaller numbers of characters than floristic comparative wood antomical studies but the comments presented here nevertheless also apply to these studies.

The notion that statistical associations might be found across clades between wood anatomical characters and features of habit or environment is predicated on an assumption of high homoplasy and little tendency for closely related taxa to resemble one another. If homoplasy were low and similarity within taxa high, then each clade would exhibit unique adaptive solutions and adaptive wood anatomical patterns would not emerge from floristic studies. Although homoplasious wood anatomical characters may be phylogenetically uninformative, as the principal focus of ecological wood anatomy, they are informative regarding the process of adaptive evolution.

Just as anatomical homologies may be discovered using well supported phylogenies, homoplasies can be discovered by finding incongruences in the distribution of wood anatomical characters on well-supported phylogenetic hypotheses (Fig. 4). Jansen *et al*. (2003) examined the adaptive role of vestures by beginning their analysis in this way. Noting that vestures occur in similar positions and are mostly of similar structure across taxa, they postulated that all cases of vestured pits were serving the same function. They then showed the homoplasious nature of vestures by tracing their occurrence in several orders on an ordinal-level molecular tree. In terms of Patterson (1982), vestures meet the similarity criterion but are incongruent with the phylogeny (i.e. do not diagnose a clade) and are thus considered homoplasious at high levels of the phylogenetic hierarchy.

Typological characters are not of interest for ecological wood anatomy, because variation in arbitrary characters cannot reveal the way that plants are responding to selection. For example, IAWA Committee (1989) defines all imperforate tracheary elements with pit cavity dimensions above an arbitrary cut-off “fiber tracheids”. The IAWA list definition is a perfectly serviceable one for wood identification; any convention will work, as long as it is clearly communicated. However, ecological questions examine the functional attributes of cell types. In any given floristic study, there is surely variation hidden within the IAWA fiber-tracheid category that would be of interest. For example, most floristic studies probably include both conductive and non-conductive cells within the “fiber-tracheid” category.

Studies of ecological wood anatomy should be very cautious when invoking the “major trends of xylem evolution” (e.g. Bailey & Tupper 1918; Frost 1930; Chalk & Chattaway 1935; Kribs 1935; Bailey 1944, 1957; terminology of Carlquist 1961), both because the aim of these studies was limited to inference of phylogeny and because some of their assumptions may be faulty. The “major trends” studies were strictly an attempt to identify the polarity of wood transformations as an aid to inferring woody plant phylogeny, e.g. vessel elements with simple perforation plates evolved from vessel elements with scalariform perforation plates. In contrast, ecological wood anatomy requires explicit hypotheses regarding structure-function relationships that might be driving evolutionary transformations in wood, e.g. simple perforation plates should be favored over scalariform ones in dry habitats. Note that to test this hypothesis, no reference to Baileyan trends is necessary. Recent examples testing structure-function hypotheses include the functional approach of Hacke & Sperry (2001) and the comparative approach of Jansen *et al*. (2003). Perhaps even more importantly, the assumptions on which the major trends paradigm is constructed are in need of critical examination. For example, the Baileyan trends depict a linear transformation series in vessel element characters from primitive to specialized. How such a linear scheme can apply to a highly branched phylogeny is not clear. Another assumption that is difficult to interpret is the notion that "specialization should result in a series of graded forms" (Frost 1930, p. 72).

A further way that studies of ecological wood anatomy may be diverted from addressing causes of structure-function correlations is by studying proximate rather than ultimate causation. From an evolutionary standpoint, it could be hypothesized that ray cells become procumbent in older stems because natural selection favors radial transport over axial transport. A very different conclusion is reached if one asks questions from an ontogenetic point of view. From this perspective, ray cells become procumbent because of transverse divisions in the ray initials. There are thus two approaches to the same question, in this case "why do ray cells become procumbent with age?": an evolutionary one and an ontogenetic or physiological one. These answers correspond to different levels of causation, ultimate and proximate, respectively (Mayr 1982). Studies of ecological wood anatomy examine hypotheses of ultimate causation (e.g. shorter vessel elements should be favored by natural selection in drier habitats). Special effort should therefore be made not to confuse them with proximate causation (e.g. vessel elements are shorter because fusiform cambial initials are shorter).

CONCLUSION

Comparative wood anatomy has much to contribute, from the practical utility of wood identification, to revealing unique characters diagnosing clades, to providing a superb system for studying adaptive evolution. Each of the branches of comparative wood anatomy requires a different set of characters and approaches. Most importantly, the characters and approach of wood identification must not be applied to studies of systematic or ecological wood anatomy. Wood identification makes use of a great number of typological characters and methods that cannot be informative regarding evolutionary processes. The goal of identification is to group diversity into ever-smaller chunks by any means; evolutionary studies attempt to order diversity based on patterns that reflect biological processes. These two approaches could not be more divergent. Employing the approach and characters appropriate to a given study, with explicit hypotheses at the appropriate level of causation, would go far in making comparative wood anatomy take its rightful place in evolutionary studies.

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