

# Linear Trends in Botanical Systematics and the Major Trends of Xylem Evolution

Mark E. Olson<sup>1,2</sup>

<sup>1</sup> Instituto de Biología, Universidad Nacional Autónoma de México, Tercer Circuito s/n de Ciudad Universitaria, México DF 04510, Mexico

<sup>2</sup> Author for Correspondence; e-mail: molson@ibunam2.ibiologia.unam.mx

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**Abstract** For nearly a century the so-called Major Trends of Xylem Evolution have guided thinking regarding wood evolution, but their conceptual foundations have not been examined. I detail and critique nine tenets of Major Trends thinking, including the use of linear schemes to infer phylogeny, the Haeckelian assumption that ontogeny recapitulates phylogeny, the use of homoplasies in phylogeny estimation, and the view of evolution as inexorable progress. In addition, I identify some six meanings of the key term “specialization,” ranging from the notion of division of labor between cell types to the relative position of a taxon in a linear hierarchy. The Trends in their original formulation of 1918–1957 show virtually no overlap with the Trends as currently construed. I suggest that the Trends were based on a conceptual foundation outdated at their outset and that they are unnecessary for any study of plant phylogeny or adaptation.

**Resumen** Las llamadas “Tendencias Mayores en la Evolución del Xilema” han orientado el pensamiento científico sobre la evolución de la madera por más de un siglo. Sin embargo, los fundamentos conceptuales de las Tendencias nunca han sido examinados de manera detallada. Aquí examino críticamente nueve preceptos de las Tendencias, tales como el uso de esquemas lineales para inferir filogenias, el supuesto haeckeliano de que la ontogenia recapitula la filogenia, el uso de homoplasias para reconstruir filogenias y la práctica de concebir la evolución como un proceso con progreso inevitable. Además, identifico seis sentidos de “especialización,” quizás el término más importante del esquema baileyano. Las varias definiciones de “especialización” incluyen “división de labores” y posiciones relativas de taxones en una jerarquía lineal. Las Tendencias, en su formulación original 1918–1957 presentan un traslape casi nulo con las Tendencias como se suelen interpretar actualmente. Concluyo que las Tendencias se basaron en un esquema conceptual anticuado desde su inicio y que son irrelevantes para cualquier estudio de evolución o adaptación vegetal.

**Keywords** Adaptation · Evolution · Great Chain of Being · Homoplasy · Systematics · Xylem

...the recent history of systematics is not simply a dispute over methods and objects; what we have seen, and continue to see, is the dying struggle of the Great Chain of Being. (O'Hara, 1992)

## Introduction

Botanists increasingly note that many traditional activities such as field collection, taxonomy, and plant anatomy are on the decline relative to other, mostly molecular lab-based pursuits (Prather et al., 2004; Wheeler, 2004; Khuroo et al., 2007; Chaffey, 2008). This is certainly borne out in my experience with comparative wood anatomy: many more students are eager to take up pipettes and sequence DNA than to toil at the microtome and microscope. At the same time, a tally of papers on flowers versus those on wood in journals such as *Evolution* or *Systematic Biology* shows that while legions of evolutionary biologists and systematists see interesting issues in flowers, only a handful consider wood. This is odd because what attracts many to plants in the first place is their incredible variety of shape and size, and xylem is perhaps the single tissue that best reflects this diversity, in addition to being ecologically and economically paramount on a global scale.

I suspect that some of this reticence to study xylem may be because those new to wood anatomy are skeptical of some of its traditional concepts and practices. I have discussed elsewhere how the traditional and inappropriate use of typological wood identification characters for phylogeny reconstruction and studies of adaptation may leave non-anatomists unconvinced regarding the usefulness of wood in general for evolutionary studies (Olson, 2005; see also Rosell et al., 2007). Another factor that in my experience causes confusion among non-anatomists and anatomists alike is the long-standing tradition of thinking about wood in terms of the so-called Major Trends of Xylem Evolution (term of Carlquist, 1961).

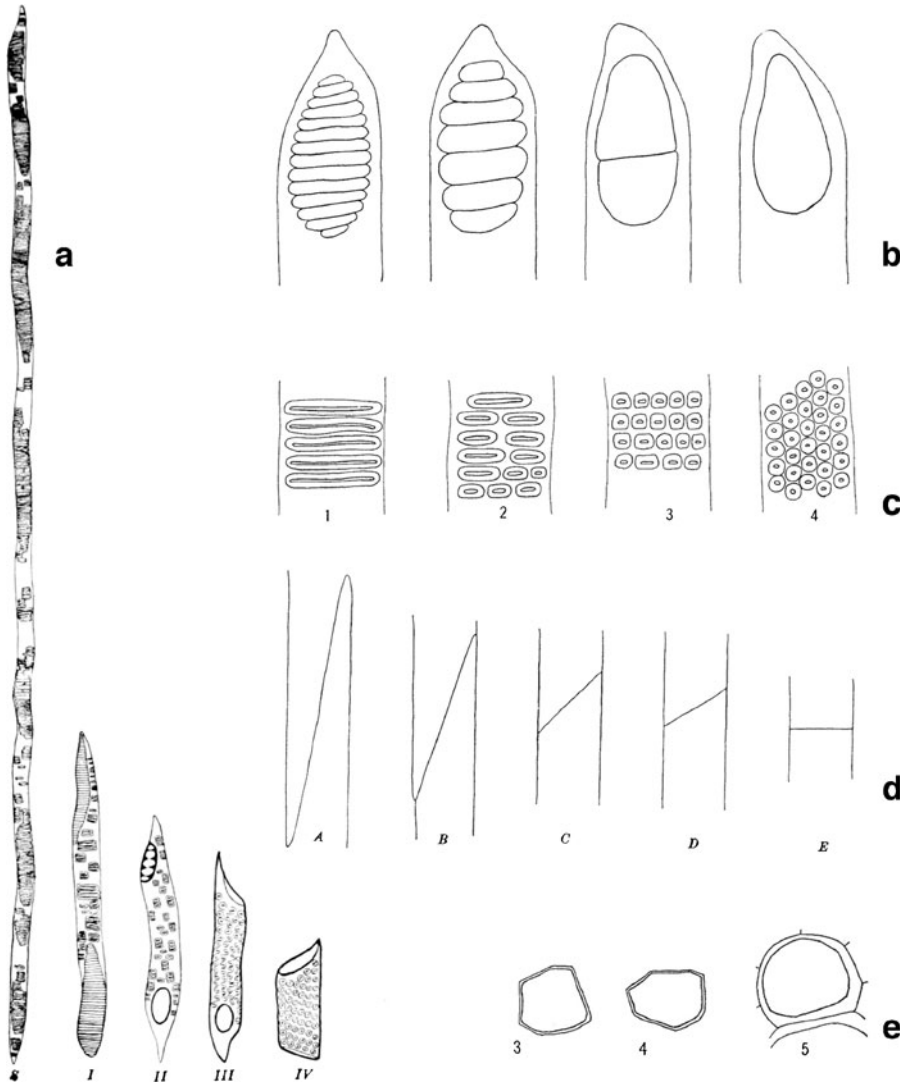
The Major Trends are a set of linear “primitive-specialized” transformation series in wood anatomical features. The Major Trends began (Table 1) with a survey of the size of the conductive cells in a very wide range of woody plants (Bailey & Tupper, 1918). The authors noticed that the conductive cells in some flowering plants shared some characteristics with those found in gymnosperms. The cells could be lined up in a continuum from cells that were similar in many features to gymnosperm cells to those that were very dissimilar (Fig. 1a). Through the 1930s, anatomists developed a list of features that distinguished “primitive,” more gymnosperm-like cells from “advanced” ones, and for the next 30 years the Trends were used as a tool for inferring phylogeny (Fig. 1b–e). Only until the 1960s was a cause finally postulated for the Trends, when Carlquist (1966, 1975) laid out the first consolidated adaptation-based framework to explain differences in wood anatomy between species (work suggesting adaptive causes for anatomical variation such as McDougall and Penfound, 1928 or Webber, 1936 was important but limited in scope and attracted no followers). Since then the Trends have become intertwined with thinking about wood and “ecology.” Even though anatomists have invoked them continuously over some ninety years, many aspects of the Trends cause confusion. For one, it is not clear how a linear primitive-advanced scheme can relate to a branched phylogeny. Confounding the bewilderment, the Trends envision ever-increasing progress toward

**Table 1** The Major Trends canon, a list of the main papers typically cited in connection with the establishment of the Major Trends of Xylem Evolution, beginning with Bailey and Tupper, 1918, the traditional starting point, and ending with Carlquist, 1966, the first paper to postulate a cause for the Trends. Morphoclines are listed from “primitive” to “advanced”

Author and year	Highlight of contribution to canon
Bailey and Tupper, 1918	established long-short primitive-advanced morphocline
Bailey and Thompson, 1918	details regarding tracheid-like vessels
Bailey, 1920	vessel elements do not elongate beyond the lengths of the fusiform cambial initials from which they are derived
Thompson, 1923	angiosperm vs gnetalean perforations
Frost, 1930a, b	tracheid-vessel transition, associations between long vessel elements and other features
Frost, 1930a, b	associations between vessel length and perforation plate type, scalariform-simple transition
Frost, 1931	scalariform-alternate lateral wall pitting series
Kribs, 1935	heterogeneous-homogenous ray type series
Kribs, 1937	diffuse scanty to vasicentric abundant axial parenchyma arrangement
Barghoorn, 1940	often cited in connection with the Major Trends, but mostly a study of ray ontogeny in “primitive” dicots
Barghoorn, 1941	ray ontogeny in “advanced” woods
Cheadle, 1943	the tracheid-vessel transition in monocots
Bailey, 1944	review of Baileyan thought
Bailey, 1953	review of Baileyan thought
Cheadle, 1953	the tracheid-vessel transition in monocots
Bailey, 1957	principles of Baileyan phylogenetics
Carlquist, 1961	coining of the term “Major Trends of Xylem Evolution”
Carlquist, 1966	first postulation of a cause for Trends, adaptation to dry habitats during radiation from moist ancestral ones

“specialization,” but this central term is rarely defined and in practice is used in a multitude of meanings.

Anatomists generally cut through the confusion to select the aspects of the Trends that they deem useful, and leave aside the rest. Although some anatomists have criticized them as being an incomplete picture of wood evolution (e.g. Herendeen et al., 1999; Horn, 2009), and at least one has rejected them (Mauseth, 1988), the Trends still guide thinking about wood (e.g. Manchester, 1979; Wheeler & Baas, 1991; Baas & Wheeler, 1996; Blokhina, 2007; Lens et al., 2008; Sano et al., 2008), and no recent textbook treatment of wood anatomy has been complete without



**Fig. 1** Major Trends morphoclines. This figure reproduces parts of original figures from Major Trends papers in which certain morphoclines, read left-to-right in these drawings, were established. **a.** Part of Bailey and Tupper's famous 1918 figure showing the primitive-specialized tracheid-vessel morphocline. "S" denotes "scalariform tracheid of *Trochodendron* or *Dioon*, not drawn to scale" (p. 191). The Roman numerals denote categories of increasingly "specialized" vessels. Where one category ends and another begins is arbitrary; moreover, the categories are polyphyletic (see text). **b.** Perforation plate morphology, from scalariform with many bars to simple. The original caption read "*Myrica inodora*, four stages showing origin of simple perforation" (Frost, 1930b, p. 201). **c.** Vessel lateral wall pitting, from scalariform to alternate; the original caption read "fig. 1, scalariform lateral pitting from *Hedycarya arborea*; fig. 2, transitional lateral pitting from *Talauma ovalis*; fig. 3, opposite lateral pitting from *Liriodendron tulipifera*; fig. 4, alternate lateral pitting from *Planera aquatica*" (Frost, 1931, p. 89). **d.** Perforation plate inclination, from highly oblique to perpendicular; original caption: "Evolution of inclination of end wall: (a) *Saurauja oldhami*, (b) *Panax edgerlegi*, (c) *Gilbertia affinis*, (d) *Diospyros virginiana*, (e) *Hicoria glabra*" (Frost, 1930b, p. 211). **e.** Vessel diameter and outline, from narrowly angular to broadly elliptical; fig. 3, *Sequoia sempervirens*, angular tracheid in transverse section; fig. 4, *Gordonia lasianthus*, angular vessel in transverse section; fig. 5, *Exothea paniculata*, common type of vessel with unevenly thickened walls" (Frost, 1930a, p. 75)

reference them (Dickison, 2000; Carlquist, 2001; Evert, 2006; Cutler et al., 2007; Beck, 2010, etc.). Major Trends issues still actively discussed include stimulating debates regarding how vessels, the conductive cells in most flowering plants, evolved, and on the reversibility of xylem evolution (Soltis et al., 2005), but some inheritances of the Trends are less constructive. For example, as I will show below, Bailey and his followers worked within a Haeckelian “ontogeny recapitulates phylogeny” framework, never citing an explicit cause for the Trends beyond a conflation of evolutionary thinking with notions of inexorable progress. This dissonance in thinking about the causal basis of wood anatomical differences between species still appears in treatments of wood evolution (e.g. Soltis et al., 2005), as do echoes of the linear hierarchy of evolutionary “levels” or “stages” of the Baileyan scheme (e.g. Feild et al., 2002).

Because of their continuing presence, it is important to examine the main assumptions of the Major Trends to help identify their profitable contributions and also where the field needs explicitly to move beyond them. I do this by identifying the assumptions and practices that underlie the Trends and attempt to clarify the multiple meanings of the key term “specialization.” This effort should be useful for comparative wood anatomy, because it can identify research priorities and rewarding directions for the field. This exercise should also be useful for those outside the field as an aid in clarifying which aspects of the Trends should be kept in mind as explicitly rejected when reading the historical wood anatomical literature, as distinguished from the ingenious inferences that the program produced and which make up part of the foundation of contemporary comparative wood anatomy. To accomplish this discussion I first need to clarify the kinds of “trends” that that are embodied by the Baileyan scheme and distinguish them from those that are not under discussion here.

### Trends in Botany: the Major Trends and Morphoclines

References to “trends” are found throughout systematics, and botany is no exception. A classic example is “Williston’s law,” the generalization that, in a group with variation in number of parts, e.g. segments, those with more or unfused segments represent the ancestral condition (Gregory, 1935; Gould, 1977; Adamowicz & Purvis, 2006), a notion that has been applied to animals and plants alike. The botanical literature is filled with linear arrangements spanning all seed plants to families to small groups of species, making it hard to overestimate their importance in botanical thought. One example is the notion of Clarke (1893) and Robertson (1916) that, in a given area, the “primitive” plants, represented by trees, flower first, followed by more and more “advanced” plants, until the culmination of the series is reached with the flowering of the annuals occupying a supposed evolutionary pinnacle. Flowering time, then, was offered as a character that could be used to diagnose relative primitiveness for the members of the flora of a given area. A major mid-century botanical trend was Corner’s “Durian Theory” (1949). Corner reasoned that, because cycads were primitive plants, the primitive angiosperms should resemble them, and selected the pachycaul papaya (*Carica*), to serve as his primitive, cycad-like angiospermal archetype. The opposite extreme, highly ramified, fine-branched trees and shrubs were considered the most advanced types of woody plants. As intermediates

between these two extremes, coarsely branched semi-pachycauls such as the Malvaean durians (*Durio*) lent their name to the theory. The theory has continued to be cited for a variety of reasons, from using it to drive or support research (e.g. Mabberley, 1974, 1982), to test interpretations of its claims of character polarity (Nyffeler & Baum, 2000), or even to deride it (Eyde, 1976). “Trends” such as Williston’s Law or the Durian theory depict graded series of morphological states and are known as morphoclines (Takhtajan, 1991). Authors such as Ehrendorfer (1973) and Takhtajan (1991) offered catalogues of botanical morphoclines running from many parts to few, trees to herbs, separate parts to fused, determinate to indeterminate inflorescences, superior to inferior ovaries, and many others. Morphoclines continue to be common in the botanical literature, where their main use has been as a tool for the inference of phylogenetic relationship (see Comstock, 1893), and the Major Trends are a perfect example of this application.

In addition to morphoclines, the word “trend” has many other meanings in biology, so it is also important to mention what the trends of interest here are not. Paleontologists study changes in character means or variances over time (McShea, 1994). Changes in means, or “driven” trends, are characterized by successive replacement of morphologies over time in a given lineage, presumably due to an external cause. “Passive” trends, in contrast, are increases in trait variance over time. For example, Cope’s rule of size increase within lineages, or the increase in plant size over time, are apparently due to an increase in the variance in size. Because smaller organisms are more numerous, have more niches available to them, and have shorter generation times, novel lineages should frequently arise from small ancestors. Following these small origins, lineages then diversify in size. In this passive trend, small species continue to arise and are not replaced by large ones but coexist with them (Wang, 2001; Gould, 2002). Another category of trend may surface when we selectively present the history of a single lineage within a branched phylogeny, such as those leading to man or horses, as linear narratives rather than one branch among many (e.g. O’Hara, 1992; Gould, 1989). Predictable relationships of virtually any sort are also often called trends. For example, frequent associations between anatomy and environment, such as vessel diameter and water availability, are often dubbed “ecological trends” (e.g. Baas et al., 1983). Despite this variation in meaning, in most cases in the botanical literature, use of the term “trend” denotes a study of morphoclines and that is the sense in which I will use the term in the rest of this paper, as I turn now to the Major Trends.

### *I.W. Bailey’s Major Trends of Xylem Evolution*

The Major Trends are a set of primitive-advanced morphoclines for characters in the wood, or secondary xylem, of flowering plants. The heart of the Major Trends are the characters related to vessel elements, the conductive cells in the majority of the flowering plants. Bailey and his followers noticed that conifers and other plants that were known to have appeared before flowering plants in the fossil record conduct water in tracheids, whereas most flowering plants do so in vessels. Bailey and his collaborators reasoned that the cell type antecedent to vessel elements was represented by tracheids and progressed via tracheid-like vessel elements to ones that were very different (Fig. 1):

“The most primitive vessels...are composed of members [elements] which closely resemble thin-walled, scalariformly pitted tracheids. Thus, the vessel-members are

long, comparatively slender in relation to their length, and (as viewed in tangential longitudinal sections of the xylem) have gradually tapered, extensively overlapping ends. They are thin-walled and angular in cross-sectional view. They differ from tracheids at functional maturity solely in the dissolution of pit membranes in a number of the bordered pit pairs in their overlapping ends...

The members of the most highly specialized vessel—in contrast to those of the most primitive ones—are short, comparatively broad for their length and tend to be oval or circular in cross-sectional view. They have truncated ends regardless of variations in their diameter. There is a single perforation at each end of the cell [Fig. 1]...

In view of such structural differences as these, it is possible to arrange the vessels of both the dicotyledons and monocotyledons in evolutionary trends of increasing specialization. It is important to bear in mind that this can be accomplished *entirely independently* of the various systems of classifying the angiosperms, thus avoiding circular arguments based upon assumptions regarding the primitive or specialized characters of various representatives of the angiosperms. In other words, primitive vessel are distinguished from specialized ones *solely* upon their own structural differences, and *entirely* without reference to the putative primitiveness of the plants in which they occur” (Bailey, 1957, p. 243–244).

The polarity of the tracheid-vessel transition and that from tracheid-like vessel elements that were long and narrow with scalariform pitting and perforation plates to short, wide elements with alternate pitting and simple perforation plates was then used to anchor inferences regarding a suite of other characters in the wood given their association with vessels of a given “level of specialization” (Table 1). In this way, in the twenty or so years following Bailey and Tupper (1918), botanists compiled a set of features in the wood that they used to infer relationships (Fig. 1), and until the 1960s the sense that the work of anatomists was largely finished pervades the literature: “Fortunately a complete phylogenetic picture of this trend of tracheary specialization is preserved among surviving representatives of the angiosperms. It is not essential to comb the rocks for missing links in the phylogenetic chains...The volumes of supporting data that have now accumulated make this evolutionary story one of the most extensive, complete, and convincing known among either plants or animals” (Bailey, 1953, p. 6). They confidently asserted that “The problem of the phylogenetic origin and specialization of vessels in the stems of woody dicotyledons can be considered as solved” (Cheadle, 1953, p. 30). Given this level of assurances in the literature, it is essential to examine the conceptual foundations of the Major Trends.

### Nine Major Trends Tenets

The following principles and practices were all essential for the development of the Major Trends. Some were invoked explicitly, such as the doctrine of Haeckelian recapitulationism, whereas others were implicit. Most, such as recapitulationism and the use of linear schemes in phylogeny reconstruction, are viewed as fallacious assumptions today and were even hotly debated during Bailey’s time.

## 1. Linear schemes to reconstruct a branched phylogeny

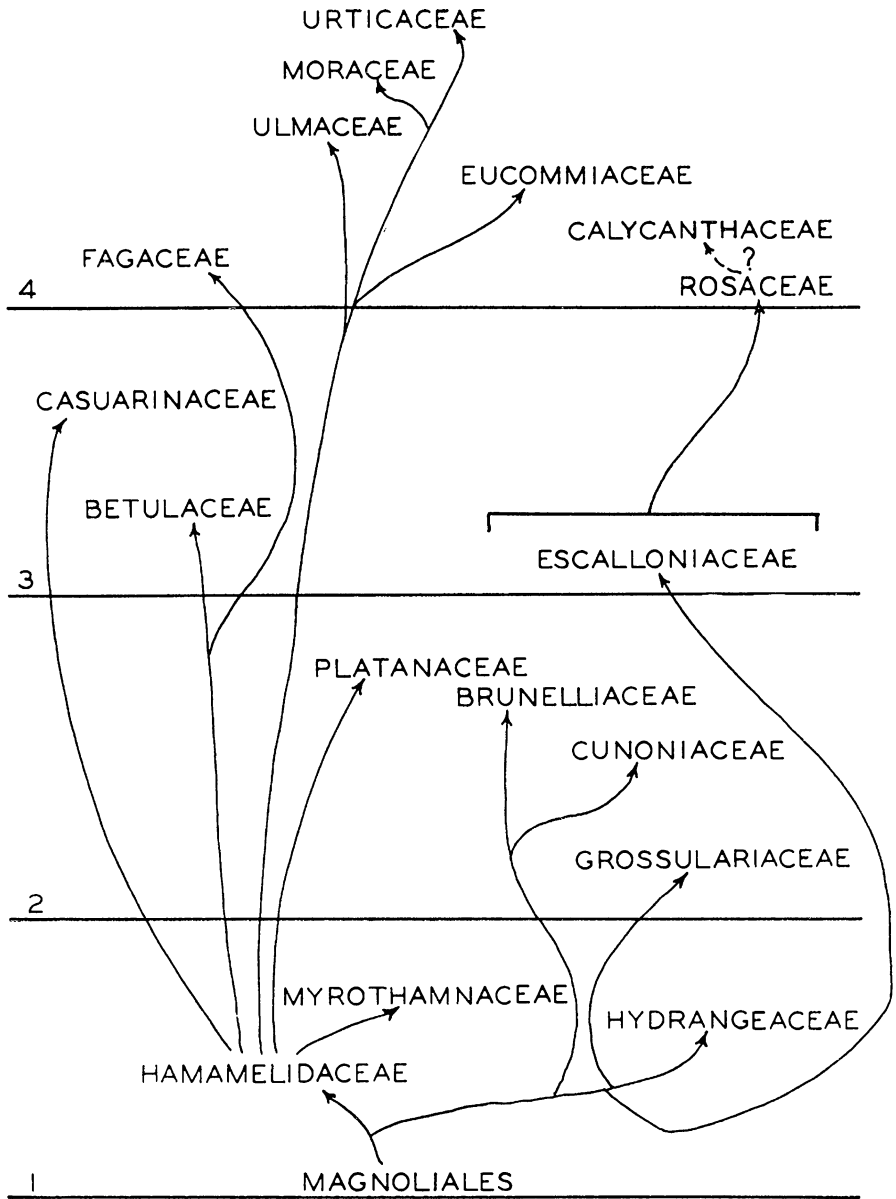
Perhaps the most conspicuous problem of linear schemes in biological systematics is that they employ linear thinking to infer what has long been known to be a branched phylogeny. One reason that this is a problem is that even if the transitions between states are all correctly inferred, a linear transformation series provides too few characters for inferring a branched phylogeny with many nodes. For example, Tippo (1938) turned to wood anatomy to help place Moraceae relative to other families. However, with only a few characters, it is difficult to obtain much resolution regarding the relationships between so many taxa. This problem is reflected in Tippo's Fig. 62, here reproduced as Fig. 2, in which the 17 families being studied are arranged into just four "levels of phylogenetic specialization" as inferred from the wood. Even in the best-case scenario, in which the transitions between states are all unequivocally inferred, the usefulness of the features included in the Major Trends was limited because the distribution of wood anatomical characters shows high levels of homoplasy, leading us to my next point.

## 2. Homoplasy = phylogeny

Virtually all of the linear schemes for the reconstruction of phylogeny, from Williston's Law to the Durian Theory to the Major Trends, employ homoplasious rather synapomorphic characters. For example, suppose it can be shown that, in all cases, hummingbird pollination has evolved from insect pollination. Just as Bailey and Tupper (1918) present a list of species with simple perforation plates (e.g. Fig. 1a), we can make a list of hummingbird-pollinated genera, e.g. *Hesperaloe* (Agavaceae), *Fuchsia* (Onagraceae), *Cestrum* (Solanaceae), *Erythrina* (Fabaceae), *Fouquieria* (Fouquieriaceae), and so on. Even though the Baileyans ingeniously postulated the polarity of the tracheid-vessel element transition, the class "all species with simple perforation plates" is not a clade, just as "all species with hummingbird-pollinated flowers" is not a clade.

The Baileyans utilized these homoplasious characters even though it was recognized by, at the latest, the time of Darwin that homoplasies are useless for the inference of relationships. Darwin (1859, p. 427) noted that "...we can clearly understand why analogical or adaptive character, although of the utmost importance to the welfare of the being, are almost valueless to the systematist." This was understood by colleagues of Bailey, e.g. "...the growth habit of plants rather than their systematic position is correlated with the climatic, geological, and zoological factors in their environment" (Sinnott, 1916, p. 292) as well as by Bailey's professor Jeffrey: "We must avoid, too, the using, for phylogenetic purposes, of characters which can be easily modified by environment" (1906, p. 297; see Wetmore 1974 for an account of Bailey's associates). Bailey and his followers were quite aware that the characters on which they based their scheme were the products of convergent evolution: "it is evident that structural similarities are not indicative necessarily of close genetic relationship...due to...parallel or convergent specializations" (Bailey, 1944, p. 426; see also Tippo, 1946; Bailey, 1953, 1957). They also recognized the phylogenetic implications of using homoplasious characters for phylogeny reconstruction, e.g. "The evidence indicates that vessels have originated from tracheids" (Cheadle, 1943, p. 17), but "...vessels must have arisen independently several times.





**Fig. 2** Linear schemes for reconstructing a branched phylogeny. Tippo's, 1938 scheme of four "levels of specialization" superimposed on a phylogeny of Moraceae and relatives. The number of character states, 4, was too few to resolve the relationships among so many groups. However, assuming that it was impossible to lower in level once attaining a higher one meant that high-low ancestor-descendant relations could be ruled out as possibilities. The original caption illustrates the arbitrary nature of the "levels": "Proposed phylogenetic relationships of families investigated in this study: (1) exclusively scalariform perforation plates; (2) scalariform and simple perforation plates; (3) simple and vestigial scalariform perforation plates; and (4) simple perforation plates" (p. 66), because the limits between categories (2) and (3) are not specified

Put in another way, some of the vesselless plants (e.g. *Sarcandra* and *Amborella*) are more closely related to other plants with vessels than they are to each other or to any other primitively vesselless forms” (Cheadle, 1953, p. 36). Because of their high levels of homoplasy, the Major Trends characters were not effective features for systematics, even though this was their principal application.

Into the mid-forties and fifties, anatomists struggled to reconcile their assertions that “the problem of wood evolution was solved” with the increasing recognition of the homoplasy of the Trends. In the mid-forties anatomists began to admit that “it is evident that structural similarities are not indicative necessarily of close genetic relationship. This is due to the fact that parallel specializations of vessels have occurred independently in diverse orders and families. Such similarities, due to parallel or convergent specializations, are not confined, however, to vascular tissue, but are of more frequent occurrence in flowers and other parts of plants than is generally recognized” (Bailey, 1944, p. 426). Bailey and his followers defended the Major Trends as a tool for inferring phylogeny in the following way: “...the evolutionary trends in the cambium and xylem of dicotyledons, when considered by themselves, have been most reliable and significant in *negations*. This is owing to the fact that plants which have retained primitive cambia and xylem cannot be derived structurally from plants which have attained uniformly high levels of structural specialization” (Bailey, 1957, p. 250). However, “Unfortunately, owing to the frequent occurrence of parallel evolutionary changes, they cannot be utilized in *positive* assertions of relationship or phylogenetic derivation...” Bailey, 1957, p. 253. This reasoning was possible only in combination with the assumption that the Trends represented irreversible evolutionary changes, a point I discuss below.

First, however, I wish to turn to the causes of homoplasy. Although the Baileyans recognized that the characters that they were studying were homoplasious, they never appealed to any process that could produce the repeated evolution of similar features, bringing me to my next point.

### 3. Evolution = progress: fusiform cambial initial length as a cause of the Trends

Part of the tradition of retaining a Baileyan veneer to comparative wood anatomy no doubt stems from the high regard in which anatomists rightly hold Bailey’s many accomplishments, arguably foremost among these the ingenious, albeit controversial (Young, 1981; Carlquist, 1987; Doyle & Endress, 2000; Feild et al., 2002; Carlquist & Schneider, 2002) inference of the polarity of the tracheid-vessel transformation and his observations on cambial behavior. Perhaps colored in this light, anatomists often seem to attribute evolutionary explanations to the Baileyans that are not there, such as when Herendeen et al. (1999) noted that “In the early and mid-1900s I. W. Bailey, Tupper, Frost, Kribs, Cheadle, and others compiled anatomical data for many angiosperm taxa, and analyses of these data documented correlations between diverse wood anatomical features, from which they hypothesized evolutionary explanations for these correlated features” (p. 280, see also De Micco et al., 2008). However, not one of the Major Trends papers (Table 1) contains anything that could be construed as an “explanation” of evolution.

Although the Baileyans used the word convergence, which implies adaptation, when it came time to discuss a driver of the Trends, they attributed size differences in mature cells across species to differences in the sizes of the cambial initial cells that

give rise to them. Changes in cambial initials were attributed to “specialization,” but the process driving specialization was not postulated before Carlquist (1966). In a 1920 paper, Bailey documented the maturation of xylem cells from their cambial precursors, establishing the idea that the lengths of vessel elements change little if at all from the lengths of the initials from which they are derived. Clearly speaking in terms of causes, Bailey (1920, p. 358) stated: “The size of the cells in the secondary xylem is determined by (1) the size of the cambial initials, and by (2) changes that take place in the derivative cells during differentiation into tracheary elements.” Cambial initial size is important because small cells can’t be derived from large initials, and ontogenetic correlation between the axial cells of the wood would seem inevitable because they are all ultimately derived from the same cambial initials. The confusion arose when these important observations were taken as sufficient to explain variation between species. Despite his impeccable ontogenetic studies, Bailey himself generated confusion from the beginning when he used the sizes of fusiform cambial initials to explain phylogenetic correlates of cell size: “...the phylogenetic shortening of vessel members is due primarily to a concomitant shortening of cambial initials...” (Bailey, 1944, p. 426). Moreover, he applied this reasoning to explain ecomorphological patterns, as when he noted that “Dwarfed and extremely xerophytic plants frequently have abnormally short vessel members owing to excessive reduction in the size of the cambial initials” (Bailey, 1944, p. 422; see also Webber, 1936; Bailey, 1957). The suggestion that tracheary cell size variation across species is explained by fusiform cambial initial cell size is reflected in the writing of numerous authors over the last 90 years (e.g. Philipson & Ward, 1965; Rock, 1972; Manchester, 1979).

The Baileyan view regarding the cause of the shortening of fusiform cambial initial length is most clearly interpreted as a notion of inexorable progress, a conflation common in Bailey’s time and often still with us today (O’Hara, 1992; Ruse, 1996). The Baileyan tradition of viewing “specialization” as inexorable progress has led to anatomists viewing adaptation and “specialization” as opposing causal explanations for the Major Trends. For example, Miller (1976) noted that “among the black walnuts, the changes in wood structure are due to latitudinal differences, which are probably related to ecological or physiological factors and not to phylogenetic specialization” (p. 375; see also Poole, 2000). Such statements can only be meaningfully interpreted from the point of view that the shortening of fusiform cambial initials is due to an inherent progressive tendency.

But Bailey’s explanatory scheme simply leaves open the question of why fusiform cambial initial length should differ through ontogeny and between species. Many explanations are possible, though current authors tend to regard differences in wood anatomy as reflecting adaptation, and cast the Trends in adaptive terms (e.g. Carlquist, 2001; Table 2). Occasional mentions of anatomy-environment correlations, such as in Bailey (1924), are only in passing, never include explicit discussions of causes and besides are never in the papers dedicated to phylogeny (Table 1). Only some fifty years after the first Major Trends paper in 1918 do we find the first suggestion that “Although major trends of xylem evolution have been established... as yet we have little information as to which factors of climate and ecology guide these trends” (Carlquist, 1966, p. 27). Carlquist’s paper ushered in the field of ecological wood anatomy, in which anatomists infer the adaptive value of anatomical features based on their repeated evolution in different lineages in similar environmental

**Table 2** Bailey's version of the Major Trends vs. the modern version, largely of Carlquist (e.g. 2001). While the visions share some elements, their differences are so prominent that they can hardly be considered the same body of thought. "Both" indicates aspects that are shared between the two versions

	Bailey	Both	Carlquist
Directionality of evolutionary change	always unidirectional from long cells to short ones along the morphoclines in Fig. 1	none	tracheid-long scalariform-short simple series accompanied lineages with tracheids or primitive vessels as they initially invaded dry habitats from ancestral wet ones; change in most features is labile, with long vessel elements being favored in moist areas and short ones in dry areas; vessel loss unlikely but possible in some cases
Cause of anatomical differences between species	differences in fusiform cambial initial length driven by "specialization" of unspecified cause	fusiform cambial initial length may be diagnostic of "division of labor" between conductive and support cells	differences in fusiform cambial initial length due to selection on adult cell size
Ontogeny recapitulates phylogeny	yes, in a strict Haeckelian sense	none	closely related species often share early ontogeny and diverge in late, but often do not, as in paedomorphic woods
Explanatory domain	phylogeny	Baileyan features may occasionally reflect phylogeny but more often are homoplasious	adaptative evolution

settings (Carlquist, 1975, 1980). However, if adaptation largely explains variation in cell size across habitats, then saying that small plants have small vessels because they have small fusiform cambial initials is akin to saying “after the advent of the Industrial Revolution, melanistic *Biston betularia* showed dark coloration due to a significant increase in the productions of dark pigmentation” rather than giving an explanation involving selection favoring dark mutants on sooty trunks.

As I discuss in the concluding section, there is surely value in asking what role cambial initial size may play in constraining or channelling wood evolution, just as there is in viewing wood evolution through an adaptive lens. All axial cells of the secondary xylem and phloem are derived from the fusiform cambial initials, so the size of the initials certainly limits the ontogenetic independence that these cells can have, and as a result, the evolutionary potential of the woody plants. On the other hand, there do seem to be clear xylem-environment associations, e.g. helical sculpture on vessels in dry areas, that likely reflect the action of natural selection. Although ontogenetic potential directly determines the array of morphologies that can be produced, there is as yet little effort to incorporate both perspectives in studies of wood evolution. In Baileyan thought, what we find instead is the spirit of Ernst Haeckel.

#### 4. Ontogeny recapitulates phylogeny

Haeckelian recapitulationism is the notion that evolutionary change occurs via the addition of stages to late ontogeny, retaining the previous stages, with the result that the adult stages of the ancestors of an organism became telescoped into its ontogeny (Gould, 1977; Richards, 2008). If this were always the case, then ontogeny would be an infallible guide to reconstructing phylogeny. Many confusing statements that mix ontogeny in phylogenetic discussions can be understood once it is clear that the Major Trends are an expression of what Bailey (1910) called “Haeckel’s law.” Frost, in particular, made explicit the Major Trends position on interpretation of ontogeny as a means for inferring phylogeny (e.g. 1930): “In view of the proof offered that the transition from the protoxylem to the secondary xylem represents a primitive to specialized sequence which is paligenetic, and the accurate portrayal this sequence gives the change from scalariform to porous perforations, there is little reason to doubt that the detailed transitions here illustrated give a connected picture of the evolution of the scalariform vessel segment from the scalariform tracheid” (1930, pp. 82–83). In the sense that Frost used the term, paligenetic ontogenies are those that recapitulate ancestral stages in the order of their phylogenetic appearance and therefore can be used to infer phylogeny; (Gould, 1977; Richards, 2008; see also the use of these terms by Thompson and Bailey 1916 and Bailey’s, 1910 discussion of recapitulation as a “canon of comparative anatomy”).

Although Haeckel was interested in inferring phylogeny, his thinking was largely linear, invoking as it did Louis Agassiz’s non-evolutionary threefold parallelism (Hyatt, 1897, Wourms, 2007). The threefold parallelism was the idea that there was a harmony of parallel linear progressions in ontogeny, across the adults of all organisms, and over time in the paleontological record. Agassiz was not an evolutionist and his parallelism was not a scheme for discovering phylogeny, and this practical deficiency, if not the stated aim, was inherited by subsequent users of the scheme. In the words of Bryant (1995): “...the threefold parallelism had no role in

delimiting taxa; it only facilitated the linear arrangements or rankings of established taxa...This epistemological framework was unchanged by Haeckel; only the causal explanation differed" (p. 207).

In this light, statements such as "The angiosperms that have been studied intensively from a developmental point of view are very limited in number and are highly specialized both as regards their growth forms and their phylogenetic level of structural modification" (Bailey, 1944, p. 427) begin to make sense: to the Baileyans, the study of ontogeny indicated the position of a species in a linear hierarchy. Realizing that the Baileyans thought of evolution as inexorable progress, the equivalence of ontogenetic explanations and evolutionary ones is more understandable. For example, "It should be noted in passing that the phylogenetic transitions between tapered and truncated vessel members may be considerably accelerated in the primary xylem particularly in the case of helically thickened, tracheary elements. Two types of developmental phenomena are significant in this regard..." (Bailey, 1944, p. 423). The rest of the paragraph is not at all about "phylogenetic transitions" but ontogenetic mechanisms, and at no point does Bailey clarify the connection between his ontogenetic observations and any phylogenetic issue. This reasoning makes no sense except in a recapitulationist framework in which ontogeny is a direct reflection of phylogenetic transitions, and in which phylogenetic transitions are a manifestation of steady, inevitable progress up an evolutionary ladder.

The role of ontogeny in evolution was a very active field of thought in the early part of the 20th century (Amundson, 2005). Haeckel's "biogenetic law" that the phylogeny of all organisms are reflected in the stages of their ontogeny was being energetically rejected in the period immediately preceding the Major Trends (see De Beer, 1930; Holmes, 1944; Gould, 1977). Russell (1916), for example, provides a long list of reasons to reject the biogenetic law as universal, including the existence of heterochronic processes such as paedomorphosis. Not only is there no trace of this controversy in the writings of Bailey and his associates, but there is a stretch of some fifty years throughout which processes such as heterochrony are not even mentioned in connection with the Trends (Carlquist, 1962, cf. Chrysler, 1937). Instead, we find the doctrine of irreversibility.

## 5. Irreversibility

That the evolutionary transitions in the wood be unidirectional is required for using the Baileyan trends in inferring phylogeny. This is explained by Cheadle (1956), who notes that "Because of [xylem's] unidirectional development [= evolution], it can always be employed as a negating factor; for example, a plant with highly specialized vessels in the secondary xylem could not have given rise to one with only normal tracheids in secondary xylem" (p.726). Irreversibility is the aspect of the Trends that has been most been discussed and subjected to testing, with findings suggesting that some traits are highly labile whereas the lability of others, especially perforation plate morphology, remains controversial (e.g. Baas & Wheeler, 1996; Carlquist, 1980, 1987; Young, 1981; Bradford & Barnes, 2001; Carlquist & Schneider, 2002; Feild et al., 2002; Soltis et al., 2005; Horn, 2009). Potentially contradicting the Baileyan's faith in irreversibility was that the Trends could be detected at any phylogenetic level, thinking that can be called fractality.

## 6. Fractality

The tracheid-long scalariform-short simple vessel element transformation series has been invoked over and over at many phylogenetic scales. Bailey noted that “In revealing salient trends of evolutionary specialization by analyses of data obtained from the dicotyledons *as-a-whole*, variations due to obtaining specimens from different parts of the plant, from plants of different growth rates, from genetically different taxa, etc., tend to neutralize one another. In addition, various localized, divergent trends of specialization do not obscure or confuse the major trends of evolution in the dicotyledons *as-a-whole*. However, when one becomes concerned with taxa of decreasing size, viz. families, subfamilies, tribes, genera and species, such variations and deviations become increasingly significant.” (Bailey, 1957, pp. 250–251). Despite this and other emphatic statements that the Trends emerge only upon examination of the dicots in their totality, perhaps the most frequent use of the Trends has not been with respect to dicots “as a whole” at all, but instead in genera or families, even, the quote above notwithstanding, by Bailey himself, e.g. “...there are salient trends of phylogenetic specialization in the vessels of the Icacinaceae which closely parallel those that occur in the other families and in the dicotyledons as a whole,” (Bailey & Howard, 1941, p. 174; Lens et al., 2008 invoke nearly identical reasoning).

It is hard to see how unidirectional, irreversible “trends” of the sort the Baileyans envisioned could be operating at the level of dicots as a whole, and in parallel between individual families. If the Trends occurred at the level of the “dicots as a whole,” then we should see the lower nodes of the angiosperm phylogeny characterized by “primitive” anatomy and the tips “specialized” with a perfect gradation in between. In such a situation, the morphological range necessary to line up features in a morphocline would be absent within any given clade. In the case of coetaneous clades with trends occurring “simultaneously and in parallel,” then each clade would show the same pattern and the Trends would be useless for inferring phylogeny at the level of the “dicots as a whole.” Fractality is thus an element of the Baileyan scheme that has always been internally contradictory in practice. The lack of correspondence to phylogeny of the Trends also illustrates the essentialistic nature of the categories of specialization the Baileyans constructed.

## 7. Essentialism

It is hard to extract useful biological information from the Great Chain of Being or *scala naturae* (Lovejoy, 1936) because many disparate elements are grouped together at a given level based on the possession of one or a few key features. Like Biblical categories such as “fish” which include anything that swims, the categories and indeed “levels of specialization” are not only based on characters that do not reflect relationship but where one category ends and another begins is arbitrary. For example, Bailey and Tupper (1918) note that “...four categories of vessels have been recognized. In group I, the perforations are prevailing scalariform; in group II, intermediate between scalariform and porous; and in groups III and IV, prevailing porous...The vessel-segments in group III differ from those in group IV in having well marked tapering ends, thus resembling tracheids in general outline” (p. 190). The category “s” of Bailey and Tupper (1918) includes the clearly unrelated cycad *Dioon*

and the angiosperm *Trochodendron*; their category “I” includes such unrelated genera as *Casuarina*, *Magnolia*, *Kadsura*, *Virola*, *Cassipourea*, *Arbutus*, etc., illustrating how these arbitrarily defined categories result in artificial groupings (Fig. 1a). Bryant (1995) could be speaking specifically about the artificiality of the Baileyan scheme’s categories when he notes that “These directional evolutionary scenarios are based on linear hierarchies of taxa defined by particular combinations of characters states rather than by ancestry...” (p. 209).

Another expression of essentialism has been dubbed statistical essentialism, which regards variation as noise and mean values to represent reality emerging from the noise (Mayr, 1982). Darwinian thought eliminated the tenability of statistical essentialism; natural variation is real and important, and mean values are constructs. Differences in height between people are real, and mean height is an artificial, if often useful, construct. Perhaps no better example of statistical essentialism can be found than “...vessel members fluctuate more or less in size and structure within the limits of a single plant...Such aberrations and internal variations are largely neutralized, and the major trends of phylogenetic specialization are clearly revealed by the statistical analysis of numerous randomly selected samples from a wide range of dictyoledons [sic]” (Bailey, 1944, p. 422). Cheadle (1956) sneered that “Frost dignified these aberrations by using them as the basis for a third concept called exceptions. It perhaps was necessary to so emphasize these aberrations, because some investigators chance upon exceptional forms and, on the basis of these relatively minor irregularities, love to dispute generalizations they have never really understood” (p. 725).

However, *pace* Cheadle the distribution of wood cell variation is real, and has significant functional consequences that have only begun to be explored. For example, rather than representing “noise” and “aberrations”, it seems just as plausible that selection should favor very high variation in features such as libriform fiber length; high variability in length could be favored by selection in that it would diminish the occurrence of fracture planes that would result if cells were aligned, while still resulting in mechanical and hydraulic characteristics that meet the needs of the stem given its size. It is of course true that the study of large datasets can reveal valuable information based on patterns of trait covariation. However, such analyses lead to inferences regarding the dynamics of ontogeny or adaptation, not phylogeny. Another example of how the Baileyans thought about causes is the case of the refugium hypothesis.

#### 8. Doctrines vs. exploring hypotheses: The “refugium hypothesis”

Bailey (e.g. 1944) and others have suggested complex scenarios that involve “primitive” characters being retained in primary xylem and the first-produced secondary xylem. Although the Baileyans never mention a mechanism, the emphasis on “retention” and the ideas that these features require a “refuge” to persist implies that these features are maintained in the face of selection pressure that should reasonably be expected to eliminate them; otherwise, they could simply be regarded as features whose presence is favored by natural selection, as one would view many other features (for views on the importance of trait historical genesis in understanding adaptation see Gould & Vrba, 1982; Larson & Losos, 1996).

Just as with irreversibility, the idea of refugia is a hypothesis to be tested against alternatives, not a dogma to be accepted. Bailey’s professor Jeffrey understood this



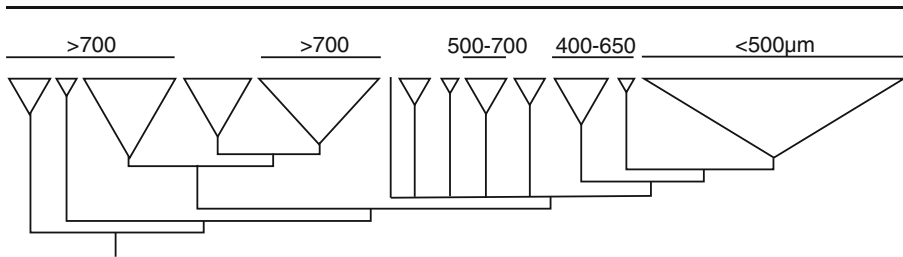
and in 1924 wrote “It is plausibly suggested that the undoubted presence of gill-arches in the mammalian embryos is an embryonic response in the maternal amniotic fluid. In other words, it is asserted that what the morphologist and the paleontologist explain in terms of the biogenetic law as vestiges of a former state represent merely a larval adaptation...” (p. 531), the point being that it is important to consider a variety of alternative explanations. In the same way, the distribution of xylem features might also be explained by adaptation to current functional contexts, with statements such as Mauseth’s (1988) decidedly rare in the literature: “The primary xylem was even described as being a refugium of primitive characters rather than being a tissue that is highly adapted to the needs of seedlings, leaves, flowers, fruits, and the tips of roots and shoots” (Mauseth, 1988, p. 124; see also Carlquist, 1975). Vestigiality, like irreversibility, is at best a hypothesis to be tested against competing ones, rather than a rule of comparative anatomy.

### 9. Modern Baileyanism and “telling the tree”

The expression “telling the tree” is O’Hara’s (1992) term for the tendency to read a linear story into a branched phylogeny in which no such story is inherent. As molecular phylogenies have become available, wood anatomists have used them to tell Baileyan stories where there may be none. Phylogenies are diagrams of nested hierarchies of synapomorphies. Successive levels of nesting in the tree denote smaller and smaller sets of species, each of which shares a given set of synapomorphic features. The two clades that descend from a common ancestor are known as sister taxa; by definition each possesses some feature that the other does not. There is no way of saying that one sister lineage is older than the other because, as products of the same branching event, the two diverged at exactly the same time. A phylogenetic tree thus provides us with a diagram of a series of successive sister taxa reflecting the nested hierarchy of synapomorphies.

Although these phylogenetic precepts are universally acknowledged, there is nevertheless a tendency to find linear stories that go beyond the information strictly contained in the phylogeny. This tendency usually takes the following form: the features of small clades or single species that are sister to large clades are taken as “ancestral” to the large ones (Krell & Cranston, 2004; Crisp & Cook, 2005). These clades are often referred to as “basal” to the large clades, even though the two groups diverged at the same moment. Examples of this tendency include Zahn et al. (2005), who referred to *Amborella* as the “basalmost angiosperm” or the title of Brown’s, 2008 account of the sequencing of the platypus genome placing the odd mammal at an “end of evolution[’s] tree.” Scientists who tell trees arrange them such that the succession of sister taxa allows recounting of a single linear story, often reading the tree left to right as in Fig. 3 (see O’Hara, 1992).

Wood anatomists may tell Baileyan stories in phylogenetic trees. For example, Lens et al. (2008) place vessel element length, a classic Baileyan feature, in the context of the molecular phylogeny of Simões et al. (2007), here simplified in Fig. 3. Lens et al. note that “Vessel element length strikingly follows the generally accepted wood trends sensu Bailey and Tupper (1918)” (p. 1211), and seem to be reading a linear story where there are only successive sister groups when they describe the tree as follows: “Compared to the rest of the family, Rauvolfioideae form a basal grade..., supporting its presumably ‘primitive’ features based on morphological observations...”



**Fig. 3** Reading Baileyan progress into phylogenies. Lens et al. (2008) discussed the distribution of vessel element lengths (numbers above clades are lengths in micrometers) in Rauvolfioideae of Apocynaceae in the context of the molecular phylogenetic hypothesis of Simões et al. (2007). Lens et al. found evidence of Baileyan progress in the shortening of vessel elements from the “basal” clades to the “most derived taxa.” In this group, the clades with the shortest vessel elements could plausibly be seen to be derived from ancestors with longer ones

The tribe Aspidospermeae is the earliest branching clade, followed by Alstonieae. The next clade is formed by a group including Vinceae” etc. (p. 1201). The interpretation of Baileyan progress may therefore stem from a reading of the tree as though the horizontal axis in Fig. 3 represented a temporal axis.

On the other hand, authors including Lens et al. (2008) have made the intriguing observation that it is fairly common to observe groups in which a clade with “primitive” features is small and is sister to a large clade with “specialized” wood. For example, Carlquist and Schneider (2004) examined the remnants of primary membranes in perforations of various groups. Tracheids have intact primary membranes, so the more primary membrane remains in perforations, the more tracheid like the cell could be considered. The authors noted that “Families with pit membrane presence in perforations are scattered throughout phylogenetic trees, but they occur most often in basal branches [i.e. small groups that are sister to large ones] of major clades (superorders) or as basal branches of orders within the major clades.” (p. 41; see also Carlquist, 2010). This pattern certainly seems conspicuous and standing in need of explanation. Because they involve sister taxon comparisons, explanations cannot involve primitive-advanced narratives, temporal or otherwise, of the Baileyan tradition. Given a widespread tendency to read linear stories into trees, and the long tradition of linear Baileyan thinking, it seems reasonable to be vigilant for tendencies to seek explanations for patterns such as these by telling the tree in terms of Baileyan “specialization.” To conclude my Baileyan survey, I now turn to the meaning of this term.

### The Diversification of Specialization

In the quotes of the Major Trends authors offered above, there are some twenty references to the notion of “specialization.” From the earliest of the Major Trends papers, the wood anatomical literature is filled with terms such as “phylogenetic specialization,” “structural specialization,” “levels of specialization,” and “evolutionary specialization.” Despite being a central notion to Major Trends thinking, there is often a lack of clarity with regard to what “specialization” actually means. None of the uses just listed seems to correspond to specialization in the sense of a restriction in organismal role, e.g. *Phoradendron* is specialized for life as a parasite or *Darlingtonia*

grows only on ultrabasic substrates, which is perhaps the most widespread use of the term. However, the term is crucial as the hallmark of Major Trends thought, and reference to “specialization” in the wood anatomical literature to the present day almost always diagnoses thinking along the lines of the Major Trends. To aid in understanding what an author is discussing when using the term, I attempt to distinguish between and to classify six different senses of “specialization” common in the wood anatomical literature.

### 1. Specialization = division of labor

The most useful application of “specialization” in the Major Trends papers refers to differentiation in the roles of tracheary elements from tracheids which support the plant and conduct water into separate support (fiber-tracheids, libriform fibers) and conductive cells (vessel elements). Individual cell types thus are regarded as specialized for a specific role, either support or conduction: “...with increasing specialization certain tracheary cells become highly modified and serve principally as conductors of liquids, whereas others gradually cease to serve in that capacity, and become modified as mechanical or skeletal elements” (Bailey & Tupper, 1918, p. 193). This is the sense used by recent authors such as Evert (2006), in statements such as “Functional specialization finds its expression in morphological differences among cells, a feature that accounts for the complexity of structure in a multicellular organism” (p. 17). Specialization in this sense as used by the Major Trends authors may be a static description of the degree to which the cells may be imagined to function distinctly in a given species, or it may be “temporalized” (cf. Lovejoy, 1936), wherein different stages describe a temporal sequence through which this separation of functions occurred, although, as mentioned above, no mechanism driving this separation was ever invoked by the Major Trends authors.

### 2. Specialization = relative position on a linear hierarchy

An extremely common sense of “specialization” in the Major Trends literature refers to levels in a linear hierarchy, and it is this sense of specialization that the Major Trends authors had in mind when discussing “successive phylogenetic levels” (Bailey, 1944, p. 426). For example, Tippe (1938) used this conception of specialization in an effort to infer the relationships among a large group of flowering plant families: “The Betulaceae are on a lower plane of anatomical specialization than the Casuarinaceae... Some of the genera are as high as *Casuarina*... whereas most of the genera are considerably lower. The Betulaceae are lower than the Casuarinaceae... [whereas] the Casuarinaceae seem more primitive in certain ways, for they have tracheids, a lower type of intervacular pitting, and heterogeneous IIB rays” (p. 37). This is the sense that is implied in statements such as “This foundation has provided the comparative anatomist, taxonomist, and evolutionist with measuring devices for gauging the relative extent of evolutionary progress among the spermatophytes” (Stern, 1978, p. 34) or “in the least advanced plants, if vessels are developed at all, they are found in the root only, and not in the stem or the leaf. The next stage of advancement is for vessels to occur in the root and the stem, and in the most advanced plants vessels occur in the root, the stem and the leaf” (Cutler et al., 2007, p. 54). As with sense 1, this sense can also be used as a static description, but also with a time dimension, with the notion that one level antecedes the other. This use of “specialization” is one of the

most pernicious aspects of the Major Trends as well as one of the most persistent. Thinking in terms of advancement on a linear scheme recalls the Great Chain of Being, in which all of nature, including living and non-living things, angels, and God, were linked in a single infinitely graded series of increasing perfection (Lovejoy, 1936), a notion springing more from the human bias to seek indications of linear progress rather than any feature of the natural world (Bryant, 1995).

### 3. Specialization = uncommon homoplasies

Sometimes “specialization” appears to refer to structures that are uncommon and restricted to one or few taxa, which may or may not be related to one another. An example of this sense is the statement of Kribs (1935) that “The so-called aggregate ray is a specialization which occurs sporadically. It is an offshoot from the main line of structural specialization [sense 2] in rays.” (p. 556). This is not sense 1 (division of labor) because there is no reference to differentiation of roles between cell types, and it is not sense 2 (position on a linear hierarchy) because the feature is an “offshoot” and not part of a linear hierarchy. Instead, this use refers to a homoplasious anatomical feature that is uncommon and can be found occasionally in various families (Carlquist, 2001).

### 4. Specialization = synapomorphy

Uncommon features can also be apomorphic and diagnose groups of related species. An example of this sense may be Soffiatti and Angyalossy (2009), when they note that “...basal genera...have only ordinary fibrous wood, similar to *Pere-skia*, with no apparent specialization” (p. 31). The xylem in the cacti referred to by these authors does have “division of labor” in that they bear both vessels and libriform fibers, so this statement cannot represent sense 1, and it is not sense 2 because there is no reference to a linear hierarchy. Instead, the authors seem to refer by “specialization” to parenchymatization of xylem and associated features that characterize many cacti, some of which seem likely synapomorphic of clades within that group. Unequivocal in the sense of synapomorphy is this statement by van Vliet and Baas (1984): “Ideally one would like to construct a phylogenetic system for the Myrtales, based on the occurrence of shared, uniquely derived specializations” (p. 794).

### 5. Specialization = evolution

Some statements by the Major Trends authors are difficult to place in the categories above and seem to be simply synonyms for evolutionary change. For example, Frost (1930a) says that “In conclusion, while these genera [*Trochodendron*, *Tetracentron*, and *Drimys*] may well represent a blind line of specialization, there is every indication that they still retain many of the characteristics of the plants which gave rise to the dicotyledons as we now know them, and that the scalariform tracheids of their primary wood are very similar to the type which gave rise to the vessel segment and thereby the vessel” (pp. 85–86). I have classified this sort of use here because the genera Frost referred to have only tracheids in their wood, with each cell contributing to water conduction and mechanical support. In these genera there is no “division of labor” and thus no “specialization” in sense 1. If it is sense 2, it is not clear what the linear hierarchy might be. It is not sense 3 because Frost refers not to unusual or apomorphic characteristics but to features that are plesiomorphic in the Baileyan

scheme. It is also not a synonym for adaptation (sense 6), because Frost does not imply the action of selection for the patterns observed. It seems possible that Frost is referring to specialization of the type in the example of *Phoradendron* or *Darlingtonia* above, but he never specifies what sort of highly specialized lifestyle these plants might lead. They are moist forest residents, but this hardly seems grounds for declaring them a “blind line” on this basis alone. As a result, it seems safest to conclude that in this and uses like it the authors are referring to “specialization” simply as a synonym for “evolution.”

#### 6. Specialization = (an) adaptation

Given the prolific use of the term, the use of “specialization” as a synonym for adaptation would seem reasonable to expect. Because the authors refer to a structure-function-environment relationship, an example may be “...before major changes in morphology and architecture occurred, cacti already had traits indicating some specializations to live in water-limited environments” (Soffiatti & Angyalossy, 2009, p. 27). Likewise, “Several specialized mechanisms for accommodating girth increase evolved: tangential interarea expansion in *Sigillaria* and *Synchysiodendron*, interarea fissuring in *Diaphorodendron*, and subcushion cellular expansion in *Lepidodendron*” (Bateman et al., 1992, p. 541) could also be construed as referring to adaptation, but on the whole unequivocal references that equate Baileyan specialization as adaptation are rare.

“Specialization” causes a great deal of confusion because the meanings described above are often used in the same paper, and sometimes in the same sentence, e.g. in the phrase “phylogenetic level [sense 2] of structural modification [sense 1].” (Bailey, 1944, p. 427). Similarly, Cutler et al. (2007) say that “This division of labour is seen as a specialization [sense 1], or advance [sense 2]” (p. 38).

I suggest that none of these uses of the term are justified and that given the confusing history of the term in comparative wood anatomy that we should avoid its use. The notion of a “division of labor” certainly seems useful, and is in agreement with the greater literature on the correlates of organismal complexity, in which greater numbers of cell types seem to correlate with increases in functional complexity (e.g. Buss, 1987; Bonner, 2006). However, to what extent different xylem cell types perform “functions” separately is an empirical issue, and it is not clear that vessels participate only in water conduction and not in mechanical support and that fibers participate only in mechanical support. In fact, recent studies suggest that selection favoring cavitation resistance affects imperforate tracheary elements as well as vessels (Hacke & Sperry, 2001; Jacobsen et al., 2007). The approach of Poorter et al. (2010) seems a productive one, in which functional differences are correlated with different proportions of different cell types. With respect to sense 2, as manifested by uses such as “degree of specialization,” “level of specialization,” and “phylogenetic specialization,” there would seem to be nothing gained in any context by reference to an imaginary linear hierarchy. The other uses of “specialization”—evolution, adaptation, apomorphy, or uncommon features—are synonyms of existing terms or are simply vague. When a term already exists in the literature with a specific connotation, it is hard to see what advantage is gained by applying a different, vaguer term. There would thus seem to be little reason to use the term “specialization” in any situation in

comparative wood anatomy, and, given its long history of fuzzy meaning, it seems best to make every effort to avoid the term altogether.

The series of conceptual disconnects within the Baileyan scheme, including confusion regarding the meaning of specialization as well as points such as linearity, fractality, and the Haeckelian worldview, are certainly a large part of why wood anatomy sat so long on the sidelines of evolutionary study, where to some extent it continues underrepresented. A prime example is the period during which Bailey and his followers were formulating the scheme. The time after Darwin in the late 1800s leading up to the Modern Synthesis of the 1930s and 1940s was a remarkably fertile time of intellectual exploration in evolutionary biology. The role of natural selection versus internal factors driving directional evolutionary change was a subject of keen debate (e.g. Eimer, 1898; Ruthven, 1909, etc., see Shanahan, 2004), and one in which wood anatomical data could have had an important role. Instead, not only did anatomists have no part in this debate, there is no trace of it in the anatomical literature of the time. Another striking example is the debate regarding the magnitude of evolutionary change, with Darwinians insisting that all change is the accumulation of infinitesimal increments and macromutationists such as De Vries advocating large changes. The Baileyans must have known of this controversy, because W. Tupper, Bailey's coauthor on the seminal Bailey and Tupper (1918), had previously worked on *Oenothera* (Tupper & Bartlett, 1916), a plant that was of major interest precisely because of the work of de Vries, which seemed to provide evidence against gradualism (de Vries, 1905; Allen, 1969). Bailey must, therefore, have been aware of the gradualism-saltationism/macromutation debate. Given that the Trends describe a perfectly graded series, Bailey would seem to have been a firm partisan of gradualism. But no trace of the debate can be found in his writings or those of his followers, no argument for or against gradualism, not even an explanation regarding why the steps in the Major Trends should be smooth. Similarly, the irreversibility or possibility of "undeviating" evolution in linear trends was a major point of contention at the time (e.g. Gregory, 1935), but this issue, essential for the Baileyan scheme, was never open to discussion. Based as they were on a conceptual framework largely out of date at their inception, adherence to the Major Trends drained wood anatomy of the chance to participate in the major issues of the day. To avoid repeating this fate, it is important to ask what wood anatomy might look like without the Trends.

### **Conclusion: Shedding Comparative Wood Anatomy of its Baileyan Baggage**

The prevailing view among wood anatomists regarding the Trends appears to be the following (see Carlquist, 2001). Angiosperms originated with tracheids or tracheid-like vessel elements. As they exploded across the landscape and invaded ever drier habitats, natural selection favored shorter, wider, more conductively efficient vessels. Some species of many clades invaded drier habitats, evolving simple perforation plates, whereas others retained scalariform plates as they remained in moist ancestral ones, and this is likely why many clades span the range from "primitive" to "specialized." Simple perforation plates are not selected against in moist habitats, so once they have been derived through invasion of dry habitats, these groups are free to re-invade moist ones and do not re-evolve scalariform perforation plates. Most vesselless

angiosperms or those with tracheid-like vessel elements have likely occupied moist habitats since the origin of the group. As species shift back and forth from dry to moist habitats, many features are free to vary, such as vessel diameter or element length. However, only species with very long scalariform perforation plates and tracheid like vessel elements could conceivably experience vessel loss and reversion to exclusively tracheid bearing wood. If we compare this view of the Major Trends with Bailey's version (Table 2), we can see that today's view bears virtually no resemblance to the Trends of Bailey. As a result, it is incorrect to think of the Baileyan trends of Bailey as current in present day thinking about wood evolution. What I wish to show in this section is that testing ideas regarding wood evolution does not require the Baileyan scheme in any form, that the Baileyanism of 1918–1957 can make little contribution to phylogeny reconstruction, has nothing to say regarding adaptation, and that subsequent views that purport to explain the Trends can in fact be formulated entirely without reference to Baileyan specialization.

With regard to the main goal of the Baileyan scheme, the inference of phylogeny, O'Hara (1988) provides a relevant exhortation: "Biologists must free themselves from the ontogenetic view of evolution, and from linear evolutionary narratives. The evolutionary narratives of the future must branch...When we rewrite our evolutionary histories in branched form the absurdity of notions of evolutionary progress and of the 'ontogeny' of taxa will be self-evident. Both of these false concepts arise out of our expectation that the central subject of an evolutionary history is a linear individual, instead of a branched tree" (p. 153). O'Hara's observations help us to separate the useful inferences regarding character polarity based on outgroup comparison that the Baileyanists have bequeathed us from the questionable ones based on linear recapitulationist notions of "specialization". It seems very likely the case that vessel elements are derived from tracheids, which would make the polarity of the tracheid-vessel element transition an example of outgroup comparison. Likewise, that simple perforation plates were first derived from scalariform ones also seems reasonable. Ultimately, however, and as pointed out by such workers as Herendeen et al. (1999), the most meaningful pattern that can be documented is the distribution of variation with respect to a robust phylogeny. Although extinction and homoplasy may make some issues difficult or impossible to resolve, careful study of anatomical characters in a phylogenetic context is the only way that putative anatomical synapomorphies can be identified (Donoghue, 1989; Carlquist & Schneider, 2002, see Rieppel & Kearney, 2002).

Much work certainly remains for systematic plant morphologists if we are to identify structural synapomorphies. Terms such as "vessel elements" and "libriform fibers" represent artificial categories if vessels and fibers have been derived various times, as the Major Trends and subsequent authors suggest. This is in contrast to the situation in animals, in which named structures generally represent features unique in the history of life, that is, synapomorphies (Wagner, 1989; Griffiths, 2007). The tetrapod femur, for example, is such a named structure that characterizes a single clade in the tree of life. As the likely products of convergent evolution, names such as "vessel elements" or "libriform fibers" cannot be synapomorphies, and as a result the naming of structures in plant and animal systematics could not be more different. Identifying which features are synapomorphic or convergent on the plant tree of life would require a massive rethinking of all the homoplasious categories that may be

closer to the idealistic morphology in the tradition of Goethe, Troll, and indeed Bailey, than to the ideals of current systematic biology. This would seem to be the sense of Herendeen et al. (1999) when they note that “The focus on general evolutionary trends rather than on analyzing character distribution patterns in a cladistic context obscures a more detailed understanding. Patterns of character evolution, including the assertions of irreversibility, need to be tested through cladistic analyses” (p. 279; see also Alverson et al., 1999; Carlquist & Schneider, 2002).

As distinct from the reconstruction of phylogeny, with respect to the causes of wood anatomical variation, abandoning the Trends means that wood anatomy can be incorporated into the study of the origin of biological diversity and treated as any other set of characters. The study of morphological form attempts to identify the different contributions of various factors in producing a given range of variation, such as adaptation by natural selection, potentialities and constraints of development systems, and the role of historical accident (Gould, 2002; Shanahan, 2004), a field that is only burdened by thinking in linear schemes. For example, searching for environment-anatomy correlations can be carried out, in fact is best done, without any reference to the Baileyan scheme. The generalization that, all things being equal, natural selection should favor narrow, cavitation resistant vessels in dry areas can be formulated, tested, and interpreted without ever referring to Baileyan thinking. For example, Mauseth (1988) explains the motivation of functional wood anatomy with no reference to Baileyan thinking at all: “...the reason that different parts of a plant have different types of vessel elements and perforation plates is that they have distinct requirements with regard to the amount of water that must be transported, the tension it might be under, and the dangers of cavitation” (p. 124). Carlquist (2007) lays out a clear association between habitat and vessel element length when he notes that “In most dicotyledons, vessel element length is markedly less in species of arid habitats than in species of mesic habitats” (p. 17). Although he was discussing vessel element length, perhaps the central Baileyan feature, to note the pattern of anatomy-environment association and to generate hypotheses regarding its origin and maintenance Carlquist had no need to recur to any facet whatsoever of the Baileyan scheme. The question of adaptation in wood is therefore not “why is there inexorable unidirectional progress in wood anatomical evolution?” but instead “what anatomy-environment correlations do we observe and why?”

With regard to the role of ontogeny in wood evolution, Major Trends authors were surely correct with assertions such as “In the case of wood rays the various types are derived phylogenetically by consecutive series of modified ontogenies” (Barghoorn, 1940, p. 918), and that morphological diversity is the result of a “phylogeny of modified ontogenies” (Bailey, 1944, pp. 424, 427). The study of ontogenetic modification in evolution is central to understanding how the diversity of anatomical modes observed has been generated (Chaffey et al., 2002). Because the cells of wood are produced in concentric rings and maintain their relative positions permanently, it is possible to reconstruct the entire history of ontogenetic decisions that a tree has made. This property offers an unparalleled and vastly underutilized system for studying the evolution of ontogeny (Carlquist, 1962, 2009; Olson 2007, Hearn, 2009).

There are many approaches to the study of why organisms and their parts display the range of shapes and sizes that they do. As just mentioned, wood anatomy has had two main schools, the Baileyan, in which causes are not explicitly discussed beyond the



effect of cambial initial size, and the adaptationist, in which “functional adaptations... can largely explain the high incidence of parallelism in xylem evolution” (Baas & Wheeler, 1996, p. 351). These approaches are most effective when used in combination. Wood shows patterns of homoplasy that plausibly seem related to the evolution of similar adaptive responses in similar environments, e.g. the tendency for plants in dry areas to have narrow vessels. However, natural selection is only part of an account of form, because the potentialities of ontogeny determine what features can be produced in the first place. In this context, interest in the sizes of fusiform cambial initials is justified, as a directing factor on the morphologies that can be produced: because all axial cell types in secondary xylem as well as phloem are ultimately derived from fusiform initials, there is a limit to the ontogenetic independence between cell types. Selection for very long imperforate cells could be limited by selection for shorter vessel elements or even phloem cells. The ontogenetic dependence between xylem cell types thus could act as a “brake” to selection, possibly limiting the space of xylem phenotypes that can be produced (see Olson & Rosell 2006). Another important issue is the degree to which homoplasy in wood reflects convergence or parallelism, which the Baileyans seem to have used as synonyms. However, convergence is generally regarded as indicating similar adaptive responses to similar environments having started from different ancestral states. Parallelism, on the other hand, suggests biases in the possibilities of ontogenetic evolution that make similar evolutionary transitions probable across species (though see Scotland, 2011). Although both terms have often been used in connection with xylem, to what extent both tendencies may operate in xylem evolution has never been addressed. Finally, exploration of how plants fill the space of morphological possibilities is sorely needed to help identify where the limits of ontogenetic possibility lie in the woody plants and thus the domain in which selection may act (Olson, 2012). Exemplary in this regard are works such as Carlquist’s (1975) monocot xylem eco-morpho-space (his Fig. 9, p. 115), Niklas’s (1999) exploration of the factors that may contribute to habit diversification in land plants, and Wilson and Knoll’s (2010) exploration of the space of tracheid-based stem constructions in extinct and extant plants.

In contrast to these promising approaches, the Trends have no role to play in modern comparative wood anatomy. They must be replaced in systematic wood anatomy by careful structural study of the characters in a phylogenetic framework to identify the nested hierarchy of synapomorphies that characterizes the plants, an effort that can be, and should be, carried out entirely free of thinking in terms of “specialization” along linear hierarchies. With regard to comparative adaptive studies of xylem structure, formulating hypotheses regarding structure-function or structure-environment relationships in no way requires or is even helped by reference to the Baileyan trends. With its relative simplicity of structure, ecological importance, and remarkable property as an “archive of ontogeny,” wood is one of the most appealing systems for studying evolutionary diversification imaginable. Only by shedding a scheme that was anachronistic at its outset can we give the evolutionary study of wood the prominence it merits.

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