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USING HETEROCHRONY TO DETECT MODULARITY IN THE EVOLUTION OF STEM DIVERSITY IN THE PLANT FAMILY MORINGACEAE

MARK E. OLSON[1,2] AND JULIETA A. ROSELL[1,3]
[1]*Instituto de Biología, Universidad Nacional Autónoma de México, 3er Circuito s/n CU, México DF 04510, Mexico*
[2]*E-mail: explore@explorelifeonearth.org*
[3]*E-mail: julietarosell@exporelifeonearth.org*

Abstract.—Organisms are made up of semiautonomous parts or modules, but identifying the limits of modules is not straightforward. Covariation between morphological features across the adults of a clade can identify suites of characters as putative modules. We contrast such an approach for delimiting modules with one that includes inferences of heterochrony, evolutionary change in the timing of developmental events. That two features show differing types of heterochrony is a strong indication that they are ontogenetically dissociated and belong to differing modules even though these features may covary across adults. We focus on xylem vessels (wood water conduits) and phloem fibers (bark support cells) in the stems of the 13 species of the plant genus *Moringa* (Moringaceae), which vary from massive bottle trees to tiny tuberous shrubs. Across adults, vessel diameter and number of phloem fibers scale positively and significantly with stem size and with respect to one another. This covariation across adults suggests that these features may be members of the same ontogenetic module, a finding that might be expected given that these cells both derive from the same tissue ontogenetically and are tightly functionally integrated in the stem. In contrast, ontogenetic data in the context of a phylogenetic hypothesis suggest that vessel elements and phloem fibers have undergone different types of paedomorphosis, heterochronic alteration to ontogeny producing adults of descendant species that resemble the juveniles of their ancestors. Vessels and phloem fibers would be expected to show differing types of paedomorphosis only if they are not ontogenetically coupled, and therefore it is likely that they are part of different modules; this ontogenetic independence was invisible to inference based only on adult covariation. Finally, we show reasons to implicate paedomorphosis in the diversification in life form of *Moringa* across the Old World dry tropics.

Key words.—Bark anatomy, *Moringa*, morphology, ontogeny, phylogenetic comparative method, phylogeny, wood anatomy.

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Organisms are composed of natural units that are recognizable as being to some extent distinct from the rest of the body. This so-called modularity is manifest in many aspects of biology, such as the assumption that the characters used by systematists reflect real, biologically defensible decompositions of organismal phenotypes. In addition, the study of modularity is key to understanding how one part of an organism can change evolutionarily without affecting the rest (Berg 1960; Wagner 1996; Bolker 2000; Raff and Raff 2000). As with concepts such as species (Pigliucci 2003) and homology (Brigandt 2003), a consensus definition of modularity has not been reached, but working criteria have been generated to guide empirical studies (Eble 2003; Rieppel 2005; cf. Patterson 1982; Wagner 1989). For example, modules can be regarded from a mechanistic point of view within a single organism, with features (e.g., genes) that interact more strongly with each other than with others constituting a putative module (Liberman and Feldman 2005). Likewise, morphological traits that display phenotypic integration may be hypothesized to be part of the same module (Klingenberg et al. 2001). This kind of empirical information is needed to help build a theoretical understanding of modularity. Numerous studies have shown evidence for modularity at the level of genes or proteins (e.g., Fraser 2005). Because the genotype-phenotype map is expected to be nonlinear (Bolker 2003), studies of modular behavior emergent at morphological levels provide a vital complement to molecular level data, especially in characters or taxa that are difficult to study in the laboratory.

Methods that include ontogenetic information should produce finer estimations of morphological modularity than those based only on information from adults. One way of describing morphological modules is what has been termed the search for ''morphological covariation sets'' (Eble 2003), in which parts that covary in an across-species analysis are members of a putative module. For example, two features that show a scaling relationship across the adults of a given clade would be considered more likely to be a part of the same module than a third feature that shows no relationship to the other two. However, this approach could overestimate the extent of modules and underestimate the number of modules present, because features that are not ontogenetically coupled but that nevertheless covary (e.g., because of a functional relationship) would be inferred as belonging to the same module. Comparing ontogenies, rather than adult morphologies only, should help to identify separate entities that would otherwise appear coupled (Fig. 1; cf. West-Eberhard 2003), because characters that covary in adults owing to functional constraints but that are ontogenetically independent are free to arrive at consistent functional outcomes via differing ontogenetic routes.

In addition, different modules may show differing types of evolutionary alterations to ontogeny. Heterochrony, one such type of alteration, results in morphological change in descendant species due to shifts in the timing of development of one part of the body relative to the rest of the organism (Gould 1977; McKinney and McNamara 1991). Heterochrony is only possible in a modular phenotype, in which some parts are dissociated ontogenetically from others (Raff and Raff 2000). Interest in heterochrony has declined somewhat over the past decade, in part in reaction to its being invoked to explain so much of evolutionary change as to lose ex-

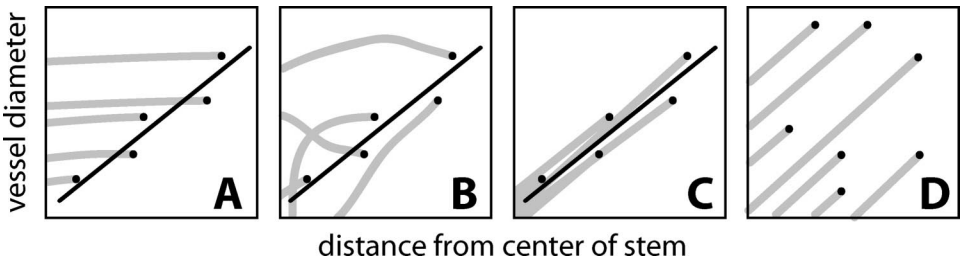

FIG. 1. Species ontogenies versus evolutionary allometry. In each graph of vessel diameter versus the distance from the center of the stem from which the sample was taken, the black points represent species means based on measurements of adults and the black line is the regression line they imply. The gray lines represent the ontogenetic trajectory for each species. (A–C) Differing ontogenetic trajectories can lead to the same interspecific (evolutionary) allometry. (A) Each species produces vessels that are nearly of mature dimensions from the earliest stages. (B) Some species have similar trajectories, but others differ. Heterochrony at this level of organization cannot explain these patterns. (C) Ontogenetic trajectories are similar between species, and heterochrony is a possible mechanism for interspecific differences. (D) Species with similar allometric relationships throughout ontogeny can fail to describe an evolutionary allometry.

planatory power (Raff 1996; Zelditch 2001), and perhaps because of observations that heterochronies observed at one level may not be caused by heterochronic processes at lower levels (e.g., Cubo et al. 2000). However, even in the absence of knowledge of lower level mechanisms, patterns of heterochrony should provide indications of ontogenetic independence between traits at a given organizational level. For example, selection favoring juvenile cranial characteristics in the adults of a lineage could move the population to a juvenile-type cranial morphology, leaving all other parts identical to the ancestral condition. Such evolutionary change would suggest the semiautonomy of the cranium from the rest of the body, even if the underlying genetic or epigenetic processes were not heterochronic. Thus, because modularity is necessary for heterochrony to occur, its study would seem to offer a way of diagnosing members of different ontogenetic modules at a given organizational level of interest, even if they covary due to functional constraints across adults or even in ontogeny.

Woody plant stems lend themselves particularly well to studies of ontogeny and modularity. They are excellent for ontogenetic studies because wood cells and some bark cells are produced in successive layers that retain their relative positions permanently. The entire ontogeny of the trunk of a tree can thus be surveyed from the cells produced when the tree was young, in the central wood, toward the most recently produced layers on the periphery (Chrysler 1937; Carlquist 1962; Cumbie 1963). This property, which allows unequivocal ordering of ontogenetic changes, makes it feasible to study ontogeny in these long-lived organisms even from wild populations. Moreover, although they have important structural differences, there are compelling reasons to expect that bark and wood should be part of the same module. First, both tissues are derived ontogenetically from the same set of cells, the vascular cambium. This meristem surrounds the stem, producing layers of wood cells internally, and bark to the outside. Second, bark and wood remain adjacent to one another and are functionally integrated into a single structure, the stem (Niklas 1999). Integration into the same module could be expected between highly functionally integrated features (Wagner 1996).

We contrast interpretations of modularity in the stem based on interspecific comparisons of adult morphologies versus those that incorporate ontogenetic information in *Moringa*, the only genus in the plant family Moringaceae. Across their range in the dry tropics of Africa, Asia, and Madagascar, the 13 species exhibit three remarkably different life forms: water-filled ''bottle trees'' up to 20 m tall, slender trees with fibrous or tuberous roots, and small shrubs with tuberous roots, the smallest of which is just 5 cm tall (Fig. 2; Olson 2001; Olson and Carlquist 2001). Across adults of *Moringa*, we test the expectation that the diameter of vessels (water conduits) in the wood (Fig. 3A, B), and the number of layers of mechanical support cells, called phloem fibers, in the bark (Fig. 3C, D) should scale positively with stem size, predictions arising from the functional roles of these cells. With respect to vessels, species with larger stems and therefore larger crowns are expected to have greater demand for water, which could lead to pressure for larger, more conductively efficient vessels (e.g., Carlquist 1975, 2001; Panshin and DeZeeuw 1980). Similarly, although little is known about the mechanical role of bark cells (Niklas 1999), greater numbers of thick-walled support cells could be expected in larger stems. To test these functional predictions, we examine the ways that vessels and phloem fibers scale in relation to stem size across the adults of *Moringa*. We also examine how vessel diameter and number of layers of phloem fibers covary in relation to one another in adults across the species of *Moringa*, because even if these cells show a strong relationship to stem size, they may nevertheless be members of different modules and fail to covary with one another. Alternatively, the finding that they strongly covary with one another would be consistent with their membership in the same ontogenetic module.

Allometric scaling across the adults of a given group is also known as evolutionary allometry, because it reflects how scaling relationships have been maintained across the adults of a given lineage (e.g., Cheverud 1982). These scaling relationships may suggest but do not necessarily indicate ontogenetic linkage between the traits (Fig. 1). Therefore, in addition to interspecific, evolutionary allometries based on measurements of adult stems, we use ontogenetic data within *Moringa* species and a phylogenetic hypothesis (Olson 2002a; Fig. 4) to infer heterochronic alterations to ontogeny that have occurred during the diversification of the clade and use these alterations to diagnose modularity. Heterochrony

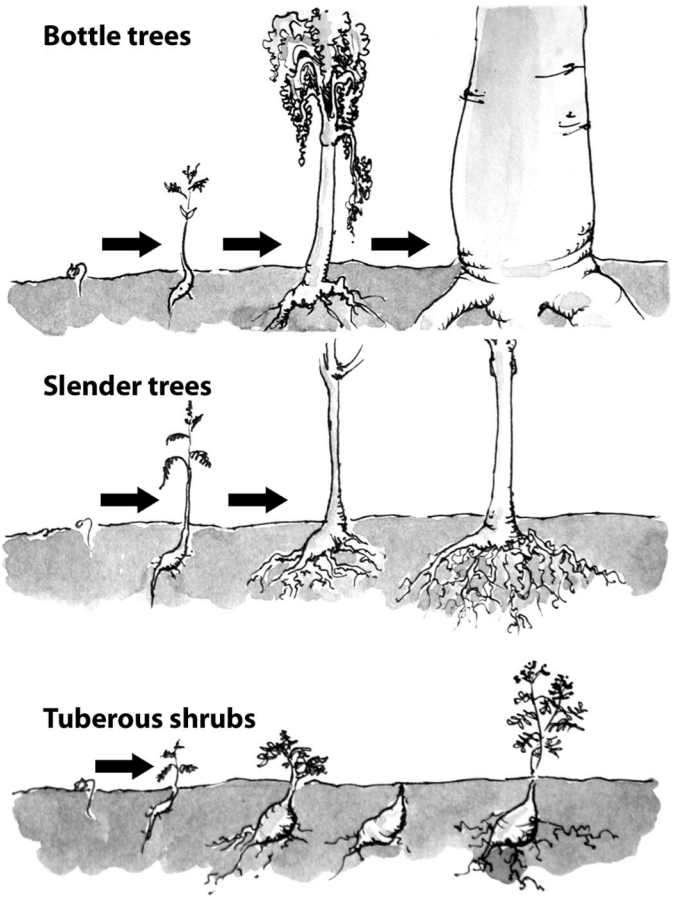

FIG. 2. Ontogenies of *Moringa* life forms. The rightmost drawings depict adult life forms. The adults of the slender trees resemble intermediate stages of the bottle trees; the adults of the tuberous herbs resemble the very young juveniles of the bottle and slender trees. The early stages of ontogeny are similar between species, making heterochrony a possible mechanism for morphological change.

in individual parts is possible because of the modular construction of organisms (Raff and Raff 2000). Therefore, differing patterns of heterochrony between bark and wood cells would strongly imply that they belong to different modules, even if the traits covary in adults.

Finally, we show reasons to suspect the involvement of heterochrony in the generation of the remarkable range of life forms in *Moringa*. Dry tropical habitats, such as those of *Moringa*, show exceptionally high diversity in plant life forms, perhaps the highest on Earth (Medina 1995; Olson 2005). Despite their diversity, these habitats have been little studied as compared to the temperate zone or the wet tropics. With so few species but a great range of shapes and sizes, *Moringa* epitomizes this diversity (Fig. 2). Via two main categories, heterochrony can lead to drastic morphological differences between species via variation of existing developmental programs, without the evolution of truly novel structures (sensu Müller and Wagner 1991; see Raff and Wray 1989; Jones 1992, 1993). Paedomorphosis or juvenilization results in a part of an adult resembling that of an ancestral juvenile, whereas peramorphosis results in the ontogenetic trajectory of a descendant species continuing beyond that of an ancestor (Alberch et al. 1979). Although there are problems with the use of heterochrony in woody plants, especially in the difficulty of finding a meaningful time axis, studies of heterochrony are of value in suggesting how populations can move from one part of morphospace to another. Heterochrony can thus be considered a proximate cause of evolutionary change, and its study offers an essential complement to studies of ultimate causation, such as adaptive evolution or any other force pushing populations through morphospace.

MATERIALS AND METHODS

Wood, Bark, and Whole-Stem Features

''Wood'' refers to the secondary xylem, that is, all of the cells produced by the vascular cambium toward the inside of the stem. As used here, ''bark'' refers to all of the cells produced to the outside by the vascular cambium (a few cells are actually derived from the apical meristem and others from a peripheral meristem called the phellogen, but they are not considered here). Within the wood, we chose to focus on vessel elements based on anatomical study (Olson and Carlquist 2001) showing that the vessel elements were readily compared between species because they lacked interspecific qualitative differences but did vary markedly in vessel diameter between adults (Fig. 3A, B).

The wood cells produced over the life of a tree remain permanently in the positions in which they were produced. This property made it possible to sample not only adult cells, but also juvenile samples from the same tree. We measured vessels from adult wood of each species to infer evolutionary allometries. Use here of the terms ''juvenile'' and ''adult'' are consistent with wood anatomical literature, with juvenile wood denoting the innermost secondary xylem and adult the outermost secondary xylem of large stems, but imply nothing regarding the onset of features such as reproductive competence (see Jones 1999). Measurements of juvenile wood, from the inner xylem, were used for comparing within-species patterns of change in vessel diameter relative to stem size with the evolutionary allometry in these variables. An ideal situation might have been a complete series of preparations from the inner to the outer wood, but this material was not available. In three cases, only adult wood was available, for a total of 23 adult and 20 juvenile samples. Vessel diameter was measured with light microscopy of transverse sections cut on a rotary microtome, following Olson and Carlquist (2001) and Olson (2001, 2002b).

Because bark is produced to the outside of the stem from the vascular cambium, it must expand tangentially to keep up with increase in stem diameter. As a result, and in contrast to the wood, the cells in the bark are usually spread apart from one another and their relative positions disrupted as the stem ages. An exception in *Moringa* is found in the wedges of phloem fibers produced in the inner bark (Fig. 3C, D). These long strands of longitudinally oriented thick-walled fibrous cells are produced from the vascular cambium, with new layers added on to the inside of the bundles. Because phloem fibers remain in organized bundles throughout the life of the stem, they provide a series of cells in the bark from which ontogenetic series can be reconstructed. In all species, after a certain amount of phloem fibers have been

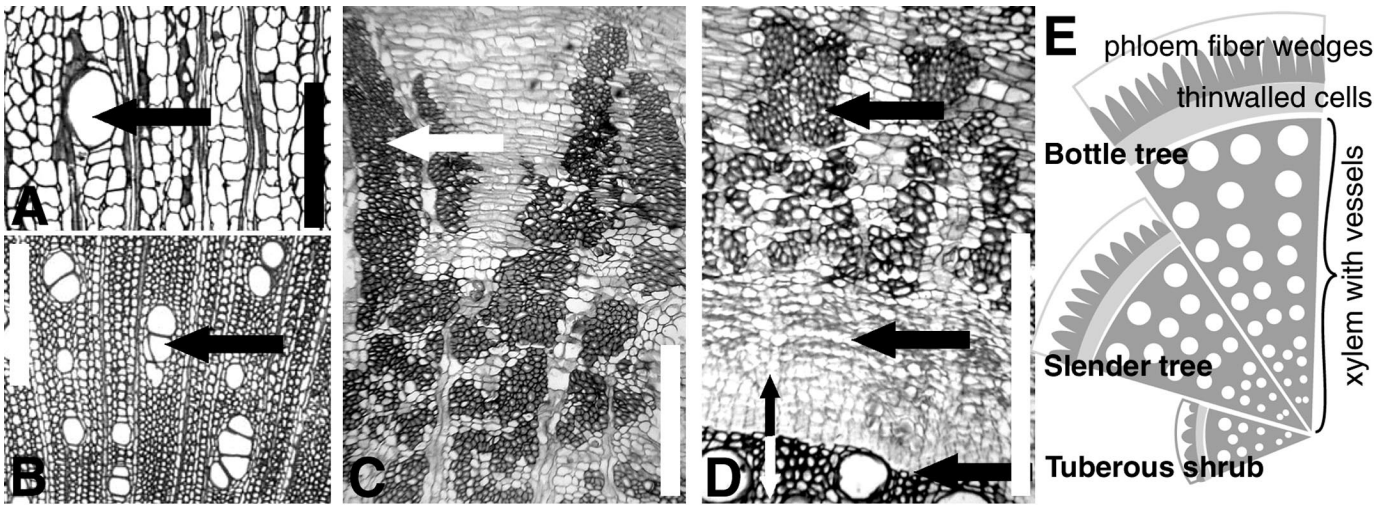

FIG. 3. Bark and wood anatomy in *Moringa* stems. All images are transverse sections, with the outer surface of the stem oriented toward the top. (A) Mature wood of the large bottle tree *M. hildebrandtii* to show very wide vessel (arrow). (B) Mature wood of the small tuberous shrub *M. longituba* showing much narrower vessels (arrow); note similar scales. (C) Outer (first-formed) bark of the large bottle tree *M. hildebrandtii* showing many layers of dark, thick-walled phloem fibers (arrow). The zone of transition to thin-walled cells is out of the frame below. (D) Bark of the small tuberous shrub *M. borziana* showing the much smaller number of layers of phloem fibers (upper arrow) formed before the transition to thin-walled cells (middle arrow). The area of the vascular cambium is indicated by the bottom arrow; the vertical arrows show the direction in which the cambium produces bark cells (black arrow) and wood cells (white arrow). The dark cells at bottom are wood, the largest cells of which are vessels. (E) Comparison of wedges of mature stem cross-sections of bottle trees, slender trees, and tuberous shrubs, to illustrate vessel ontogenies and differing quantities of phloem fibers in the different life forms. Note that all life forms stop producing phloem fibers and make the transition to thin-walled cells. Scale bars all = 500 μm.

produced, their production is halted and the cambium begins producing very thin-walled cells (Fig. 3D), whose function is apparently storage of water and starch, in contrast to the mechanical support role of the phloem fibers. We term bark samples that are still producing phloem fibers as ''juvenile,'' and those in which the shift to thin-walled cell production has occurred as ''mature.'' Adult bark samples were available from 10 individuals from six species. Over 50 juvenile samples, which were still actively producing thick-walled cells, were sampled from five species. The number of layers of thick-walled cells produced before the transition to thin-walled cells was represented by the mean of measurements of five sectors of the same bark sample. Number of phloem fiber layers was counted from transverse sections prepared by either hand or microtome as for the wood sections.

Most material came from living plants collected in the wild in Kenya, Namibia, Madagascar, Oman, and India (locality and voucher information is given in Olson and Carlquist 2001). Some juvenile samples were derived from cultivated plants that were grown together from seed in two locations:

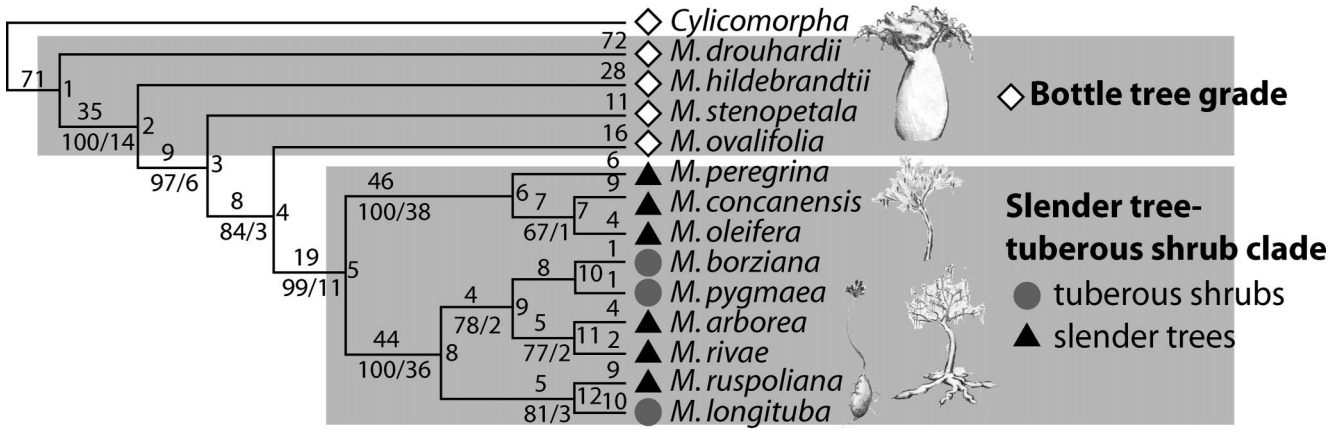

FIG. 4. Phylogeny of Moringaceae based on Olson (2002a), the single most parsimonious tree resulting from analysis of a combined dataset consisting of DNA sequences from two nuclear and one chloroplast region and morphological data. Branch lengths are given above branches, bootstrap/decay indices below. Nodes are numbered 1–12 (number to the right of each node). Important groups are boxed in gray; the basal four species form a grade of large bottle trees; the remainder of the species are much smaller. Most are slender trees with woody or tuberous roots, and three species are small shrubs or woody herbs with few thin stems and massive underground tubers. *Cylicomorpha* is a member of the outgroup Caricaceae.

the greenhouse facility at Washington University, St. Louis, Missouri, and a private greenhouse in Santa Barbara, California, starting in 1997–1998 and ending in 2001.

Evolutionary Allometries: Scaling in Stems across Adults

To describe the evolutionary allometric scaling relationships of the adult wood and bark characters examined to adult stem dimensions and to each other, we fit the following regressions (the complete datasets used in these regressions are given in the Appendix): (1) mean species values of adult vessel diameter on the distance from the center of the stem from which the sample was taken ($\log_{10}$ transformed); (2) number of layers of thick-walled phloem fibers produced before the transition to thin-walled cells versus xylem cylinder thickness ($\log_{10}$ transformed); and (3) vessel diameter versus number of layers of phloem fibers. Because closely related species commonly resemble each other more than distantly related ones, species cannot be assumed to be statistically independent (Felsenstein 1985). Therefore, we fit these regressions using an approach that takes into account this nonindependence.

The phylogenetic comparative method that we used is an implementation of the phylogenetic generalized least squares approach of Martins and Hansen (1997; PGLS). In addition to the regression slope and intercept, their method involves the estimation of a parameter α, which describes the observed decay in trait similarity between species given their phylogenetic distance. As implemented by Martins (2004) in the computer program COMPARE version 4.6, which we used to fit PGLS regressions, if the differences in trait values between species are linearly proportional to branch lengths and the tree topology, $\alpha = 0$. This situation approximates a Brownian motion model of evolution, and PGLS produces results that are identical to those of Felsenstein's independent contrasts method (Felsenstein 1985; Martins and Hansen 1997). Higher values of α imply that the differences in trait values between species vary exponentially with respect to branch lengths in the context of a given topology. In addition to being used in the estimation of the other parameters, the value of α is of interest for its own sake, because it gives an idea of how labile traits are with respect to the phylogeny, a characteristic little examined in plants. To provide an independent estimate of trait lability to compare with α, we also calculated the *K* statistic of Blomberg et al. (2003), which reflects how well the phylogeny predicts trait similarity between species given a Brownian motion model of evolution. This index was calculated using the PHYSIG code of Blomberg et al. (2003) and Matlab 6.5 (Mathworks, Boston, MA). The variance-covariance matrices for PHYSIG were generated using PDDIST of the PDAP program package version 6.0 (Garland et al. 2002; see Garland et al. 1993, 1999; Garland and Ives 2000). PHYSIG and PDAP were kindly provided by Ted Garland. Conventional statistical analyses employed Statistica 6 (Statsoft, Inc., Tulsa, OK). Parameters of PGLS regressions are designated with the subscript PGLS. The significance of the slope β_{PGLS} was tested by dividing the estimated β_{PGLS} by its standard error and comparing the resulting quotient with a *t*-distribution with $n - 2$ degrees of freedom (Kutner et al. 2005). The phylogeny used for these analyses (shown in Fig. 4) is well supported (bootstrap values $> 70\%$ at all nodes) and is the single most parsimonious tree resulting from analysis of a combined dataset consisting of DNA sequences from two nuclear and one chloroplast region and morphological data (Olson 2002a). Branch lengths are numbers of molecular substitutions.

Evolutionary Allometries Versus Ontogenetic Data

Figure 1 shows different ways in which within-species ontogenetic patterns can produce the same allometric relationship between adult structures across species. Comparing ontogenetic and evolutionary allometries between traits gives the opportunity to detect ontogenetic dissociation. If trait 1 shows a different pattern of ontogenetic allometry, say as in Figure 1A, with trait 2 showing a pattern such as that in Figure 1B, then this would suggest that these characters do not covary in ontogeny and therefore may belong to different modules. To determine which of these scenarios, if any, applies in the case of *Moringa*, we computed 95% confidence and prediction bands for the PGLS evolutionary allometry regression lines based on adult values by using the sigma-squared obtained with COMPARE 4.6 as an estimate for mean squared error in the standard formula for these confidence intervals (Kutner et al. 2005, p. 63). The ontogenetic vessel diameter and phloem fiber measurements were then overlain on their respective evolutionary allometries and the distribution of ontogenetic data was evaluated with respect to the evolutionary allometry prediction intervals. For a heterochrony scenario to be applicable as conceived here, then the ontogenetic data (i.e., all of the raw data, including adult and juvenile) should fall within the evolutionary allometry prediction intervals, analogous to Figure 1C. In such a situation, the ontogenetic allometry of any given species is equivalent to the fitted evolutionary allometry line (that part of the regression line where the empirical data fall) or some segment of it. The hypothesis of heterochrony being responsible for differences in wood vessel diameter would be falsified by finding that ontogenetic data fail to conform to the evolutionary allometry (e.g., Figs. 1A, B).

To compare regression slopes between evolutionary allometries and those based on ontogenetic data, we used standard, nonphylogenetic statistics. Although a PGLS based method specifically developed for incorporating ontogenetically autocorrelated data is needed, one could be approximated by a phylogenetic tree with many, very short within-species branches for the many ontogenetic data per species. We did not use this approach because it leads to a likelihood function for α that apparently increases asymptotically (data not shown), suggesting that the data behave independently of the phylogeny and that their relationships can be adequately represented with conventional statistics. The vessel diameter ontogenetic regression used ordinary least squares (OLS), whereas a weighted least squares (WLS) approach was used for the regression of the ontogenetic bark data on stem size because of unequal variances. For WLS regressions, the response variables were weighted with the inverse of the square of their expected standard deviation, which was obtained from the regression of the absolute value of the residuals against stem size (Kutner et al. 2005). Comparisons of re-

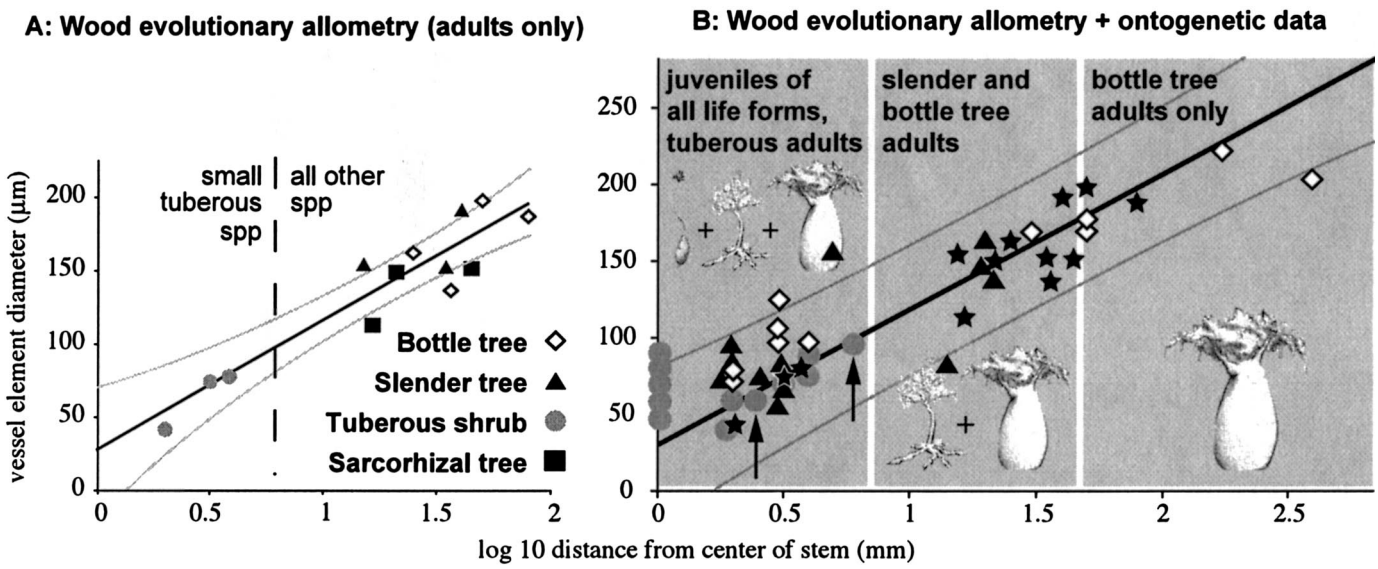

FIG. 5. Evolutionary allometry versus ontogenetic data in *Moringa* wood. At left (A), evolutionary allometry of vessel diameter on stem size, based only on the adult mean values of each of the 13 species of *Moringa*. PGLS regression line is shown with 95% confidence interval. The tuberous shrubs have the smallest stems and narrowest vessels, whereas the largest, the bottle trees, have the widest vessels. The slender life forms have intermediate values. In the graph at right (B), the same evolutionary allometry regression line is shown with 95% prediction interval. The same datapoints as at left are shown in this graph as stars. Overlain on the evolutionary allometry are raw juvenile and adult values from all species to show coincidence between evolutionary allometry and ontogenetic data. The ontogenies of the slender and tuberous life forms can be thought of as successive truncations of the ancestral bottle tree ontogeny: in the gray band at the left of the graph, juveniles of all species and adults of the tuberous shrubs share the smallest stems and vessels. In the center, adults of some bottle trees are found, whereas all of the adults of the slender life forms occur here. Finally, only the adults of the bottle trees reach the upper right. The arrows indicate two samples of *M. borziana* of differing ages; the sample on the left is five times older than the one on the right, but vessels scale with stem size and not age.

gression coefficients used the procedure of Sokal and Rohlf (1995, p. 495).

Life Form Ontogenetic Stage

Ontogenetic changes in life form or habit were taken from earlier observations in the field and in cultivation (Olson 2001; Olson and Carlquist 2001). Development in life form of the largest species of *Moringa* was divided into three stages comparable to the array of adult morphologies observed throughout the genus: a tuberous stage, a slender tree stage, and a bottle tree stage (Fig. 2). Because they have a similar set of ontogenetic stages, the slender trees with fibrous roots and those with tuberous roots (the ''sarcorhizal trees'' of Olson and Carlquist 2001) are both included in the slender tree category here.

The phylogeny was used to infer the directionality of evolutionary changes in life form, wood, and bark ontogeny (cf. Jaecks and Carlson 2001). Ancestral states of life form ontogeny type (illustrated in Fig. 2; distribution given in Fig. 4) were reconstructed on the tree of Figure 4 with maximum likelihood using the StochChar module of the Mesquite computer program version 1.05 (Maddison and Maddison 2004a,b). A Markov one-parameter model (Lewis 2001) was used, with the varying parameter being the rate of change in states. Such reconstructions are necessary to infer the type of heterochronic change, if any, in life form ontogenetic patterns because they permit identification of the type of ontogeny that is ancestral to another.

RESULTS

Wood and Bark Evolutionary Allometries, and Inference of Heterochrony

Both vessel element diameter and number of phloem fiber layers are strongly predicted by stem size, and it is therefore reasonable to speak of these variables as describing evolutionary allometries (as opposed to a situation such as Fig. 1D). The regression of mean values of adult vessel diameter against stem size ($n = 13$, $r^2 = 0.85$, $\beta_{PGLS} = 88.44$, $P < 0.001$; $\alpha_{PGLS} \sim 16.5$) is presented with its 95% confidence interval in Figure 5A. The analogous regression in the bark, of the number of layers of thick-walled phloem fibers produced in the bark before the transition to thin-walled cells regressed on stem size, is shown in Figure 6A ($n = 9$, $r^2 = 0.94$, $\beta_{PGLS} = 71.87$, $P < 0.001$; $\alpha_{PGLS} \sim 20.5$). The regression of the number of layers of phloem fibers on vessel diameter indicated a somewhat weaker but significant relationship ($n = 9$, $r^2 = 0.62$, $\beta_{PGLS} = 0.62$, $P = 0.012$; $\alpha_{PGLS} \sim 24$). The *K*-index values seem congruent with the values of α obtained, because all suggest less similarity between species than would be expected given tree topology and branch lengths (see Appendix) under a Brownian motion model.

The raw juvenile and adult measurements of vessel diameter vs. stem size for all samples are shown superimposed on the wood evolutionary allometry in Figure 5B. All but four of the samples fall within the prediction interval of the evolutionary allometry regression, a situation analogous to

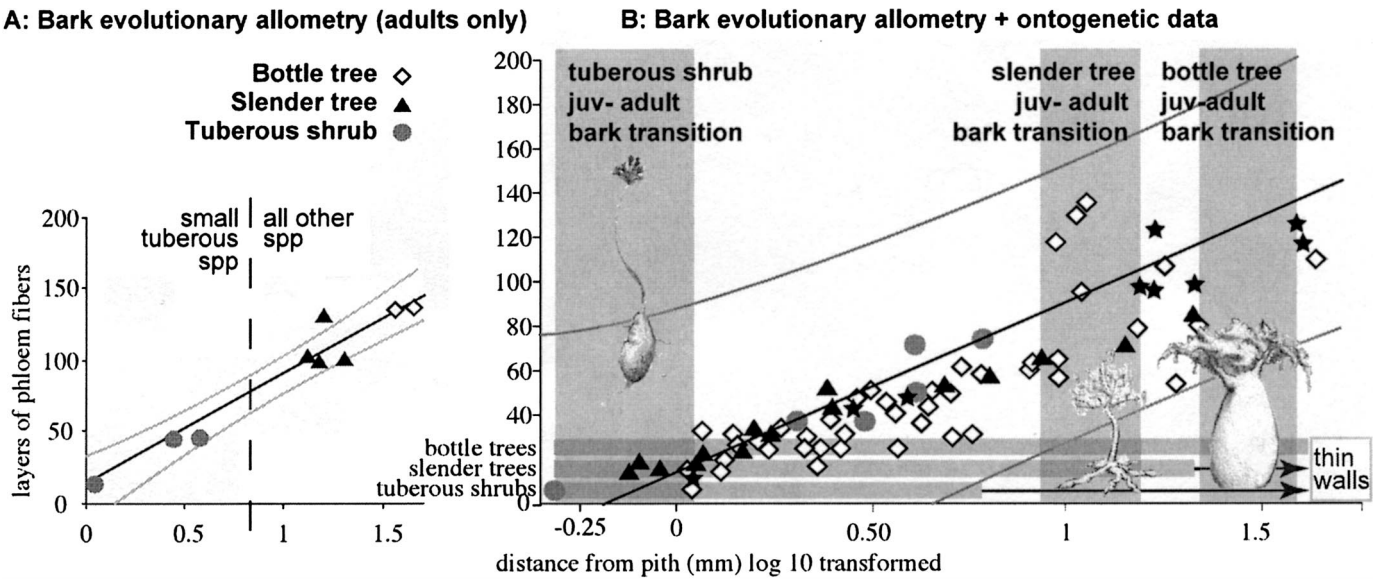

FIG. 6. Evolutionary versus ontogenetic allometry in *Moringa* bark. At left (A), PGLS evolutionary allometry with 95% confidence interval of the number of layers of phloem fibers on stem size, based on the adult values of nine species. In the graph at right (B), the same evolutionary allometry regression line is shown with its 95% prediction interval; the evolutionary allometry data points from the graph at left are shown here as stars. Overlain on the evolutionary allometry are raw juvenile and adult values, showing coincidence between evolutionary allometry and ontogenetic data. Gray bands indicate the juvenile-adult transition zone for each life form, delimited by the largest juvenile sample at left and the smallest adult at right. To the left of these bands, all samples are juveniles for that life form; to the right, all samples are adults. The gray band at right shows that the bottle trees stop producing juvenile thick-walled cells and transition to adult thin-walled cells very late, whereas this transition in the tuberous shrubs occurs very early. In the slender life forms, this transition occurs at intermediate stages. The bands at bottom represent the entire span of phloem fiber production of each life form type. The arrows represent the section that corresponds to the ancestral bottle tree type ontogeny that is omitted before the transition to thin-walled cells, which occurs in all species.

Figure 1C, with the juvenile samples of all life forms falling in the lower left half of the trajectory along with the adult measurements of the tuberous shrubs, the smallest of the *Moringa* life forms. The rest of the points, in the center and to the upper right, are adult measurements. A nonphylogenetic regression for all samples, adult and juvenile ($n = 38$, $r^2 = 0.80$, $\beta_{LS} = 64.08$, $P < 0.001$) had a slope that is not significantly different ($P = 0.07$) from that of the evolutionary allometry based only on adult species means.

Similarly, the ontogenetic bark data are shown in Figure 6B. Most of these ontogenetic data fall along the evolutionary allometry regression line, and all fall within the prediction interval. Juvenile-adult transition zones can be identified for each of the three life forms (shown in Fig. 6B), with the lower bound corresponding to the largest juvenile sample observed for a given life form and the upper bound the smallest adult. We refer to these as transition zones because only juvenile samples of that life form are found to their left, whereas only adults are found to the right. They thus indicate, for each life form, where the shift from juvenile (phloem fibers still being produced) to adult (thin-walled cells) occurs. The tuberous shrubs make this transition extremely early, producing few layers of thick-walled cells before transitioning to thin-walled ones. This transition occurs at larger stem sizes in the slender trees and at even greater diameters in the bottle trees. The nonphylogenetic weighted least-squares regression for all bark samples, adult and juvenile ($n = 65$, $r^2 = 0.83$, $\beta_{WLS} = 49.17$, $P < 0.001$) has a slope that is not significantly different ($P = 0.06$) from that of the evolutionary allometry based only on adult species means.

Reconstruction of ancestral character states unequivocally suggests that the smaller life forms in *Moringa* evolved from large bottle tree ancestors (Fig. 7). Similarly, the tuberous life form appears to have arisen twice within the genus, with key nodes ancestral to the tuberous species having proportional likelihoods of approximately 0.64 in favor of a slender ancestor (Fig. 7).

The comparison of vessel element evolutionary allometry with ontogenetic data is exactly analogous to Figure 1C, with all of the species describing longer or shorter versions of the same ontogenetic trajectory (Fig. 5B). For example, the vessel element ontogeny of a bottle tree is described by the regression line in Figure 5B; that of a slender tree shares the early parts of this trajectory. Because ancestral character state reconstruction shows that the bottle trees represent the ancestral type ontogeny with respect to the slender trees and tuberous shrubs (Fig. 7), the vessel element ontogeny of the smaller species could have been derived via truncation of an ancestral bottle tree ontogeny.

Likewise, the different amounts of phloem fibers in the bark also can be regarded as variations of a single ontogenetic program (Fig. 6B), with the adult bark of the small species resembling in some respects the juveniles of the large species. However, in contrast to the wood, the tuberous shrub and slender tree ontogenetic patterns involve deletion of intermediate ontogenetic events of the bottle tree type ontogeny

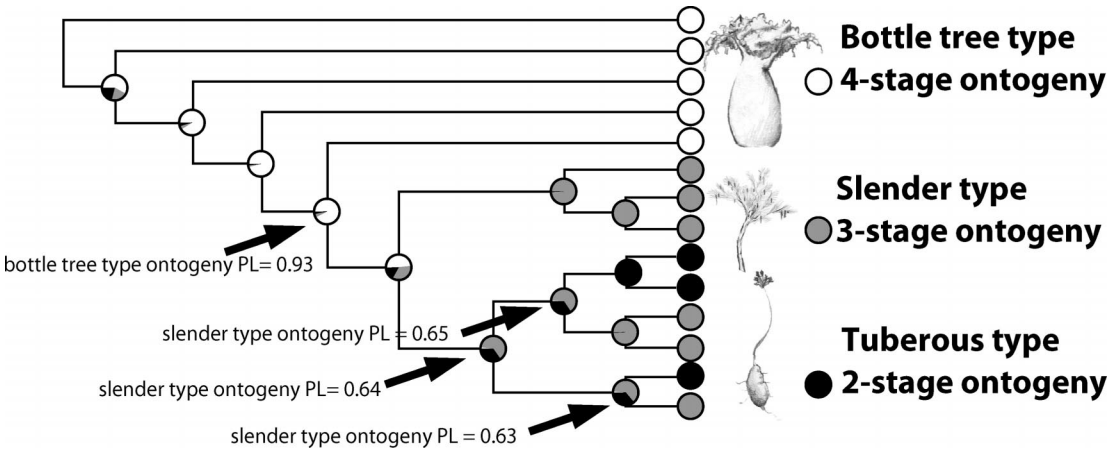

FIG. 7. Ancestral state reconstructions for the life form ontogeny types in Figure 2 on the phylogeny of Figure 4. Filled circles at tips represent observed states; pie charts at internal nodes represent proportional likelihoods of reconstructions. Key nodes are labeled with the proportional likelihood of the ontogeny type that was reconstructed as most likely at that node, to show that the slender and tuberous life forms are almost certainly derived from bottle tree type ancestors and that the tuberous type probably evolved from slender ancestors.

(Fig. 6B; cf. Mabee 1993). If the tuberous and slender tree bark ontogenies were derived via simple truncation of an ancestral ontogeny, as in the wood, we would expect to find species that never make the transition to thin-walled cells. Instead, in all species, juvenile stems produce thick-walled phloem fibers, and adults produce thin-walled cells. That is, the thick-walled to thin-walled transition occurs in all species. The only interspecific ontogenetic differences are in the number of cell layers produced before this transition occurs. Instead of simple truncation, the latter stages of phloem fiber production are omitted in the smaller species and the transition to production of thin-walled cells occurs after fewer layers of phloem fibers have been produced.

DISCUSSION

The functions of woody plant stems, such as mechanical support, result from the interaction of wood and bark, rather than being the domain of one of these tissues individually. Because wood and bark interact functionally and are derived ontogenetically from the same set of cells, it would not be surprising to observe ontogenetic integration between their characters. In *Moringa*, the strong scaling relationships between stem size and vessel diameter and phloem fiber number suggest functional synergy between these characters and the stem as a whole. This functional relationship belied the ontogenetic independence between the wood and bark characters from one another, which was only inferred by examining ontogenetic data in a phylogenetic context.

Inference of Modularity Based on Adult Characteristics Versus Ontogeny

Across species, greater vessel diameter and greater numbers of phloem fibers in adult stems were strongly and significantly associated with greater stem size (Figs. 5, 6). Based on this information alone, it is difficult to infer whether these cell types are ontogenetically associated. However, these correlations are consistent with expectations regarding the functional roles of these cells. Thus, the high correlations in the evolutionary allometries of both wood and bark features with stem size are consistent with their expected functional roles, so it is reasonable to consider both vessels and phloem fibers tightly integrated into the function of the stem as a whole. If structures that interact functionally are likely candidates for integration into the same module, it would not be surprising to find that the wood and bark features examined would covary strongly with one another, as would be expected if they were members of the same module. However, vessel diameter and the number of layers of phloem fibers were more weakly albeit significantly associated with each other. This weaker association hints that the vessel elements and the phloem fibers are not ontogenetically coupled, but the significant association makes it impossible to reject the notion entirely.

Studying ontogeny rather than focusing exclusively on covariance of adult traits permitted inference of ontogenetic independence that otherwise would have been undetectable. Across adults of the *Moringa* clade, both wood and bark traits show clear evolutionary allometries, scaling positively with stem size. If these traits were ontogenetically coupled as part of the same module, they would be expected to show similar patterns of evolutionary alterations to ontogeny. Indeed, both vessels and phloem fibers can be said to show types of paedomorphosis or juvenilization. However, the types of paedomorphosis inferred are different. Because the phylogeny implies that the slender tree type ontogeny is derived from the bottle tree type, and that the tuberous shrubs, in turn, have repeatedly arisen from slender type ancestors (Fig. 7), the array of vessel element dimensions seen in adult moringas are consistent with a pattern of successive truncation of the ancestral bottle tree ontogeny. The vessels of the adults of the smaller *Moringa* species thus resemble the juveniles of their ancestors. In contrast, in the bark, all species reach the thick-walled phloem fiber to thin-walled cell transition (Fig. 3). The species differ only in how many layers of phloem fibers are produced before this transition occurs. The smaller species can be considered paedomorphic in that the adults have similar amounts of phloem fibers as the juveniles of the

species with the ancestral type ontogeny. However, this pattern cannot be considered one of simple truncation, as in the wood, because the adults of all species, regardless of the number of layers of thick-walled cells present, shift to production of thin-walled cells at maturity. Therefore, the kinds of paedomorphosis observed in the wood and bark cells have qualitative differences and thus help to reject the idea that these features are part of the same module. If these two cell types were ontogenetically coupled, similar evolutionary alterations to ontogeny in both cell types would be expected, regardless of the nature of the covariation between the cell types (Raff and Raff 2000). Therefore, vessel elements and phloem fibers are likely ontogenetically dissociated and are best considered as belonging to different modules. Instead, the correlation observed between them seems indirect and most likely to be a consequence of their functional integration into the stem as a whole.

Heterochrony Versus Allometry

The use of features other than absolute time as frameworks against which to study heterochrony have been criticized because surrogates for age such as body size are often not correlated linearly with age (e.g., Klingenberg and Spence 1993; Godfrey and Sutherland 1995). Nevertheless, there are reasons to expect that our inferences of heterochrony are robust to these considerations. In animals, body size has many strong biomechanical and metabolic correlates and is often used as a proxy for age. In woody plants, however, stem size is not simply a proxy for age, but also an archive of ontogeny (e.g., Carlquist 2001). Cells produced at a diameter x in a tree can be unequivocally ordered as being produced before cells produced at diameter $x + 1$ and after $x - 1$. Thus, in addition to being of crucial functional significance, stem size also permits unequivocal ordering of ontogenetic data.

In addition, there are strong reasons to suspect that absolute time is not associated in any necessary way with ontogenetic events in woody plants. For example, although the tuberous shrub species of *Moringa* may be long lived (e.g., based on our field work: Olson 707, collected in 1998 and Van Praet 71, a specimen in the East Africa Herbarium from 1967, are likely the same individual), individual stems grow relatively briefly before dying back (Fig. 2). Organismal age is clearly not an appropriate x-axis in this case, because the life of an individual stem is brief with respect to the entire life span of the plant. It might be thought that regarding the individual stem as an organ and gauging its ontogeny relative to stem age would provide a comparable x-axis between individuals, but stem features appear to track stem allometry more strongly than absolute age. For example, the wood cylinder of *M. borziana* 678 was just 5 mm in diameter, but growth increment scars on the stem indicated a minimum age of 20 years. In contrast, the wood cylinder of *M. borziana* 707 was 12 mm in diameter and just four years old. In both samples, vessel elements and bark features were correlated with stem diameter, just as in the rest of the samples from all species, and bore no relation either to the age of the stem or to the age of the individuals (these samples are highlighted in Fig. 5B). Because dry tropical plants such as *Moringa* add new cell layers to stems only during rainy seasons of uncertain occurrence and erratic duration, stem size is almost certainly a more relevant measure of ''biological time'' (cf. Strauss 1987) than is absolute age.

The patterns of paedomorphosis in the wood and bark are congruent with a pattern of paedomorphosis at the life-form level. Phylogeny reconstruction indicates that the large, bottle tree life form represents the ancestral type with respect to the smaller species (slender trees and tuberous shrubs; Fig. 7). Adults of the smaller species resemble juvenile stages of the bottle tree ontogeny (Fig. 2). Therefore, as for vessel element diameter, the array of life forms in *Moringa* could be regarded as derived via successive truncation of a single ontogenetic program. The Moringaceae-Caricaceae clade within Brassicales shares the bottle tree life form, which is unique within the order (Olson 2002b). Bottle trees differ markedly from most trees in having the wood converted into water storage tissue of very low mechanical support value, with the bark playing a major role in supporting the tree (Olson and Carlquist 2001; Carlquist 1998). Yet from this highly modified morphology, simple ontogenetic alterations have apparently led to dramatic differences in stature, changes in trunk length-diameter relations, and differences in root-shoot allocation seen among the array of life forms in *Moringa*.

Plants, Modularity, and Hierarchy

Difference in degree of modularity could lead to differences in the propensity of a given lineage to diversify (cf. Nagy and Williams 2001). Because they are made up of repetitions of serially homologous parts, plants are often described as ''modular'' (e.g., Takhtajan 1954; Preston and Ackerly 2003). However, an organism could be made up of serially homologous metamers but still show high integration between parts in ontogeny, and therefore show a low degree of modularity from an evolutionary perspective. Plants that have been studied to date appear to be highly disconnected between parts (e.g., Pigliucci et al. 1991). The degree of variability within major plant clades certainly seems to show that plants are extraordinarily labile as compared to animals; it is difficult to mistake one order of mammals for another, whereas many plants from different orders resemble each other strongly. Wagner (1996) posits that one way for modularity to evolve is via parcellation, in which greater modularity is achieved by successive compartmentalization of a highly integrated and therefore constrained system. Suggestive of this patterns is the striking life-form diversity in eudicot clades such as *Moringa*, or to an even more spectacular degree in groups such as *Euphorbia*, which may be a result of greater modularity as compared to groups with apparently very little variation, such as cycads, pines, or many basal angiosperm lineages.

The approach used here, and in studies of modularity in general, implicitly assumes that modularity is a within-level property. In *Moringa*, we examined tissue-level phenomena. But at a lower level, individual cells likely behave to some degree independently of others, and at a higher level, individual stems may behave as units to some extent independent of the rest of the plant. There does not seem to be any reason that modular interactions between levels could not be estab-

lished and that a single module should involve only components at a single level of organization. The assumption that modules occur at single levels strongly affects the methods used and conclusions reached. For example, we assumed that the relationship between stem size and wood and bark anatomical features was due to a functional relationship and not to ontogenetic coupling between hierarchical levels. Just as the conclusion of a heterochrony study depends on the level of organization studied, understanding of modularity will certainly be improved as studies integrate more levels of organization.

Modularity is a key element in understanding major issues such as homology and adaptation. Ontogenetic data, especially in a phylogenetic context, can help identify units of covariation that diagnose phenotypic modules. The notion that heterochrony can explain all evolutionary change is likely exaggerated (Raff 1996; Zelditch 2001), but because modularity is necessary for heterochrony to occur, the study of heterochrony does offer a useful way of recognizing members of different ontogenetic modules. Moreover, beyond their use as tools for studying modularity, ontogenetic alterations are themselves of profound interest as doubtlessly playing a role in the proliferation of organisms, including highly morphologically diverse dry tropical plant taxa, across the physical landscape and throughout morphological space.

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Appendix

Datasets for wood and bark evolutionary allometries, and *K*-statistics (Blomberg et al. 2003). Species means (in parentheses) are of all the available samples for that species, except those with a collection number (e.g., Olson 675), which represent the value of that sample only. The *K*-statistic is an index of how hierarchically distributed the data are in the context of a given topology and set of branch lengths. This index is standardized for comparison between studies. Values <1 indicate less similarity between species than would be expected given the tree topology and branch lengths.

	Vessel element diameter versus distance from the center of the stem at which sample was taken		No. of layers of phloem fibers versus radius of xylem cylinder	
	Vessel diameter, in μm	Distance from center of stem, in mm, $\log_{10}$-transformed	No. of layers of thick-walled phloem fibers	Xylem cylinder wall thickness, in mm, $\log_{10}$-transformed
Tip data	*M. drouhardii* (187.43)	*M. drouhardii* (1.9)	*M. hildebrandtii* Olson 697 (126)	*M. hildebrandtii* Olson 697 (1.7)
	M. hildebrandtii (197.82)	*M. hildebrandtii* (1.7)	*M. stenopetala* Olson 675 (125)	*M. stenopetala* Olson 675 (1.602)
	M. stenopetala (136.8)	*M. stenopetala* (1.56)	*M. peregrina* Olson 567 (97.8)	*M. peregrina* Olson 567 (1.18)
	M. ovalifolia (162.7)	*M. ovalifolia* (1.40)	*M. concanensis* Olson 700 (98)	*M. concanensis* Olson 700 (1.16)
	M. peregrina (152.9)	*M. peregrina* (1.18)	*M. rivae* Olson 701 and 677 (123.3)[1]	*M. rivae* Olson 701 and 677 (1.22)[1]
	M. oleifera (152.31)	*M. oleifera* (1.54)	*M. borziana* Olson 678 and 707 (47.8)[1]	*M. borziana* Olson 678 and 707 (0.59)[1]
	M. concanensis (191.4)	*M. concanensis* (1.60)	*M. pygmaea* Nugent 25 (11)	*M. pygmaea* Nugent 25 (0.04)
	M. borziana (77.85)	*M. borziana* (0.59)	*M. longituba* Olson 704 and 708 (42.6)[1]	*M. longituba* Olson 704 and 708 (0.45)[1]
	M. pygmaea (42.5)	*M. pygmaea* (0.30)	*M. ruspoliana* Olson 702 and 703 (98.7)[1]	*M. ruspoliana* Olson 702 and 703 (1.32)[1]
	M. rivae (113.19)	*M. rivae* (1.22)		
	M. arborea (151.5)	*M. arborea* (1.65)		
	M. ruspoliana (149.55)	*M. ruspoliana* (1.32)		
	M. longituba (74.58)	*M. longituba* (0.5)		
K-statistic	0.29	0.34	0.23	0.27

[1] Mean of the two samples.