

# Reinvestigation of Leaf Rank, an Underappreciated Component of Leo Hickey's Legacy

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## ABSTRACT

The widespread recognition of the scientific importance of leaf architecture, the description and interpretation of leaf shape and venation, is a cornerstone contribution of Leo Hickey's career. One leaf architectural trait that Hickey developed is leaf rank, which describes the level of organization of leaf venation in a single, discrete, ordinal variable. He used this scoring system to provide a rapid summary of overall venation complexity and organization in modern and fossil leaves. Leaves with the most reduced and disorganized venation are scored as low rank, whereas leaves with complex and well-organized venation are given high values. Leaf rank data facilitated comparisons of early angiosperms in fossil floras and were invoked in hypotheses regarding angiosperm evolution and ecology. This study presents a large data set of leaf ranks that Leo Hickey scored while he was a researcher at the Smithsonian Institution from 1969 to 1982. The data set represents at least 2,435 observations of US National Herbarium specimens. These formative observations of leaf venation have never been published. Here, we examine Hickey's data in light of current angiosperm phylogeny as a way to reinvestigate several of his hypotheses regarding leaf rank and angiosperm evolution: (1) leaf ranks tend to be consistent within a family; (2) leaf rank was low in early angiosperms, and high-rank venation occurred later; and (3) leaf rank is correlated with environmental conditions, often with reduced leaf rank values appearing in xeric taxa compared with close relatives under mesic conditions. These hypotheses have not been tested in the light of DNA-based, angiosperm-wide phylogeny, which was not available at the time when leaf rank was developed. We show that even with a DNA-based phylogeny, family-level comparisons show significant differences in average leaf rank; inferred leaf rank states along the early backbone of the angiosperm phylogeny are low, with high-rank taxa occurring across derived lineages; and there is a definite trend toward reduced leaf rank in xeric taxa, all consistent with Hickey's hypotheses. This taxonomically rich set of observations can serve as a foundation for further investigations of the evolution of leaf vein organization.

## KEYWORDS

Angiosperm evolution, leaf architecture, leaf rank, leaf venation

## Introduction

The study of angiosperm leaves and their fossils represents the lion's share of paleobotanical

research, in part because leaves are the most abundantly preserved plant megafossils (Behrensmeyer et al. 1992; DiMichele and Wing 1998; Wilf 2008). Fossil leaf floras have long been used to

infer paleoenvironmental conditions at the time of preservation (Bailey and Sinnott 1915, 1916; Wolfe 1971, 1993; Little et al. 2010; Peppe et al. 2011; Breedlove et al. 2013; also, see supplementary bibliography in Little et al. 2010). Much of Leo Hickey's legacy resides in the modern development of leaf architecture, the description of leaf shape and venation (Hickey 1971, 1974, 1977, 1980; Hickey and Doyle 1972, 1977; Hickey and Wolfe 1975; Ash et al. 1999; Ellis et al. 2009). These works provide the most widely used approaches for describing modern and fossil angiosperm leaves.

Leaf rank was an early method for describing leaf vein complexity and organization in a single variable (Hickey 1971, 1977; Doyle and Hickey 1972, 1976; Ash et al. 1999). Rank is based on an assessment and classification of the overall organization of the vein orders. Leaves with fewer distinct orders of venation that are not consistently patterned are assigned a low rank, whereas leaves with several distinct vein orders that are regular in pattern are assigned higher ranks. This ordinal classification of venation organization first appeared in the literature as an abstract at a Botanical Society of America Annual Meeting (Hickey 1971), but it was most elaborately described as a method with clear criteria and illustrations in Hickey's (1977) Golden Valley monograph.

Leaf rank data were important in developing the picture of early angiosperm evolution through the Cretaceous (Hickey and Doyle 1977; Wing and Boucher 1998; Cúneo and Gandolfo 2005). It was noted that preserved leaves tend to be of lower rank in older strata, with a trend toward higher-rank leaves occurring in younger rock layers. However, leaf rank as a useful tool for the paleobotanist has received little attention, and it is not part of standard leaf architectural descriptions (Ellis et al. 2009).

More recent attention to modeling the evolutionary physiology of angiosperm leaves has resulted in a renewed interest in the leaf traits of early fossil angiosperms. As a result, ancient angiosperm biology and early evolutionary trends are regularly inferred using leaf venation traits in the context of the modern DNA-based phylogeny of plants (Roth-Nebelsick et al. 2001; Feild et al. 2004; Brodribb et al. 2007; Feild and Arens 2007; Boyce et al. 2009; Feild et al. 2009; Brodribb and Feild 2010; Feild, Brodribb et al. 2011; Feild,

Upchurch et al. 2011; Walls 2011; Boyce and Leslie 2012; De Boer et al. 2012; Price et al. 2012; Price et al. 2013; Roddy et al. 2013; Sack and Scofoni 2013). Most of this work is quantitative in nature, but there have also been preliminary observations that leaf rank scores may be correlated with quantitative leaf vein measurements (Green et al. 2009; Brodribb and Field 2010; Green et al. 2014).

In spring 2008, the authors were provided with more than 2,000 handwritten leaf rank scores, with notes on habit, from Leo Hickey. These data comprised the basis of Hickey's written statements on leaf rank patterns across angiosperm phylogeny, but they were never formally published. In this study, we analyze Hickey's data and show that his hypotheses, regarding similar rank scores within families and low leaf rank in early angiosperms, are compatible with the current phylogenetic framework of angiosperms. The hypothesis that reduced leaf rank values occur in xeric taxa compared with close relatives under mesic conditions is confirmed statistically. Our more quantitative approach illustrates and corroborates Hickey's sense of the trends and patterns in leaf rank and leaf evolution across angiosperm history.

## Materials and Methods

### *LJH Leaf Rank Data Set*

The leaf rank data set (LJH) was transcribed into a digital format from handwritten notes received from Leo Hickey in spring 2008 (see supplementary material available online). These digital notes were organized to provide taxonomic information, leaf rank score(s) and habit information (if present). The original notes also contained several hand drawings and comments; they are archived at the Peabody Museum of Natural History, Yale University. Most of the data are genus-based observations, with a high score and a low score typically given to account for the variability observed, and rarely with separate lines for species in the genus that exhibit differing ranks or habits. After transcription and error checking, each genus was assigned an order and family-level name based on the current synthesis of the molecular-based angiosperm phylogeny (Stevens 2001).

Hickey's method for ranking (Hickey 1977; Ash et al. 1999) involves assigning leaves to one of

TABLE 1. Parsimony ancestral state reconstructions of leaf rank for early angiosperms. Angiosperm base node refers to the earliest state in the phylogeny of taxa present in the LJH leaf rank data set; eudicot base node refers to the ancestral state inferred for crown eudicots. All “name” to sister conventions refer to state inferred for the branch/backbone of the angiosperm phylogeny that links the named group to the derived sister in the phylogeny (i.e., the sister clade of all angiosperms after the named group). *Abbreviations:* LJH, original leaf rank score set from Leo Hickey; LJH +, original leaf rank score set with the addition of our leaf rank scores for the genera *Amborella*, *Illicium* and *Trimenia*; NA, not applicable.

| Backbone/clade             | Inferred node state LJH  |      | Inferred node state LJH + |         |
|----------------------------|--------------------------|------|---------------------------|---------|
|                            | Minimum, median, maximum | Rank | Minimum, median, maximum  | Rank    |
| Angiosperm base node       | 7.9, 8.1, 8.3            | 2r3  | 6.9, 7.1, 7.2             | 2r2     |
| <i>Amborella</i> to sister | NA                       | NA   | 6.3, 7.2, 7.5             | 2r1–2r3 |
| Nymphaeales to sister      | 7.9, 8.0, 8.1            | 2r3  | 6.6, 6.8, 7.4             | 2r2     |
| Austrobaileyales to sister | NA                       | NA   | 6.8, 7.1, 7.8             | 2r2–2r3 |
| Eudicot base node          | 8.1, 8.2, 8.3            | 2r3  | 7.9, 8.3, 8.7             | 2r2–3r0 |

four levels or ranks along a continuum of increasing organization. These four ranks (abbreviated 1r, 2r, 3r and 4r) were further subdivided by Hickey as [1r0], 1r1, 1r2, 1r3, [2r0], 2r1, 2r2, 2r3, [3r0], 3r1, 3r2, 3r3, [4r0], 4r1, 4r2 and 4r3, where the ranks in square brackets with zeroes for second numbers are transitional between the four main ranks; the rank 1r0 describes reduced leaves with little to no venation. We converted all ranks to numbers from 0 (1r0) up through 15 (4r3) to provide 16 ordered categories for the purposes of quantitative analyses. The consistency and repeatability of this scoring method has been quantified by Green et al. (2014). In this case, the scores were all done by a single individual (Hickey) and therefore can be presumed to be somewhat more consistent than the data analyzed by Green et al. (2014), which included leaves scored by several people with different backgrounds.

To assess whether the lack of taxa that are currently considered to be early divergent, extant angiosperm lineages has an effect on the ancestral state inference of early angiosperm evolution, three additional key genera were scored from the National Cleared Leaf Collection, housed at the Smithsonian Institution: *Amborella*, *Illicium* and *Trimenia* (see supplementary material available online).

#### Analyses of the LJH Leaf Rank Data Set

The R programming language (R Development Core Team 2008) was used to perform all analyses and plots, exclusive of phylogenetic analyses (see

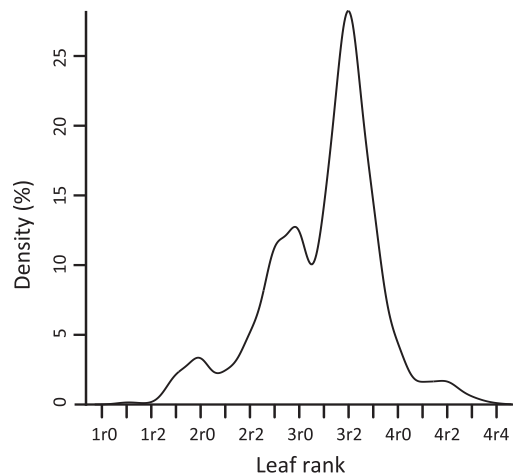


FIGURE 1. Distribution of leaf rank scores in the LJH leaf rank data set. The distribution is based on mean leaf rank for 1,828 angiosperm genera (2,218 specimens, 259 families). The most common rank (3r2) corresponds to a stereotypical higher dicot leaf with clearly organized and distinguishable primary-, secondary- and tertiary-order venation.

supplementary material available online for script file documenting all statistical analyses). Two linear least-squares models were examined, using family and order as predictors for mean rank. A density plot was made to illustrate the distribution of ranks in the LJH leaf rank data set, based on genus rank averages. In addition, box-and-whisker plots were produced for each family (based on among-genera average ranks) to illustrate the range of variation in ranks by family, and for rank scores of taxa scored as xeric compared with nonxeric.

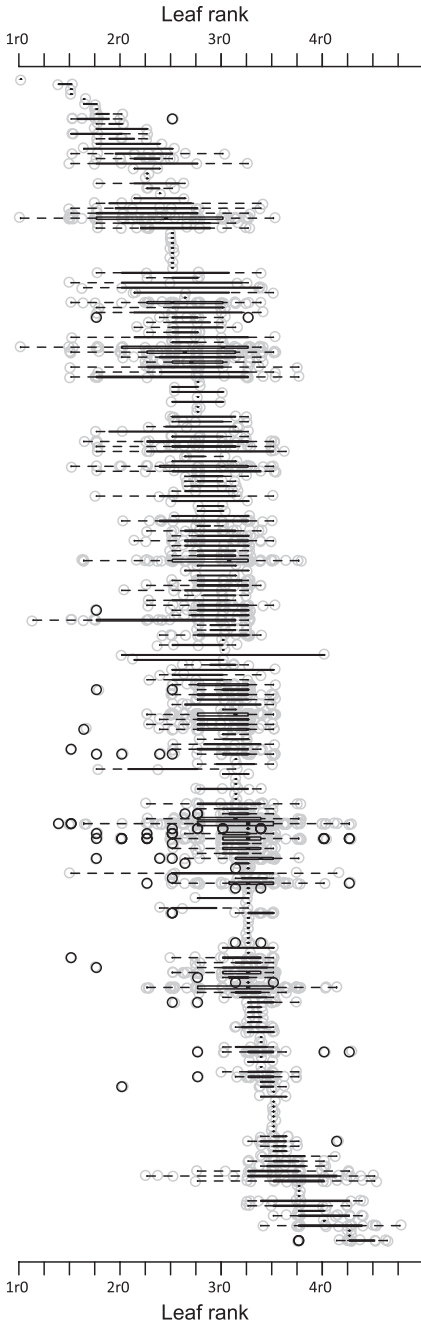


FIGURE 2. Box-and-whisker plot showing the conditional distribution of leaf rank by family for 259 families (1,828 genera) in the LJH leaf rank data set. Gray circles (slightly jittered to reduce overplotting) represent each genus, boxes and whiskers show interquartile ranges and expected variation within each family, and solid black circles show outliers. Families are ordered from top to bottom in order of increasing median leaf rank. The observed range within many families covers a large proportion of the total variation.

A phylogeny of the taxa present in the LJH data set was produced using the web-based tool Phylomatic, Version 3 (<http://phylodiversity.net/phyloomatic/>, Webb and Donoghue 2005; Stoltzfus et al. 2013). The taxon list is the input and is compared with the angiosperm supertree such that nonpresent taxa from the supertree are pruned away to provide a phylogeny of all taxa in the LJH data set. The supertree represents the current consensus view of the major branches in the land plant phylogeny, and for angiosperms, it is typically resolved to the family or order level, which we consider a reasonably conservative framework for investigation of evolutionary patterns using ancestral state reconstruction (i.e., many genera form a polytomy above the family node). As an inferred ancestral state is largely influenced by the states of adjacent sister lineages, an arbitrary resolution of polytomies could produce a biased ancestral state reconstruction. A more averaged ancestral node value is inferred for a polytomy when using least-squared parsimony reconstruction (Maddison and Maddison 2011), and thus we consider the supertree a conservative first test of his hypotheses.

Averages for minimum, mean, and maximum rank score were calculated for each genus and used to form the character matrix for tree-based trait analysis using Mesquite (Maddison and Maddison 2011). Ancestral state values of leaf rank were reconstructed using least-squares parsimony over genus terminals on the supertree, which minimizes the sum of squared change along all branches of the tree to reconstruct the values of internal nodes based on the trait values of the species terminals (Maddison and Maddison 2011). Inferred ancestral state numbers were rounded off and converted back to ranks (Table 1).

## Results

All 16 possible ranks are present in the data set (Figure 1). The modal observation (approximately 30%) is of leaves scored as 3r2. There is another peak of observations scored between 2r2 and 3r0, and thus the majority of the data are from what are considered high-rank leaves. Leaf ranks by family show substantial variation in median rank and spread among families; however, the majority of the families have high within-family median ranks (3r2 or higher; Figure 2). A

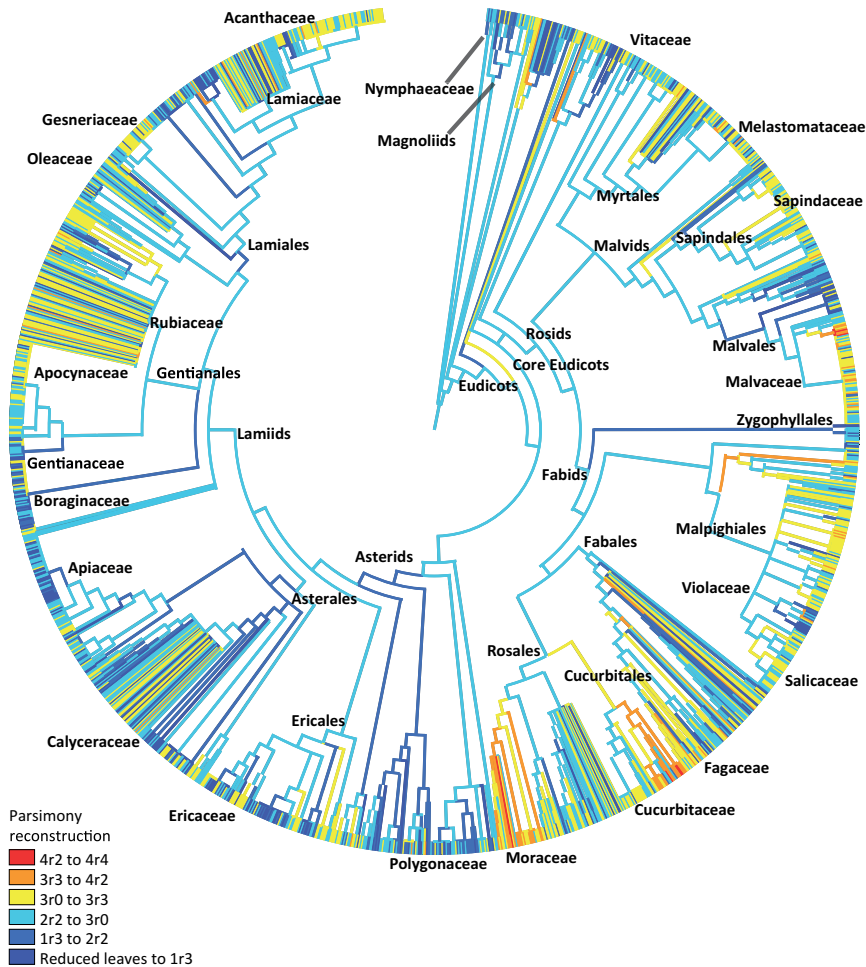


FIGURE 3. Phylogenetic tree of all genera represented in the LHJ leaf rank data set. A subset of clade names is shown adjacent to their node or at the clade tip. The genus-level ancestral state reconstruction shows low-rank taxa (cool colors) along the early backbone of the angiosperm phylogeny with a pulse of high-rank taxa (warm colors) in the eudicot clade and scattered across the tree, mostly in derived positions. Low-rank genera also occur across the tree in derived positions; some of these are represented by taxa scored as xeric by LJH.

linear least-squares model ( $F = 6.571$  on 234 and 1,962 degrees of freedom [df]) using family as an unordered factor to predict mean rank is highly significant ( $P < 2.2e-16$ ) with an adjusted  $r^2$  of 0.37. This suggests a strong systematic component to the mean rank scores, although sparse, overdispersed sampling may be increasing the apparent explanatory power of the model. A similar model to predict mean rank using order instead of family as a predictor has greatly reduced, but still highly significant, explanatory power ( $F = 9.759$  on 45 and 2,172 df,  $P < 2.2e-16$ ; adjusted  $r^2 = 0.15$ ).

Ancestral state reconstructions for the basal branches of the angiosperm phylogeny showed uniformly low ranks (Figure 3; Table 1). The state inferred for each basal ancestral node was uniformly 2r3 for the LHJ leaf rank data set, but there was more variation, including lower-rank states, with the inclusion of the three additional basal angiosperm genera (LJH+ *Amborella*, *Illicium* and *Trimenia*; Table 1). Visual inspection of the supertree (Figure 3) shows that the highest-rank taxa only occur in derived positions but do so across many subclades (warm colors: orange and red; e.g., Rosales, Cucurbitales, Fagaceae and

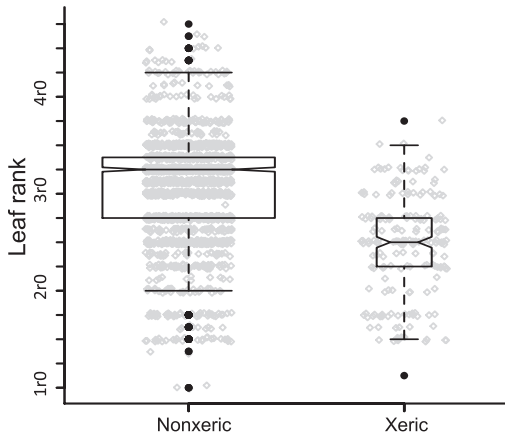


FIGURE 4. Box-and-whisker plot showing the conditional distribution of leaf rank for xeric compared with nonxeric taxa (1,828 genera) in the LJH leaf rank data set. Gray circles (slightly jittered to reduce overplotting) represent each genus, boxes and whiskers show interquartile range, and solid black circles show outliers. Genera scored as xeric by LJH (see supplementary material available online) tend to have lower leaf rank scores compared with nonxeric/mesic genera as shown by the notch test described in Chambers et al. (1983) or using an unpaired, two-sided  $t$  test ( $t = -15.3146$ ,  $df = 254.039$ ,  $P < 2.2e-16$ ).

Dipterocarpaceae). Cool-colored branches (blues in Fig. 3) indicate low-rank values, which occur throughout the phylogeny, particularly along the backbone of the phylogeny.

The box-and-whisker plot of average leaf rank by genus for xeric compared with nonxeric taxa shows substantial spread (Figure 4), but statistically different medians, according to the “notch” test for the equality of medians (Chambers et al. 1983). Taxa scored as xeric tend to have lower-rank scores than nonxeric taxa, as shown, for instance, by an unpaired, two-sided  $t$  test ( $t = -15.3146$ ,  $df = 254.039$ ,  $P < 2.2e-16$ ).

## Discussion

Overall, our results corroborate Leo Hickey’s formative hypotheses about leaf trait evolution in early angiosperms (Hickey 1977; Hickey and Doyle 1977). Specifically, these hypotheses are as follows: (1) leaf ranks tend to be consistent within a family; (2) leaf rank was low in early angiosperms, with high-rank venation occurring later, and what seems to be independently, across lineages; and (3) leaf rank is correlated with environmental

conditions, often with reduced leaf rank values appearing in xeric taxa compared with close relatives under mesic conditions. Overall, our results support these hypotheses. We did not expect, a priori, that all hypotheses would remain supported given that with the advent of DNA-based phylogenies there have been changes in both family circumscriptions and in the sister-group relationships along the backbone of the angiosperm phylogeny.

The model to predict mean rank from family is highly significant, which suggests that in spite of changes in phylogenetic hypotheses since the 1970s, there remains a strong systematic component in rank scores. The possibility of sparse, overdispersed sampling may have increased the seeming explanatory power of the model, thereby overemphasizing the phylogenetic signal in the data set. Future work, with more selective and even sampling across the angiosperm tree of life, could more strictly test whether within-family similarity of ranks is valid. Further, more detailed sampling at the species level (i.e., high resolution genus- and family-level phylogenies) could reveal hitherto unknown patterns of evolution in leaf venation complexity. There have been very few studies that systematically sample families and genera using leaf venation complexity as a trait (e.g., Rury and Dickson 1977; Todzia and Keating 1991; Wang et al. 2001; Luo and Zhou 2002; Eklund et al. 2004; Horn 2009; Pacheco-Trejo et al. 2009; Zhang et al. 2011). Some studies show a marked similarity of rank among all members of a family (e.g., Luo and Zhou 2002). However, these studies at the family and genus level have several observations of high and low ranks within families and even genera, suggesting that venation complexity may have a more convoluted evolutionary history compared with the prevailing narrative of a broad escalation of venation complexity over angiosperm evolution (Hickey and Doyle 1977; Feild, Brodribb et al. 2011).

Our results, using the LJH data set, show the weaker explanatory power of rank provided by orders compared with families, which indicates that much of the phylogenetic signal in leaf venation complexity does occur at finer scales. If the phylogenetic signal was very high, then deep time ancestral states would be highly predictive of descendant states (i.e., orders would be as good or better at predicting leaf rank values). However,

the predominately low rank inferred for the backbone of the phylogeny is also consistent with escalation (Hickey and Doyle 1977; Feild, Brodribb et al. 2011). Thus, our data support a broadscale escalation in rank (independent occurrences of high rank in clades derived from low-rank ancestral states) but also provide room for a more complex evolutionary history (many low-rank genera in families with predominantly high-rank genera; i.e., Acanthaceae). Investigations into leaf venation complexity at various phylogenetic scales are needed to more robustly test whether there is conflict between the hypotheses of overall escalation compared with a highly labile evolution of leaf venation complexity.

Even more interesting than the maintained support for family-level leaf rank similarity is the stability of ancestral state reconstruction along the basal backbone of the phylogeny. In fossil floras, the observation of low leaf ranks earlier compared with later in the Cretaceous is now classic (Hickey and Doyle 1977). However, the systematic placement of isolated fossil leaves is notoriously difficult (Wilf 2008). Thus, the hypothesis that leaf ranks tended to increase over evolutionary time independently among lineages requires a test from the fossil record that can only be accomplished if most of the Cretaceous leaf morphotypes were part of whole-plant reconstructions. However, with the advent of independently derived, DNA-based phylogenies, this hypothesis is at least partially testable by inferring ancestral states of extant taxa only. Such tests are limited but are also highly conservative because fossil stem taxa of low leaf rank would unequivocally cause state inference deeper in the tree to be of low rank. Thus, our inferred low leaf ranks on the basal-most backbone of the tree, with or without additional basal genera (*Amborella*, *Trimenia* and *Illicium*), represent strong support for Hickey's ideas about leaf rank evolution with low-rank ancestors giving rise to higher-rank descendants. The many low-rank taxa found in derived positions in the phylogeny is an interesting phenomenon that could be ascribed, in part, to Hickey's hypothesis that low-rank taxa among high-rank close relatives are often from xeric habitats. The LJH data set quantitatively supports this idea, but further work is needed to disentangle the relationships between phylogenetic signal and environmental selection.

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## Literature Cited

- ASH, A.W., B. ELLIS, L.J. HICKEY, K.R. JOHNSON, P. WILF AND S.L. WING. 1999. *Manual of Leaf Architecture: Morphological Description and Categorization of Dicotyledonous and Net-veined Monocotyledonous Angiosperms*. Washington, DC: Leaf Architecture Working Group. 67 pp.
- BAILEY, I.W. AND E.W. SINNOTT. 1915. A botanical index of Cretaceous and Tertiary climates. *Science* 41(1066):831–834.
- 1916. The climatic distribution of certain types of angiosperm leaves. *American Journal of Botany* 3(1):24–39.
- BEHRENSMEYER, A.K., J.D. DAMUTH, W.A. DiMICHELE, R. POTTS, H.-D. SUES AND S.L. WING. 1992. *Terrestrial Ecosystems through Time*. Chicago: University of Chicago Press. 568 pp.
- BOYCE, C.K. AND A.B. LESLIE. 2012. The paleontological context of angiosperm vegetative evolution. *International Journal of Plant Sciences* 173(6):561–568.
- BOYCE, C.K., T.J. BRODRIBB, T.S. FEILD AND M.A. ZWIENIECKI. 2009. Angiosperm leaf vein evolution was physiologically and environmentally transformative. *Proceedings of the Royal Society B* 276(1663):1771–1776.
- BREEDLOVESTROUT, R.L., B.J. EVRAETS AND J.T. PARRISH. 2013. New Paleogene paleoclimate analysis of western Washington using physiognomic characteristics from fossil leaves. *Palaeogeography, Palaeoclimatology, Palaeoecology* 392: 22–40.
- BRODRIBB, T.J. AND T.S. FEILD. 2010. Leaf hydraulic evolution led a surge in leaf photosynthetic capacity during early angiosperm diversification. *Ecology Letters* 13(2):175–183.
- BRODRIBB, T.J., T.S. FEILD AND G.J. JORDAN. 2007. Leaf maximum photosynthetic rate and venation are linked by hydraulics. *Plant Physiology* 144(4):1890–1898.
- CHAMBERS, J.M., W.S. CLEVELAND, B. KLEINER AND P.A. TUKEY. 1983. *Graphical Methods for Data Analysis*. Monterey, CA: Wadsworth. 395 pp.
- CÚNEO, R. AND M.A. GANDOLFO. 2005. Angiosperm leaves from the Kachaiké Formation, Lower Cretaceous of Patagonia, Argentina. *Review of Palaeobotany and Palynology* 136(1–2):29–47.

- DE BOER, H.J., M.B. EPPINGA, M.J. WASSEN AND S.C. DEKKER. 2012. A critical transition in leaf evolution facilitated the Cretaceous angiosperm revolution. *Nature Communications* 3:1221. doi: 10.1038/ncomms2217
- DI MICHELE, W.A. AND S.L. WING, EDs. 1998. *Methods and applications of plant paleoecology*. Paleontological Society Special Publications 3:1–171.
- DOYLE, J.A. AND L.J. HICKEY. 1972. Coordinated evolution in Potomac Group angiosperm pollen and leaves [abstract]. *American Journal of Botany* 59(6):660.
- 1976. Pollen and leaves from the mid-Cretaceous Potomac Group and their bearing on early angiosperm evolution. In: C.B. Beck, ed. *Origin and Early Evolution of Angiosperms*. New York: Columbia University Press. pp. 139–206.
- EKLUND, H., J.A. DOYLE AND P.S. HERENDEEN. 2004. Morphological phylogenetic analysis of living and fossil Chloranthaceae. *International Journal of Plant Sciences* 165(1):107–151.
- ELLIS, B., D.C. DALY, L.J. HICKEY, K.R. JOHNSON, J.D. MITCHELL, P. WILF AND S.L. WING. 2009. *Manual of Leaf Architecture*. Ithaca, NY: Cornell University Press. 190 pp.
- FEILD, T.S. AND N.C. ARENS. 2007. The ecophysiology of early angiosperms. *Plant Cell and Environment* 30(3):291–309.
- FEILD, T.S., N.C. ARENS, J.A. DOYLE, T.E. DAWSON AND M.J. DONOGHUE. 2004. Dark and disturbed: A new image of early angiosperm ecology. *Paleobiology* 30(1):82–107.
- FEILD, T.S., T.J. BRODRIBB, A. IGLESIAS, D.S. CHATELET, A. BARESCH, G.R. UPCHURCH, B. GOMEZ, B.A.R. MOHR, C. COIFFARD, J. KVACEK AND C. JARAMILLO. 2011. Fossil evidence for Cretaceous escalation in angiosperm leaf vein evolution. *Proceedings of the National Academy of Sciences USA* 108(20):8363–8366.
- FEILD, T.S., D.S. CHATELET AND T.J. BRODRIBB. 2009. Ancestral xerophobia: A hypothesis on the whole plant ecophysiology of early angiosperms. *Geobiology* 7(2):237–264.
- FEILD, T.S., G.R. UPCHURCH, D.S. CHATELET, T.J. BRODRIBB, K.C. GRUBBS, M.S. SAMAIN AND S. WANKE. 2011. Fossil evidence for low gas exchange capacities for Early Cretaceous angiosperm leaves. *Paleobiology* 37(2):195–213.
- GREEN, W.A., L.J. HICKEY, S.A. LITTLE, C. PRICE, J. WEITZ AND S. WING. 2009. Disentangling ecological and phylogenetic signals in leaf venation patterns [abstract 563]. *Botanical Society of America Annual Meeting*; 2009 July 25–29; Snowbird, UT.
- GREEN, W.A., S.A. LITTLE, C.A. PRICE, S.L. WING, S.Y. SMITH, B. KOTRC AND G. DORIA. 2014. Reading the leaves: A comparison of leaf rank and automated areole measurement for quantifying aspects of leaf venation. *Applications in Plant Sciences* 2(8):1400006; doi: 10.3732/apps.1400006
- HICKEY, L.J. 1971. Evolutionary significance of leaf architectural features in the woody dicots [abstract]. *American Journal of Botany* 58(5):469.
- 1974. A revised classification of the architecture of dicotyledonous leaves. In: C. R. Metcalfe and L. Chalk, eds. *Anatomy of the Dicotyledons*, Volume I. 2nd ed. Oxford: Clarendon Press. pp. 25–39.
- 1977. Stratigraphy and paleobotany of the Golden Valley Formation (Early Tertiary) of western North Dakota. *Geological Society of America Memoir* 150:1–183.
- 1980. Paleocene stratigraphy and flora of the Clark's Fork Basin. *University of Michigan Papers on Paleontology* 24:33–49.
- HICKEY, L.J. AND J.A. DOYLE. 1972. Fossil evidence on evolution of angiosperm leaf venation [abstract]. *American Journal of Botany* 59(6):661.
- 1977. Early Cretaceous fossil evidence for angiosperm evolution. *Botanical Review* 43(1):3–104.
- HICKEY, L.J. AND J.A. WOLFE. 1975. The bases of angiosperm phylogeny: Vegetative morphology. *Annals of the Missouri Botanical Garden* 62(3):538–589.
- HORN, J.W. 2009. Phylogenetics of Dilleniaceae using sequence data from four plastid loci (Rbcl, Infa, Rps4, Rpl16 intron). *International Journal of Plant Sciences* 170(6):794–813.
- LITTLE, S.A., S.W. KEMBEL AND P. WILF. 2010. Paleotemperature proxies from leaf fossils reinterpreted in light of evolutionary history. *PLoS ONE* 5(12):e15161. doi: 10.1371/journal.pone.0015161
- LUO, Y. AND Z. ZHOU. 2002. Leaf architecture in *Quercus* subgenus *Cyclobalanopsis* (Fagaceae) from China. *Botanical Journal of the Linnean Society* 140(3):283–295.
- MADDISON, W.P. AND D.R. MADDISON. 2011. *Mesquite: A modular system for evolutionary analysis* [computer program]. Version 2.75. Available from: <http://mesquiteproject.org>
- PACHECO-TREJO, J., T. TERRAZAS AND H. OCHOTERENA. 2009. Leaf architecture of the genus *Didymaea* Hook. f. (Rubiaceae). *Plant Systematics and Evolution* 281(1–4):137–149.
- PEPPE, D.J., D.L. ROYER, B. CARIGLINO, S.Y. OLIVER, S. NEWMAN, E. LEIGHT, G. ENIKOLOPOV, M. FERNANDEZ-BURGOS, F. HERRERA, J.M. ADAMS, E. CORREA, E.D. CURRANO, J.M. ERICKSON, L.F. HINOJOSA, A. IGLESIAS, C.A. JARAMILLO, K.R. JOHNSON, G.J. JORDAN, N. KRAFT, E.C. LOVELOCK, C.H. LUSK, Ü. NIINEMETS, J. PEÑUELAS, G. RAPSON, S.L. WING AND I.J. WRIGHT. 2011. Sensitivity of leaf size and shape to climate: Global patterns and paleoclimatic applications. *New Phytologist* 190(3):724–729.
- PRICE, C.A., S.-J.C. KNOX AND T.J. BRODRIBB. 2013. The influence of branch order on optimal leaf vein geometries: Murray's law and area preserving branching. *PLoS ONE* 8(12):e85420. doi: 10.1371/journal.pone.0085420
- PRICE, C.A., S.L. WING AND J.S. WEITZ. 2012. Scaling and structure of dicotyledonous leaf venation networks. *Ecology Letters* 15(2):87–95.
- R DEVELOPMENT CORE TEAM. 2008. *R: A language and environment for statistical computing* [computer program]. R Foundation for Statistical Computing, Vienna, Austria. Available from: <http://www.R-project.org>
- RODDY, A.B., C.M. GUILLIAMS, T. LILITTHAM, J. FARMER, V. WORMSER, T. PHAM, P.V.A. FINE, T.S. FEILD AND T.E. DAWSON. 2013. Uncorrelated evolution of leaf and petal venation patterns across the angiosperm phylogeny. *Journal of Experimental Botany* 64(13):4081–4088.
- ROTH-NEBELSICK, A., D. UHL, V. MOSBRUGGER AND H. KERP. 2001. Evolution and function of leaf venation architecture: A review. *Annals of Botany* 87(5):553–566.
- RURY, P.M. AND W.C. DICKISON. 1977. Leaf venation patterns of genus *Hibbertia* (Dilleniaceae). *Journal of the Arnold Arboretum* 58(3):209–256.
- SACK, L. AND C. SCOFFONI. 2013. Leaf venation: structure, function, development, evolution, ecology and applications in the past, present and future. *New Phytologist* 198(4):983–1000.
- STEVENS, P.F. 2001. *Angiosperm Phylogeny Website*. Version 13 [September 2013]. St. Louis, MO: Missouri Botanical



- Garden. Available from: <http://www.mobot.org/MOBOT/research/APweb/>
- STOLTZFUS, A., H. LAPP, N. MATASCI, H. DEUS, B. SIDLAUSKAS, C.M. ZMASEK, G. VAIDYA, E. PONTELLI, K. CRANSTON, R. VOS, C.O. WEBB, L.J. HARMON, M. PIRRUNG, B. O'MEARA, M.W. PENNELL, S. MIRARAB, M.S. ROSENBERG, J.P. BALHOFF, H.M. BIK, T.A. HEATH, P.E. MIDFORD, J.W. BROWN, E.J. MCTAVISH, J. SUKUMARAN, M. WESTNEAT, M.E. ALFARO, A. STEELE AND G. JORDAN. 2013. Phylotastic! Making tree-of-life knowledge accessible, reusable and convenient. *BMC Bioinformatics* 14:158. doi: 10.1186/1471-2105-14-158
- TODZIA, C.A. AND R.C. KEATING. 1991. Leaf architecture of the Chloranthaceae. *Annals of the Missouri Botanical Garden* 78(2):476–496.
- WALLS, R.L. 2011. Angiosperm leaf vein patterns are linked to leaf functions in a global-scale data set. *American Journal of Botany* 98(2):244–253.
- WANG, Y.F., D.K. FERGUSON, R. ZETTER, T. DENK AND G. GARFI. 2001. Leaf architecture and epidermal characters in *Zelkova*, Ulmaceae. *Botanical Journal of the Linnean Society* 136(3):255–265.
- WEBB, C.O. AND M.J. DONOGHUE. 2005. Phylomatic: Tree assembly for applied phylogenetics. *Molecular Ecology Notes* 5(1):181–183.
- WILF, P. 2008. Fossil angiosperm leaves: Paleobotany's difficult children prove themselves. *Paleontological Society Papers* 14:319–333.
- WING, S.L. AND L.D. BOUCHER. 1998. Ecological aspects of the Cretaceous flowering plant radiation. *Annual Review of Earth Planetary Sciences* 26:379–421.
- WOLFE, J.A. 1971. Tertiary climatic fluctuations and methods of analysis of Tertiary floras. *Palaeogeography, Palaeoclimatology, Palaeoecology* 9(1):27–57.
- 1993. A method of obtaining climatic parameters from leaf assemblages. *US Geological Survey Bulletin* 2040:1–71.
- ZHANG, Q., A. ANTONELLI, T.S. FEILD AND H.Z. KONG. 2011. Revisiting taxonomy, morphological evolution, and fossil calibration strategies in Chloranthaceae. *Journal of Systematics and Evolution* 49(4):315–329.