

FOSSIL ANGIOSPERM LEAVES: PALEOBOTANY'S DIFFICULT CHILDREN PROVE THEMSELVES

PETER WILF

Department of Geosciences
Pennsylvania State University
537 Deike Building
University Park, PA 16802

Abstract—The great bulk of the angiosperm fossil record consists of isolated fossil leaves that preserve abundant shape and venation (leaf architectural) information but are difficult to identify because they are not attached to other plant organs. Thus, poor taxonomic knowledge has tempered the tremendous potential of fossil leaves for constructing finely resolved records of biodiversity through time, extinction and recovery, past climate change and biotic response, paleoecology, and plant-animal associations. Moreover, paleoecological and paleoclimatic interpretations of fossil leaves are in great need of new approaches. Recent work is rapidly increasing the scientific value of fossil angiosperm leaves through advances in traditional paleobotanical reconstruction, phylogenetic understanding of both leaf architecture and the response of leaf shape to climate, quantitative plant ecology using measurable, correlatable leaf traits, and improved understanding of insect leaf-feeding damage. These emerging areas offer many novel opportunities to link paleoecology and neoecology. Increased collaboration across traditionally separate research areas is critical to continued success.

INTRODUCTION

Leaves, the most visible plant organs, are by far the most abundant type of plant fossil. However, fossil leaves, especially those of angiosperms (flowering plants), are notoriously difficult to identify. They are often found in isolation and without preservation of organic material (i.e., as impressions). A fossil leaf considered “excellent” on the outcrop due to its beauty and apparent completeness (Fig. 1) typically preserves only a size, a shape, and a venation pattern. Less often, organic materials with additional characters are present, such as cuticular remains, or attachments to other leaves or leaflets are preserved. Very rarely, leaves may be attached to diagnostic flowers or fruits. These problems are especially acute for the angiosperms, due to their high diversity, abundance, and phenotypic plasticity from Cretaceous to Recent. Early angiosperm paleobotanists, though deserving great credit as scientific pioneers, filled the literature with an apparently intractable legacy: thousands of incorrect assignments to extant genera based on superficial comparisons (discussed in Dilcher, 1974; Hill,

1982). For these and other reasons, the broader field of paleobotany tends to avoid the angiosperm leaf record, paleobotany courses typically “run out of time” before the topic arrives, and the most voluminous source of potential data that paleobotany has to offer is generally kept out of sight or considered mostly decorative.

Despite this difficult history, fossil floras dominated by isolated angiosperm leaves are somehow providing data for a large number of recent publications in respectable journals, especially paleoecological and paleoclimatic studies related to past climate change and extinction. How can this be? I focus here on a selection of developing research areas where fossil angiosperm leaves play a central role. I first discuss the legacy issues mentioned above and how overcoming them is an important and interesting research goal, combining subdisciplines that often work separately. I then give an overview of recent developments, in plant functional ecology, paleoclimate, and plant-animal interactions, that have much potential to provide important new links between paleoecology and neoecology.

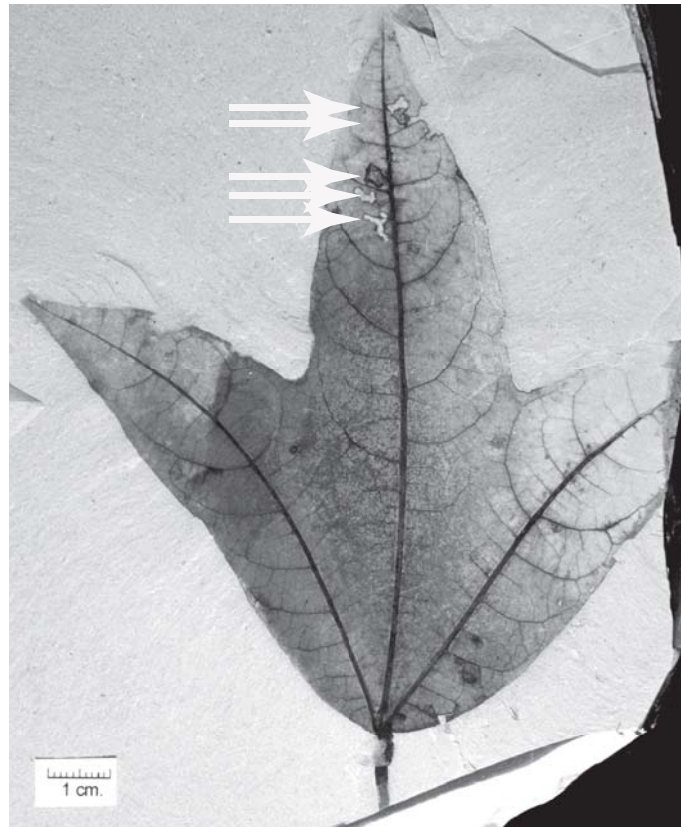


Figure 1—A typical ‘problem child’ from the Laguna del Hunco flora, early Eocene of Patagonia, Argentina (Museo Paleontológico Egidio Feruglio, MPEF-PB 979; note 1 cm scale bar). This cosmetically attractive, three-lobed leaf is one of 109 specimens of this morphotype in the flora; the morphotype has not been found attached to other plant organs and also apparently lacks organic preservation. The distinctively regular primary veins originating from a single point at the base, along with other features, allow placement in the large family Malvaceae s.l. (> 240 genera, > 4200 species). Further taxonomic placement is unlikely, although there are similarities to the genus *Brachychiton*. Leaf shape in the morphotype, known currently as “Malvaceae sp. TY23,” shows wide variation in lobe incision and width as well as leaf size, though placement in a single morphotype is aided by the large sample size, which allows observation of the continuum of variation. Consistent features across the sample include palmate lobation with three (sometimes two) lobes and primary veins originating from a single point; the lobes convex-sided, with pointed acute apices; the lobe sinuses rounded, incised up to >50% to >80% of the distance to midvein; the leaf margin typically untoothed; and the secondary veins brochidodromous (prominently looped) apically but interior (joining the primary veins together) basally. Malvaceae sp. TY23 is a good example of the many types of data fossil leaves typically provide; its presence contributes to the high estimated plant richness of this flora (over 150 leaf morphotypes), its relative abundance to paleoecological data and diversity analyses, its stratigraphic positions to the timing of paleoenvironmental events, its lack of teeth to a warm paleotemperature estimate from the whole flora (16.6 ± 2.0 deg. C; interestingly, there are teeth on a single specimen), its generally large leaf area (reconstructed as 5344 mm^2 on this specimen) to a moist paleoprecipitation estimate from the whole flora ($114 +49.1, -34.3 \text{ cm/y}$), its area and petiole width (2.5 mm on this specimen) to estimated leaf mass per area (for this specimen: 89 g/m^2 , 95% prediction range 68 to 117 g/m^2), and its abundant and diverse associated insect damage, found on many other plant hosts in the flora as well, to interpretations of elevated plant-animal associations and ecosystem diversity in Eocene Patagonia (Wilf et al. 2003a, 2005a, 2005b). Insect damage on this specimen includes, from top to bottom arrow, polylobate hole feeding (damage type 3 of Labandeira et al. 2007), deeply incised margin feeding (DT15), surface feeding (DT29), and curvilinear hole feeding (DT7, bottom two arrows), all of which are generalist damage types conceivably made by a single feeding insect.

THE LEAF MORPHOTYPE - TAXONOMY DIALECTIC

When anatomical and epidermal features are not preserved, fossil angiosperm leaves are most often reliably assigned using attachments, which are rare (Crane and Stockey, 1985; Manchester et al., 1986; Boucher et al., 2003; Zamalola et al., 2006), or repeated co-occurrence (Wing and Hickey, 1984; Manchester and Hickey, 2007) with other organs considered diagnostic, most often flowers, fruits, and seeds. This approach attains high botanical precision but usually for a small minority of the leaf species inferred to be present. Thus most leaf floras, including many with high apparent richness, remain poorly known taxonomically. There are exceptions: sustained efforts by S.R. Manchester and colleagues on the typically low-diversity Paleocene floras of the Western Interior USA have deciphered a large percentage of leaf taxa (e.g., Crane et al., 1991; Manchester et al., 1999; Manchester and Hickey, 2007). One significant outcome of botanical reconstructions, underscoring the hazards of identifying isolated fossil leaves, is the frequent recognition of extinct genera. These often incorporate specimens previously diagnosed to extant genera before attachment or associational evidence emerged (Manchester, 1989, 2001; Manchester et al., 1998).

For leaves without recognized attachments, co-associations, organic material, or anatomy, i.e., the great majority of the record, we turn to the leaf impressions themselves, where we typically find a great deal of data on shape and the fine details of venation (leaf architecture). These features are highly variable and quite subtle among living plants, and it is here that early fossil workers made many mistakes. Widely used, detailed descriptive terminology now exists for leaf architecture (e.g., Hickey, 1973; Ash et al., 1999; Ellis et al., 2009), which has been studied for several extant groups (e.g., Carr et al., 1986; Keating and Rاندrianasolo, 1988; Hickey and Taylor, 1991; Todzia and Keating, 1991; Gandolfo and Romero, 1992; Liu, 1996; Premoli, 1996; González et al., 2004; Fuller and Hickey, 2005; Martínez-Millán and Cevallos-Ferriz, 2005). However, since a major overview paper by Hickey and Wolfe (1975), which showed systematic signal in leaf architecture with great utility for identifying fossils (e.g., Hickey, 1977; Wolfe, 1977; Wolfe and Wehr, 1987), there has been no detailed or updated

guide to character distribution across the angiosperms; two useful contributions have come from tropical plant identification guides that make extensive use of leaf architecture (Gentry, 1993; Keller, 2004). Thus, fossil leaf identification requires great first-hand knowledge, derived from personal experience of cleared-leaf collections (available in very few institutions), herbaria, and living specimens, of immensely complex visual patterns and their distributions among the world's plants. The need for this broad geographic knowledge is greatest for Cretaceous and Paleogene floras (and many Neogene, especially Miocene assemblages), which typically have little compositional relationship to that of the modern site, or even to the continent where they are found.

A great opportunity now exists to re-evaluate angiosperm leaf architecture within the overhauled phylogenetic context offered by molecular data (Angiosperm Phylogeny Group, 2003). The phylogenetic signal, homoplasy, and character evolution of leaf architecture can be investigated quantitatively, and this will eventually lead to greater confidence in the phylogenetic significance of particular characters when they are found in fossils. Preliminary work already shows phylogenetic signal and evolutionary patterns across the angiosperms in broad traits such as vein organization, leaf shape, and major venation category (Doyle, 2007; Green and Little, 2007), as well as confirmation and possibility of refinement for many of the patterns noted by Hickey and Wolfe (1975). Phylogenetic signal also emerges in leaf shape variables, long assumed to be convergent, that are significant for paleoclimate estimates (Little et al., 2008, discussed below). Within plant lineages, leaf architectural characters are increasingly used in cladistic evolutionary studies, including characters selected for investigation precisely because they are often preserved in fossil leaves (Doyle and Endress, 2000; Eklund et al., 2004; Fuller and Hickey, 2005; Scharaschkin and Doyle, 2005; Manos et al., 2007).

Although advancement of phylogenetic leaf architecture will greatly improve hypotheses about the botanical affinities of many fossil angiosperm leaves, the bulk of taxa, especially from older (Cretaceous and Paleogene) floras will remain unidentified for some time to come, especially because the discovery rate of new forms remains high. In addition to taxonomy, there is a strong need to estimate the total number of

species in a flora and analyze their characteristics, as a major data source that can be tied to robust stratigraphy, geochronology, and paleoclimate records. Leaf architecture allows the discrimination of morphologically discrete sets of species-like entities, called morphotypes, within fossil (and extant) floras (Johnson et al., 1989; Ash et al., 1999). Morphotypes are highly defensible compared to the old practice of assigning all fossils, no matter how fragmentary and questionable, to extant genera. They derive from vouchered specimens and are subject to review by later investigators. Leaf morphotypes may or may not be equivalent to named entities; if not, when they are eventually taxonomically assigned they carry no nomenclatural baggage.

The major advantage of morphotypes is that they can comprise a parataxonomy for an entire fossil flora, usually associated with abundance, paleoecological, and stratigraphic data. They make possible important treatments of whole-flora ecology, diversity, climate analysis, and many other topics, as well as illustrations and descriptions that are free of taxonomic errors. For example, leaf morphotypes play a major role in many studies of regional biodiversity through time, including extinction, recovery, and response to climate change (Wolfe and Upchurch, 1986; Johnson et al., 1989; Wing et al., 1995; Wilf, 2000). Their obvious disadvantage is that they are to various degrees unknown as botanical entities, and their widespread use in high-profile publications perhaps sends a message to students that taxonomy doesn't matter very much. Thus, leaf morphotypes generate reproducible science that has greatly increased the profile of paleobotany in diverse fields such as climate change and paleoclimatology, geochemistry, stratigraphy, ecology, and the other major branches of paleontology. At the same time, they are "difficult children" that often cause unease among botanists and paleobotanists.

The resolution to this dialectic is collaboration, cooperation, and diversification of interests. Leaf morphotypers typically pursue large sample sizes and statistical significance to test large-scale patterns, and some of the largest and stratigraphically best-constrained fossil plant collections in the world are the result. However, these collections must be made with great attention to the relatively rare fossil flowers, seeds, fruits, cuticles, and attachments that allow systematics to be done. In addition, eventual publica-

tion and proper illustration of all the morphotypes in a flora is essential, even as a parataxonomy, though this rarely occurs (e.g., Hill, 1982; Crane et al., 1990; Dilcher and Lott, 2005; Danehy et al., 2007). Conversely, collections made in pursuit of a small number of targeted botanical entities are much more valuable if a full suite of associated taxa and organs is collected, including leaves, and more so yet if abundance data are captured. These statements are easily made, but in practice it can be quite difficult in the field to broaden one's search image and resource investment beyond the initial target that motivated the field work. Linking morphotyping and systematics from the start of a project is therefore a robust recipe for diverse successes.

An example of this type of collaboration is a current project on latest Cretaceous and Paleogene fossil floras of Patagonia, Argentina. We have collected more than 12,000 plant fossils with precise stratigraphic control, including more than 400 leaf morphotypes, to answer a set of initial questions about plant diversity, plant-insect associations, paleoclimate, and geochronology (Wilf et al., 2003a, 2005a, 2005b; Iglesias et al., 2007, 2008a). At the same time, the collections allow systematic delineation of many important botanical entities, usually based on leaves with cuticles or attached or associated reproductive structures (Zamaloa et al., 2006; Gandolfo et al., 2006, 2007; González et al., 2007; Wilf et al., 2007, 2008), as well as new ichnotaxonomic entities from fossilized insect folivory (Sarzetti et al., 2008). Thus, simultaneous advances in geological and ecological as well as systematic aspects of paleobotany are being made in a large and productive field area, little investigated since the 1920s and 1930s (Berry, 1925, 1937, 1938). The morphotypes create a stable organizational substrate for hundreds of species represented by thousands of specimens, from which taxonomic entities can be recognized and large-scale questions of pattern can be asked. Less formal cooperation also yields results: bulk collections of late Paleocene leaves in Wyoming that were used in a study of insect damage through time (Wilf et al. 2006) included well-preserved fossil fruits that contributed to resolving an associated Paleocene leaf species long considered enigmatic (now *Browniea serrata*, Nyssaceae: Manchester and Hickey, 2007). In addition, prospecting for fossil plants in the area led to the discovery of an important, ^{40}Ar - ^{39}Ar dated volca-

nic ash that precisely constrains the floras, including the *Browniea* occurrences (Secord et al., 2006).

I note in passing the great potential for reinvestigating leaf fossils with epifluorescence microscopy (e.g., Friedrich and Schaarschmidt, 1979; Schaarschmidt, 1982; Kerp and Krings, 1999), which allows rapid scanning of numerous specimens to reveal detailed, informative features on an overlooked few that may have appeared only to be impressions or coalifications under conventional light microscopy. The technique has been highly productive in our lab. For example, in-situ pollen grains in fossil flowers may fluoresce brightly but be invisible under SEM because they are located just under the matrix surface (Iglesias et al., 2008b). Leaf cuticles too fragile to isolate safely with chemicals, and so thin as to be nearly undetectable under ordinary light, can be investigated in-situ and non-destructively (Wilf et al., 2008; Iglesias et al., 2008a).

FUNCTIONAL LEAF TRAITS: A QUANTITATIVE LINK FROM PALEOECOLOGY TO NEOECOLOGY

Fossil plant deposits contain a vast reserve of under-tapped, diverse ecological information (recently reviewed comprehensively by DiMichele and Gastaldo, 2008). Deep-time paleoecology, in general, continues to be dominated by the production of diversity and turnover metrics and relative abundance curves via taxon counting, and by interpretations of taphonomy and depositional environments. Direct quantitative links to neocological data remain weak but fundamental for testing which current ecological observations have temporal generality, and how current ecosystems evolved. Adding to the paleoecologist's difficulty is a plethora of contending neocological theories that are difficult or impossible to test with fossils, a prominent example being Hubbell's (2001) neutral theory of biodiversity.

Quantitative trait ecology is one of the most promising avenues for new breakthroughs in paleoecology because it is built from measurements, usually continuous, of critical functional variables that are strongly tied to the performance and environmental tolerances of organisms (e.g., McGill et al., 2006). Trait values can then be correlated to each other and to variables representing ecological gradients (Wright et al., 2004;

Swenson and Enquist, 2007), using straightforward metrics such as R^2 and p , to reveal how the constituent species of a community vary in resource deployment and life strategy. Traits that typically have high variance within a community are especially informative for interpreting ecology at the species level. However, it is challenging to identify traits that can be measured in fossils or estimated by proxy. For fossil vertebrates, body size has a long history of ecological interpretation from fossils via scaling from tooth dimensions (e.g., Alroy, 1998).

For plants, leaf mass per area has emerged from a wealth of recent literature in plant ecology as centrally important in defining communities along resource gradients (Reich et al., 1991, 1997, 1999; Ackerly and Reich, 1999; Wright et al., 2004, 2005a, 2005b). Leaf mass per area (which is also the inverse of specific leaf area) varies significantly within sites and correlates significantly with related traits including leaf lifespan (+), leaf toughness (+) and thickness (+), nitrogen content (-), and photosynthetic capacity (-). In turn, these intercorrelated traits also correlate with plant defense and palatability to herbivores; for example, leaves with high leaf mass per area tend to have low concentrations of nitrogen and are thus demonstrably less palatable to insects (Coley, 1983; Coley and Barone, 1996).

A recent collaboration of 16 ecologists and paleobotanists produced an easily-applied, well-calibrated proxy for fossil leaf mass per area based on the biomechanical scaling relationship between leaf mass and petiole dimensions, normalized to leaf (blade) area (Royer et al., 2007; Fig. 2). Specifically, petiole width is used because it is much more commonly preserved than full petiole length, and when squared, petiole width scales to the petiole's cross-sectional area that supports the leaf mass. Thus, all that is needed from fossil leaves (or leaflets if compound leaves) is petiole (petiolule) width and estimated leaf area. The calibration was based on angiosperms, but importantly for deep-time fossil applications, preliminary gymnosperm data fit the angiosperm calibration well (Royer et al., 2007).

Royer et al. (2007) quantified fossil leaf mass per area for two well-sampled, taxonomically well understood (MacGinitie, 1969; Wolfe and Wehr, 1987) Eocene lake floras with insect-herbivory data: Republic (early Eocene, Washington, humid warm temperate)

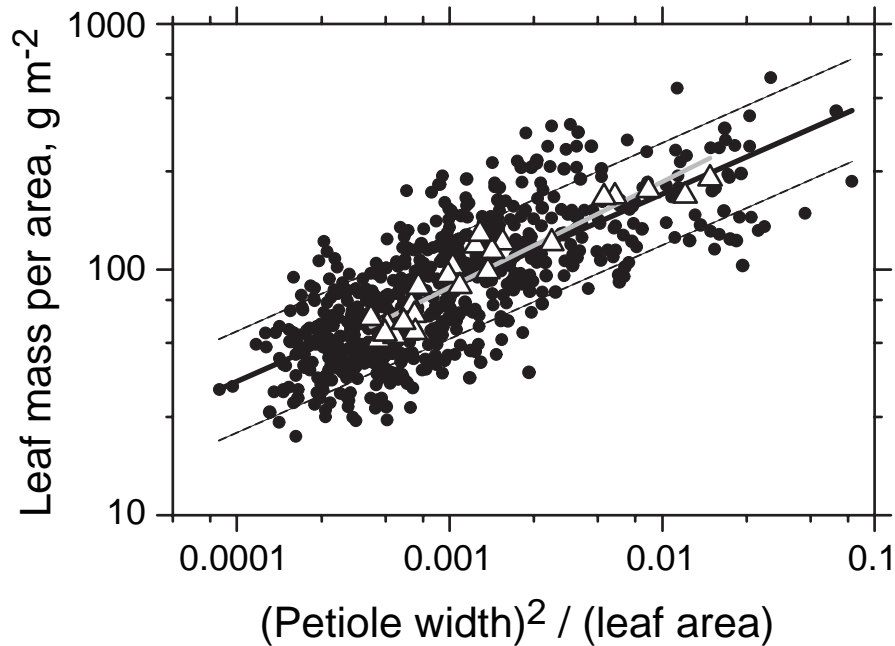


Figure 2—Scaling between petiole width² (mm²) and leaf dry mass (g), normalized by leaf area (mm² and m², respectively), for 667 species-site pairs of extant woody angiosperms from 65 globally distributed sites, redrawn from Royer et al. (2007). Note that the vertical axis shows the desired trait variable, leaf mass per area (g m⁻²), and that the only input needed from fossil leaves is petiole (petiolule for compound leaves) width and leaf (leaflet) area (horizontal axis). Dots represent the species-site pairs, and triangles represent the site means for sites where ten or more species were sampled. The black and gray lines are the linear regressions for species and sites, respectively (see Royer et al. 2007 for details). Dashed lines represent 95% prediction intervals for the species data.

and Green River (middle Eocene Bonanza site, Utah, seasonally dry subtropical). From modern observations of how leaf mass per area and plant-insect ecology vary with climate (Coley, 1983; summarized in Wilf et al., 2001), Royer et al. predicted, and found, a greater variance of both leaf mass per area and herbivory for the seasonally dry Green River flora than at Republic, as well as an overall negative correlation of herbivory and leaf mass per area. These results showed the Green River sample to contain a mixture of lake-margin species (of Platanaceae and Salicaceae) with high resource availability, presumed fast growth strategy, and high palatability (low leaf mass per area), versus the presumably drought-tolerant, slow-growing, and unpalatable species occupying the rest of the landscape (high leaf mass per area). This study quantitatively confirmed a previous characterization of the variance within Green River plant and plant-insect community ecology based on traditional, qualitative interpretation of fossil plant growth strategy and herbivory in modern analog environments (Wilf et al., 2001). Thus, the approach is ready to use

on less understood fossil floras (for an application to past climate change and herbivory, see Currano et al., 2008). The results also indicate a higher likely rate of nutrient recycling, which increases at lower leaf mass per area, among woody angiosperms at Republic than at Green River.

This example from paleobotany brings together both plant trait ecology and plant-insect ecology into a straightforward predictive framework for paleoecology. More importantly, it demonstrates the potential for trait ecology to allow direct, productive comparison of fossil and extant communities in terms of niche ecology, climate gradients, plant-animal interactions, and nutrient recycling (see also Royer, 2008).

PALEOCLIMATE FROM LEAF FOSSILS: WHICH WAY FORWARD?

I am fairly certain that “paleoclimate estimates” would be the top response to any poll of geologists asked the question: “what good are fossil leaves?”

Indeed, quantitative paleoclimate estimates are in all likelihood paleobotany's most frequent export to other fields. "How warm was it there?" and "how fast and how much did it cool here?" are core questions for understanding Earth history, and fossil plants have long been major contributors to paleoclimate reconstructions, fossil biome interpretations, intercontinental migration hypotheses, climate simulation constraints, etc. The leaf data have come in two principal forms: analysis of the climatic tolerances of nearest living relatives (e.g., Mosbrugger and Utescher, 1997), which relies on correct taxonomic placement of fossils, and analysis of leaf size and shape variables (i.e., leaf physiognomy; starting with Bailey and Sinnott, 1915), which does not, and is therefore a common use of leaf morphotypes. Many paleotemperature trends quantified from fossil leaf physiognomy, especially leaf-margin analysis (the robust linear correlation of mean annual temperature with the percentage of woody dicot species in a mesic flora that have untoothed leaf margins: Bailey and Sinnott, 1915; Wolfe, 1979), have been validated by marine isotopic and other independent data for important intervals of global warming and cooling near the Cretaceous-Paleogene, Paleocene-Eocene, and Eocene-Oligocene boundaries (Wolfe and Poore, 1982; Wolfe, 1992; Wing et al., 2000, 2005; Wilf et al. 2003b). This general topic, its rich history, and many associated issues have been reviewed exhaustively elsewhere, most recently and effectively by Greenwood (2007), and I concentrate here on a few directions I consider most productive.

The first is the future of multivariate leaf physiognomy. In a major breakthrough, Wolfe (1993, 1995) showed the significant contribution to climate signal in extant floras that comes not only from the among-species mean of leaf margin state (toothed or untoothed, i.e., leaf-margin analysis) at a site but also from 28 other shape characters, and he developed a method for using this signal in paleoclimate estimates known as CLAMP (climate leaf analysis multivariate program). In my first paper (Wilf, 1997), I found that the additional characters, unfortunately, did not improve temperature estimates in extant floras over leaf-margin analysis, despite requiring many times more work. This straightforward conclusion has been repeatedly validated (see Greenwood, 2007 for review), and no defense of CLAMP has emerged that has refuted it. Other work has shown that temperature seasonality

signals in CLAMP are statistical byproducts of the modern correlation of temperature and temperature seasonality (Jordan, 1996) and that leaf sizes are significantly biased towards small leaves in the CLAMP database, particularly affecting rainfall estimates by inflating them (Wilf et al., 1998, 1999). I note here that the leaf-size bias in the calibration data is also very likely to distort paleoaltitude estimates using CLAMP, which use fossil leaves to estimate differences in mean annual enthalpy between coeval coastal reference and inland target floras (e.g., Wolfe et al., 1997, 1998). This is because enthalpy (which has a specific humidity component that correlates with leaf size) will be overestimated more for the coastal reference flora, due to its larger leaves, than for the targeted inland flora, inflating the enthalpy difference and thus the paleoelevation estimate for the inland site.

Seeking an alternative to CLAMP, I began a new project to improve multivariate leaf physiognomy and to recover the additional climate signal that Wolfe first identified in the CLAMP project. Two significant problems to overcome were first, that CLAMP relied on discrete character states rather than continuous measurements, and second, that after observing many colleagues scoring leaves, it was clear that different investigators were not likely to score the same leaf the same way using Wolfe's instructions (Wilf, 1997). Rapid, computerized measurement of leaf outlines on ordinary desktop computers had just (ca. 2000) become possible and seemed to be an excellent procedure for solving both problems.

Working with two undergraduates (Huff et al., 2003), I developed a set of computer-assisted, highly reproducible, continuous measurements including various combinations and ratios of area, perimeter, tooth count, and tooth area measurements, and showed that these varied in the predicted way between one wet tropical site (Panama) and two temperate (Pennsylvania) extant sites: the tropical site's leaves (or leaflets when compound) were, by among-species mean, more circular and less dissected, with smaller and fewer teeth. Due to the central role of digital leaf images, we coined the method "digital leaf physiognomy" (Huff et al., 2003). A major follow-up paper using leaf collections by E.A. Kowalski and D.L. Dilcher examined these and 14 additional sites from the Eastern USA, finding significant linear correlations between most of the digital leaf physiognomy characters and mean

annual temperature (Royer et al. 2005). Importantly, several correlations passed digital fragmentation tests and showed promise for use in fossil floras. Another benefit of the method is that it appears to dampen an important bias, whereby species near bodies of water analogous to depocenters are more often toothed than those in adjacent forest from the same climate (Burnham et al., 2001). However, additions of a few floras from outside the Eastern USA altered the correlations somewhat (Cariglino, 2007), and it is clear that a great deal of additional calibration data from more regions will be needed before major applications can be made to fossil floras (D.L. Royer et al., work in progress). Moreover, the amount of labor needed to measure the new variables from imperfectly preserved fossil leaves exceeds CLAMP (Cariglino, 2007), and thus future acceptance of the method depends on whether the labor is justified with significantly improved climate estimates.

The digital leaf physiognomy project has had many synergistic outcomes, currently in very early stages, that are at least as interesting for future investigations as the initial climatic correlations and applications because they provide new, explicit, and quantitative links between paleoecology and neoecology. The wealth of continuously measured, novel leaf-shape data that is emerging has high statistical significance and ecological importance (Royer et al., 2008). The data can be placed on phylogenetic trees to measure historical effects, and they can also be correlated to other vegetational traits (Royer et al., 2005, and see above).

Preliminary work (Little et al., 2008) shows that nearly all of the leaf traits used in leaf-margin analysis and digital leaf physiognomy, and presumably in CLAMP as well (including tooth traits), have slight to strong, significant historical (phylogenetic) signal. Thus, Little et al. are demonstrating that the core assumptions underlying leaf-physiognomic methods need overhaul: that leaf shape is primarily controlled by climate, that phylogeny is insignificant, and therefore that the species at a site can be treated as statistically independent entities. Continued investigation along these lines is likely to help explain the much-debated “regional differences” in leaf-climate responses (e.g., Greenwood et al., 2004; Aizen and Ezcurra, 2008) and to allow phylogenetic adjustments of paleo-

climate estimates for fossil floras with no modern regional analogs. The Little et al. initial results are also validated by the work mentioned above that showed phylogenetic signal in leaf-shape data mapped on trees (Doyle, 2007; Green and Little, 2007).

Leaf physiognomy science is entering a new phase wherein high reproducibility of measurements and improved phylogenetic context both allow significant improvements in characterizing the taxonomy, paleoclimate, and ecology of fossil floras. This is a far more productive and interesting route forward than the continuing proliferation of papers on “equation-testing” and revisitation of old arguments about CLAMP (for review see Greenwood, 2007). A broad approach is also more likely to keep leaf physiognomy involved in relevant and diverse science while geochemical paleoclimate proxies for the terrestrial realm advance quickly (Weijers et al., 2007; Snell et al. 2007; Schouten et al., 2008).

CALIBRATING INSECT-DAMAGE RICHNESS FOR PALEOECOLOGY AND NEOECOLOGY

Clearly one of the most productive contributions of fossil leaves is their uniquely diverse and abundant preservation of insect-feeding damage. No other type of fossil preserves such rich, direct evidence of two levels of the food web in a single specimen, often combined with the full stratigraphic context, high sample size, and other contextual data offered by fossil leaf collections such as paleoclimate data, leaf trait data (see above), and host-plant abundance and phylogeny. Thus, fossil insect damage offers a tremendous opportunity to study and time the response of plant-insect feeding associations to major environmental stresses and climate change (Labandeira et al., 2002a; Wilf et al., 2006; Currano et al., 2008). This topic, with obvious relevance to today’s changing ecosystems, has been extensively reviewed recently (Labandeira, 2005; Wilf, 2008), and the example of Eocene herbivory in the context of leaf mass per area and climate (Royer et al., 2007) is given above. Here, I briefly discuss some important aspects of the bedrock data source, insect damage types (DTs) that occur on fossil leaves (a few examples shown in Fig. 1), what is needed to under-

stand them better, and their potential as a strong link to neoecology.

Ecologists have living herbivores available for counting, and they have not needed a system for quantifying richness of insect damage (but see below). Instead, insect damage is usually quantified as a rate: amount of leaf tissue removed per unit time. Recognition of insect damage types originated to quantify the full richness of insect feeding on Paleocene and Eocene floras from Wyoming (Wilf and Labandeira, 1999). The fossil DTs have since been expanded, illustrated, and described using several fossil floras (e.g., Labandeira, 2002; Labandeira et al., 2002b). The working catalog of fossil DTs, now numbering more than 150, is maintained in an open-access, fully illustrated, continuously updated, printable Internet guide (Labandeira et al., 2007).

The DTs parallel leaf morphotypes in many ways in terms of taxonomic issues. They are informal, operational units that represent the insect-feeding richness on a flora. Although some may find the inherent concept of “morphotypes on morphotypes” unsettling, this allows characterization of the full spectrum of damage richness on all the host plants in a flora. As for leaf morphotypes, the eventual incorporation of DTs into formal taxonomic entities is essential, especially for those that can be linked to a well-defined culprit (Wilf et al., 2000; Sarzetti et al., 2008), but the discovery rate is much higher than the description rate. A major difference from leaf morphotypes, which usually correspond to inferred species entities, is that the correspondence of DTs to real herbivore species is highly variable, and for the most part unquantified. Whereas the mine, gall, and other “specialized” damage types on a particular plant host typically each represent one or only a few herbivore species (Johnson and Lyon, 1991; Russo, 2007), generalized feeding, such as most external foliage feeding, is much harder to pinpoint. A few herbivore species at a site may make many kinds of damage on many plant species (Basset and Höft, 1994).

Therefore, a major effort is needed in living forests to calibrate the insect damage types to the number of herbivore species that make them. This work, underway in a pilot project, will lead to more informed interpretations of fossil damage occurrences and will also produce important natural history data. More-

over, calibration should make possible an alternative measure of past arthropod diversity through time and enable this conspicuous data source to be used for ecological studies in living forests. For example, insect feeding richness can be monitored for its response to current climate change, a natural and relevant extension of results from the deep-time fossil record, projected to neoecology.

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