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SPOTLIGHT

DOI 10.2110/palo.2005.S05

Sticks and Mud, Fruits and Nuts, Leaves and Climate: Plant Taphonomy Comes of Age

It's conceivable that just about every natural scientist first started out as a plant taphonomist. As far-fetched as this statement seems, think back to when you were a child. Didn't you ever toss a handful of maple fruits into the air to see them flutter down, whipping around like little helicopters? Or blow hard at a dandelion to see how long the seeds floated in the air? You must have thrown leaves or sticks into a stream to see them swept away by the current. Even Winnie-the-Pooh undertook a series of taphonomic experiments on the transport of detached plant parts, throwing fir cones and Poohsticks, one after another, from an elevated structure oriented perpendicular to flow into a low-energy fluvial system to observe empirically which plant clast passed under the bridge first (Milne, 1926).

At some point, however, serious scientists feel compelled to put their childhood games aside, but this is exactly when plant taphonomists become engaged intellectually. This is because most plant taphonomists are paleobotanists, and one of the most basic questions in studying any fossil flora is: How faithfully does my assemblage represent the ancient vegetation? Are there biases favoring the preservation of certain species or plant organs over others? Will my Poohstick beat your fir cone to the other side of the bridge?

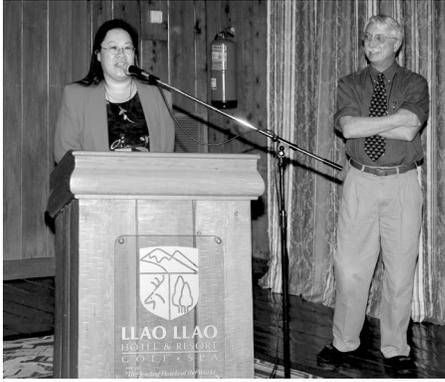
There are several approaches to answering questions in plant taphonomy. The first is to do as Winnie did and look at patterns in the transport, sorting, settling, and preservation of various plant parts in modern depositional systems. These actualistic studies, also called actuopaleobotany, are fundamental to elucidating the taphonomic filters that act upon plant material. Another approach is through laboratory experimentation. Unlike animals, plants readily lend their organs—leaves, wood, fruits, and seeds—to testing. It was in the 1980s, for example, when basic research on leaves was carried out in which dicot (broad-leaved) foliage was put into a bucket of water to see how long it would take until it settled to the bottom (Ferguson, 1985, 2005), a simple but essential experiment that nobody had thought to do (and publish on) before then. A third approach is to start at the fossil assemblage and to work back through the processes of time, deciphering the taphonomic history of individual plants or of an entire paleoflora with the hope of reconstructing the once-living plant, community, or landscape. Most studies involve two or more of these approaches, as it is application of the insights gained through actualistic study that intimately couples plant taphonomy with paleobotany.

Alternatively, plant taphonomy can be viewed from a process-oriented perspective. The major phases, or sets of processes, through which plant material must pass before fossilization are necrology, biostratinomy, and diagenesis. Necrology involves the death of a plant or the loss of a plant part, either by traumatic causes (wind, storm, animal damage) or by pre-programmed physiological changes on the part of the plant (abscission, dehiscence). Biostratinomy is the transition of the plant or plant part from the living world to the inorganic realm, up to and including burial. Diagenesis encompasses the physical and chemical processes acting on and interacting with the buried plant debris and the sediment that convert them into a fossil and enveloping matrix. Up to now, biostratinomy has gotten the lion's share of attention among plant taphonomists, but the diagenesis of plant tissues always has been of great interest to geobiochemists and paleobotanists alike.

Plant taphonomy began as an offshoot to paleobotany in the Northern Hemisphere in the 1970s (Ferguson, 2005). At that time, both plant and animal taphonomy became established as separate subdisciplines of paleontology. In the past three decades, plant taphonomy has expanded its focus and developed in sophistication.

The papers presented in this Plant Taphonomy Special Issue reflect the increasing maturity of our field. Instead of remaining exclusively in the domain of temperate floras in the Northern Hemisphere, plant taphonomy has been disseminated to the Southern Hemisphere (Gastaldo et al., 2005; Greenwood, 2005; Steart et al., 2005) and to Neotropical regions (Burnham et al., 2005), and now is used to solve questions that specifically or even uniquely pertain to Gondwanan or tropical floras. Similarly, investigations in plant taphonomy no longer merely impact paleobotanical interpretations, they also are integral in wide-ranging, global issues, including complex climate modeling (Spicer et al., 2005) and the recognition of shifting taphonomic regimes at critical extinction boundaries in Earth history (Gastaldo et al., 2005). Furthermore, it is no longer a one-act show with only leaves in the main roles, since woody fruits and seeds are now moving into the limelight (Gee, 2005). At other times, logs as (non-)indicators of paleocurrent and even plant hash have made their appearance on the taphonomic stage as well (Gastaldo, 1994, 2004).

One current driving force behind the continual progress of plant taphonomy is its significance for paleoclimate reconstruction. Leaf morphology has been used as a proxy for climatic conditions for nearly a century now (Bailey and Sinnott, 1915, 1916), and paleoclimate estimation programs long have been in the refinement stage. The understanding of taphonomic forces on leaves and leaf floras is instrumental in the fine-tuning of these systems. Two major climate programs have arisen that are based on leaf morphology: Leaf Margin Analysis (LMA) and Climate Leaf Analysis Multivariate Program (CLAMP); for another conceptual approach to climate reconstruction—the Coexistence Approach—see: Mosbrugger and Utescher, 1997; Uhl et al., 2003). LMA correlates the proportion of woody dicot species in a flora with entire (non-toothed) leaf margins and mean annual temperature (MAT), while CLAMP takes a multivariate approach, involving 31 different characters of leaf morphology and 11 climate variables. LMA is faster and simpler to use, but



Carole Gee and Bob Gastaldo convene the Plant Taphonomy Symposium at IOPC-VII in Argentina, held at the fabulous Llao Llao Resort Hotel in Bariloche, March, 2004.

Carole Gee is a native of Los Angeles, and developed her passion for plants in the lush botanical gardens and chaparral-covered hills of southern California. Her formative years as a botanist and paleobotanist were spent at the University of Texas at Austin, where she produced a monographic revision of the Late Jurassic Hope Bay flora of the Antarctic Peninsula for her Ph.D. with Ted Delevoryas. At the time, UT-Austin was a hotbed of depositional systems analysis. A research year as a Fulbright scholar at the Natural History Museum in Stockholm and a 3-year post-doc in paleopalynology at the ETH Zurich helped to hone Carole's paleontological skills before she moved on to the University of Bonn in Germany. There, Carole has been a paleobotanist at the Institute of Paleontology for the last 15 years, where she works primarily on Tertiary fruits and seeds, and plant taphonomy. She continues to dabble in Mesozoic floras and maintains a lively interest in Eocene mangroves. Although perpetually dismayed at the gray skies and cold winters in Bonn, Carole takes great delight in the biodiversity of her Mediterranean garden, as well as in the paleobotanical richness of the lignite mines and Tertiary Fossilagerstätten in the Rhineland, which will surely keep her busy and off the street for some time to come.

Bob Gastaldo became the Whipple-Coddington Professor of Geology and Department Chair at Colby College in 1999, after spending 21 years in the Deep South at Auburn University, Alabama, where he co-edited this journal with Chuck Saurda. Who would have thought that upon arriving at the opposite end of the continental U.S. latitudinal spectrum, Bob would have moved to projects focused both down (to the Devonian) and up (to the Permian) the stratigraphic column, and become a Quaternary limnologist at the same time? Bob was mentored early in his career by William C. Darrah at Gettysburg College, Pennsylvania, and received his degrees with Lawrence C. Matten at Southern Illinois University in Carbondale, Illinois, studying Carboniferous paleobotany. Since then, he has researched both Recent and ancient coastal deltaic/estuarine systems in the subtropics and tropics, conducted experimental and empirical plant-taphonomic investigations, and, among other things, applied biostratigraphy to solving tectonic problems in the Appalachians. He has been a Fulbright Research Scholar (Utrecht, The Netherlands), a Forschungpreisträger of the Alexander von Humboldt Stiftung (Göttingen, Germany), and held an Alumni Professorship (Auburn University). Currently, he and colleagues from the U.S., Poland, Ukraine, and the Czech Republic are assessing the causes for ecosystem stability and perturbation in the Mississippian coal-bearing sequences of Euramerica. And, at times, he does get some sleep.

CLAMP offers the computation of a number of different climate variables. Although both sides have rather vocal proponents and opponents, it is beyond the scope of this special issue to pit the two schools of modeling against one another, however fiery and entertaining a confrontation that would be. But, what is being considered here are the results of taphonomic forces on plant assemblages and on leaf floras being sampled by these programs and their implications for accurate paleoclimatic predictions.

In both CLAMP and LMA, calibration of the programs is based on living vegetation in the mesic Northern Hemisphere. Any floras outside of this default environment or assemblages with incomplete or fragmentary leaves (the usual state of affairs with fossil material) may result in skewed climate predictions. But how skewed is skewed? And why?

Spicer et al. (2005) took a sample of present-day vegetation from the Crimean peninsula that had not been absorbed into the CLAMP data set and used it to test the robustness of CLAMP's predictive powers. Starting with an ideal assemblage of leaves from living plants, individual leaf characters were omitted, one by one, or by sets

(e.g., all margin data), to assess the resulting deviation from known climate parameters. It turns out that the loss of margin characters had the greatest effect, especially on temperature-related parameters (mean annual temperature, warm-month mean temperature, cold-month mean temperature, and length of growing season). This apparently is linked to the loss of information encoded in the leaf teeth, however these are related. In contrast, a taphonomic selection against large leaf size, the loss of apex or base, or shape characters had little effect. This is good news, as the tip is the most taphonomically vulnerable part of a leaf, something that anyone who has ever mounted leaves on a herbarium sheet knows. On the other hand, the loss of both tip and base information or many of the marginal characters in all leaf taxa in an assemblage renders the flora impotent for climate estimation using CLAMP.

Assessing the accuracy of LMA in estimating MAT was carried out by Greenwood (2005), who applied it to leaf assemblages in extant tropical and temperate Australian forests. He found that autochthonous leaf samples from the forest floor in these Australian habitats predict MAT accurately—for the most part. However, MAT was underestimated when analyzing streambed assemblages, owing to a greater proportion of leaves with toothed margins. It also was determined that the proportion of taxa with toothed margins in the forest-floor samples corresponds to those in the canopy at the same sites.

Another taphonomic phenomenon observed in the Southern Hemisphere flora is differential leaf-litter production and standing biomass (measured by stem basal area) in two quintessential Australian trees, *Nothofagus* and *Eucalyptus*. These plants are canopy-dominants in the cool temperate rainforest and wet sclerophyll forest, respectively. Steart et al. (2005) found that *Nothofagus* sheds more leaves relative to its standing biomass than *Eucalyptus*, and this taphonomic pattern may be used to assess more accurately the relative abundance of these genera in Cenozoic floras. Furthermore, when there are large differences in leaf size, leaf counts do not accurately reflect rank-order dominance patterns in the vegetation. Rather, total leaf area generally reflects dominance patterns.

Can we not see the forest for the trees? It is well known that Earth's cornucopia of species is located in the tropics. Does this high diversity have a taphonomic effect on climate interpretation? Burnham et al. (2005) evaluated rank order of dominance (by stem basal area) against mean annual temperature (MAT) and mean annual precipitation (MAP) in eight Neotropical floras extending from Costa Rica to southern Peru with a range of precipitation regimes. They found that high biodiversity, in itself, is not detrimental to interpreting climate (MAT) if at least 50% of the species are included. Samples with only 25 species, the standard minimum number generally used in MAT studies, are acceptable, but compromise the accuracy of MAT predictions. Estimates of MAP, on the other hand, are considerably and consistently underestimated, although this issue appears to have little to do with high biodiversity.

Although taphonomic influences on leaves and unraveling the forces acting on fossil-leaf assemblages have been studied for many years (Ferguson, 2005), those involved in the formation of paleocarpological (fruit and seed) deposits have received much less attention. In the early 1990s, the leading paleocarpologists in Europe all were asked in which facies they thought carpollological deposits formed (Gee, pers. survey). Most could give no definite answer, and those who did replied that fruits and seeds most likely accumulated at the bottom of river channels. Accepting this as a challenge, as well as perplexed with the mass accumulations of Neogene fruits and seeds in the lignite-bearing sequences of western Germany, Gee (2005) discovered a sedimentological link between medium- to very coarse-grained sand and lignified diaspores that results in their concurrent transport as bedload and co-occurrence in flood deposits. Thus, these "bedload carpodeposits," as coined by Gee (2005), are analogous to sedimentary structures and may be formed when certain hydrological conditions are met, namely during high-discharge events. Hence, the taphonomic signature of these accumulations account for their occurrence in a variety of fluvial and lacustrine facies.

The greatest terrestrial crisis of all geologic time occurred at the Permian-Triassic boundary, and has been correlated previously with a land-plant die-off. However, the recognition and comparison of isotaphonomic assemblages are essential before evolutionary trends over such a critical time interval can be drawn. To this end, Gastaldo et al. (2005) launched an interdisciplinary investigation of pre-, trans-, and post-boundary plant-fossil assemblages in the Karoo Basin, South Africa, to study the sedimentology and taphonomy

of 14 localities. They found that the fluvial depositional regimes and plant taphonomic character of these Late Permian to Middle Triassic deposits changed through time, shifting from well-preserved, leaf-mat, parautochthonous assemblages to poorly preserved, fragmentary, allochthonous assemblages that do not coincide with the time boundary, but occur on either side of the P/Tr extinction event. Thus, caution should be exercised before extrapolating from these data to a global biotic catastrophe. Moreover, plant fossils in the Early Triassic of the Karoo Basin indicate that the landscape indeed was stabilized by vegetation and not subjected to changes in fluvial sedimentation caused by a land-plant die-off.

These, in a nutshell, are some of the implications of the studies presented in this issue. Of course, such brief descriptions do not do justice to the wealth and breadth of these taphonomic studies, but are presented here merely to whet the appetite of readers to partake heartily of the Plant Taphonomy Special Issue.

The papers in the special issue grew out of the Plant Taphonomy Symposium at the 7th International Organization of Paleobotany Conference (IOPC-VII) held in Bariloche, Argentina, from March 21 to 26, 2004. Every four years, an IOP Conference is held at some new meeting point on the planet, and provides for the largest and most important forum for paleobotany. Last year's vibrant IOPC-VII in NW Patagonia reflected the breathtaking Andean environs and the vivacious Argentine people. The lectures and subsequent discussions at the Plant Taphonomy Symposium were no less stimulating and lively.

The symposium consisted of 10 half-hour talks, and topics embraced the entirety of the paleobotanical record, from the Silurian to the Recent. Not all of the talks could be included in this special issue, owing to previous or concurrent publication. But in many ways, the symposium presentations represent a microcosm of plant taphonomy at the start of the 21st century. Silurian charcoal as verification of the earliest wildfire (Ian J. Glasspool), anatomical evidence in the detection of early wildfire in the Devonian (Dianne Edwards), and the hot-springs provenance of the Rhynie Chert flora (Hans Kerp and Hagen Hass) concern the oldest representatives of the terrestrial flora, the early land plants. In the fossil record, *in-situ* forests in a Carboniferous cyclothem attested to large-magnitude, coseismic base-level changes in the Pennsylvanian (Robert A. Gastaldo and colleagues; Gastaldo et al., 2004), while mass carpological deposits in Neogene sands revealed their origin as floodwater-propelled, bedload-transported plant clasts (Carole T. Gee). Actualistic studies on modern floras and the application of these insights for understanding the taphonomic filters acting on specific fossil floras were discussed in two presentations: the biodiversity of leaves in extant Neotropical forests and the highly diverse early Paleocene Castle Rock Flora (Robyn J. Burnham and colleagues), and differential biomass production among canopy trees in modern Australian forests and the fossil record of *Nothofagus* and *Eucalyptus* in the late Oligocene Berwick Quarry Flora (David C. Steart and colleagues).

A second carpological talk compared the taphonomic fidelity of seed size between modern vegetation in hardwood-forest and salt-marsh communities, and core samples from a tidal estuary (Hallie J. Sims and Jason A. Cassara). Seed size is thought to be linked to ecological characters, but if seed assemblages in fossil deposits are biased by taphonomy, it is hard to uphold paleoecological interpretations based on this parameter. Taphonomic constraints on climate estimation also formed a focal point at the symposium, when their impact on CLAMP (Robert A. Spicer and colleagues) and LMA (David Greenwood) were delineated. Those twirling, brightly colored, computer-generated, three-dimensional CLAMP axes of Spicer et al. were indeed something wondrous to behold!

Thus, we find plant taphonomy not only alive, well, and kicking, but also happily integrated into interdisciplinary areas of research and unabashedly meeting the new challenges of the cyberworld head on. Flagrantly paraphrasing Mark Twain, the rumors of plant taphonomy's demise (Ferguson, 2005) have been greatly exaggerated!

In closing, let us return to our experimental plant taphonomist,

Winnie-the-Pooh. After successfully running trials with a natural flume and lignified rods of aerial plant parts (i.e., Poohsticks), Winnie and colleagues swiftly expanded their research horizons to include animal taphonomy when Eeyore drifted by unexpectedly, having fallen in upstream. But that's another story.

—CAROLE T. GEE and ROBERT A. GASTALDO

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