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INTEGRATIVE PALEOBOTANY: AFFIRMING THE ROLE OF FOSSILS IN MODERN PLANT BIOLOGY—INTRODUCTION AND DEDICATION

Ignacio H. Escapa,* Alexandru M.F. Tomescu,[1],† Michael T. Dunn,‡ and Ruth A. Stockey§

*Consejo Nacional de Investigaciones Científicas y Técnicas, Museo Paleontológico Egidio Feruglio, Trelew, Chubut 9100, Argentina; †Department of Biological Sciences, Humboldt State University, Arcata, California 95521, USA; ‡Department of Agriculture, Biology, and Health Sciences, Cameron University, Lawton, Oklahoma 73505, USA; and §Department of Botany and Plant Pathology, Oregon State University, Corvallis, Oregon 97331, USA

Gar Rothwell was named Distinguished Professor at Ohio University in 2004. Photo courtesy of Fred C. Tom of Lamborn's Studio, Athens, Ohio.

If you are interested in plant evolution, try this quick exercise: take a phylogenetic tree of the plant kingdom, close your eyes, and point your finger randomly to a node of the phylogeny. Irrespective of the clade to which you are pointing, there is one thing you should know about it: the living representatives of that clade have evolved as a result of a long process in which failed attempts are the rule, and as a result, the diversity of extinct forms accumulated in the fossil record far exceeds that recorded in the extant flora. From this simple concept, Gar W. Rothwell made his career. Because of that, here is a second thing you should know about the plant clade to which you pointed at random: Gar has, more likely than not, contributed information about evolution

[1] Author for correspondence; email: mihai@humboldt.edu.

in that clade at some point in his career. Gar was one of the principal contributors to the revival of paleobotany from a largely descriptive discipline to a vibrant field of investigation at the forefront of modern evolutionary sciences that contributes crucial insights into plant evolution, equal in importance to those provided by genetics and molecular biology. Because of this, the impact of Gar's scientific contributions reaches far beyond the field of paleobotany, with important implications for wide areas of plant biology, including anatomy and morphology, development, systematics, phylogeny, and evolution.

Gar earned a master's degree in the laboratory of Thomas N. Taylor (University of Illinois at Chicago, 1966) studying Paleozoic seeds in the genus *Conostoma* (Rothwell and Eggert 1970; Rothwell 1971*a*). He subsequently earned his PhD degree in the laboratory of Wilson N. Stewart (University of Alberta, 1973), where he reconstructed the plants in the seed fern genus *Callistophyton* (Rothwell 1972*b*, 1975, 1980, 1981). His work was instrumental in ushering in studies of fossil plants as whole living organisms, looking at both structure and development. These early experiences launched Gar on a career in plant evolutionary biology that stretched over a half century, during which he occupied positions at the University of Alberta, University of London–Chelsea College, Ohio University, and Oregon State University. Throughout his career, Gar's scholarly work and contributions have been recognized by numerous awards and honors: the Isabel Cookson Award, the Edgar T. Wherry Award, the Michael A. Cichan Award, the Merit Award of the Botanical Society of America, and honorary membership in the International Organization of Palaeobotany, where he served for 12 years as secretary-treasurer and president.

Gar is the author, with Wilson Stewart, of one of the most impactful and widely used textbooks in the field of paleobotany and plant evolution—*Paleobotany and the Evolution of Plants*. Published in 1993, this textbook explains in direct and engaging prose the crucial role of fossils, and of their anatomy and morphology, in understanding the origin and evolution of all major plant groups. For more than a quarter century it has provided inspiration to numerous paleobotanists and structural botanists worldwide.

The results of the research program that Gar has led are reflected in the more than 250 peer-reviewed journal articles and book chapters published in more than 30 scientific journals that cover the fields of botany and paleobotany (e.g., *International Journal of Plant Sciences*, *American Journal of Botany*, and *Review of Palaeobotany and Palynology*) and the broader area of the natural sciences (e.g., *Science* and *Nature*). However, Gar's influence in the field of plant biology cannot be reduced to a number of publications—it is best reflected in the quality, relevance, and impact of these contributions, which combine a classic perspective derived from detailed anatomical and morphological descriptions of fossil species with innovative methodologies and approaches. Gar conducted most of these studies in collaboration with his students and other fellow paleobotanists and plant biologists.

Gar is a time traveler: the species he has described belong to a time slice that spans more than 400 million years. His studies have investigated plants and other organisms from the Paleozoic to the present and have addressed an incredibly large number of lineages, many of them described as new species, genera, families, and even classes. He has made detailed descriptions of prokaryotes, fungi, liverworts, mosses, lycopsids, sphenopsids, ferns of a wide variety of lineages, pteridosperms, conifers and coniferophytes, cycads, ginkgophytes, bennettitaleans, and angiosperms—nothing has escaped Gar's inquisitive eye. These descriptions of fossil taxa, which led to the development of several now-classic whole-plant concepts, have always represented for Gar only the first step in understanding broader and deeper processes in plant evolution and development. Gar has also used these fossils to develop innovative ideas and approaches for documenting the natural history of species long extinct and to inform some of the most vexing unanswered questions in plant evolution and phylogeny. Over the past few decades, no scientist has been more influential in affirming and expanding the potential of paleobotany as an integral contributor to evolutionary plant biology than Gar. In terms of organismal biology and natural history, in landmark studies Gar documented several aspects of reproductive biology of the early seed plants, including the hydrasperman reproductive syndrome (Rothwell 1971*a*, 1971*b*, 1986; Rothwell and Scheckler 1988; Serbet and Rothwell 1995), pollination drops (Rothwell 1977) and pollen tubes (Rothwell 1972*a*) of Carboniferous seed ferns (pteridosperms), and seed dormancy in Paleozoic conifers (Mapes et al. 1989). Together with collaborators, Gar described what is still the oldest seed plant reconstructed as a whole plant, the pteridosperm *Elkinsia* (Rothwell et al. 1989; Rothwell and Serbet 1992; Serbet and Rothwell 1992). His studies of the apical organization of lepidodendralean rooting structures (rhizomorphs; Rothwell 1984; Rothwell and Pryor 1991), the lepidodendralean embryo anatomy (Stubblefield and Rothwell 1981; Pigg and Rothwell 1983*b*), and the body plan of the Chaloneriaceae (Pigg and Rothwell 1979, 1983*a*) led to a paradigm shift in our understanding of the structure and evolution of the body plan of isoetalean lycopsids (Rothwell and Erwin 1985). Gar's continued exploration of coal ball floras put on firm footing the idea that the rise and the first major radiation of leptosporangiate ferns occurred in the Carboniferous (Rothwell 1978, 1987*a*, 1996, 1999; Trivett and Rothwell 1988; Rothwell and Good 2000; Tomescu et al. 2006; Rothwell and Stockey 2008). His studies spanning several decades also painstakingly documented the evolution of conifer reproductive structures, from the early conifers of the Paleozoic (Rothwell 1982; Mapes and Rothwell 1984, 1991, 1998; Rothwell et al. 1997, 2005, 2007; Hernandez-Castillo et al. 2001, 2009; Rothwell and Mapes 2001) to the origins of modern conifer families (Falder et al. 1998; Ratzel et al. 2001; Klymiuk et al. 2011; Rothwell et al. 2011, 2012; Serbet et al. 2013; Atkinson et al. 2014*a*, 2014*b*; Rothwell and Ohana 2016). In studies of broader scope, Gar surveyed the diversity of fossil and extant plants, contributing novel perspectives on the evolution of sporophyte body plans and branching patterns across the entire embryophyte clade (Rothwell 1995; Tomescu et al. 2014) and on the diversity and evolution of stelar architecture across the tracheophyte clade (Rothwell 1976; Beck et al. 1982).

The inclusion of fossil plants in phylogenetic analyses ranks among Gar's most important contributions to evolutionary biology. Extinct species exhibiting novel combinations of characters refashion our understanding of evolutionary relationships and are key to studies of deep phylogeny. Gar's work has been at the forefront of the integration of fossils in studies of systematics and phylogeny. He was one of the pioneering paleobotanists to empirically address the influence of fossils on the resolution of phylogenetic relationships. Based on numerous analyses focused on different plant groups, Gar has repeatedly demonstrated that the inclusion of fossil species in a phylogenetic context, aside from broadening the scope of analyses, can change traditionally held views on the relationships of living organisms. Among the most relevant of these studies, Rothwell and Serbet (1994) undertook an analysis of lignophyte evolution, which supports the monophyly of seed plants and has been at the base of subsequent developments and discussions (e.g., Doyle 2006; Hilton and Bateman 2006; Toledo et al. 2018). In another study, Gar took on the depths of pteridophyte phylogeny, developing an extensive morphological matrix that included the broad diversity of extinct fern lineages alongside living ferns (Rothwell 1999). The study supports a paraphyletic grade of pteridophytes along the euphyllophyte backbone, providing a solid counterpoint to the results of studies based exclusively on living plants, which recover ferns, psilotophytes, and sphenopsids as a monophyletic group sister to the seed plants (revisited by Rothwell and Nixon in 2006). Branching off from many of Gar's extensive studies of fossil gymnosperms and conifers are collaborative treatments of phylogeny within these groups, aimed at voltzialeans (Rothwell et al. 2005), Pinaceae (Ryberg et al. 2012; Gernandt et al. 2016; Smith et al. 2017), Cupressaceae (Rothwell et al. 2011), gnetophytes (Rothwell and Stockey 2013), and broader samplings across these groups (Rothwell and Stockey 2016). In the same vein, Rothwell et al. (2009) queried the Paleozoic and Mesozoic fossil record of seed plants, garnering renewed support for an anthophyte clade and, at the same time, emphasizing the need for total evidence analyses in the resolution of recalcitrant areas of plant phylogeny. The state of the art in the integrative assessment of plant phylogeny based on living, as well as fossil, diversity has been presented recently in a special issue of the *American Journal of Botany* in the article "Tree of Death: The Role of Fossils in Resolving the Overall Pattern of Plant Phylogeny" that Gar coedited with two of us (Rothwell et al. 2018*a*). Many of the articles in the special issue—to which Gar contributed an extensive treatment of marattialean phylogeny (Rothwell et al. 2018*b*)—are authored by his former students and collaborators.

Another major direction pioneered by Gar involved integrating the extensive knowledge of the morphology and anatomy of fossil plants with the growing understanding of developmental regulation at the genetic and molecular levels to undertake "paleo-evo-devo" studies in plant biology (Rothwell 1987*b*). In doing this, Gar searched the fossil record for structural evidence supporting the action of specific genes and growth regulators. This type of anatomical evidence, which he introduced as "structural fingerprints" (Rothwell and Lev-Yadun 2005; Rothwell et al. 2014), allows for tracing the history of those mechanisms in phylogenetic space and time and is crucial to understanding the origin and evolution of the regulatory processes that these fingerprints reflect, thus refining our understanding of the patterns and processes of morphological evolution. Gar was the first paleobotanist to explore such structural fingerprints and the first to explicitly articulate and consistently pursue the integration of plant fossils in the evo-devo paradigm (Rothwell and Tomescu 2018). His studies that integrate data from the fossil record to address the evolution of lycophyte body plans (Rothwell and Erwin 1985), leaves (Sanders et al. 2007, 2009), polar auxin transport (Rothwell and Lev-Yadun 2005), gravitropism (Sanders et al. 2011), and secondary growth (Rothwell et al. 2008) are now classic landmarks for integrative studies of the evolution of plant morphology.

This special issue is the outcome of both Garfest 2017, a joyful paleobotanical banquet held in Gar's honor at the 2017 meeting of the Botanical Society of America in Fort Worth, Texas, and a daylong colloquium organized in recognition of Gar's scientific achievements at the 2018 meeting of the Botanical Society of America in Rochester, Minnesota. The articles collected in this issue celebrate Gar's prolific, wide-ranging, and far-reaching career and fittingly explore a very diverse array of plants, time periods, and questions. Our original idea was to publish a single volume including all the contributed articles. However, the large number of articles we received (27), a testament to the respect and appreciation that Gar commands among his peers, has required a change of plan. Thus, this issue contains a subset of those articles, selected solely based on the order in which they were accepted for publication. The remaining articles are scheduled for publication in Rothwell special sections that will be included in subsequent issues of the *International Journal of Plant Sciences*. Together, these articles cover a broad spectrum of plant and nonplant lineages (e.g., chytridiomycetes, bryophytes, lycopsids, sphenopsids, ferns, pteridosperms, coniferophytes, conifers, gnetophytes, and angiosperms) and address questions that range from ecology to anatomy and morphology of various plant parts, whole-plant reconstructions, systematics, phylogeny, developmental regulation, and the evolution of plant development. The studies investigate plants from throughout the geologic timescale (Paleozoic, Mesozoic, Cenozoic), as well as living plants, in all corners of the world: Australia, Argentina, Canada, China, Finland, Germany, Italy, Panama, Portugal, Russia, Scotland, Switzerland, Turkey, Venezuela, and the United States.

As Andrew Knoll recounts: "Many years ago, I received a phone call from Gar. His opening words were, 'I have a theory.' Sensing the irony oozing down the phone line, I took the bait, 'Gar, what's your theory?' 'I think,' replied Gar, 'that my fossils were once living plants.'" Paleobotany is the science that endeavors to bring the terrific spectrum of extinct species back to life, and for several decades Gar has been one of its foremost luminaries. This collection of articles provides a crystal clear image of the impetus and relevance of the studies of fossil plants in today's integrative world of plant biology. It is an honor and a great pleasure to dedicate it to our colleague, mentor, and friend, Gar Rothwell, for the legacy of his insatiable curiosity, his innovative ideas, and the abundant inspiration he has engendered throughout the discipline of botany. In closing, we rejoice that this is but one milestone in Gar's story, which continues and never ceases to keep us guessing—or in Steve Manchester's words: "Gar moves so gracefully up and down the stratigraphic column and across plant phylogeny that it can be difficult to know where he will strike next." Wherever that may happen, we look forward to it!

Acknowledgments

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Intersection of Evo-Devo and Phylogeny: Celebrating the Contributions of Gar W. Rothwell to Biodiversity and Evolution." We also thank all of Gar's colleagues, both for contributing articles to the colloquium and to this special issue and for volunteering to review one or more of the 27 contributed articles. They are too numerous to be listed here. We are indebted to the editors of the *International Journal of Plant Sciences*, Christina Caruso and James Ellis, for their invaluable support and guidance. Fred C. Tom at Lamborn's Studio (Athens, Ohio) graciously provided the photograph of Gar shown here.

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