DONALD PINKAVA'S JOURNEY FROM ASTERACEAE TO CACTACEAE: FROM THE OHIO STATE UNIVERSITY TO ARIZONA STATE UNIVERSITY

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ABSTRACT

Donald J. Pinkava is best known for his application of cytogenetics in unraveling the complex interspecific hybridization in the prickly pear genus *Opuntia* Mill. in the southwestern United States extending down into northern and central Mexico. Using cytogenetics, Pinkava delimited species boundaries within *Opuntia* for taxonomic treatments. His work on *Opuntia* in the Chihuahuan Desert led to later comprehensive contributions in the *Flora of North America* and the *Flora of Arizona* that include opuntias not only in the Southwest but in every US state. Pinkava's systematic knowledge, as reflected in his taxonomic treatments provided the basic scientific framework needed for ongoing conservation of Cactaceae in the Southwest to the present day. Interestingly, the starting point for all of Pinkava's contributions in Cactaceae began with his initial studies of Asteraceae as a student of T. Richard Fisher at The Ohio State University (OSU), an institution with longstanding research interests in the Asteraceae. It is there that he selected a genus, *Berlandiera* DC as his dissertation topic. Ironically, this genus has a range from the drier sites of the Eastern Coastal Plains, into the Ozark and Ouachita Mountains, with a disjunct distribution in the mountain floras of southeastern Arizona and Northern Mexico. Like *Berlandiera*, Pinkava's own work reflects techniques and training in the eastern US, that migrated and was used as the basis for his groundbreaking studies of Cactaceae in the Southwest.

RESUMEN

Donald J. Pinkava es mejor conocido por su aplicación de la citogenética para desentrañar la compleja hibridación interespecífica de tuna, género *Opuntia* Mill., en el suroeste de los Estados Unidos extendiéndose hacia el norte y centro de México. Usando citogenética, Pinkava delimitó los límites de las especies de Opuntia para tratamientos taxonómicos. Su trabajo sobre *Opuntia* en el desierto de Chihuahua condujo a posteriores contribuciones integrales en la 'Flora of North America' y 'Flora of Arizona' que incluyen opuntias no solo en el suroeste sino en todos los estados de EE. UU. El conocimiento sistemático de Pinkava, como se refleja en sus tratamientos taxonómicos, proporcionó el marco científico básico necesario para la conservación continua de Cactaceae en el suroeste hasta el día de hoy. Curiosamente, el punto de partida de todas las contribuciones de los cactus de Pinkava comenzó con sus estudios iniciales de Asteraceae como estudiante de T. Richard Fisher en la Universidad Estatal de Ohio (OSU), una institución con intereses de investigación a largo plazo en Asteraceae. Es allí donde seleccionó un género, *Berlandiera* DC, como tema de su disertación. Irónicamente, este género tiene un rango desde los sitios más secos de las planicies costeras del este hasta las montañas Ozark y Ouachita, con una distribución discontinua en las floras montañosas del sureste de Arizona y el norte de México. Al igual que *Berlandiera*, el propio trabajo de Pinkava refleja técnicas y capacitación en el este de los EE. UU., que migraron y se utilizaron como base para sus estudios innovadores sobre las cactáceas en el suroeste.

KEY WORDS: Asteraceae, Berlandiera, Chemotaxonomy, Opuntia, plant systematics

INTRODUCTION

When asked what we could learn about the Creator by studying biology, J.B.S. Haldane provided the following, often cited, response: "If one could conclude as to the nature of the Creator from a study of creation it would appear that God has an inordinate fondness for stars and beetles (Haldane 1949)." One could say that the Creator was also smitten by plants. Besides the power to photosynthesize and skip the hassle of foraging for food, there had to be at least one family of flowering plants the Maker was inordinately fond of. It seems the logical candidate would be the Asteraceae (= Compositae).

The Asteraceae is one of the most widely dispersed families of angiosperms and contains 1,900 genera with more than 32,000 accepted species (WFO 2022). Numerous experts in Asteraceae were necessary to fully survey its diversity and provide treatments for manuals and floras. In the 1950s and '60s, the ability to obtain chromosome numbers had a major impact on elucidating speciation in vascular plants (Stace 2000).

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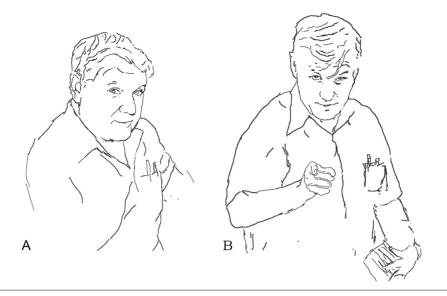


Fig. 1. Two views of Dr. Pinkava as A. Scholar and B. Educator. Redrawn from photographs A. Photograph by William P. Sharp. B. Unknown photographer.

Because of its complex and modified inflorescence, the "head" or capitulum, containing numerous flowers, in the Asteraceae provided an excellent opportunity to obtain meiotic chromosome counts for systematic studies. Cytology permitted evolutionary processes to be assessed, including polyploidy and hybrid crosses. Many of the taxa in the family are annuals, permitting breeding and crossing studies to be completed, and many are of economic value as food (e g , sunflower, artichoke, lettuces, chicory), ornamental plants (chrysanthemum, aster, daisies), industrial products (e.g., guayule) and medicines (Rolnik & Olas 2021). Add to this phenetics, or numerical taxonomy (Nixon 2001), a powerful tool to assess boundaries among Asteraceae species and putative hybrids, and you have a set of research tools to study hybrids and polyploidy not only in Asteraceae, but a model applicable to other families.

Donald Pinkava (Fig. 1A, B) entered graduate school in the early 1960s at The Ohio State University (OSU), and pursued systematic studies of *Berlandiera* DC. Heliantheae (Asteraceae) under the supervision of T. Richard Fisher. Fisher was an expert in Asteraceae, particularly the genus *Silphium* L. and contributed a treatment of the family for Ohio (Fisher 1989). Fisher's own career began at Indiana University, where he was guided by one of the most respected economic botanists, Charles B. Heiser, Jr. an authority on *Helianthus*. Heiser did his undergraduate work at Washington University where he was strongly influenced by economic botanist Edgar Anderson and went on to Berkeley for his Ph.D. (Pickersgill and Anderson 2011). Heiser applied cytogenetic findings to investigate the domestication of the sunflower *Helianthus annus* L. by Native American Indians (Heiser 1951). Fisher brought this expertise of his mentor to OSU where, he used it as a basis for making that institution one of the major centers for studying Asteraceae.

Like Fisher, Pinkava translated the influence of *his* mentor into a solid framework for a research program that highlighted both Asteraceae and Cactaceae. Clearly, being the herbarium-based systematist at Arizona State University (ASU) would need more than a research expert on Cactaceae. It would also require an excellent field botanist to dovetail with that institution's strength in Sonoran desert ecology.

During his career at ASU, Pinkava and his students made substantial contributions to floras of the Sonoran and Chihuahuan deserts of the Southwest, developed specialized techniques for preserving bulky glochid-covered specimens of cacti onto herbarium sheets, and studied the cytogenetics and hybrid complexes of *Opuntia* and other Cactaceae. Yet he also continued to publish papers on Asteraceae and train students to become experts in the family. Pinkava's first student at ASU, David J. Keil did his M.S. degree on the

flora of the White Tanks, AZ, and continued the focus of his graduate studies at OSU, earning his Ph.D. with Tod Stuessy in 1973. Pinkava and his collaborators, including Keil, added significant additional chromosome counts of Asteraceae from the US Southwest and Mexico throughout his career.

In this contribution, highlighting Donald Pinkava, we would like to illustrate his branch in the phylogeny of Compositae research. We wish to put his scholarly contributions in the context of the OSU Department of Botany in the 1960s, to note the environment in which Pinkava was trained. We also wish to demonstrate his place in the wider network of Asteraceae specialists and other botanists who find themselves academically related to him (Keil et al. 2018; Makings 2018).

The Fisher Years

Donald Pinkava's advisor, T. Richard Fisher earned a Ph.D. in botany in 1954 at Indiana University as one of Heiser's 29 doctoral students, along with ethnobotanists W. Hardy Eschbaugh (Ph.D. 1964) and Gregory Anderson (Ph.D. 1971) and legume systematist Jeffrey Doyle (Ph.D. 1981). Fisher's dissertation research focused on the systematics of the genus *Heliopsis* Pers. (Compositae, Fisher 1957).

Born in Brownstown, Illinois in 1921, Fisher served in the Philippines during World War II, earned his B.A. at Eastern Illinois State (now University) Teachers College in 1947 and taught high school for several years before his dissertation work with Heiser. Upon graduation Fisher was on the faculty at Appalachian State Teachers College (now University) in Boone, North Carolina for 2 years before his arrival as a faculty member at OSU in 1956, where he worked until 1968. After that Fisher went to Bowling Green State University in northwestern Ohio from 1968–1983. As department chair he led the department to its Ph.D. accreditation. He also became very involved in what would become the Schedel Arboretum and Gardens in Elmore, Ohio (https://www.schedel-gardens.org/ where he remained active the rest of his life (Stuckey 2000).

At OSU Fisher developed the plant systematics graduate program for which he designed several courses and acquired funding for research. He also designed and taught a field botany course for twelve summers at OSU's F. T. Stone Laboratory on Lake Erie (Welcome to Stone Laboratory, https://ohioseagrant.osu.edu/education/stonelab, accessed 18 April 2022). During his dozen years at OSU, he advanced to full professor in eight years. Eight M.S. and eight Ph.D. degrees were earned by 13 students under his advisership, and in 1965 he made possible the hiring of Ronald L. Stuckey, an additional plant systematist, into the program. Stuckey would go on to become Director of the OSU herbarium from 1967 to 1975 (History of the OSU Herbarium https://mbd.osu.edu/collections/herbarium/history-osu-herbarium, accessed 18 April 2022).

Donald Pinkava at OSU

Donald John Pinkava was born on 29 August, 1933 of Czech heritage in Cleveland, Ohio and spent most of his early years in the Orange Village area. He proceeded to Ohio State for all three academic degrees, a B.S. in the College of Education in 1955, and his M.S. in 1961 and Ph.D. with Fisher in Botany in 1964 (Pinkava 1963; Pinkava 1964). He took a brief hiatus from his education from 1955–1960 during which he taught high school in Solon (Cuyahoga County), Ohio.

Beyond the Fisher laboratory the world of Ohio State botany that Don Pinkava entered in the early 1960s was rich with the likes of herbarium curator Clara G. Weishaupt, who contributed to a summary of the monocots of Ohio (Weishaupt 1967) and to a floristic guide to Ohio vascular plants (Weishaupt 1960). Another contemporary, Richard A. Popham was a meticulous plant anatomist whose later published lab manual was "not for use by the student in the drowsy solitude of drab laboratory in the absence of the instructor"...not as "a crutch for the ill-prepared, tired or too-busy instructor" but "is a sparking device for lively observationdiscussion sessions" (Popham 1966). Weishaupt, Popham, and plant physiologist Bernard Meyer had received all of their academic degrees from OSU and were to stay on and teach there, Weishaupt from 1946 to 1968, remaining active up until her death in 1991. Meyer taught at Ohio State from 1940–1971, passing in 1987. Popham taught for 40 years (1940–1980) and continued to haunt the department for another 8 years as an emeritus professor. These faculty followed a tenure similar to that which Don Pinkava would do at Arizona State, with 36 years of teaching and another 17 as Emeritus Professor. Other botanists at OSU included renown lichenologist Emanual "Rudy" D. Rudolph, whose research contributions included some of the first descriptions of Antarctic lichens. Rudolph also contributed studies of the history of botany, particularly women in botany (Rudolph 1990, 1996), and served many years as department chair (Stuckey 1994). Rudy and his wife Ann were intrepid collectors of scientific books and botanical prints, donating a collection of 53,000 to OSU libraries (Stuessy et al. 1997a). Weishaupt, Rudolph, plant physiologist Carroll A. Swanson, and horticulturalist and statistician Dale A. Ray all served on Pinkava's dissertation committee. Pinkava also acknowledged morphologist John M. Speer for photography (Pinkava 1964).

Two things occurred a few years after Pinkava left Ohio State in 1964: in1968 Fisher also left Ohio State for Bowling Green State University in Bowling Green, Ohio, where he remained for the rest of his life (Stuckey 2000). Then, in 1968 Ohio State continued in its Asteraceae tradition by hiring Tod Stuessy, a student of Billie Turner's at the University of Texas at Austin (UT Austin).

Billie Turner and UT Austin

A year before Fisher completed his doctoral degree at Indiana University, Billie Turner finished his dissertation at Washington State University, under Marion Ownby, in 1953. Like Fisher, Turner's graduate work focused on a genus within Asteraceae, *Hymenopappus* L'Hér. A prolific researcher and advisor, Billie Turner mentored over 60 students during 55 years of his career at UT Austin (Powell 2020; Lipscomb 2020; Turner 2020). In addition to Tod Stuessy, other students of Billie Turner include Matt Lavin (Ph.D. 1987), Tina Ayers (Ph.D. 1986), Spencer Tomb (Ph.D. 1970) and Wayne Elisens (Ph.D. 1982; Turner 2015).

Like Ohio State, UT Austin was another major center for the study of Asteraceae (Fig. 2). There Billie Turner collaborated heavily with Ralph Alston with whom he coauthored a textbook in biochemical systematics (Alston & Turner 1963). In 1962, Tom J. Mabry accepted a position at UT Austin to establish a natural products chemistry program in the Department of Botany. The phytochemical systematic research was groundbreaking, particularly in the work on flavonoids and their use to delimit relationships among legumes and among Asteraceae. Among Mabry's students was W. Dennis Clark, who later joined the ASU faculty (Fig. 2).

It was not surprising that a replacement from UT was hired when Fisher left for Bowling Green. In his place came Tod Stuessy. However, it was not Stuessy who would be the architect of chemosystematics and molecular systematics at Ohio State, that would be the role of Daniel J. Crawford, who left the University of Wyoming to join the Department of Botany in 1977 (Les 2011). Crawford joined forces with Stuessy to establish a strong, collaborative research program focusing on the evolutionary processes of vascular plants, and in particular, those present in the Juan Fernández Islands (Stuessy et al. 1997b). Crawford continued his studies of Coreopsidae while at Ohio State and had a strong interest in plant speciation, a theme in his upper division course offerings. However, it was Stuessy who continued to train students in the monography, cytology, and in the 1980s phylogenetics of Compositae. Over his 30 years at Ohio State, Stuessy mentored 16 doctoral students, the majority of them in studies of Asteraceae (Fig. 3).

Among Stuessy's most prolific and influential students, Vicki A. Funk, completed her degree in 1980 and, after a year at the New York Botanical Garden where she worked with Arthur Cronquist, she obtained a position at the National Museum of Natural History (Smithsonian Institution) in 1981. There Funk became a major voice of Asteraceae for the next 40 years until her passing in 2019 (Marck 2019). Among her greatest contributions to Asteraceae systematics was the comprehensive volume *Systematics, evolution and biogeography of the Compositae* (Funk et al. 2009). Funk's rare combination of the ability to collaborate, combined with her drive to accomplish a goal, was a major reason this monumental treatment of the family was possible. While on her postdoc in New York she became involved at the American Museum of Natural History with the techniques of cladistics. In addition to her huge contribution to monographic studies of Asteraceae Funk was instrumental in introducing the use of cladistics to plant systematics in the 1980s. She became as much a presence in the evolutionary phylogenetics community as in botany. She remained a generous colleague whose *joie de vivre* permeated her life and a fierce advocate for the importance of herbaria (Funk 2003, 2018).

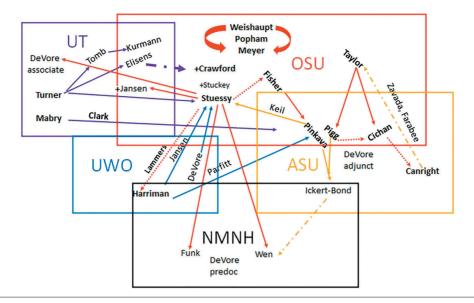


Fig. 2. This diagram indicates the complex web of relationships between faculty, students and postdoctoral associates at The Ohio State University (OSU, in red), Arizona State University (ASU, in orange), The University of Texas, Austin (UT, in purple), The University of Wisconsin Oshkosh, (UWO, in blue) and the National Museum of Natural History (Smithsonian Institution, in black). Arrows go from mentor to student, mentors are bolded. Uniform dotted line depicts new faculty pointing to individuals they replaced on retirement, + indicates additional individuals hired. Postdoctoral associates are represented by irregularly dashed lines. See text for details.

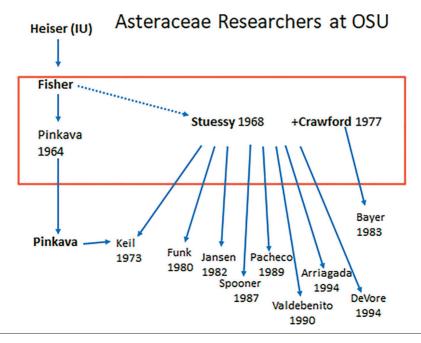


Fig. 3. This diagram depicts the students of Asteraceae from The Ohio State University with arrows going from mentor to student and year of Ph.D.s indicated.

Other Stuessy students who studied Asteraceae at OSU included David M. Spooner, (Ph.D. 1987) who studied the genus *Simsia* Pers. (Spooner 1990). Spooner went on to the University of Wisconsin at Madison and the USDA where he studied the origin and genetic diversity of domesticated potatoes. The Stuessy/ Crawford research group included three Chilean botanists Patricia Pacheco (Ph.D. 1989), Hugo Valdebenito (Ph.D. 1990) and Jorge E. Arriagada (Ph.D. 1994) who collaborated on studies of the Juan Fernández Islands and Latin America (Stuessy et al. 1997). Melanie L. DeVore (Ph.D. 1994)'s dissertation was a systematic study of the family Calyceraceae, the outgroup for the Asteraceae and her work served as an important inroad for Stuessy to begin systematic studies of the basal subfamily of Asteraceae, Barnadesioideae (Stuessy et al. 1996; Fig. 3).

At this same time Crawford's lab produced a group of students who emphasized phylogenetics, isozymes and molecular techniques. In the early 1980s evolutionary biologist G. Ledyard Stebbins spent a sabbatical at OSU where he worked with the young graduate student of Crawford's, Randall J. Bayer on *Antennaria*. This was an interesting coincidence because Stebbins was at Berkeley during Heiser's graduate student time there. Although Mason was Heiser's official advisor, Stebbins was a strong influence on Heiser 's interest in hybridization decades before (Pickersgill & Anderson 2011).

Along with Ohio State and UT Austin's major programs on Asteraceae, two other institutions come to mind: the University of Wisconsin at Oshkosh and the National Museum of Natural History (Smithsonian Institution). The migration and interconnections of Asteraceae researchers and other botanists as students, faculty and postdocs among these institutions and Arizona State weave a complex web that illustrates how the influence of inspirational teachers and their research spreads (Fig. 2).

INTERCONNECTIONS BETWEEN OSU, ASU, UWO, UT, UMNH

After completing his dissertation on *Berlandiera* in 1964 and contributing to the ongoing OSU herbarium fascination with the Asteraceae, Pinkava accepted the position at ASU, which he would hold for the rest of his career. Pinkava's first graduate student at ASU, David Keil, went on to OSU where he completed his Ph.D. at OSU in 1973, and went to a job at California State Polytech, San Luis Obispo until his recent retirement. Other connections between OSU and ASU developed in the ensuing years, and they include our own academic connections.

Pinkava's colleague at ASU James E. Canright taught plant anatomy and paleobotany and directed his graduate students in areas of developmental anatomy and palynology. Two of his graduate students, Michael S. Zavada and Michael J. Farabee completed their M.S. degrees at ASU looking at Cretaceous pollen assemblages from western North America (Zavada 1976; Farabee 1983). Both later held brief post doc positions in the 1980s with Thomas N. Taylor at OSU. (Fig. 2).

In the meantime, Robert Jansen, who had been mentored by Neil Harriman from the University of Wisconsin at Oshkosh graduated from the Stuessy lab in 1982. Jansen held a position at the University of Connecticut and then joined the botany department at UT Austin in 1991 where he is presently. The hiring of Robert Jansen at University of Texas Austin was one more way Billie Turner managed to obtain the personnel resources to maintain the most cutting-edge tools for addressing classification of Asteraceae. It was Robert Jansen who co-advised Mary E. Cosner's dissertation (1993) with Daniel Crawford that permitted the further expansion of molecular techniques applied in research at OSU. Additional Turner students made an OSU connection. Wayne Elisens who finished his Ph.D. with Turner at UT, later held a postdoctoral position in Daniel Crawford's lab at Ohio State. Another Turner student, Spencer Tomb finished in 1970 and accepted a position at Kansas State University in Manhattan, KS. There he mentored Swiss palynologist Marie Kurmann who completed her M.S. with Tomb in 1981 and later completed her dissertation on pine pollen development at OSU under Dean William Jenson (Fig. 2).

Then there are additional connections between OSU and ASU. Michael A. Cichan studied floral development of chicory ovules for his M.S. thesis with Barbara F. Palser at Rutgers (Cichan & Palser 1982). He then came to OSU where he developed a dissertation on vascular cambium dynamics in Paleozoic fossil plants

DeVore and Pigg, Pinkava's journey from Asteraceae to Cactaceae

under the mentorship of Thomas N. Taylor, graduating in 1986. He held a postdoc position with Charles B. Beck at the University of Michigan that next year and accepted a position to fill James E. Canright's plant anatomy job at ASU where he taught briefly before starting a second postdoc at University of Wisconsin with Ray Evert. His tragic death in a plane crash in August of 1987 left the ASU position open, which was filled in 1988 by Kathleen B. Pigg who also worked with Taylor at OSU. Stuessy student Thomas L. Lammers, studying Campanulaceae of Hawai'i, finished his degree the same week as Pigg in 1988. He eventually filled Neil Harriman's position at the University of Wisconsin, Oshkosh from 1999–2017.

In addition to Harriman's student Bob Jansen who went to Stuessy's lab at OSU, another Oshkosh student Bruce Parfitt (Ph.D. 1991) went on to ASU to work with Pinkava for his dissertation and additional papers on cacti. He accepted a position at University of Michigan at Flint. Melanie L. DeVore, also from the Harriman herbarium at Oshkosh worked with Stuessy at Ohio State, finishing her degree in 1994. She took a position at Sam Houston State in Huntsville, Texas, and held an associate position at nearby UT Austin; she then moved on to her current position at Georgia College in 2000. DeVore and Pigg began a long-term collaboration in 2000 that continues today.

A prolific researcher from China, Jun Wen, completed her degree in the Stuessy lab in 1981. Wen went on to a postdoc at Harvard, held positions at Colorado State University and the Field Museum, eventually taking a job at the Smithsonian which she holds today. Steffi M. Ickert-Bond, co-chaired by Pinkava and Kathleen Pigg completed her M.S. in 1997 and Ph.D. at ASU in 2003, and then went on to a post-doc at the Field Museum and NMNH with Jun Wen. She is now Professor & Herbarium Director, University of Alaska, Fairbanks (Fig. 2).

Pinkava's lasting contribution to the ASU herbarium was to prepare it for the next phase: digitalization and databasing. Pinkava lived to see the advent of SEINet (https://swbiodiversity.org/seinet/) and other efforts which all relied on the presence of well curated herbaria. Pinkava's insistence of students learning floristics, alpha taxonomy (including nomenclature), and expanded field collecting were essential for assuring the presence of clean data, accurate determinations and locality data, essential for the next generation of ASU students who practice niche modeling and use other geospatial tools.

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