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Author(s): Jon E. Keeley, V. Thomas Parker and Michael C. Vasey

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CHARACTERS IN *ARCTOSTAPHYLOS* TAXONOMY

JON E. KEELEY¹

U.S. Geological Survey, Western Ecological Research Center,
Sequoia-Kings Canyon Field Station, Three Rivers, CA 93271;
Rancho Santa Ana Botanic Garden, Claremont, CA 91711;
Department of Ecology and Evolutionary Biology, University of California,
Los Angeles, CA 90095
¹jon_keeley@usgs.gov

V. THOMAS PARKER AND MICHAEL C. VASEY

Department of Biology, San Francisco State University, San Francisco, CA 94132

ABSTRACT

There is value in understanding the past and how it has affected the present. Science focuses on empirical findings, and we know that our prior experiences and those of our predecessors play important roles in determining how we interpret the present. We learn from accomplishments and foibles of predecessors and appreciate the real life experiences we have gone through. In our studies of the genus *Arctostaphylos* Adans. we have been struck by the fascinating stories surrounding taxonomists who have played roles in the development of our current understanding of the group. In addition to providing insights, they sometimes provide humor and lessons on the value of competition versus collaboration. We offer this history of the humans that forged the taxonomy behind *Arctostaphylos* classification in this light.

Key Words: Competition, collaboration, Eastwood, Jepson, manzanita, Roof, Wells

Manzanitas are the largely Californian shrubby genus *Arctostaphylos* Adans. that has long presented a challenge for taxonomists. Unlike other Ericaceae taxa such as *Erica* L., where floral traits differ radically, *Arctostaphylos* are rather homogenous in floral traits but distinguished by vegetative characters including postfire resprouting, leaf shape, inflorescence bracts, glandularity, and hairiness of foliage. We have studied the history of this genus and are here to report that the most fascinating characters are those behind the naming of *Arctostaphylos* taxa. Although this colorful genus has attracted more than two-dozen botanists who have addressed the taxonomy of the group, Alice Eastwood, Willis Jepson, and Phil Wells are perhaps the best known. Many more played a role and in the history of plant taxonomy, and few taxa have attracted a more colorful group of scientists.

One of our earliest introductions to this topic was from the enigmatic Philip V. Wells who had a keen interest in *Arctostaphylos* and a contumacious perspective on other scientists studying this genus. He often spoke of the sharp and sometimes bitter rivalry between Willis Linn Jepson and Alice Eastwood, both of whom in the first half of the 20th century seemed locked in a competition to name new *Arctostaphylos* taxa and provide an appropriate treatment. In the context of this background, it was noted from *A California Flora* (Munz and Keck 1959) that a synonym for *A. viscida* Parry was *A. jepsonii* Eastwood. When one of us queried Wells about this incongruity, he explained (to paraphrase) that *A. jepsonii* is a synonym because it was considered a hybrid and Eastwood realized this and published the

name with the recognition that it would never be an acceptable name and, based on rules of botanical nomenclature would bury forever the name of Jepson as a legitimate species of *Arctostaphylos*. Although other taxonomists have acknowledged hearing this, we have no way of vetting the story and it may indeed be apocryphal, but in our minds it is part of the *Arctostaphylos* mythology.

Our objective in this article is to describe some aspects of these human characters. Just as new insights into morphological or genetic characters help us understand the evolution of a genus and relationships with their lineages, so too we think that understanding a little of the personalities of those whose work we depend upon will improve our own interactions. Early on we note that most botanists were quite competitive with one another, yet sometimes collaborated. Our lesson from this is that collaboration may well be an avenue to more rapid insights and understanding. We also suggest that progress in this group arose from two processes, one being simply exploration and description, and the second the origin of literally new systematic characters. We view our discussion not as a sociological statement, but as an observation that progress occurs in multiple ways, but collaboration is frequently more successful as issues become more complicated.

18TH AND EARLY 19TH CENTURIES

The modern era of systematically naming plants dates to Carolus Linnaeus (1707–1778), who was also the first to name a manzanita. He called it *Arbutus*

uva-ursi L., later transferred by Sprengel to Adanson's *Arctostaphylos*. Linnaeus was known as quite a character and, with his new classification system, sometimes offended decent society by drawing parallels between plant flowers and human genitalia, e.g., "[t]he calyx is the bedchamber, the filaments the spermatic vessels, the anthers the testes, the pollen the sperm," (Miller 2002, p. 57) all of which seemed rather scandalous. One clergyman noted "Linnean botany is enough to shock female modesty" (Fara 2003, p. 71).

Most of the Europeans involved in the naming of manzanitas during this period were either explorers like von Humboldt, or recipients of specimens from others who were exploring North America. These herbarium specimens were the basis for new taxa. For example, Swiss botanist de Candolle (1778–1841), without leaving home, classified a number of manzanitas from California in the genus *Andromeda* L., all of which were transferred to *Arctostaphylos* by Lindley (1799–1865) from London College.

Two botanical competitors from Europe were Frederick Pursh (1774–1820) and Thomas Nuttall (1786–1859), both of whom moved from England to North America. Ironically, both were hired sequentially by Benjamin Smith Barton of the University of Pennsylvania who was trying to write a new *Flora of North America* (Pennell 1936). Pursh also was hired by President Thomas Jefferson to work up the collections of the Lewis and Clark expedition, a project that moved him away from Barton's project. Thomas Nuttall was an English botanist who lived much of his life traveling and writing about American plants and was next hired by Barton. Pursh and Nuttall both replicated much of the journeys of Lewis and Clark early on, and explored many other areas later in life. Barton died before completing his work and afterwards both Pursh and Nuttall published independent work that moved North American botany forward: Pursh's *Flora Americae Septentrionalis* (containing *Arctostaphylos tomentosa* [Pursh] Lindl.) (Pursh 1814), and Nuttall's *The Genera of North American Plants...* (Nuttall 1818).

Nuttall for a time also was curator of the botanical garden at Harvard and named *Arctostaphylos* species based on material he had collected in California. Sometimes though he would name species on the skimpiest of material, e.g., *A. pumila* Nuttall was based on just leaf samples (Parry 1887). Ironically, Nuttall complained that Pursh did the same, arguing that he named a species from "merely an imperfect capsule" and because of incidents like that "[t]his unfortunate want of fidelity, prevented me from communicating to Mr. Pursh, many of the plants which now appear in this work." (Nuttall 1818, p. 298). Nuttall also had a keen eye for generic differences and clearly articulated reasons for recognizing *Xylococcus bicolor* Nuttall as distinct from *Arctostaphylos*. Something that even 20th century botanists grappled with.

Asa Gray (1810–1888) succeeded Nuttall at Harvard and named several *Arctostaphylos*, though from material collected by others. Gray's opinion carried more weight with some botanists than others, for example, when he moved *X. bicolor* back into *Arctostaphylos*, Willis Jepson accepted it throughout his career, in contrast to Alice Eastwood who did not. Charles C. Parry (1823–1890) was an Englishman who moved to the U.S. and studied under Asa Gray. He collected extensively as part of the U.S. and Mexican Boundary Survey and published an impressive six new *Arctostaphylos* in one year (Wells 1990). Marcus Jones (1852–1934), who it seemed seldom had a nice thing to say about any botanist, wrote that "Parry was a typical toady, as most men had to be to get a position in the Government service. He was a suave, well-groomed society man with little brains, a great feeder of hot air, who slobbered over the great to keep in their good graces" (Jones 1930, p. 3).

FOCUS ON THE WEST COAST

Willis Linn Jepson

Towards the end of the 19th century, a growing academic community on the West Coast shifted the focus of naming *Arctostaphylos* to local taxonomists. A good starting point is with Edward Lee Greene (1843–1915), who was forced to resign his teaching position from a Baptist College in Illinois (Jercinovic 2005), became an Episcopal missionary and headed west, prolifically collecting and naming new plants along the way. His travels led him to the West Coast and an appointment as rector at St. Mark's Episcopal Church in Berkeley. However, when he started teaching Roman Catholic doctrine to the Episcopalians it caused many to leave his church (Jercinovic 2005), which ended badly in "an amazing little tale involving priestly insubordination, fist-cuffs, locked church doors, filibustering sermons, and the Standing Committee, Chancellor, and Bishop of the diocese" not to mention the State Supreme Court (Ridout 1958, p. 51). By the time he named his first manzanita, *Arctostaphylos patula* Greene in 1891, he had been booted from the Episcopal church and was now a devout Roman Catholic.

Greene named several hundred new species mostly from California, of which a respectable two-thirds have withstood the test of time and are still considered valid (Jercinovic 2005). He was well known in the Berkeley community and was an obvious choice for the first botany professorship at the newly founded University of California. During his tenure there, he had a profound influence on California botany. He was a voluminous writer and, according to Jepson (1918), was a classical scholar whose work deserves high praise for its clear and forceful treatment. As seemed to be the case with early California botanists, he founded his own journals for publishing, including *Pittonia*, and with Jepson's cooperation, *Erythea* (Jepson 1918). How-

ever, not everyone shared Jepson's admiration as illustrated by a letter from the botanical explorer John Coulter to Asa Gray "[w]hat in the world is going to become of us with Greene stirring up synonymy with a pitchfork?... has *Pittonia* No. 3 come to your hands? It reads like the work of a crazy man, at least one lost to all sense of propriety." (Jercinovic 2005, p. 5). However, Greene's character exemplifies many of those in our *Arctostaphylos* story, as Charles E. Bessey wrote in a letter to Greene in 1910 "I have a great leaning towards any man who has something of heresy in him... You have dared to be original and that is what pleases me immensely" (Jercinovic 2005, p. 7).

In reference to his professor, Jepson wrote, "[h]e must have been, I think a very lonely man. The circumstances of his life served to bring this about. He was given to solitary botanizing" (Jepson 1943, p. 4), words that later seem to describe Jepson himself. Student Jepson was primed to excel in California botany and Greene's belief that understanding plants could only be gained through field studies likely reinforced Jepson's own predilections. Apparently Reverend Greene's anti-Darwinian view had little effect on the growing evolutionist Jepson, although conflicts did arise. Conflicts also with the University of California led to Greene's resignation in 1895, and he took his herbarium and moved east, ultimately spending most of the last 11 yr of his life at the Smithsonian Institute in Washington, D.C. (Jercinovic 2005).

Willis Linn Jepson (1867–1946) is one of just a handful of California *Arctostaphylos* taxonomists, a son of pioneer parents who moved by covered wagon from Missouri to California (Figure 1). Born near the present day community of Vacaville (Solano Co.), he grew up with a marked affection for the natural landscape around him. He graduated from the University of California in 1889, and in 1891, as a new graduate student, demonstrated an extraordinary appetite for botany and the natural world. He was one of the signatories incorporating the Sierra Club in 1892 and played a key role in the creation of the Chamisso Botanical Club (named for the French/German botanist, poet and world traveler, authority for *Eschscholzia californica* Cham. and the inspiration for the genus *Camissonia* Link). This latter organization potentially played a significant role in Jepson's career development as Ertter noted "Different members staked out territories, in which trespassing by rivals was discouraged, ..." (2000, p. 243). This is a theme that reverberates throughout the history of *Arctostaphylos*. Indeed, it appears that competition with LeRoy Abrams (who later published the four volume *Illustrated Flora of the Pacific States*, Abrams and Ferris 1923) from Stanford University compelled Jepson to found, in 1913, the California Botanical Society and "advance his position of leadership in the botany of the state" (Ewan 1987, p. 13).

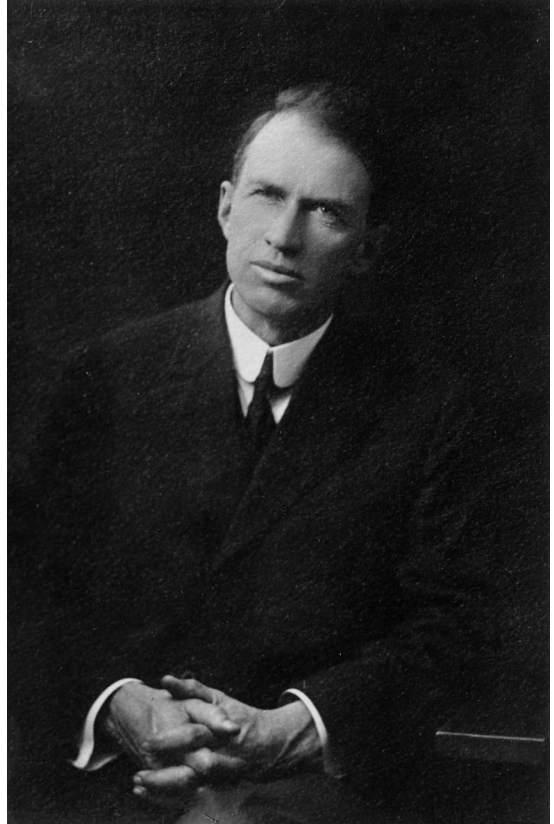


FIG. 1. Willis Linn Jepson, Professor of Botany at the University of California (Image courtesy of the University and Jepson Herbaria Archives, University of California, Berkeley).

Jepson's affection for the state is illustrated by his early graduate student goal of writing a flora of California. This magnum opus was to be published in several volumes as they were completed, the first coming out in 1909. Marcus Jones (1910) was highly critical of this project, and of Jepson in general, however, Jones was an equal opportunity offender as he was highly critical of most western US botanists. Philip Munz, for example, described Jones' *Contributions to Western Botany*, as being "marked by its cutting criticism of almost all contemporaries" (Munz and Keck 1959, p. 1563). With respect to Jepson's flora project, Jones wrote "[i]t is the judgment of the writer wrong to publish a work in this way for many people unable to buy will subscribe for without counting the final cost and it will work great hardship on them (Jones 1910, p. 71)." He then proceeds to criticize many of the treatments in this first volume, and blasts Jepson for his poor Latin descriptions.

Jones went on to comment "[t]he writer hopes that Mr. Jepson may successfully complete the herculean task he has assumed, and that before it is too late he may modify his methods and improve the quality of

his work and let others labor alongside of him without friction. The work can never become a school manual because of its bulk and cost. There will be a clear field for Prof. Hall or some other botanist to supply that crying need of a handy and compact school book on Californian botany (Jones 1910, p. 75).” We wonder if, despite the critical nature of this comment, it may not have been the impetus for Jepson interrupting his *Flora of California* project to later write his more compact, single volume of *A Manual of the Flowering Plants of California* (Jepson 1925)?

Without question, Jepson was an outstanding field botanist, with an appetite for collecting and a keen eye for ecological patterns and new variants, skills perhaps more keenly developed than his taxonomic astuteness with *Arctostaphylos*. As a graduate student, he and Professor Greene started the journal *Erythea*, and in the first volume he published his first species of *Arctostaphylos*, *A. elegans* Jepson (1895). However, in the long run, Jepson did not have great success with naming of *Arctostaphylos*. Although he published several taxa, which apparently passed immediate peer review, as with science in general, the real peer-review system is how the scientific community accepts the findings in subsequent years and decades.

Arctostaphylos is largely a chaparral genus and Jepson wrote one of the first papers describing California chaparral (Jepson 1896). However, in this paper he mistakenly indicated *A. glauca* Lindl. was found in the Sierra Nevada, an error we bring up only because it suggests he didn’t have sufficient interest at the time in the genus to follow what other botanists were writing about manzanitas; five years earlier C. C. Parry made clear that the very distinct *A. glauca* with large coalesced stones was restricted to the coast ranges, and the Sierra Nevada plants with much smaller separable stones were *A. viscida* Parry (Parry 1887). By the time Jepson published his first book based on his Ph.D. dissertation, *A Flora of Western Middle California* (Jepson 1901), he also made this mistake and even in the second edition (Jepson 1911) he was still mistakenly calling the Sierra Nevada plants *A. glauca*. Considering that he made countless trips to the Sierra Nevada during that first decade of the 1900s (Beidleman 2000), suggests that Jepson was slow in developing an interest in this genus. This is also suggested by the fact that his one paragraph description of *A. elegans* in 1895 (Jepson 1895) was followed by a 21-year hiatus until his next publication on *Arctostaphylos*.

In contrast to his taxonomic perspectives, when it comes to *Arctostaphylos*, Jepson’s lasting contribution was his ecological and evolutionary astuteness, in particular the recognition of crown sprouting in some manzanita species. This was an ecological trait previously overlooked by all prior *Arctostaphylos* investigators. However, even more profound was his recognition that several *Arctostaphylos* taxa lacked resprouting ability and concentrated seedling recruit-

ment to a single pulse in the first postfire year. The importance of these observations is illustrated by the fact that in 1916 when Jepson founded the journal *Madroño*, he chose for the lead off article “Regeneration in Manzanita” (Jepson 1916). Later, in biological notes in his treatment in *A Flora of California* (1939), Jepson contended that the non-resprouting species that delayed reproduction to the postfire environment represented true “fire-type shrubs.” This represents the first suggestion in the literature of an adaptation evolved in response to fire, not just in chaparral but also for any ecosystem. In some respects, this was an idea before its time as it seemed to capture very little attention until 30 yr later when Phil Wells published his classical paper on chaparral evolutionary strategies (Wells 1969).

With respect to *Arctostaphylos* nomenclature, Jepson had less impressive successes and some inexplicable failures. Perhaps the most perplexing mistake Jepson made is related to a localized endemic manzanita in coastal San Diego County. Just as Einstein’s cosmological constant was self-acknowledged as the biggest blunder of his career, perhaps Jepson’s biggest blunder was his flip-flopping on the naming of this unique taxon. The story begins in the late 1890s with the report of a new manzanita, *A. glandulosa* Eastwood (Eastwood 1897). In Jepson’s first treatment of *Arctostaphylos* (Jepson 1922) a new, but very poorly defined variety was published, *A. glandulosa* var. *crassifolia* Jepson. However, later Jepson (1925) made a new combination, *A. tomentosa* var. *crassifolia* (Jepson) Jepson but much later (Jepson 1939) he protested that his original placement of this variety under *A. glandulosa* was an example of *lapsus calamitosus typographicus* (i.e., a calamitous typographical error). However, based on distinctly different leaf anatomies between *A. tomentosa* and *A. glandulosa*, we now know this San Diego taxon is appropriately placed in *A. glandulosa* and Jepson’s real *lapsus calamitosus* was reversing himself in 1925.

Jepson’s initial taxonomic error in this regard reminds us of the importance of distinctive morphological characters to taxonomy in this challenging genus, such as the presence of stomata restricted to the lower leaf surface in some species but equally distributed on abaxial and adaxial leaf surfaces in others. Early on, Jepson apparently failed to recognize the taxonomic significance of bifacial (*A. tomentosa*) versus isofacial (*A. glandulosa*) leaves. However, his returning the local San Diego taxon to *A. tomentosa* and writing off the original treatment as a typographical error (Jepson 1939) was purely a lapse of attention to details. In his 1939 volume he did recognize this stomatal feature, but never applied it to *Arctostaphylos glandulosa* subsp. *crassifolia*, which he described as a subspecies of *A. tomentosa*. The concept of two different leaf types was beginning to be more widely appreciated at this time (e.g., Adams 1940), and Howell (1945) produced a review

of these two leaf types in *Arctostaphylos* and stressed their taxonomic value.

A similar scenario occurred with his publication of *A. elegans* Jepson, which was followed a couple years later with a note in *Erythea* “[t]his form, I now decide, is to be referred to *A. manzanita* Parry. I do not regard it as even worthy of a varietal name and so make record for the benefit of monographers and others. The name was published in this journal for January, 1893. (Vol. i. p. 15)” (Jepson 1895). However, later Jepson reversed himself once again and included *A. elegans* in Jepson (1922, p. 81) stating, “The note in *Erythea*, 3:178, was an inadvertence.” Later, Benson (1940) formally treated this taxon as a variety of *A. manzanita*.

Another unsuccessful taxonomic revision by Jepson appears to have arisen due to his distaste for C. Hart Merriam’s (of Life Zone fame, Merriam 1898) naming of *A. mewukka* Merriam and *A. nissenana* Merriam, both species recognized in honor of Native American tribes in California where these species were geographically situated. Regarding *A. mewukka*, Jepson (1922, p. 83) noted, “[t]he specific name, borrowed from the Miwok tribe, seems barbarous. Dr. Merriam has cultivated Indian lore and tribal habits so long that *mewukka* [sic] to him is probably as pleasing as the lucent phrases of the *Ars Poetica* to the ear of Horace.” Perhaps as a consequence, Jepson (1922, p. 83) felt Merriam’s description of *A. mewukka* was “insufficiently described to be placed with certainty. . .” and so Jepson erected a new name, *A. pastillosa* Jeps., which has never been accepted by other *Arctostaphylos* taxonomists. However, by 1939 he resurrected Merriam’s *A. mewukka* and *A. nissenana* and dissolved *A. pastillosa* (Jepson 1939).

One of Jepson’s last students was J.E. Adams (1903–1981), who published his systematic study of *Arctostaphylos* a year after Jepson’s 1939 treatment (Adams 1940). Although Adams’ treatment was broadly similar to his professor’s, it was much closer to contemporary thinking about the genus, including rejection of Jepson’s claim of *lapsus calamitosus typographicus* vis a vis *A. glandulosa* var. *crassifolia*. He also rejected Jepson’s persistence in subsuming *Xylococcus bicolor* as an *Arctostaphylos* as done by Gray. Adams clearly understood the fruit characteristics that separated *Xylococcus* from *Arctostaphylos* as described by Nuttall in his original description (Nuttall 1843). In addition, for the first time in *Arctostaphylos* taxonomy, Adams included subspecies in addition to varieties to cover subspecific variation.

One of the more unfortunate parts of the Jepson *Arctostaphylos* story is that his former student, A. Everett Wieslander (1890–1992), accused him of essentially pilfering three new *Arctostaphylos* species and publishing them without consultation (Wieslander and Schreiber 1939). An opening footnote to that paper read:

“While this article was in press, Dr. W. L. Jepson, to whom a copy of the manuscript was submitted for

criticism on November 17, 1938, published two papers, “Embryonic Panicles in *Arctostaphylos*” (*Erythea* 8:97. December 22, 1938). . . “Three New Californian *Arctostaphyli*” (l.c. 8:99). The use of my name as co-author of *A. pilosula* Jepson & Wieslander, *A. rudis* Jepson & Wieslander, and *A. silvicola* Jepson & Wieslander was unauthorized and without my knowledge or consent. A. E. Wieslander.”

According to Wieslander the proofs of this paper, which were to be published in *Madroño*, were sent to Jepson, despite a warning by the editor Herbert Mason to not share them with him (Lage and Wieslander 1985). It appears that in order to have his name attached to these species, Jepson resurrected the journal *Erythea*, which he had co-founded and was editor of but had last been published in 1922. In December 1938, he published “Three New *Arctostaphyli*” in which he named these taxa (Jepson 1938a), but did include “Jepson and Wieslander” as authorities for the new species indicating Wieslander’s role in their discovery. According to Wieslander (Lage and Wieslander 1985), Jepson had never seen or designated a type specimen of the three taxa.

In Wieslander and Schreiber (1939), the authors republished these three species as “sp. emend” providing more complete descriptions and designating type specimens. Given these facts, the most parsimonious conclusion is that Jepson was trying to preempt the naming of these three manzanita species so that he would have his name associated with them. Up to this point, as suggested above, Jepson had recognized very few species of *Arctostaphylos*. For someone who related so strongly to this genus, perhaps his lack of success in the discovery of new taxa, and the opportunity to more firmly attach his name to *Arctostaphylos* nomenclature, were important drivers behind this seemingly desperate attempt to “scoop” his former student in naming the three Wieslander and Schreiber taxa. An alternative view is that Jepson for some reason (lost in the mist of time) believed that his name should be associated with these three taxa and some evidence for this hypothesis is that in the Wieslander and Schreiber (1939) paper there were two species, *A. morroensis* Wieslander & Schreiber and *A. otayensis* Wieslander & Schreiber, that Jepson did not name, suggesting he had his reasons for believing he was a rightful authority for the three species he did publish. We will never know.

When Wieslander was put in charge of the Forest Survey for the Vegetation Type Mapping project in 1926, he was requested to determine the sprouting capacity of each species of the chaparral because of its practical bearing on the construction and maintenance of firebreaks (now known as fuel breaks), “sprouting” or “nonsprouting” became the first point of observation in the field. However, since this trait is generally most evident after cutting or burning, he noted “In an effort to clear up this difficulty we were rewarded by the observation that the burl is not a reaction of the species to mutilation by fire or

cutting, as many have understood it to be, but a normal structure which appears early in the life of the seedling... even where fires have never occurred" (Wieslander and Schreiber 1939, p. 39). This detail was unknown to Jepson when he first elaborated on resprouting (Jepson 1916, p. 3); with respect to *A. glandulosa* "After the stems are fire-killed, young plants begin to form a root-crown, which becomes turnip-shaped or globose," suggesting this might be a coppicing effect. Wieslander and Schreiber (1939) set the record straight by presenting a photograph showing the early stages of burl formation in *A. glandulosa* seedlings and saplings, thus demonstrating that burl formation was an ontogenetic trait initiated early in development. However, how much of this were Wieslander's own observations was unclear, since by then Jepson had incorporated this thinking into his own writings (Jepson 1939).

In the Wieslander and Schreiber (1939) footnote, there was also mention of a second paper Jepson hastily published on embryonic panicles (Jepson 1938b). Wieslander and Schreiber were planning on introducing observations regarding panicle development in their 1939 paper and point out that panicles were of taxonomic value in sorting out *Arctostaphylos* species because "[b]otanists had never used them to identify the manzanitas" (Lage and Wieslander 1985, p. 174). In the year prior to publication, Wieslander stood up after a Berkeley botany department seminar and stated how his field assistant "Mr. Jensen had found that the panicles had characteristics that were very helpful in identifying different species of manzanita, and they were present on the plants longer than the flowers and fruits. Then I [Wieslander] got a four page-letter written by Professor Jepson. He said he had never been so mortified in all his life. He said, "I discovered the differences in embryonic panicles myself. You embarrassed me... There was something wrong with him, I think" (Lage and Wieslander 1985, p. 175). This is consistent with Herbert Mason's (1947, p. 62) description of Jepson "Almost every incident of his stormy life was a drama, a fact that was always in his consciousness even to the point of histrionics."

In his 1938 embryonic panicle paper, Jepson contended that he had known and understood the taxonomic importance of these structures since 1915, and went on to describe many of the differences in these structures that set species apart. A similar discussion is given in the opening to his treatment of *Arctostaphylos* the following year (Jepson 1939), however, nowhere in the treatment does he describe embryonic panicles of the different species or use them to separate the taxa, so it would appear this discussion of embryonic panicles was an afterthought, added hastily before publication. Today these traits are critically important to distinguishing among *Arctostaphylos* taxa, however, Jepson's descriptive term for this trait did not endure the test of time as today we follow the suggestion of Mr. Jensen in calling them "nascent inflorescences."

As a teacher, Jepson was an exponent of the theory of self-reliance and personal experience. Apparently this worked for him in his career and he viewed it as the correct path for all students. Although there are numerous reports of positive interactions with a wide variety of people Jepson encountered throughout his travels (Ertter 2000), at home he was often an irascible colleague or professor. One of his students, Herbert L. Mason (1896–1994), contended that Jepson was very protective of his time and suggested this was one reason why Jepson never married (Mason 1947). However, he was an early suitor of Alice Eastwood, but apparently she never encouraged it and Moore (1996) suggested she never married either for similar reasons. Herbert Mason was a student who graduated under Jepson in 1932 and in his somewhat over the top obituary Mason (1947, p. 62) described the trials of being a Jepson student; Jepson "almost never took a student into the field with him and students could not knock on his perpetually closed office door, but rather they needed to send a letter requesting an appointment."

Finally, in contrast to many who have worked in *Arctostaphylos*, Jepson appeared to look more for similarities among taxa rather than differences. Consequently, Jepson tended to "lump" taxa together as varieties of more wide-ranging species (e.g., lumping several taxa as varieties of *A. andersonii* Gray, *A. montana* Eastw. into *A. pungens* Kunth, *A. franciscana* Eastw into *A. hookeri* G. Don, and *A. virgata* Eastw. as a variety of *A. glandulosa* in Jepson's 1922 treatment). This philosophy possibly influenced his taxonomic approach and resulted in the relatively few species he named. It was also adopted to a degree by Adams (1940) and later by Munz and Keck (1959) in his treatment in *A California Flora*. This taxonomic approach was also the polar opposite from Alice Eastwood, and later manzanita taxonomists (e.g., Phil Wells), who tended to fall on the "splitter" side. With this contrast in mind, we turn our discussion to another one of the most remarkable characters in *Arctostaphylos* lore, Eastwood.

Alice Eastwood

Alice Eastwood (1859–1953) was a self-taught botanist, and although high school valedictorian, she never pursued a college education. At an early age her mother died and her father had financial difficulties so she grew up during her formidable early teenage years in a convent near Toronto (Dakin 1953). Her first interests in botany were cultivated by the convent priests and relatives who were interested in experimental horticulture. She eventually moved to Colorado to live once again with her father, but he was not terribly successful at business and so she had to work several jobs to earn her way through high school. The freedom of exploring the Rocky Mountain landscape instilled in her an interest in native

plants and she acquired a significant personal herbarium.

In 1890–1891, as an amateur botanist she made a plant collecting trip to California and visited Katharine Brandegee and her husband at the California Academy of Sciences in San Francisco (Crosswhite and Crosswhite 1985). The Brandegees were impressed with Eastwood's expertise in botany and ultimately offered her a position at the California Academy of Sciences. Eventually, in 1894 Eastwood took over as head of the botany department, a position she held until retirement in 1949. Her early perambulations around Mount Tamalpais in Marin County yielded three important new manzanita species: *A. glandulosa*, *A. canescens*, and *A. montana* (Eastwood 1897). Her fascination with manzanitas was thus launched and her outdoor explorations were likely enhanced by being one of the few women ever admitted to the Cross Country Boys Club (Thompson 2016). Also early in her career at the academy, she gained notoriety nationally for her heroic saving of nearly 1500 type specimens when most of the collection was otherwise destroyed by fire following the 1906 San Francisco earthquake. This feat was greatly facilitated by the fact that, contrary to the convention at the time, she had stored all type specimens separately from the main collection, allowing her easy access during fires (Moore 1996).

Eastwood apparently guarded her time and avoided getting married because she wished to pursue her career without hindrances (Moore 1996), but this was not uncommon for the time as nearly three quarters of all 19th century female botanists remained single throughout their careers (Rudolph 1982). However, she did come close to marrying on a couple of occasions, while she was still in Colorado, the sudden death of her intended, had encouraged the move to accept Brandegee's job offer at the Cal Academy (Moore 1996). During Sierra Club outings she became acquainted with geologist Grove Karl Gilbert (1843–1918) and their relationship matured so that by 1918 they decided to marry (Pyne 1980). Gilbert though was reluctant because as he put it, "Alice and I have been lovers for years but for a long time I would not propose marriage because it seemed like asking her to give up a life that satisfied her to become the nurse of my broken health" (Pyne 1980, p. 262). However, his health improved and they planned on marrying, but he died that year of a heart attack at the age of 75.

Eastwood was well poised to deal with the complicated genus *Arctostaphylos*. Particularly *apropos* to this genus was a letter in which she regarded species as a human abstraction imposed on nature. "While I do not hope to straighten out a genus which is not straight in Nature I hope to make the relationships a little clearer than they are now" (Moore 1996, p. 45). Throughout her life she was a risk taker, spending years at a time traveling to herbaria in the east and overseas, hoping her Academy job would still be there when she returned.

As she described it "When one has little one can afford to take risks" (Moore 1996, p. 175). Privately she criticized many herbarium taxonomists on their lack of field knowledge of the species with which they were dealing (Moore 1996). We would expect that she would have held Jepson in high regard in this respect.

Perhaps the interactions between Alice Eastwood and Willis Linn Jepson were to some degree pre-ordained through the negative relationship of their mentors. Alice Eastwood's career was strongly influenced by Brandegee while Edward L. Greene played a significant role in Willis Linn Jepson's early career. Brandegee, however, despised Greene for a number of reasons and her vitriolic prose about his deficiencies were extreme. Part of Brandegee's dislike of Greene was that he was an outspoken critic of Darwin and she published comments such as "This kind of botany was taught, probably in the Middle Ages to which Mr. Greene properly belongs" (Carter 2011, p. 200).

The earliest communication we can find between Eastwood and Jepson was a cordial letter in response to Jepson sending his published dissertation to her for review. She congratulated him on his accomplishment and noted, "Of course we differ in opinion on some points but that is to be expected if both are honest and independent" (Eastwood 1901, no pagination). After that there is relatively little correspondence between the two and Moore (1996) suggested that Jepson and Eastwood did not particularly get along. Nonetheless, although not close colleagues, she maintained a cordial relationship with Jepson in their early years (Daniel 2008).

It seems likely that her professional interest in *Arctostaphylos* taxonomy may have been irritating to Jepson, and presumably *vice versa*. Indeed, Eastwood over her career had substantially greater success in discovering and naming *Arctostaphylos* species. Eastwood had a careful eye with a keen appreciation for subtle differences among taxa. Over her long career, she would name the most manzanita species of all other manzanita taxonomists (30), fourteen of which would ultimately stand the test of time (Parker et al. 2012). By contrast, as discussed above, Jepson described only a few *Arctostaphylos* taxa that have stood the test of time.

Despite Alice Eastwood's keen eye for detail, not all of her decisions have weathered the long-term peer review process, e.g., her separating four species into the genus *Schizococcus* Eastw. (Eastwood 1934, 1937). This separation was largely based on their fruit pulp, which shattered prior to dispersal. However, this characteristic of dehiscent fruits has been reported from other species in the genus *Arctostaphylos* (Keeley 1995), and for this and other reasons (e.g., Howell 1955) few botanists recognize *Schizococcus* and later, molecular genetic data confirmed that these four species are solidly embedded within *Arctostaphylos* (Hileman et al. 2001); indeed one *Schizococcus* species (*A. nissenana*) is in a

different deep lineage than the other three *Schizococcus* (Boykin et al. 2005, Wahlert et al. 2009).

Eastwood is often quoted as having said “I count my age by friends, not years—and I am rich in friends.” She took special delight in honoring friends by using their names for the specific epithet of new species, and over 100 species were so named (Cantelow and Cantelow 1957, p. 83). One of her closest friends and colleagues was John Thomas Howell who worked alongside her for many years and eventually took over the reins of the herbarium at the California Academy of Sciences when Eastwood died. J.T. Howell (1903–1994) was a native Californian born in Merced and an avid botanist by the time he entered high school. He studied under Jepson but notes he was rather underwhelmed by Jepson’s preference for research over teaching (McHoul 1975), and he later received a master’s degree from UC Berkeley in 1927. He was the first resident botanist at the Rancho Santa Ana Botanic Garden, back when it actually was in Santa Ana Canyon, as opposed to residing in Claremont, as is the case today. However, he and the garden founder did not get along well and when Eastwood offered Howell a position as her assistant at the Academy, he reportedly said “Miss Eastwood, I have to tell you I’ve just been fired from a job as resident botanist by Mrs. Susan Bryant at the Rancho Santa Ana Botanic Garden;” to which Eastwood replied, “Mr. Howell, coming from Mrs. Bryant I consider that a recommendation” (Smith 1989, p. 13).

Howell’s and Eastwood’s careers at the Academy overlapped by more than 20 yr, although Howell was usually viewed as Alice’s assistant. Moore (1996) suggested that this was illustrative of Eastwood’s safeguarding her status in the Academy. More than likely the fact that Eastwood was 70 when she hired 26 yr-old Howell (Figure 2) had more to do with their dynamic than professional jealousy. Certainly nothing in the writings of Howell suggested any level of resentment, but when it came to *Arctostaphylos*, both worked rather independently. Ultimately, Howell named only one species, *A. edmundsii*, a coastal endemic from the Big Sur region. This was in 1952, a year before Ms. Eastwood’s death in 1953. Considering their different talents, he with his keen observations on stomatal pattern distribution (Howell 1945) and she with her trained eye for slight taxonomic distinctions among *Arctostaphylos* taxa, suggests that a strong collaboration between these two may have proved synergistic.

One of the significant collaborative efforts between Eastwood and Howell was the creation of the journal *Leaflets of Western Botany* in 1932, apparently for the purpose of expediting their publications of new species. According to Moore (1996), Eastwood started the journal since previous outlets had been closed. The Academy’s official scientific journal was being popularized by the director and would not publish descriptions of new species in Latin. Plus, Eastwood intimated that both she and Howell were



FIG. 2. Alice Eastwood and John Tomas Howell, Washington state, 1936 (with permission from the Anne T. Kent California Room).

frozen out of publication in *Madroño* due to a disagreement with Jepson. Thus, after *Leaflets of Western Botany* was founded in 1932, Eastwood went on a proverbial tear, describing 18 new species of *Arctostaphylos* in 1933 and 1934. Of these, five are still recognized as species today, and seven are recognized at the subspecific level.

This possible conflict with Jepson, and her contention that she was being blocked from publishing in *Madroño*, is consistent with the story Philip Wells relayed in the introduction above, particularly since *A. jepsonii* Eastwood was published following more than two decades of silence on the manzanita front (Eastwood 1934). Perhaps Eastwood and Jepson were not on good terms by this time; Jepson’s *Arctostaphylos* treatment in 1922 omitted several taxa previously recognized by Eastwood and possibly this contributed to Eastwood to independently publish her own revision of the genus (Eastwood 1934). The tension between Jepson and Eastwood was later underscored by the *Arctostaphylos* treatment by Jepson in his *A Flora of California* (Jepson 1939), in which several taxa described by Eastwood in the 1930’s were not recognized. Nonetheless, despite her age and these obstacles, Eastwood published another six species during the war years

(1942–1945), of which one, *A. australis*, expanded her sphere of influence to Baja California. Another, seemingly good taxon, *A. cushingiana* was ignored by Wells, but now recognized as *A. glandulosa* subsp. *cushingiana* (Keeley et al. 2007).

POST-WORLD WAR II

Philip A. Munz (1892–1974), who began his career in 1946 as a botanist at Rancho Santa Ana Botanic Garden (Munz 1947), brought *Arctostaphylos* treatments up to date with *A California Flora* (Munz and Keck 1959). This treatment was the first to replace Jepson's crown-sprouting description with the term basal burl, which persists to the present in manzanita keys (although the term was apparently first used by Dobzhansky 1953). Like Adams (1940), Munz mixed both varieties and subspecies designations, made about a half dozen new subspecific combinations and named the new variety of *A. glandulosa* var. *adamsii* Munz in Adams's honor, describing him as author of a notable study of the genus *Arctostaphylos* (Munz 1958). As noted by Wells (2000), Munz (1958) also added the new species of Wieslander and Schreiber (1939). He additionally elevated some of the Eastwood species that had previously been submerged by Jepson and colleagues.

A new surge of manzanita mania was brought about by Jim Roof, sometimes known as the cantankerous curmudgeon of Tilden Park (Edwards 1999). James B. Roof (1910–1983) was as eccentric as any of the *Arctostaphylos* characters in this story. He was founding director of the Regional Parks Botanical Garden in the East Bay of San Francisco and ran the garden from 1934–1974. During that time, he was editor of the parks botanical journal *Four Seasons*, which he utilized as his primary mechanism for publishing *Arctostaphylos* names and observations - a notable tradition among his immediate *Arctostaphylos* predecessors, several of whom had their own institutional journal for publishing. He was also well known for interrupting the bulldozers leveling Laurel Hill Cemetery in San Francisco, the type locality for *A. franciscana*, and engaging them to help salvage plants that he then moved to the garden in Tilden to conserve this rare species. Roof rightly perceived the conservation implications of *Arctostaphylos* endemism and pursued them vigorously. Despite being a bachelor and living much of his adult life in a one room shack at the garden, he also had an eye for the ladies and raised eyebrows with his repeated use of attractive young models to highlight plant photos on the cover of *Four Seasons* (Figure 3), and in his "research" papers (e.g., Roof 1972).

Using the *Four Seasons*, he published extensively on his philosophy of *Arctostaphylos* taxonomy. He had rather unconventional ways of thinking about *Arctostaphylos* relationships and later designed *Arctostaphylos* alliances that have not stood the test of time. These were often based on a combination of

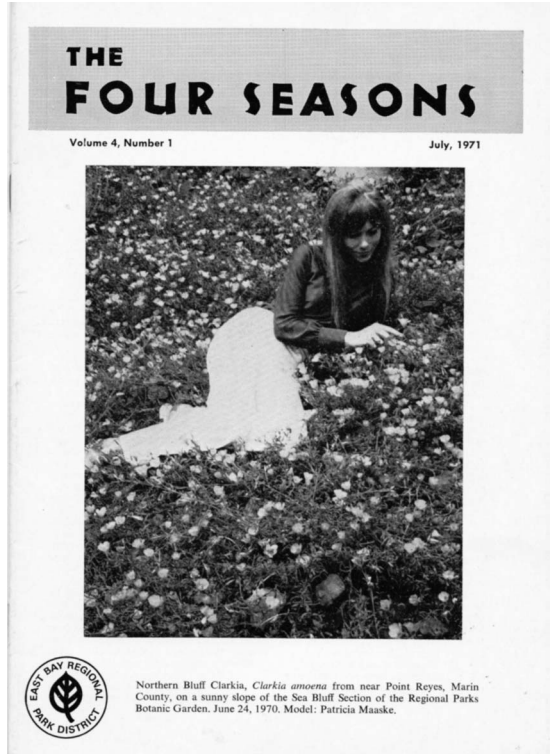


FIG. 3. An example of James Roof's *Four Seasons* (with permission of the East Bay Parks).

morphological and cytological traits, and when he found taxa that did not conform, he would invent colorful terms to describe them (Edwards 1999).

His most extensive writings were on *Arctostaphylos* collections from Pinnacles National Monument and the surrounding landscape of central coastal California. This region is dominated by *A. glauca* and *A. pungens* and Roof described an interesting array of variants, most of which he ascribed to variants of *A. pungens* (Roof 1978). His approach to alliances was to lump together many well-defined taxa such as *A. pungens*, *A. manzanita*, *A. parryana* and numerous other lesser taxa. While we recognize there are some as yet undefined *Arctostaphylos* problems in this central coast region, including potential variation in ploidy level that have not yet been totally resolved, most subsequent botanists have not agreed with his approach. Despite these philosophical perambulations, Roof did describe seven new species of *Arctostaphylos* including three (*A. montaraensis*, *A. cruzensis*, and *A. pacifica*) that are still recognized today (Parker et al. 2012).

Certainly one of Roofs enduring contributions to *Arctostaphylos* was his horticultural and conservation work on *A. densiflora* Baker, a narrow endemic in Sonoma County. Ironically, despite being reduced to just a single small population in the wild, it is without doubt the most widely planted manzanita in the state, thriving in a wide range of conditions. A

collecting party headed by Howard McMinn in 1941 selected an individual they considered best represented the species (Roof 1972) and this is the type from which contemporary cultivars known as "Howard McMinn" were propagated. Roof recalled that for many years this horticultural selection was erroneously referred to as the type specimen of *A. densiflora* but later expressed his "apologies for errors offered and suffered" (Roof 1972, p. 6). Roof was an avid protector of the natural population and not tolerant of offenders, e.g., visiting the roadside population soon after road crews had sprayed engine oil on some of the remaining *A. densiflora*, something he termed "official vandalism," exclaimed "No savages would have been so heedless of beauty: it was an act of morons" (Roof 1972, p. 6). Roof did much to try to protect this species in the wild although repeated collections from this population by him, Wieslander, Knight and others by transplanting seedlings to their private and public gardens were perhaps misguided since at the time the total known population numbered 41.

James Roof was editor of the Regional Parks botanical journal *Four Seasons* until he had some conflict with the board and created another, very short lived journal, *Changing Seasons*. He bitterly described this as "a necessary replacement for the FOUR SEASONS, the internationally recognized research journal of the now defunct [sic] Regional Parks Botanic Garden" (Roof 1979). Conflicts over the garden earlier in the 1960s, in fact, were critical events leading to the origin of the California Native Plant Society (Stebbins 1990).

Walter Knight (1914–2002) was a great field botanist with a keen eye for manzanitas. He honed his botanical expertise generating plant lists for environmental impact reports dealing with areas planned for development. He also worked for a time at the East Bay Regional Park's garden. He published a dozen papers; all in *Four Seasons*, on new and interesting *Arctostaphylos* discoveries, and during the years 1966–1985 co-authored a book on the flora of San Bruno Mountain (San Mateo Co) and one on the flora of Sonoma County. He is the author of *A. truei* (Knight 1969), which later was recognized as a subspecies of *A. mewukka* and he was a key contributor to two important species, *A. klamathensis* and *A. malloryi*. Knight was an enthusiastic field botanist and enjoyed going on *Arctostaphylos* forays with others such as James Roof, Steve Edwards, Roman Gankin, and Phil Wells, to name just a few. He was particularly helpful to Philip Wells from 1984 to 1989 while Wells prepared for his 1993 treatment in *The Jepson Manual* (1st edition) (Hickman 1993). Several new taxa were discovered during these trips.

Roman Gankin (1938–) also made important contributions through his dissertation that was a classic on the autecology of the very rare and restricted endemic, *Arctostaphylos myrtifolia* Parry (Gankin and Major 1964). Gankin has always been a

great *Arctostaphylos* explorer and described one of the very unique restricted manzanitas discovered in recent years, *A. refugioensis* Gankin, apparently "scooping" Phil Wells who recognized the unusual characters of this species on herbarium specimens (Wells 2000) but did not make field collections necessary for description. Many of the taxa discovered by this new wave of manzanita taxonomists subsequently made it into the *Supplement to A California Flora* by Munz and Keck (1968). While the academic community was largely convinced that *Arctostaphylos* was "done" after Munz and Keck (1959) (G.L. Stebbins, personal communication), the actions of these field scientists and inclusion in the *Supplement* suggested the contrary. Thus, the "table was set" for the new *Arctostaphylos* "expert" to emerge, Phillip Wells.

PHILIP WELLS ERA

Philip V. Wells (1928–2004) awakened the *Arctostaphylos* community by his appearance with an extensive assessment of chromosome numbers in 1968 that greatly extended our knowledge of manzanita systematics (Wells 1968). Wells was not a native Californian, and he completed his Ph.D. under the great ecologist Dwight Billings at Duke University, sharing an office with another noteworthy California ecologist, Harold A. Mooney. His dissertation was an autecological study of desert tobacco species, and this work seems to have garnered little attention. However, his time in the desert paid dividends because he discovered that ancient desert packrat middens harbored amazing collections of late Pleistocene and early Holocene plant matter that provided an unparalleled opportunity for analyzing temporal shifts in vegetation during past climatic episodes (Wells and Jorgensen 1964). His ability to detect interesting and important ecological patterns extended to studies on the link between Great Plains conifers and fire regimes (Wells 1983), substrate and disturbance impacts on vegetation distribution in central California (Wells 1962), and climatic shifts in chaparral and desert vegetation in central Baja California (Wells 2000). These insights also, of course, contributed to his interest in *Arctostaphylos* (Figure 4), one of the more biogeographically fascinating genera in California.

Wells (1990) credits his interest in *Arctostaphylos* to Cornelius H. Muller. One of his first academic positions following graduate school was a yearlong replacement for Muller at UCSB. In discussions with Muller, he was encouraged to find a genus for taxonomic work that would be a sidelight to his ecological research, an attitude almost certainly offensive to taxonomists who devote their careers to taxonomy (Wells 2000). With Muller this approach was certainly fulfilling in that he continued throughout his career to make occasional contributions to *Quercus* taxonomy, despite his focus on the ecology of allelopathy. With Wells it also turned out

to be a good strategy and as he described it “Although I studied the manzanitas over a period of 32 yr, I really did most of it in concentrated bursts totaling maybe only about three years of full-time activity (maybe enough for 1 Ph.D.)” (Wells pers. comm. to JK).

His contributions to *Arctostaphylos* nomenclature were second only to Alice Eastwood. Wells described 11 new species of which nine are still recognized and two exist as subspecies (100% retention). Wells was also important for three major revisions in the genus in 1968, 1987, and 1988. In 1968, he made 27 new taxonomic rearrangements including adding two new species descriptions (Wells 1968). These were largely driven by his work on *Arctostaphylos* chromosome insights and unfortunately did not make it into the 1968 *Supplement* (Munz and Keck 1968). In 1987, he made six rearrangements including the addition of four trinomials featuring the rank of forma (Wells 1987). Then, in 1988 prior to submission of his taxonomic treatment for *The Jepson Manual* (Hickman 1993), he added 32 new revised taxonomic arrangements (Wells 1988). Species descriptions by Eastwood and Wells combined make up more than one-third (37%) of the currently recognized species (63) in *Arctostaphylos*. Interestingly, neither Eastwood nor Wells included other colleagues as co-authors of their species treatments although both undoubtedly had assistance in their field surveys.

One of the important impacts of Wells’ taxonomic work was his decision early on to submerge the rank of variety and to describe all infraspecific taxa as subspecies (Wells 1968). The primary motivation for this was to recognize variation that was geographically circumscribed. However, it is well known that some species, particularly crown-sprouting species such as *A. tomentosa* and *A. glandulosa*, have morphological variants that persist through repeated fire cycles (Keeley et al 2007); to recognize these, and other widespread variants without a clear geographic range, Wells proposed the term forma (Wells 1988).

Wells (1968) presented chromosome counts for over 60 *Arctostaphylos* taxa and used this information to formulate hypotheses on species origins. One notable example was the origin for the tetraploid *A. mewukka* Merriam. Wells hypothesized that this mid-elevation species originated by amphidiploidy from a cross between the higher elevation *A. patula* Greene and lower elevation *A. viscida* Parry. Wells’ hypothesis was supported by cytological and genetic work by Kristina Schierenbeck (1956–) (Schierenbeck et al. 1992).

Although Schierenbeck did not pursue a career in *Arctostaphylos* taxonomy she did demonstrate some valuable lessons about the use of manzanitas in forensic science (Schierenbeck 2003). Butte County Sheriff deputies consulted with Dr. Schierenbeck to determine if plant samples found in the back of a pickup truck could assist in tracking down a young girl. A leaf of *A. patula*, in combination with other associated plant species pointed her to a site where



FIG. 4. Philip V. Wells at Mill Creek Summit, Los Angeles County with *A. glandulosa* subsp. *gabrielensis* (P.V. Wells) J. E. Keeley, M.C. Vasey & V.T. Parker, 10 March 1986 (photo by Jon Keeley).

she suspected they came from, and quite unfortunately she led them to the discovery of the young girl’s body.

One of the most important contributions by Wells was a paper that discussed obligate-seeding and crown-sprouting species in chaparral (Wells 1969). This work relied heavily on Jepson (1916), whose brilliant insights into the true fire-type shrubs, which were the obligate seeding (Wells’ term obligately-seeding) species. However, Wells was able to extend this beyond *Arctostaphylos* to include *Ceanothus* and exclude other genera in chaparral, as well as apply an evolutionary model to explain the advantages of obligate seeding.

Wells did not collaborate with other *Arctostaphylos* aficionados. He did correspond with others (e.g., Walter Knight and Jon Keeley), and used them to guide him on field trips, and discovery of new taxa, but did not include them in his publications. Indeed, type specimens were collected in collaboration with these *Arctostaphylos* experts, but colleagues were never included in his papers or as authorities for his new species. This was perhaps a shortcoming in his work since for the last few decades of his life he had relatively limited access to field work in California and might have benefited from collaboration with active *Arctostaphylos* field botanists.

ABOUT THE AUTHORS

Jon E. Keeley (1949–; first author) grew up in rural San Diego County and spent much of his early childhood exploring the natural history of chaparral

and sage scrub ecosystems around the community of Bonita. He started systematically collecting plants as an undergraduate and pursued a master's degree on postfire chaparral recovery following the massive 1970 Laguna Fire. Philip Wells' paper on the evolution of *Arctostaphylos* and *Ceanothus* life history strategies (Wells 1969) was largely responsible for selecting this thesis topic, and it played a key role in his future career direction (Keeley 2014).

Keeley's keen interest in *Arctostaphylos* evolution was further stimulated by an early paper on hybridization in *Arctostaphylos* written by the renowned Russian emigrant Theodosius Dobzhansky (1953), perhaps most widely known for his maxim "Nothing in biology makes sense except in the light of evolution." Dobzhansky (1953) and UCLA botanist Carl Epling (1947) used a very subjective approach to classifying individuals as hybrids or F1 backcrosses and concluded that *A. patula* and *A. mariposa* (now *A. viscida* subsp. *mariposa*) from near Yosemite National Park were a textbook demonstration of introgression. Although convincing because of their reputation, a clearer demonstration of hybridization was Leslie Gottlieb's (1968, see also Schmid et al. 1968) quantitative analysis of *Arctostaphylos* hybridization. Gottlieb went on to have a very successful career as a plant geneticist, however to some of us he is best remembered for his insightful essay contrasting Herman Melville's and Charles Darwin's reaction to the Galapagos Islands landscape (Gottlieb 1975). Keeley (1976) applied a similar approach to a mixed population of *A. glauca* and *A. pungens* in San Diego County and presented evidence not of just plants with intermediate characteristics of both putative parental species, but also individuals that recombined combinations of traits from both species, highly suggestive of hybridization and introgression.

Keeley's interest in *Arctostaphylos* further developed through his explorations and discovery of new taxa in Southern California (Keeley et al. 1997a) and Baja California (Keeley et al. 1997b, Keeley et al. 2007). One early specimen from northern San Diego County was sent to Wells and he disagreed with Keeley's assessment and claimed it was just a range extension of *A. peninsularis*, a Baja species, one which Wells had recently named (Keeley 1974). Eventually, Keeley realized it actually was a new species and named it *A. rainbowensis* (Keeley and Massihi 1994). Wells, however, continued to insist he was correct, and in his 2000 monograph, submerged *A. rainbowensis* as a subspecies of *A. peninsularis* (*A. peninsularis* subsp. *keeleyi*). Having known Phil Wells personally it is hard to not believe that this is similar in intent to the story of *A. jepsonii* Eastwood, recounted in the opening paragraphs.

In 1985 Virgil Thomas Parker attended his first workshop on *Arctostaphylos* at UCSB because of an interest in resprouting and seeding life histories in *Arctostaphylos*. The guest speakers at the workshop were Philip Wells (University of Kansas) and Jon

Keeley (Occidental College in Los Angeles), and each were given 50 min to speak and were told they had to adhere closely because the room had to be vacated immediately after the two talks. In a style later recognized as typical Wells, at 50 min Phil wasn't close to finishing and turned to Keeley rhetorically saying "you won't mind me taking some of your time" and without waiting for an answer continued for another half hour. Perhaps one of the better parts of this meeting, though, was the after lunch lab display of a rich diversity of live *Arctostaphylos* collected by Wayne Ferren and other UCSB botanists. It was here that Keeley and Parker had a chance to meet and they have continued to correspond on similar interests in *Arctostaphylos* taxonomy and ecology over the following years.

Tom Parker and Michael C. Vasey (1947–) got serious about *Arctostaphylos* taxonomy following a 1992 discussion between Vasey and an editor for the *Flora of North America* (FNA) project, in which some concerns were raised about turning the FNA *Arctostaphylos* treatment over to Philip Wells, the natural heir since he had recently completed the *Arctostaphylos* treatment for the 1993 *Jepson Manual* (Hickman 1993). Apparently, word had reached them of difficulties in dealing with Wells and particularly his insistence upon using a trinomial nomenclatural system (including the rank of *forma*) for several important groups (Wells 1988), although *forma* was never used in *The Jepson Manual*. As a consequence, the editors were willing to consider alternatives. This FNA representative recognized Vasey was very knowledgeable on the genus and challenged him to do the treatment. Vasey agreed as long as he could collaborate with Parker, and, in order to do more than just "rearrange the deck chairs," FNA needed to help them investigate molecular data with funding, which subsequently did come through. During these early studies in 1990, there was a discussion between Parker and Keeley about ways to collaborate on *Arctostaphylos* problems. In 1994, Parker suggested that he and Keeley collaborate on a National Science Foundation research proposal to further the understanding of *Arctostaphylos* evolution through molecular methodologies. However, this proposal was not funded and this rejection instilled in Parker the need for collecting "proof of concept" data that would ultimately allow a fuller understanding of the phylogeny of this group.

Ultimately, the first study using nuclear ribosomal DNA in *Arctostaphylos* (Markos et al. 1998) showed promise for altering our view of *Arctostaphylos* evolution as it raised the likelihood that Wells' perspective on the phylogeny of the group was in need of reexamination. Throughout Wells' career, he expressed strong opinions on the appropriate subgeneric classification system and species affinities. His morphologically based cladistic analysis employed 70 traits that he contended pointed clearly to two subgenera, each with three sections, and these conclusions were presented in Wells (2000), but to our knowledge the cladistic analysis was never

published. The subsequent molecular work (Markos et al. 1998, Hileman et al 2001, Boykin et al. 2005, Wahlert et al. 2009) provided evidence to revised Well's *Arctostaphylos* phylogenetic concepts.

This molecular rDNA work also cast light on evolution within the subgenus *Arbutoideae*. Particularly surprising was the discovery that although *Arbutus* is a close relative to *Arctostaphylos*, manzanitas are more closely related to Mediterranean *Arbutus* species than to North American *Arbutus* (Hileman et al. 2001). This unexpected finding, however, is consistent with phenological patterns of flowering. *Arctostaphylos* flower from nascent inflorescences on old wood from the previous year, and this is also the pattern for Mediterranean *Arbutus*, but not with North American *Arbutus*, which do not produce persistent nascent inflorescences and flower from new growth (Keeley 1997).

Another direction Parker and Vasey took was holding 2-day *Arctostaphylos* workshops for manzanita aficionados, most often hosted by the Jepson Herbarium and held at Hastings Natural History Reservation in the Carmel Valley. These outings not only made this difficult genus more accessible to non-specialists but the specialists seemed to learn more and more about manzanita mysteries with each workshop. The most significant contribution was the development of a workable key to the genus, polished by participants over the years in these workshops.

By the early 2000's the FNA project was still in the works and now the invitation for *The Jepson Manual* revision came through. In light of California's large latitudinal range there are substantial differences between the north and the south. Parker and Vasey, realizing they needed help on the southern California manzanitas, contacted Keeley about providing input and collaboration, which seemed like the best solution (Figure 5). One of the first collaborative projects was an attempt to sort out the complex of *A. glandulosa* interspecific variation (Keeley et al. 2007). Using a collection of 1400 sheets of this species, based on a decade of collecting from Oregon to Baja California, they were able to make quantitative trait comparisons that sorted out the taxa and interpreted the results as comprising two lineages, a glandular and non-glandular line, each of which have given rise to various subspecies. The next collaborative effort was a paper presenting a number of changes in taxonomy within the genus (Parker et al. 2007), necessary before incorporating these changes into the final treatment. What was most interesting about these two papers was the review process. In the case of the former, which used large datasets and statistical analyses, the paper invoked substantial review critiques that were rather difficult to address. The latter paper involved just expert opinion and received almost no critiques and was published more or less as is. Both *Arctostaphylos* treatments were eventually published (Parker et al. 2009, 2012). This collaboration continues with the most recent project one that has addressed Jepson's



FIG. 5. Tom Parker, Mike Vasey, and Jon Keeley at type locality (Gabilan Range, San Benito Co.) for *A. gabilanensis* circa 2005 (photo by Jon Keeley).

(1916) early interest in resprouting and seeding 100 yr later (Keeley et al. 2016).

CONCLUSIONS

Over the past three centuries, nearly fifty authors have described over three hundred *Arctostaphylos* taxa. Our principal objective has been to introduce others to the small group of those individuals who have been most involved in the naming of species in this charismatic genus. Undoubtedly, other complicated genera have similar humans that were part of the history of systematic research and we encourage researchers to also investigate the history of their preferred organisms, as it will be fruitful from a research perspective, as well as insightful about the course of human endeavors within challenging groups. Early on, we thought that this might be an exposition on the advantages of collaboration versus competition in science, but clearly examples of both arise throughout the history of this group. Indeed, we are convinced that one thing held in common with most if not all who pursue manzanita studies is the pleasure of joining others in field explorations in such a rich and diverse environment as the California Floristic Province. We feel that considerable progress has been made on understanding the evolution and diversity of this impressive genus, and yet we suspect that the diversity of personalities working in the group has probably been as important an element in that progress as other factors.

We end with a few quotes that summarize to us some of the lessons gleaned from this the history of *Arctostaphylos* taxonomy. "The basic trouble, you see, is that people think that 'right' and 'wrong' are absolute; that everything that isn't perfectly and completely right is totally and equally wrong. However, I don't think that's so. It seems to me that right and wrong are fuzzy concepts, . . ." (Asimov 1989, p. 35). "An expert is a man who has made all

the mistakes which can be made, in a narrow field.” (Niels Bohr as quoted by Edward Teller in Coughlan 1954, p. 62). “If we knew what we were doing, it wouldn’t be called ‘research’, would it?” (Albert Einstein as quoted by Hawken et al. 1999, p. 272). It seems these characters and their philosophies perfectly capture the on-going reality of work in a genus as challenging and fascinating as *Arctostaphylos*. We have no doubt that other authorities will emerge, new insights will be gleaned, and different arrangements of relationships will be fashioned based upon other perspectives. In this era of shifting taxonomic identities, it is well to keep in mind that species are always hypotheses of phylogenetic relationships based upon the best information and interpretation of data available at a given time. Taxonomic characters shape these interpretations but it is the interplay of human characters, with all their various foibles and differing strengths, which ultimately shape taxonomic treatments! Most importantly we need to keep in mind that the true ‘peer-review’ process is something that unfolds over years or decades following publication of a scientific paper.

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