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Sherwin Carlquist—Recipient of the 1993 Asa Gray Award

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The American Society of Plant Taxonomists has awarded Dr. Sherwin Carlquist the 10th annual Asa Gray Award. The award, presented "for outstanding accomplishments pertinent to the goals of the Society," was given to Sherwin Carlquist because of his broadly based contributions in systematics, island biology, and systematic wood anatomy, and because he has been so widely influential during his fruitful career at Pomona College, Claremont Graduate School, and Rancho Santa Ana Botanic Garden. Throughout the years the research of many colleagues and students has been strongly influenced by Sherwin's investigations and theories, as a number of the letters supporting his nomination attest. Sherwin Carlquist epitomizes the most meritorious type of scientist: an indefatigable and innovative researcher, a dedicated teacher, and one who has an incessantly probing mind.

Sherwin has been extremely productive during his career, publishing seven books and 200 research papers in which he has worked on more families of plants than most systematists would think of attempting. In planning his 1993 retirement from Rancho Santa Ana Botanic Garden and Claremont he conceived of about 40 new anatomical projects for which he has obtained plant material and prepared slides, clearly demonstrating his tremendous curiosity, drive, and organization. He will surely continue to stimulate and inform us with many more insightful and provocative publications while continuing his work in Santa Barbara.

The works that have earned Sherwin the most renown are his studies of islands on which he has published three widely read and influential books: *Island Life* (1965), *Hawaii: A Natural History* (1970, 2nd ed. 1980), and *Island Biology* (1974). Portions of these works resulted from his research papers on Pacific Asteraceae and his influential five-part series "The biota of long-distance dispersal" (1966, 1967). This work on islands has enticed a substantial number of

young investigators to address relevant questions in adaptive radiation, loss of vagility, insular (secondary) woodiness, and evolution of breeding systems. In fact, Sherwin's books are among the most widely consulted and cited publications on islands, whether as part of an in-depth study or as an initiation to island biology. Because these works have appealed to a wide audience, his work has been pivotal in awakening the general consciousness to the significance of plant systematics. Notably, the wide influence of these books has caused many people to appreciate and thus care for the natural world.

Plant anatomy has made wide and fundamental contributions to understanding the evolution of plants, and Sherwin has been and continues to be a major contributor to the field. In addition to his island studies, Sherwin has produced a prodigious series of systematic anatomical studies. His success in using anatomy to find the relationships of *Fitchia*, undertaken for his graduate studies, motivated him to pursue numerous other anatomical studies to elucidate relationships among a wide array of plant taxa. His studies encompass a broad selection of plants, from *Ephedra* to the Onagraceae and many sympetalous angiosperm families, with special emphasis on herbaceous groups. He has also effectively used anatomical data to further understanding of numerous anomalous groups such as the Roridulaceae, Byblidaceae, Tremandraceae, Geissolomataceae, Grubbiaceae, Cneoraceae, and Coriariaceae. He has made a major contribution with his anatomy books: *Comparative Plant Anatomy* (1961), *Ecological Strategies of Xylem* (1975), and *Comparative Wood Anatomy* (1988).

Sherwin's studies of wood anatomy have given us new insights into the principles of wood evolution. Particularly relevant is his now universally accepted theory of paedomorphosis, which explains how and why the wood of herbs and herb-derivatives is different from that of typically woody plants. Sherwin is one of few anatomists to study the wood of non-arboreal species. His studies of primitive angiosperms (Chloranthaceae, Degeneriaceae, Illiciaceae, Trimeniaceae, and Winteraceae) as well as the gymnosperm *Ephedra* have continued the important tradition of I. W. Bailey's contributions to comparative anatomy and its evolutionary significance.

When Sherwin began studying wood anatomy the idea that wood was adapted to the species' habitat was all but ridiculed. In his book, *Ecological Strategies of Xylem Evolution* (1975), he attempted to elucidate the relationship between habitat and woodiness. While not all of his speculations have been borne out, patterns of ecological distribution of anatomical features are clear. Most notable in recent years has been the discovery that vasicentric tracheids, a subsidiary conductive system thought to be characteristic of only a few families, are actually rather widely distributed in a large number of families, in shrubs of desert and Mediterranean climates and trees of the dry tropics. While much work remains to be done in wood physiology, Sherwin's studies in ecological wood anatomy have helped to bridge the gap between anatomy and physiology.

Sherwin's publications always include interesting and insightful syntheses and often new biological and evolutionary hypotheses. However, he has also made significant contributions directly to taxonomy, most notably in his studies of the Stylidiaceae (1979). His taxonomic work includes new species in Goodeniaceae (1969) and Grubbiaceae (1977), and the curious new genus of Restionaceae, *Alexgeorgea* (1976)—the only known wind-pollinated plant with underground flowers!

His ability to combine excellent and stimulating research with concern and assistance for students is rare indeed. In addition to his scholarly publications covering a broad range of taxa and topics, Sherwin has been an active teacher at Claremont Graduate School for more than three decades. As a teacher, Sherwin has displayed an enthusiastic concern and involvement with students. Throughout his career he consistently took time to listen to students and to guide them to make their own discoveries. His lectures at Pomona College and Claremont Graduate School were always exciting because he interjected many fascinating examples from his botanical travels, presenting a hard to match spectrum of the plant world that ignited students' imaginations. He has played an important role in the education of 16 Ph.D. students, as well as a number of M.A. students. The list includes: Edward F. Anderson, Loren C. Anderson, Donald R. Bissing, Gary D. Cromwell, Christopher Davidson, Larry E. DeBuhr, Warren S. Drugg, Arthur C. Gibson, James S. Hen-

drickson, R. John Little, David C. Michener, Theodore H. Mortenson, Leila M. Shultz, Gary D. Wallace, Ruth C. Wilson, and Scott Zona.

The American Society of Plant Taxonomists is pleased to recognize Sherwin Carlquist as the recipient of the 1993 Asa Gray Award. We are enriched both by his science and by our access to autobiographical notes recounting certain milestones in his interesting and distinguished career. Thus I am able to conclude this brief tribute with Sherwin's own insightful words.

"I was born in Los Angeles (July 7, 1930) and grew up in various suburbs surrounding Los Angeles. This fact would be of little importance except that one of these suburbs contains the Huntington Botanical Gardens. I often walked through the Gardens on weekends, fascinated by the diverse forms, especially in the outstanding desert gardens of the Huntington. I had no mentor to explain to me that the red flowers of *Cleistocactus* do not open because they admit hummingbirds but not other visitors. Curiosity about the adaptive significance of forms such as these undoubtedly motivated me to become interested in the adaptive significance of the structure.

At the University of California, Berkeley, I had the good fortune to take a plant taxonomy class from Lincoln Constance, whose sophisticated wit and personal warmth appealed to me; I asked him if I could do an undergraduate research with him, although I had no ideas for a project. He suggested I read the literature on a large family of angiosperms, and I suggested the largest (or second largest), Asteraceae. The following semester he guided me into investigative work and suggested I find the chromosome numbers of the species of *Eriophyllum*, a genus of that family on which he had once worked. With the aid of a primitive microscope, I did that, deciding I was not enthusiastic about chromosome cytology.

While Lincoln Constance was on sabbatical leave in Chile, I browsed through the Asteraceae in the herbarium and came across *Fitchia*, a tree with large pendent heads from southeastern Polynesia. I discovered various authorities placed *Fitchia* in Heliantheae, Cichorieae, or Mutisieae, respectively, despite the quite disparate characters of these tribes. I had taken a course in plant anatomy from Adriance Foster; the course made plant anatomy seem very lucid and accessible, and I thought perhaps using plant anatomy I could determine the true relationships of *Fitchia*. With Constance, Foster, and Stebbins as thesis advisors, I embarked on this study, which contained so many of the themes I was to pursue: anatomy as an indicator of relationships; evolutionary change on islands (increased woodiness, loss of vagility); and comparative anatomy, particularly comparative wood anatomy.

There was no hope as a beginning graduate student that I could reach the various islands where *Fitchia* grows, but the Rarotongan species *F. speciosa* had once been cultivated near Honolulu and was still growing as an escape there. My mother had given me a moderate sum of money as a graduation present, telling me I could go wherever I wanted; the sum seemed sufficient for an airplane ticket to Hawaii and about two weeks there. I did find the *Fitchia*, and also used the Hawaii trip to collect material for cytological and anatomical studies on the silverswords (*Argyroxiphium*) and their relatives (*Dubautia*, *Wilkesia*).

Sitting beside a silversword in Haleakala crater one day in July, 1953, I noticed the thickness of the leaf, and broke it open to see if it was succulent. To my surprise, strands of a gel could be squeezed out of the leaf, and I thought this might be a water storage mechanism that permitted the silversword to survive in the arid cinders of Haleakala (that has subsequently been demonstrated physiologically). I wanted to study the anatomical genesis of these gels, which fill intercellular spaces, as well as see what the relationships of the silversword are. The significance here is that if I hadn't been in the field myself, I would likely not have discovered the gels (which dissolve in typical pickling fluids), nor would I have been able to obtain materials of so many species of a group. But, more significantly, I would not have become acquainted with the diverse ecological settings in which these species grew, so I wouldn't have understood the relationship between anatomical structures and ecology. At that time, attempting to explore that relationship was unfashionable: anatomists wore lab coats and rarely collected the materials they studied; field botanists did collect and saw field ecology, but didn't use microtomes or look through compound microscopes. I saw no reason why one person couldn't do both, and I proceeded to do so. Thus, anatomical differences between species became for me not just taxonomic characters but also possible strategies for adaptation to ecological situations.

I followed my studies of the silverswords and their relatives with studies of the California tarweeds (Heliantheae, subtribe Madiinae), and reached the conclusion that the silversword alliance belonged to the tarweeds. This required hypothesizing long-distance dispersal of a seed from California to Hawaii across at least 2500 miles of ocean, but I saw no difficulty in that—although I soon learned others (especially vicariance biogeographers) regarded that as an impossibility. Fortunately, molecular and genetic data from workers such as Bruce Baldwin and Gerald Carr have come to my rescue. Plant anatomy may appear a dull tool for establishing phylogenetic relationships, but one shouldn't disregard evidence from any source, and plant anatomy has the additional advantage of telling much about the biology of a species.

Islands seemed to have many instances of second-

ary woodiness on them, and I became fascinated with the anatomy of wood that has evolved in this direction. To study wood of predominantly herbaceous families such as Asteraceae, Lobeliaceae, and Goodeniaceae, I applied for grants for field and laboratory work. The grants permitted me to travel to island areas all over the world. I did complete the laboratory studies on woods, but I also satisfied a hidden agenda: understanding more about evolution on island areas. This latter interest led me to write *Island Life*, a popular book (I wrongly assumed that would be easier to write than a scientific book); *Hawaii: A Natural History*, followed, and *Island Biology*, a book incorporating some scientific papers and adding chapters on other topics, concluded the trio. I never thought I was primarily a worker in the field of evolution on island areas, I always thought of myself as a comparative plant anatomist. These three island books therefore appeal to me as amateur works in a sense, and they have had the merit of interesting younger generations in evolutionary questions on islands—questions that their newer methods would be able to solve ever so much more adeptly than the techniques I had been using. And thereby I could enjoy the achievements of these youngsters and not compete with them.

About 1972, I decided to devote myself largely to studies in wood anatomy. Wood is the most complicated tissue of a plant, and I reasoned that it would be accordingly rewarding. At that time, few workers were active in the field, and rather than finding that discouraging, I sensed opportunity. At that time, differences among woods were categorized systematically and the literature implicitly suggested that while leaf anatomy might be an important tool in how a plant managed its water economy, wood certainly wasn't. I challenged that interpretation in a book that was necessarily premature, *Ecological Strategies of Xylem Evolution*. Comparative wood anatomy yields data that suggest particular physiological functions and can offer ideas to wood physiology. I see the two fields as building a bridge that will eventually unite the two fields intimately.

In order to develop ideas about wood evolution, I began not by asking particular questions and finding the right material to answer those questions, but by investigating the wood anatomy of numerous dicotyledon families. I reasoned that hitherto unappreciated evolutionary modes would emerge if I accumulated data that showed how wood of numerous dicotyledon families had responded to a range of situations independently. Explanations thereby presented themselves for such phenomena as vessel grouping, occurrence of vasicentric tracheids, growth ring intricacies, helical thickenings in vessels, and raylessness. At the same time, each group studied yielded data of systematic interest (e.g., woods of Aristolochiaceae and Lactoridaceae are very similar to those of Piperaceae). Some of the systematic hypotheses so generated are of use to molecular phylogenists, who must select a limited number of species to investigate in order to determine the relationships of a particular family.

Favorable institutional settings seem important to happy careers, and I count myself fortunate to have found, after a year of post-doctorate work at Harvard University, a position that I kept from 1956 until retirement on 1 January 1993. The exact financial auspices of this position varied, but it essentially involved a half time commitment to the Graduate Program in Botany in Claremont, a program hosted by the Rancho Santa Ana Botanic Garden (degrees through Claremont Graduate School); and a half time commitment to undergraduate teaching at Pomona College, one of the five affiliated Claremont Colleges. These institutions have offered me wonderful teaching opportunities, good facilities, and helpful and tolerant colleagues: all of these factors have permitted me to enjoy a research career that continues unabated. I now live in Santa Barbara, California, where I am associated with the Santa Barbara Botanic Garden and am an unpaid adjunct professor at the University of California at Santa Barbara."

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