Antecedent Wetland Ecologists - German and Austrian in the Ninetieth Century

Arnold van der Valk[1], Ecology, Evolution and Organismal Biology, Iowa State University, Ames, IA

Please note that this is the first of a series in WSP. Many of the people, and even institutions, who influenced the development of the wetland science as a field have recently died or closed, and many other pioneering wetland scientists have retired or will soon retire. Given this, we would like to capture the early history of our science by getting the people who created it to write about their reasons for becoming wetland scientists and their contributions to the field. This series of articles will focus on two major topics: (1) the contributions of major scientists working in wetlands to the development of wetland science, and (2) the roles of major wetland institutions and organizations in the development of wetland science. Each article will highlight major advances, organizational and/or intellectual, that have shaped wetland science in the United States and around the world.

We have invited a number of distinguished wetland scientists to contribute articles in the series. We also like to invite anyone interested in the history of wetland science to submit an article for this series. We are particularly interested in accounts of the history of wetland science outside of the United States. If you would like to contribute an article to this series, please contact either of the editors of this series, Arnold van der Valk, Ecology, Evolution and Organismal Biology, Iowa State University, Ames, IA 50011 (valk@iastate.edu) or Gordon Goldsborough, Department of Biological Sciences, University of Manitoba, Winnipeg, MB R3T 2N2, Canada (gordon.goldsborough@umanitoba.ca).

ABSTRACT

The ideas of three nineteenth-century German-speaking, academic scientists (Anton Kerner, Karl Möbius, and Heinrich Schenck) greatly influenced the development of wetland ecology. Anton Kerner in his landmark book, *Das Pflanzenleben der Donaulaender*, described hydrarch succession as an orderly process and also discussed the implications of large-scale drainage of wetlands in Hungary on regional climate. Studies of oyster beds by Karl Möbius resulted in the formulation of the concept of ecological communities being in equilibrium due to the interaction of their constituent species, unless they are disturbed. Heinrich Schenck pioneered the study of aquatic plants and their adaptations for life under water. All three raised the visibility of wetlands and wetland plants in the scientific community in the nineteenth century.

INTRODUCTION

As originally formulated in the 19th century by Ernst Haeckel (1834-1919) in his *Generelle Morphologie*, ecology was the study of organisms and their interactions in their natural environment, as opposed to their study in the laboratory (Haeckel 1866). In other words, ecology is the study of organisms in nature. Haeckel, an early supporter of Darwin, saw it as a new, much needed science that focused on the study of natural selection. For an account of the development of an ecological perspective among thinkers interested in natural history in the early nineteenth century like Alexander von Humboldt, Charles Darwin, and many of their contemporaries, see Donald Worster's *Nature's Economy* (1977).

Ecology did not develop in a systematic way, however, but as an accumulation over time of numerous, disparate studies done on a variety of organisms (algae, invertebrates, plants, birds, fish, mammals, etc.) in a variety of environmental contexts (grasslands, forests, lakes, oceans, rivers, wetlands, etc.). From its inception, ecology has always consisted of a myriad of subdisciplines often focused on a specific type of ecosystem such as grassland ecology, forest ecology, tropical ecology, limnology, etc. or on a group of organisms such as animal ecology, insect ecology, plant ecology, etc. Because they were typically trained as either botanists or zoologists, most pioneering ecologists in the late ninetieth and early twentieth centuries thought of themselves as either plant ecologists or animal ecologists, if they thought of themselves as ecologists at all.

How did the science of wetland ecology develop? Wetland ecology is clearly a subdiscipline of ecology. As I will demonstrate in a later installment in this series, wetland ecology did not become a self-conscious science, i.e., a science with a recognized name with which scientists identified themselves, until the 1970s. Nevertheless, prior to the 1970s, there were many scientists who worked exclusively,

1 Corresponding author: valk@iastate.edu, 515-294-4374

primarily, or occasionally on wetlands or wetland organisms. Their studies collectively form the basis for what came to be called wetland ecology.

At this point, I would like to make an important distinction between what have been called protoecologists and what I will call antecedent ecologists. Protoecologists are individuals who made observations that in retrospect would be considered to fall within the science of ecology. Such observations can be found in numerous writings from classical antiquity to those of Darwin. Frank Egerton's book *Roots of Ecology: Antiquity to Haeckel* (2012) provides a detailed account of many protoecologists and their observations. Antecedent ecologists are individuals in a variety of disciplines, mostly scientific, whose research work or writings on organisms, populations, communities, or ecosystems created an interest in ecology as an object of scientific study and/or who raised the visibility of ecology both within the scientific community and outside it. Most, but not all antecedent ecologists were academic scientists, but some were not scientists at all.

In this paper, I am going to examine the contributions of three nineteenth-century German-speaking, antecedent wetland ecologists, two academic botanists (Anton Kerner, Heinrich Schenk) and one academic zoologist (Carl Möbius), to the development of wetland ecology. In my brief discussions of their scientific contributions, I will emphasize how novel ecological insights from their studies of wetlands or wetland organisms contributed to a greater awareness of the importance of wetlands among their contemporaries and how this helped lay the foundation for wetland ecology. Two of these scientists (Kerner and Möbius) are widely recognized for their contributions to the development of "scientific ecology" in Europe (McIntosh 1985, Acot 1998, van der Valk 2011). The influence of the third, Schenck, has been more limited, and he is little known today (Les 2003). Nevertheless, he was an important contributor to the study of wetland plants and their adaptations to aquatic life. In the writings of these men are found many of the important ideas about wetlands and wetland plants that shaped the development of wetland ecology.

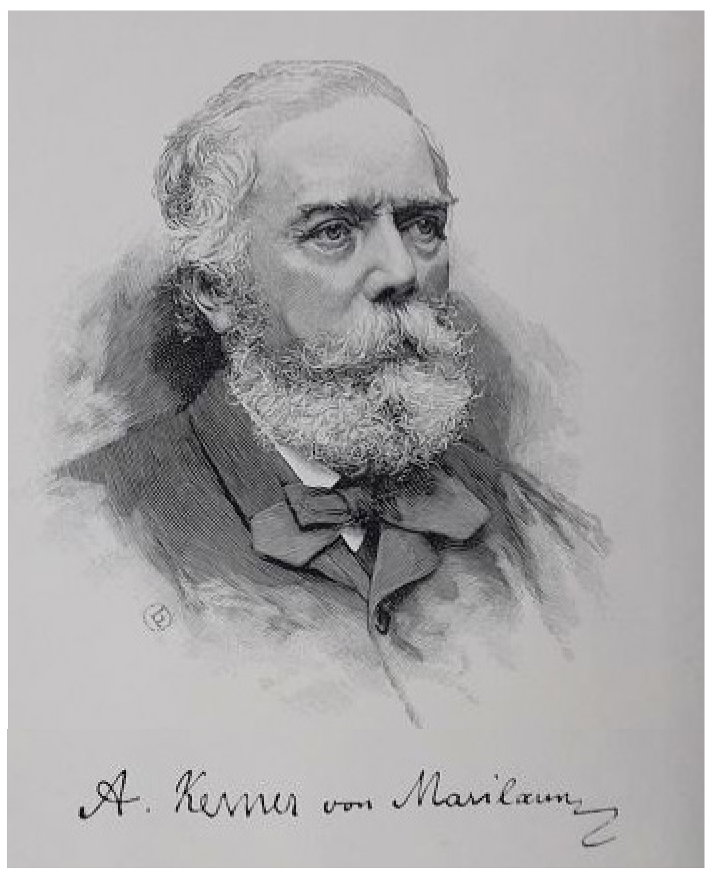
ANTON KERNER VON MARILAÜN (1831-1898)

Anton Kerner (Figure 1) grew up in what is now Austria. As a boy, he developed a life-long interest in plants. Although he studied medicine at the University of Vienna (1848-1854) and became a medical doctor, he quickly gave up medicine after a cholera epidemic in 1855. For the rest of his life, he worked as a botanist and eventually became a professor of botany and director of the botanical garden at the University of Innsbruck (1860-1878) and then the University of Vienna (1878-1898).

In 1863, Kerner published his most influential book, *Das Pflanzenleben der Donaulaender* or *The Plant Life of the Danube Basin*. It was translated into English by Henry S. Conard (1951) as *The Background of Plant Ecology*. In the Foreword to his translation, Conard described Kerner's book as the "immediate and direct parent of all later works on Plant Ecology." This book made Kerner famous in Europe, and it is still considered to be a landmark work on the classification of vegetation (Conard 1951, McIntosh 1985).

"The horizontal and vertical assorting of large plant communities is by no means accidental in spite of its apparent lack of order. It follows certain immutable laws. Every plant has its place, its time, its functions, and its meaning. In every zone, plant life has been developing through an inconceivably long time according to the same pattern to build up its green structure over naked earth. In every zone the plants are gathered into definite groups, which appear either developing or as finished communities, but never transgress the orderly structure and correct composition of their kind." (Translation from Conard 1951). According to Kerner, it is the role of plant geographers to define and characterize these recurring plant communities and their development. Kerner notes that it was the descriptions of exotic vegetation types in "word and picture" from around the world that poured into Europe in the early and mid-

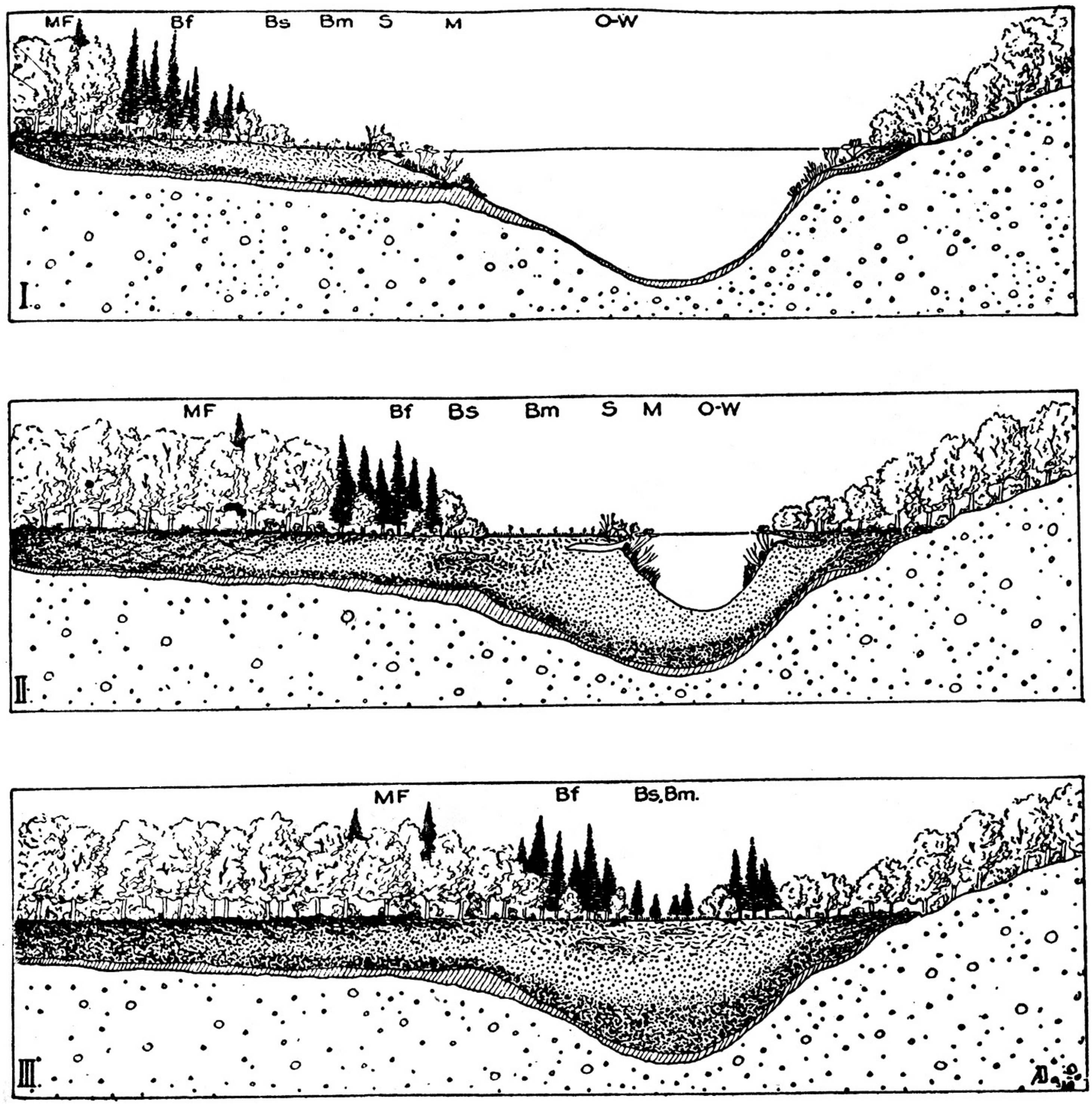
FIGURE 1. Anton Kerner von Marilaün. (From F. W. Oliver 1904)



ninetieth century that stimulated an interest, including his own, in the natural vegetation of Europe.

It is Chapter 9, How a Swamp becomes a Meadow, in *The Plant Life of the Danube Basin* that particularly influenced the development of wetland ecology. In it, Kerner describes what came to be known as hydrarch succession. "In the shore of every pond which is not disturbed by the hand of man one notices a growth of "rushes," and in the water, wherever it is not too deep, countless floating and submerged water plants, which beneath the clear water

FIGURE 2. "Diagram illustrating the gradual filling up of lakes by the encroachment of vegetation, and also the stages in the origin of peat and marl deposits in lakes. The several plant associations of the Bog series, displacing one another, belong to the following major groups: (I) O. W., open water succession; (2) M., marginal succession; (3) S., shore succession; (4) B., bog succession, comprising the bog-meadow (Bm), bog-shrub (Bs) and bog-forest (Bf); and (5) M. F., mesophytic forest succession." (From Gager 1916)



at the edge of the pond, give rise to moor soil, or a peaty mass. The runners of the reeds on the shore sink their roots into this mass, the roots become enmeshed together, hold the peaty residues between their strands, and build a shelf of peat which is not always firmly attached to the bottom of the pond. Portions of this may break loose and become floating islands. Thus the cane-break reaches ever further from the shore toward the middle of the pond, the open water surface is more and more narrowly confined and finally changed to a reed formation. But in nature there is no ending and no standing still, but only an ever coming and ever going." (Translation from Conard 1951). Kerner closes Chapter 9 with the following sentence, "Having now learned how unaided nature reclaims the swamp lands in the Hungarian lowlands, it will be profitable to take a look at the results of reclamation by the hand of man." Chapter 10 is titled "Draining the Swamps."

In Chapter 10, Kerner examines the environmental implications of a very large (300 square miles, "as large as the Kingdom of Würtemberg") wetland drainage project in Hungary to create more farmland. The question that Kerner asks himself is, how this will affect the climate of the region and its vegetation? He predicts "increases in the extreme differences in temperatures" between summer and winter. Summer rainfall he also predicts will decrease because of reduced evapotranspiration in the region. Eventually, these climatic changes will cause changes in the upland vegetation.

Kerner's book made wetlands an exciting and productive object of study for ecologists. He emphasized the potential importance of wetlands for understanding succession, their significance for regulating regional climates, and the potential negative impacts of their drainage for an entire region. Kerner was one of the first to appreciate the services provided by wetlands. His description of a pond going from open water to meadow due to the annual deposition of dead plant material became the textbook example of succession (Figure 2). Versions of Figure 2, which is from a 1916 introductory botany text (Gager 1916), that are based on Kerner's description of hydrarch succession, are still readily available today on the internet as classic examples of succession. Kerner's emphasis on the orderly and predictable development of vegetation during hydrarch succession would greatly influence the thinking of both later European and America ecologists interested in succession, e.g., Frederic E. Clements. It would not be for another hundred years that more detailed studies of actual hydrarch successions would provide a more nuanced and very different paradigm of hydrarch succession. More on this in a later installment.

KARL AUGUST MÖBIUS (1825-1908)

Karl Möbius (Figure 3) was born in Saxony, a province of Prussia, now part pf Germany. Because his parents could not afford to send him to university, he was trained to become a primary school teacher, and he taught in an elementary school for five years. He developed an interest in natural history after reading Alexander von Humboldt's books. In 1849, he began studying natural history at the University of Berlin. In 1853, he obtained a job in Hamburg as a high school teacher and completed his doctorate. His natural science studies eventually resulted in a position at the Hamburg Museum of Natural History. Möbius also was one of the founders of the Hamburg Zoo and the first public aquarium in Germany. His main research interests were in marine invertebrates like corals, and he is credited with discovering symbioses in marine invertebrates. While in Hamburg, Möbius began working on the invertebrates of the Baltic Sea near the coastal city of Kiel. In 1868, he was appointed to a professorship at the University of Kiel and the directorship of the Kiel Zoological Museum. While at Kiel, he began to study oysters and oyster cultivation. In 1877, he published an influential monograph, *Die Auster und die Austernwirtschaft* (The Oyster and Oyster Farming). In it, he described in detail the interactions among different organisms in a community, an oyster bank. In 1887, Möbius was appointed the director of the Zoological Museum in Berlin. For more information about Möbius and his later career, see Nyhart (1998, 2009) and Glaubrecht (2008).

It is Möbius' studies of oyster banks that establish the idea in ecology that assemblages of organisms in an area, because they interact with each other, form a stable com-

FIGURE 3. Karl August Möbius. (From Museum für Naturkunde, Berlin, Germany)

munity. In other words, not just abiotic factors (salinity, temperature, light, etc.), but also biotic factors (competition, predation, parasitism, etc.) control the composition and relative abundance of species in an area. He coined the term *biocönose* to describe such living communities. His monograph on oysters was translated into English by H. J. Rice for the U.S. Commission of Fish and Fisheries (Rice 1883) which brought Möbius' ideas about communities to the attention of English-speaking ecologists.

According to Möbius , an oyster bank "is thus, to a certain degree, a community of living beings, a collection of species and a massing of individuals, which find here everything necessary for their growth and continuance, such as suitable soil, sufficient food, the requisite percentage of salt, and a temperature favorable to their development. Each species that lives here is represented by the greatest number of individuals which can grow to maturity subject to the conditions which surround them, for among all species the number of individuals which arrive at maturity at each breeding period is much smaller than the number of germs produced at that time. … Science possesses, as yet, no word for a community where the sum of species and individuals, being mutually limited and selected under the average external conditions of life, have, by means of transmission, continued in possession of a certain definite territory. I propose the word *Biocoenosis* for such a community. Any change in any of the relative factors of a biocönose produces changes in other factors of the same. If, at any time, one of the external conditions of life should deviate for a long time from its ordinary mean, the entire biocönose, or community, would be transformed. It would also be transformed, if the number of individuals of a particular species increased or diminished through the instrumentality of man, or if one species entirely disappeared from, or a new species entered into, the community." (Rice's translation as quoted in Nyhart 1998).

FIGURE 4. Heinrich Schenck. (From Les 2003)

Möbius' definition of community stressed four things: (1) physical conditions largely determine which species can live in an area; (2) the interactions among different species regulated their abundances; (3) there is a large difference between the number of propagules (colonizers) and the number of mature individuals in a community; and (4) the community exists in a balanced state (equilibrium) that would only change if a factor controlling its composition and/or interactions among its component species changed, including human interference like harvesting. His ideas about the nature of communities still resonate with ecologists today.

HEINRICH SCHENCK (1860–1927)

Heinrich Schenks (Figure 4) was born in Siegen, Germany, received a doctorate from the University of Bonn (1884), became a lecturer at Bonn in 1889, and, starting in 1896, taught at the Polytechnic Institute of Darmstadt, where he was also the director of the botanical garden. Unlike Kerner and Möbius. Heinrich Schenck is not a major figure in the development of ecology. But Schenck is a major contributor to the development of wetland ecology.

Plant ecology arose primarily in Germany in the 1880s (Cittadino 1990). This happened because of three important developments: (1) Darwin's publication in 1859 of *The Origin of Species* with its emphasis on adaptations and natural selection, (2) an increased interest in plant geography (spatial distribution of plants) that resulted from European explorations in Asia, South America, and Africa, and (3) the rapidly developing field of plant physiology in Germany due to major advances in chemistry and optics. This resulted in an interest among German antecedent ecologists in trying to explain how plant anatomical and morphological adaptations enabled plant species to live in different climatic regions, e.g., deserts and the wet tropics. This fusion of plant geography and plant physiology to form plant ecology resulted in the development of a central ecological tenet: the distribution of organisms is largely determined by their physiological tolerances.

One of the major figures in the development of plant ecology was Simon Swendener (1829-1919), especially after he arrived at the University of Berlin in 1878 (Cittadino 1990). Swendener encouraged his students to study plants in their natural environments in order to understand how the anatomy and morphology of their organs (leaves, stems, roots, etc.) make it possible for them to live in regions with different climates. Although Swendener himself was not a believer in natural selection, his students were heavily influenced by Darwin. In effect, Swendener's students took German botanical laboratory science and applied it to the study of plant distribution.

Heinrich Schenck was one of these students who was greatly influenced by Swendener. Schenck studied primarily at the University of Bonn, starting in 1880 and receiving his doctorate in 1884, but he spent 1881-1882 at the University of Berlin where he came into contact with Swendener. After completing his doctorate, Schenck began to study the adaptations of aquatic plants. How did the anatomical and morphological features of aquatic plants allow them to survive under water?

In 1886, Schenck published a major monograph, *Die Biologie von Wassergewaechse* (*The Biology of Aquatic Plants;* Les 2003). Agnes Arber (1920) called Schenck's book "... one of the most important general contributions ever made to the study of water plants...." In it, Schenk noted that "… they [aquatic plants] inhabit such a strange medium, in which the physiological process is partially carried out differently than in air, in which the demands to the mechanical construction of the plant are also different, and in which special adaptations must arise in floral organization, in the means of fertilization, in the formation of fruits and seeds, in their dispersal, and in their germination." Schenk's work on aquatic plants highlighted their amazing anatomical and morphological adaptations, and thus focused attention on wetlands as an important habitat that could be profitably studied by scientists who were becoming interested in ecology. As Les (2003) notes, Schenck's classic work is today almost completely unknown, but this should not be the case. Like Kerner and Möbius, he greatly raised the visibility of wetlands and wetland plants in the scientific community in the nineteenth century and beyond. ■

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