

October 2014

Herbert W. Conn: Formative decades of microbiology and evolutionary biology

Frederick M. Cohan

Wesleyan University, fcohan@wesleyan.edu

Alexa Boesel

Wesleyan University, aboesel@wesleyan.edu

Follow this and additional works at: <http://wescholar.wesleyan.edu/div3facpubs>



Part of the [Evolution Commons](#), and the [Microbiology Commons](#)

Recommended Citation

Cohan, Frederick M. and Boesel, Alexa, "Herbert W. Conn: Formative decades of microbiology and evolutionary biology" (2014).
Division III Faculty Publications. Paper 387.
<http://wescholar.wesleyan.edu/div3facpubs/387>

This Popular Press is brought to you for free and open access by the Natural Sciences and Mathematics at WesScholar. It has been accepted for inclusion in Division III Faculty Publications by an authorized administrator of WesScholar. For more information, please contact dschnaidt@wesleyan.edu, ljohnson@wesleyan.edu.

Herbert W. Conn: Formative Decades of Microbiology and Evolutionary Biology

Conn's early contributions continue to inspire microbiologists, particularly those facing the renewed challenge of defining bacterial species

Frederick M. Cohan and Alexa Boesel

The Wesleyan Biology Department conference room showcases several portraits of distinguished biologists from its history, including one depicting Herbert W. Conn (1859–1917) as a dashing young man sporting a double-breasted suit, pince-nez, and a perfect Van Dyke beard. Conn made outstanding contributions to both microbiology and evolutionary biology, showing how bacteria share fundamental properties with more familiar animals and plants, and thus making microbes more comprehensible to lay people and scientists alike. His breadth of knowledge comes through in the many books and articles he published, reflecting his intellectual command of several biological disciplines.

Conn founded the Wesleyan University Biology Department in 1884 and served as its chairman until he died in 1917. From 1905, he also directed the Connecticut State Board of Health Laboratory, building and organizing both institutions from the ground up during this formative time for both microbiology and evolutionary biology. By the beginning of his career, microbiol-

ogists recognized the bacterial causes of several major diseases, were beginning to realize that the principle of natural selection extends to the microbial world, and also began to appreciate the immense biodiversity of that microbial world.

Conn Made Microbiology Accessible to the Public

Conn endeavored to make the unseen world of microbes familiar, real, and consequential to the public. In his 1903 book *Bacteria, Yeasts, and Molds in the Home*, he described food preservation as a battle against all organisms that would consume our food before we could. “Preserving [our] food . . . simply means protecting it from consumption by other living organisms, . . . some of the larger animals with which everyone is familiar . . . rats and mice and the various insects . . . [and] a host of small animals and plants that go by the name microbes or microorganisms.” He also noted that the bacteria of concern in food preservation are much like animals, requiring complex foods such as sugars, starches, and proteins.

Conn taught lay audiences that microbes are organisms with many of the properties that we find in more familiar animals and plants. For instance, he described how bacteria create waste products from their consumption of food. He likened microbial conversion of food into waste to wood embers that follow when wood burns during a fire—in both cases, the end products differ chemically from the original material. As a practical matter, the decay of foods into materials with vile tastes and odors is the result of waste products produced by bacteria and molds.

In another article aimed at the general public, Conn explained how waste products bring about an ecological succession, drawing on similarities to processes occurring in plant communities of

SUMMARY

- ▶ Herbert W. Conn (1859–1917) made outstanding contributions to both microbiology and evolutionary biology, reflecting his intellectual command of several biological disciplines.
- ▶ Conn endeavored to make the unseen world of microbes familiar, real, and consequential to members of the general public.
- ▶ He presciently considered the role of bacteria in our own bodies, describing them as being both harmful and beneficial to our health.
- ▶ He also contributed to our understanding of the concept of species, how they originate, and what those ideas might mean in terms of bacterial speciation.
- ▶ In Conn's spirit, microbial ecologists studying speciation eschew the “species” taxa of bacterial systematics, considering it to be too broadly defined to allow investigation of the origins of diversity.

open fields in the American Northeast. A set of grass species in an open field, first populated by a diversity of plants, “crowd[s] out . . . the large number of . . . species which sprang up at the outset,” he wrote. Building upon this notion, he compares a similar struggle occurring among bacteria when milk turns sour or when it forms cheeses and yogurt. Conn explains how one initially abundant group of bacteria begin to putrefy milk, but do not persist when they are crowded out by another group, then called the “lactic bacteria.”

During this ecological succession, the lactic bacteria sour the milk by secreting lactic acid, creating a hostile environment for putrefying bacteria, Conn explained. The lactic bacteria “are like the vigorous growing grass which covers the fields and prevents the profuse growth of the numerous weeds that would spring up were the grass not in possession of the soil.” He made the struggle for existence among bacteria important to anyone eating cultured products such as cheese and yogurt, but also made this example fit with the more familiar concepts of plant ecology.

Conn Used Microbiological Examples To Explain Ecology and Evolution

Conversely, Conn used microbiology to explain processes in ecology. For example, he described how the fungal decay of wood returns organic resources from fallen trees to the ecosystem and fosters the livelihood of many insect species. In his 1892 article, “Some Uses of Bacteria,” Conn substantiated the profound and essential role of bacteria in nature, focusing on how they help to cycle elements in ecosystems.

He presciently also considered the role of bacteria in our own bodies, describing them as being both harmful and beneficial to our health. “We look upon bacteria in our bodies as causes of disease rather than things which are of any value, and yet a healthy person always has bacteria in large quantities in his mouth, in his stomach, and in his intestines,” he wrote. “They may be possibly beneficial to us either in the line of scavengers in removing material, which ought not to remain in our bodies . . . or in assisting digestion. This point, however, is not yet demonstrated, and I merely allude to it as a possibility.” More than a century later, we more fully appreciate the manifold benefits of what we now call our gut microbiome for digesting foods and providing nutri-

ents as Conn suggested, but also contributing to our development, immunity, behavior, and resistance to disease.

Conn contributed seminal ideas to the theory of evolution, again through illustrating processes in the context of familiar organisms. In the early days of evolutionary biology, Conn objected to deeming natural selection responsible for every detail of divergence among species. In his rebuttal to what we now call “panselctionism,” he remarked that “the conditions of life are too complicated to make . . . a rigid selection possible. . . .” Conn credited the “many naturalists [who] think there are specific characters of demonstrably no use,” and provided his own model for how useless characters could evolve. Here he made a very early case for random evolution by genetic drift. “A whale swimming into a school of small mollusks opens his huge mouth and takes in hundreds of individuals indiscriminately, no question of fitness affecting the survival of the remainder, but only the accident of happening to be out of the reach of the huge mouth. . . . The fittest do not always survive, for many of them are destroyed.”

Like Darwin, Conn remarked on the prodigious reproductive capacity of organisms. “Certain bacteria multiply so rapidly that the descendants of a single individual, if allowed to multiply unhindered for three days, would be represented by . . . 47,000,000,000,000.” More generally, he added, “No animal or plant has been found that does not have powers of multiplication which surpass the possibilities of sustenance.” While Darwin argued that this prodigious reproduction is what makes natural selection possible, Conn conversely asserted that natural selection is what makes reproductive extravagance possible and even expected. “It may seem a little strange that nature should be thus prodigal, for we do not commonly expect to find such wastefulness,” he noted. “In general . . . nature seems to be quite parsimonious. . . . There must be some reason for this prodigality here amid a general parsimony. It is this prodigality alone that makes natural selection a possibility.”

Conn speculated on which form of natural selection might be most significant for humans in the modern era. “[Our] most serious contest is with parasitic foes,” he wrote. “Microscopic organisms, producing as they do various infectious diseases, are man’s most serious enemies, and the most efficient agencies in preventing many indi-

viduals from producing offspring. . . .” This assessment was assuredly correct for humans living in cities before water-borne microbes became appreciated as a threat to public health, before prevention of contagion was seen as a personal responsibility, and before the development of antibiotics. While the mid-20th century provided a respite from deadliness from some infectious diseases for some populations, humans are very much at risk from emergent and re-emergent infectious diseases, including from drug-resistant pathogens, amid multifarious global changes. His assessment of the important role of infectious disease in evolution once again rings true.

So far as we know, Conn never wrote about the evolution of microbes, although he came close. In *Bacteria, Yeasts, and Molds in the Home*, he noted that some epidemics of a given disease were more severe than others. It would have been a small step to speculate on how changes in virulence could involve natural selection, but Conn did not take that step, at least in his writing. Indeed, evolutionary microbiology did not take off as a field until the 1980s, nor evolutionary medicine until the 1990s.

Conn Sought To Refine the Species Concept

Conn made a seminal contribution to our understanding of the concept of species and how species originate, and these efforts contributed to contemporary explorations of bacterial speciation. Darwin saw species of animals and plants as not profoundly different from varieties within species, and viewed the origin of species as simply the result of selection favoring divergent forms in different populations.

Conn, however, in his 1888 article, “The Significance of Varieties and Species,” viewed species as unique and qualitatively different from varieties within a species. He advanced the hypothesis that species’ origins depended on evolution of reproductive incompatibility. “Where the reproductive system is constant, there may arise a highly variable species; but where the reproductive system is highly variable, there will be a tendency to the production of numerous closely allied species,” he wrote. “All of this will lead to a new understanding of the significance of species as groups of animals in which variations have largely affected the sexual organs.”

Conn, along with the French biologist Georges-Louis Leclerc, Comte de Buffon (1707–1788), helped to stir a discussion that led to the

Biological Species Concept, focusing on sexual isolation as instrumental to how a new species originates. That concept, later championed by Ernst Mayr, led many 20th-century biologists to embrace the idea that species transcend human cognition. Systematists and evolutionary biologists eventually extended the idea of speciation to encompass all kinds of organisms, including bacteria and other microorganisms that do not reproduce sexually.

Species are now widely seen to have the following properties: cohesion, in the sense that divergence within a species is constrained by some evolutionary force; irreversible separateness, such that once two groups are considered distinct species, they then can diverge indefinitely; and ecological distinctness, in that two groups can coexist indefinitely because they can partition their resources.

Conn Set Stage for Reconsidering the Microbial Species Concept

Following Conn’s approach, our group and others have sought to identify which of these properties, originally attributed to animals and plants, might also apply to bacteria. More generally, we are studying what processes underlie the origins of ecological diversity in bacteria. Toward this end, microbial ecologists studying speciation eschew the “species” taxa of bacterial systematics, considering it to be too broadly defined to allow investigation of the origins of diversity.

It is useful instead to define a species, or an “ecotype,” as a phylogenetic group of close relatives that share genetic adaptations to a particular set of habitats, resources, and conditions. More specifically, different microbial species are predicted to coexist indefinitely as a result of their ecological differences, while lineages within one species are ecologically too homogeneous to allow indefinite coexistence.

How, then, does one bacterial species become two? A theory of bacterial speciation can draw on the findings of zoologists and botanists, as Conn would probably suggest today, but we need to take into account the ways in which recombination and population size differ when going from bacteria to multicellular animals and plants. Most importantly, recombination occurs at extremely low rates in bacteria, never much more frequently than mutation; bacterial recombination can occur between vastly divergent microorganisms; bacteria can acquire novel genes and biochemical

pathways through horizontal genetic transfer; and because of the astronomical sizes of bacterial populations, mutations and recombination events that are rare on a per-capita level can become accessible to a population.

How do these properties affect speciation of bacteria? One consequence of the rarity of recombination is that speciation does not require either geographic isolation or reduced recombination. Indeed, several lines of evidence show bacterial populations poised to diverge into distinct species, even within a single region, according to findings from our group as well as from Martin Polz at the Massachusetts Institute of Technology in Cambridge, Mass., and his collaborators.

Horizontal genetic transfer appears to foster speciation. Thus, there are many examples of closely related, ecologically distinct bacteria species having acquired niche-specifying genes that proved responsible for their ecological divergence. However, important questions about horizontal transfers remain to be addressed, including identifying which ecologically important traits transfer easily, such as antibiotic resistance and virulence traits, or less readily, such as traits encoding the osmosis-resisting cell wall of Firmicutes, and also determining the extent to which speciation depends on horizontal transfers versus changes in existing genes.

One outstanding issue with profound consequences for the properties of bacterial species is the rate of their extinction. We have hypothesized that some bacterial species have cohesion, meaning that they remain capable of exchanging genes, but cohesion is contingent on extinction rates. In a process known as “periodic selection,” each adaptive improvement creates a genome-wide sweep of diversity and thus brings about cohesion within an ecologically homogeneous bacterial species. However, we have shown that this cohesion depends on whether periodic selection can occur before a given species goes extinct.

Also fundamentally important is the rate of speciation. One view is that, owing to the high rates of horizontal transfer and consequent high rates of speciation, most species may contain no more than a mother and a daughter, according to Ford Doolittle of Dalhousie University in Halifax, Nova Scotia, Canada.

In some cases, the closest bacterial relatives are already ecologically distinct and members of different species, according to our studies of *Bacillus* species from Death Valley soils. These findings appear to support Doolittle’s view. However, *Synechococcus* bacteria growing in hot springs suggest that speciation occurs at a much slower rate in this taxon, with large, ecologically homogeneous groups being easily identified, according to our other studies done in collaboration with David Ward of Montana State University, Bozeman, and his group. Discovering the phylogenetic breadth of individual bacterial species is a critical but unresolved issue for microbial ecology, evolution, and systematics.

Frederick M. Cohan is Professor of Biology and Environmental Studies and Alexa Boesel is an undergraduate in the Department of Biology, Wesleyan University, Middletown, Conn.

Suggested Reading

- Becraft, E., F. M. Cohan, M. Kühl, S. Jensen, and D. M. Ward.** 2011. Fine-scale distribution patterns of *Synechococcus* ecological diversity in the microbial mat of Mushroom Spring, Yellowstone National Park. *Appl. Environ. Microbiol.* **77**:7689–7697.
- Cohan, F. M.** 2011. Are species cohesive?—a view from bacteriology, p. 43–65. *In* S. Walk and P. Feng (ed.), *Bacterial population genetics: a tribute to Thomas S. Whittam*. ASM Press, Washington, D.C.
- Cohan, F. M.** 2013. Species, p. 506–511. *In* S. Maloy and K. Hughes (ed.), *Brenner’s encyclopedia of genetics*, 2nd ed. Elsevier, Amsterdam.
- Conn, H. W.** 1888. The significance of ‘varieties’ and ‘species.’ *Science* **11**:253–254.
- Conn, H. W.** 1896. *The story of germ life*. D. Appleton and Company, New York.
- Conn, H. W.** 1900. *The Method of evolution*. Silver, Burdette and Co., New York.
- Conn, H. W.** 1902. Struggle for existence among bacteria. *The Independent* **54**:887.
- Doolittle, W. F., and O. Zhaxybayeva.** 2009. On the origin of prokaryotic species. *Genome Res.* **19**:744–756.
- Hunt, D. E., L. A. David, D. Gevers, S. P. Preheim, E. J. Alm, and M. F. Polz.** 2008. Resource partitioning and sympatric differentiation among closely related bacterioplankton. *Science* **320**:1081–1085.
- Wiedenbeck, J., and F. M. Cohan.** 2011. Origins of bacterial diversity through horizontal gene transfer and adaptation to new ecological niches. *FEMS Microbiol. Rev.* **35**:957–976.