Int Microbiol (2002) 5: 145–150
DOI 10.1007/s10123-002-0079-7

PERSPECTIVES

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Paul Buchner (1886–1978) and hereditary symbiosis in insects

Accepted: 17 June 2002 / Published online: 23 July 2002
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Paul Buchner Fig. 1; Nuremberg, 1886 – Ischia, 1978) is sometimes referred to as "the founder of systematic symbiosis research." His research on hereditary symbiosis in insects aimed to usher in a new era in bacteriology and the theory of infection, and it has also had a great impact on theorizing about the importance of symbiosis in evolution [12, 13, 26]. Some 26 doctoral students studied symbiosis in insects in collaboration with Buchner, 7 of which continued their careers as symbiosis researchers with students of their own [11]. Buchner is especially known for his great compiled work, *Endosymbiose der Tiere mit pflanzlichen Mikroorganismen*, the fourth edition of which was published in English as *Endosymbiosis of Animals with Plant Microorganisms* [4].

Buchner was born in Nuremberg, Germany. His father, Wilhelm, was a physician and obstetrician, with a deep interest in botany and a large herbarium. He introduced his son to science at an early age, especially to the flora of his own region and the Alps. In 1907, Paul Buchner enrolled at the University of Würzburg with the intention of becoming a botanist. But that was a time when cytology and experimental embryology were at the cutting edge of biology. He became enthralled by the lectures of Theodor Boveri, Professor of Zoology and Comparative Anatomy, and one of the world's leading experimental embryologists. Buchner switched his major field to Zoology. In his third semester, he attended the lectures of Richard Hertwig, one of the world's leading cytologists and great protozoologists, in Munich. At that time, Richard Goldschmidt was also a lecturer (*Privatdozent*) at the University of Munich, and Hertwig's assistant. Buchner chose Goldschmidt, about 8 years his senior, as his major Professor for his doctoral dissertation. Goldschmidt is well-remembered today for his genetic studies of sex in moths and especially for his reluctance to the theory of small gene changes as the basis for the origin of species and his advocacy of saltationist change: "hopeful monsters" perhaps resulting from chromosomal rearrangements. Buchner's dissertation was on *Das Akzessorische Chromosom in Spermatogenese und Ovogenese der Orthopteren, zugleich ein Beitrag zur Reduktion* (The accessory chromosome in spermatogenesis and ovogenesis in the Orthoptera, along with a consideration of reduction). He earned his doctorate in 1909 (*Magna cum Laude*). However, his preoccupation with chromosomes was short-lived, as he found himself wandering far off the main paths of twentieth century life sciences.

Immediately after his examination, he began a year-long stay at the Stazione Zoologica in Naples, then famous especially among German experimental biologists, writers and intellectuals of the late nineteenth century. He became familiar with the study of marine animals, the model organisms of embryologists. His switch to microbial symbiosis sprang from lectures he heard at the University of Naples by Umberto Pierantoni (1876–1959) on microbial symbionts of sap-sucking insects such as cicadas and aphids.

At that time, microbial symbiosis was barely a field of activity, and almost exclusively European. The famed German botanist Anton de Bary had coined the term symbiosis in a speech given to Naturalists in 1879 to highlight the studies led by Simon Schwendener, himself, Albert Bernhard Frank and others, who showed that lichens were double organisms, and that microbes living in hosts resulted in rather dramatic morphological changes of considerable importance for evolution [6, 22]. Frank subsequently reported his studies indicating that fungi beneficial to their hosts were attached to the roots of many plants including forest trees, for which he coined the term "mycorrhiza" in 1885 ([9], p. 195). He had also introduced the term "symbiotismus", a year before de Bary's usage of symbiosis [8]. There were also notable studies of nitrogen-fixing bacteria in the root

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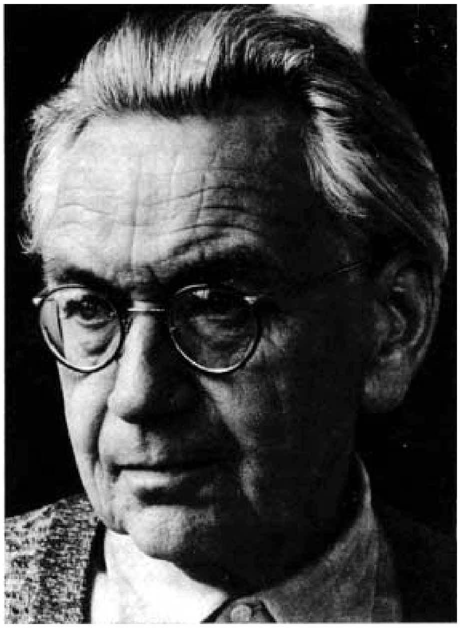

Fig. 1. Paul Buchner (1886–1978)

nodules of legumes, and reports in the 1880s of algae living inside cells of hydra and sea anemones. But there was precious little work on symbiosis in organisms "higher up on the scale of beings" and much of the evidence that fungi and bacteria, organisms most commonly associated with disease, were beneficial to their hosts was either denied or ignored [22].

The door to symbiosis in insects was pulled wide open when Umberto Pierantoni (1876–1959) in Naples (later in Turin) and Karel Šulc in Moravia, Brünn, independently published works which interpreted the "pseudovitellus" of the Homoptera (as T.H. Huxely had called it in 1858 because it simulated the vitellus of an impregnated ovum) to be a primitive gland organ in the gut tube populated with intracellular symbiotic microbes (they called them "yeast fungi"). In 1909, Pierantoni spoke before the Società dei Naturalisti in Naples on the symbiotic organs he discovered in the scale insect *Icerya*, and the following year, on those of the aphids and of *Pseudococcus* [16, 17, 18]. In 1909, Šulc reported on the symbiosis of cicada in front of the Naturwissenschaftliche Gesellschaft of Mährish-Ostrau [25], and the following year he introduced the term "mycetome" (letter from E.A. Steinhaus to Paul Buchner, 30 January 1947; supplied by Giorgio Buchner) which was generally used throughout the twentieth century for the symbiotic organ of many (10%) insect species including cockroaches, leaf hoppers and aphids.

These early discoveries of Pierantoni and Šulc captured Buchner's imagination. As he later recalled, "With the publication of these studies it seemed as though a blindfold had been removed from the eyes. Numerous examples of symbiosis in the Homoptera were described in rapid succession, and numerous other important insect families or smaller systematic entities were recognized as symbiont barriers" ([4], p. 29). Pierantoni also extended his studies of symbiosis with his discovery of luminescent bacteria in the cells of the light organs of certain beetles and cephalopods [18]. In some cases, the symbionts were transmitted from generation to generation. He called this "hereditary symbiosis", and asserted that what others had mistaken as endogenous organelles were actually bacteria adapted to intracellular life. All this, he argued, "would assign to the cytoplasmic inclusions and perhaps to many constituents of the protoplasm an autonomous life and a specific activity, to the benefit of the organism in which they live" ([5], p. 279). But Buchner distanced himself from such speculations, which, as he saw it, pushed "the symbiosis principle into infinity and thus is too speculative to use as a scientific tool." ([4], p. 73).

Following his sojourn in Naples, in 1910 Buchner returned to the University of Munich as an assistant to Hertwig, under whose direction he and his friend Karl von Frisch "habilitated" in 1912. Frisch succeeded Hertwig as Professor at the University of Munich, a position Buchner had hoped for. However, that same year Goldschmidt was appointed director of one of the institutes of the newly founded Kaiser Wilhelm Institutes in Berlin; Buchner took over Goldschmidt's vacated position as custodian and curator at the Zoological Institute in Munich for the next decade. During these years, he investigated intracellular symbionts in sap-sucking insects. He demonstrated that insects such as aphids, scale insects and cicadas, which suck plant juices, have symbiotic microorganisms contained in the symbiotic gland cells, the mycetocytes of mycetomes. He also showed how symbionts were inherited through the egg cytoplasm in aphids, coccoids, aleurids and psyllids. He showed the process of embryo infection, and that numerous species of aphids had a second symbiont. He also called attention to the symbiosis of the cicadas with two to three different kinds of microbes in the mycetomes. These studies provided a broad platform for his studies of hereditary symbiosis in other insects including ants and cockroaches. He suspected that the microbes produced enzymes for digesting food for the insect. In 1920, he turned to the study of blood-sucking insects: lice, bed-bugs, ticks, mites, tsetse flies, mosquitoes and fleas all contained symbiotic bacteria; their relatives that suck invertebrate blood had none. He assumed therefore that the symbionts helped break down the red blood corpuscle in vertebrates.

He subsequently investigated symbiosis in the large singing cicadas and described in detail the inheritance of the two kinds of symbionts always present in them. By 1925 he had listed 34 varieties of cicadas, including a succession of polysymbiotic forms, and all three microbes were harbored in the egg cells. He was even able to examine the sequence of the acquisition of polysymbiotic species, opening up what he called a veritable "fairyland of insect symbiosis." In 1921, he published his first book, *Tier und Pflanze in intracellularer Symbiose* [1]. When the second edition appeared at the end of

the decade, the book had grown to about twice the size of the original [2].

Buchner held several academic positions throughout his career. In 1923, he moved from Munich to Greifswald as Professor of Zoology. There, he remodelled the old Zoological Institute and Museum and reorganized the exhibits and, the following year, he founded *Zeitschrift für Morphologie und Okologie der Tiere*. In 1929, he moved to Breslau where he remained until 1936, when he moved again to Leipzig. By that time he had also established roots in the bay of Naples. With his first visit, Buchner had fallen under the magic of the blue gulf itself and its islands, one of which, Ischia, he adopted as his home with his Italian wife and their son Giorgio (born 1914). In 1927, he bought land in Ischia, laying the foundations for his home a year later; the house was completed in 1930. He received a small grant from the Deutsche Forschungs Gemeinschaft for microscopes and microfilm and other apparatus for a laboratory in the house, after which all work he published on symbiosis was carried out there.

Post-war renaissance

During the war, Buchner worked in Leipzig, while his wife, son and daughter-in-law lived in Ischia. He frequently travelled to Ischia on research trips, and, in the summer of 1943 – when the allied forces were already in Sicily – he did not return to Leipzig, which was in the Russian zone after the war. He did not return to Germany until 1956. In 1947, he was invited to become Director of the Zoological Institute in Munich, but the situation was so bad travelling back and forth between Munich and Ischia that he did not go. During the war, he had founded the *Museo dell' Isola d'Ischia*, in which he and Giorgio, an archaeologist, classified and exhibited geological, prehistoric, and archaeological findings from the island. The war years and the post-war years were difficult for the Buchners. When Italy was occupied by allied Armed Forces, they had no income and no food, and they feared that their house would be confiscated.

On 13 May 1946, Buchner wrote to his friend and mentor Goldschmidt about his impoverished conditions. As a Jew, Goldschmidt had been forced to leave Germany in 1933, when he took refuge in the United States at the University of California, Berkeley. He received Buchner's letter in mid-July, and subsequently put a notice in *Science* (September 27) describing the Buchners' difficult, almost starvation, conditions [10]:

"Paul Buchner, formerly of the University of Leipzig and authority on cellular symbiosis, has been living with his family on the Island of Ischia since before the invasion of Italy. Prof. Buchner's wife and son are Italian citizens. Since the departure of the English Army from the Island the entire family has been without work and income and is now existing near starvation level. Although Prof. Buchner could not do any zoological work during the war years, he continued his prehistoric and archaeological survey of the island, and with the help of the English has founded a small museum built around his material. He is now in danger of being evicted from his house as an alien. Since he cannot return to Germany and cannot work in Italy, his plight is extreme. His address is Porto d'Ischia San Alessandro, Italy."

Goldschmidt's note had vital impact. Because of it, Buchner renewed old contacts and made new ones with American biologists, several of whom sent food and clothing. Goldschmidt himself sent a sack of 100 pounds of flour. Ernst Mayr, who had been a student of Buchner's at Greifswald, sent him a care packet and a copy of his book *Systematics and the Origin of Species*, and notified Buchner that they were going to launch the first volume of a new journal, *Evolution* (interview, Cambridge, Mass., 21 November 1996). Mayr informed him that the distance between geneticists on the one hand, and paleontologists and taxonomists on the other was not as great as it had been earlier. Certainly there were some who remained outside, such as Goldschmidt, but Mayr had not seen him since 1940 (letter from E. Mayr to Paul Buchner, 12 January 1947).

One of the most important new contacts for Buchner was Edward A. Steinhaus, one of the United States' best known insect pathologists, at the University of California at Berkeley. During the war years, Steinhaus had worked at the Rocky Mountain Laboratory of the United States Public Health Service, concerned principally with certain of the rickettsial diseases, studying the relationships between intracellular microorganisms and ticks. He then moved to Berkeley where he established the Laboratory of Insect Pathology and Microbiology. In 1946, his laboratory was concerned with (1) various diseases of insects and their possible use in biological control; (2) the various biological relationships between insects and microorganisms; (3) attempts to connect the relationship between the mycetomes and symbiotes of the mealybug with their phylogenetic and systematic characteristics.

During the war, Steinhaus had written a major book on *Insect Microbiology*, in which he introduced Buchner's work to American biologists with one chapter on the intracellular "bacterium-like" symbiotes and another on the intracellular "yeast-like" symbiotes [24]. It was the first extensive review in English but it was not comprehensive, and Steinhaus compiled it under great handicaps during the war at a time when publishing difficulties were considerable due to paper shortages. "Nevertheless," Steinhaus wrote to Buchner on 30 January 1947, "with all its faults, I think it is, so far, one of the most complete reviews of your work in the English language and now perhaps some other English or American author will be prompted to give your work the attention and justice it deserves" (letter from E.A. Steinhaus to Paul Buchner, 30 January 1947; supplied by Giorgio Buchner).

Buchner's book pointed to many problems that needed attention. How did symbiosis evolve? How did

symbiont and host affect each other? How wide-spread was the phenomenon of symbiosis in insects? One also needed to know exactly what the microbes were. Buchner referred to them as "plant-microorganisms" in the title of his book. We should remember that "microbes" at this time had no natural history. Apart from their importance for the beer industry, and for production of bread, cheese and wine, they were primarily studied either as underdeveloped animals ("protozoa"), as models for studying cells ("unicellular organisms") and/or as disease-causing entities ("germs") in the case of bacteria. Institutionalized biology remained largely bifurcated in Linnean fashion, as botany and zoology. (We would do well to remember too that the 400–500 "species" of bacteria that inhabit our guts are still today sometimes referred to as "flora".) Classifying microbes was no easy matter. Naming them was difficult to do in accordance with taxonomic procedures for plants and animals. Microbiologists often relied on physiological characteristics and they often classified bacteria in terms of their disease-causing attributes. Investigating the physiology of microbes in hereditary symbiosis such as those of aphids was difficult because one cannot cultivate the microbes outside their hosts.

Buchner planned to write a revised version of his book and have it translated into English, and asked Steinhaus if he could do the job. Despite his German name, Steinhaus's German was elementary; his ancestors on his father's side originally came to the United States along with other Lutheran immigrants, and his mother's ancestors were among the English Pilgrims and other early European settlers. Although he had learned German for his doctorate, his ability to read German had decreased. "If I had the ability I should be most happy to agree to such a proposition, but under the circumstances I cannot." he wrote to Buchner, "...However, I do agree that some steps should be taken to see that your work gets into the English language and is recognized by zoologists in America, England, and other parts of the world. Your work is far too important and valuable to exist in only one language" (letter from E.A. Steinhaus to Paul Buchner, 30 January 1947; supplied by Giorgio Buchner).

At that time there were no comprehensive books in the English language on symbiosis, especially detailing the extensive research on hereditary symbiosis. During the first half of the twentieth century, American genetics, led by T.H. Morgan and H.J. Muller, maintained the all-exclusive importance of chromosomal genes in heredity. American geneticists explicitly excluded the cytoplasmic inheritance of symbionts from genetics as a source of error [21, 22]. This began to change after the war when a new generation turned to study microbial genetics and found new evidence of cytoplasmic inheritance in microorganisms, and some particles, such as kappa in *Paramecium*, that could also be transmitted artificially by infection. Genetic studies of bacteria indicated that the transfer of genetic material could occur by means of lysogeny, transduction, and transformations. In 1952, Joshua Lederberg attempted a new synthesis and enlarged the term heredity to include infectious heredity [12]. He argued that symbiosis could lead to macro-hereditary changes; it was possible, perhaps even likely, that mitochondria and chloroplasts had evolved as symbionts, but that techniques were not yet available to resolve that question.

Lederberg was one of the very few American biologists who had read Buchner's treatise, and he also pushed to have it translated into English [22]. The main problem was finding a suitable translator. In his view, the ideal candidate would have been Richard Goldschmidt. Unfortunately, Goldschmidt could not consider doing the translation himself since he was in the midst of writing his own book and was ill with heart trouble and still working at home [22]. Lederberg also wrote to Walter Carter, Head of the Entomology Department at the Pineapple Research Institute of Hawaii. Carter had worked in Buchner's institute in Leipzig for a short time during the war, and investigated *Pseudococcus*. He would collaborate in checking the translation of Buchner's book, which was begun in 1958. Dr. Bertha Mueller of the University of Hawaii took on the onerous job of translating it. Partly financed by a grant from the National Institutes of Health, and from the Unites States Department of Health, Education and Welfare, the translation took place over several years, and involved several biologists.

The new book appeared in 1965 just before Buchner's 80th birthday. By that time, he had received many awards, including honorary doctorates from the Universities of Pavia, Greifswald, and Munich, where he was made Professor Emeritus in 1959. An institute of experimental research on symbiosis (Koch) was named after him, the Austrian Society of Zoology awarded him the Erzherzog Rainer medal and, in 1961, the Federal Republic of Germany honoured him with the Gran Cross of the Order of Merit.

Symbiosis in evolution

Like several other symbiosis researchers, Buchner remained a life-long sceptic of the belief that natural selection acting on random genetic changes was the sole basis of evolution [22]. But at the same time he was cautious in delimiting what he called "the symbiosis principle" from the excesses of evolutionary and cytological speculation. That symbiosis was a primordial characteristic of life, and that mitochondria were symbionts had been advocated by several biologists, most notably Paul Portier [20] at the Institute Océanographique de Monaco, and Ivan Wallin [26] at the University of Colorado. Pierantoni himself had also repeatedly equated mitochondria with bacteria between 1923 and 1948 [19], as did plant bacteriologist Hugo von Schanderl at the Botanical Institute in Geisenheim, in a detailed presentation of his theory in a large book in 1947 [23]. That chloroplasts were symbiotic microorganisms

had also been suggested by many biologists including Andreas Schimper – who coined the term "chloroplast" in 1883 – and later Constantin Mereschkowsky (who rejected the idea that mitochondria arose as symbionts). Still others, most prominently Shôsaburô Wastasé and Mereschkowsky, had argued that the nucleus may also represent a symbiosis [21].

Speculations about the symbiotic origin of cell organelles had often led to absurdly elaborate theories, including bogus claims – by Portier, who speculated that new mitochondria-like bacteria came in with food to fuse with and vitalize old mitochondria; by Wallin, who claimed that he had cultivated mitochondria outside their "host" and that chloroplasts were derived from them; and by von Schanderl, who claimed that he had "regenerated symbiotic bacteriods" from many sterilized plant parts, and that he had observed the transformation of mitochondria into free-living bacteria. ([4], p.71). Buchner saw such fantastic claims and the controversies that surrounded them as a liability; they only hampered symbiosis research, "because theoretical misjudgments tended to obliterate the limits of what is understood as endosymbiosis today and thus to discredit the results achieved" ([4], p. 69).

Buchner opposed all such concepts about symbiosis as a primordial aspect of cell life. As he put it, "for us who have remained aloof from such speculations, endosymbiosis between animals and plant micro-organisms represents, though always supplementary, device, enhancing the vital possibilities of the host animals in a multiplicity of ways. For us it is but one manifestation of that principle of interdependence prevalent in all animate nature, which is the prime basis of the plant and animal kingdoms and of the existence of humankind" ([4], p. 74).

He had his own oppositions to confront. Two of them. First, there was the prevalent view that symbiosis was a rare phenomenon. Many biologists were still reluctant to accept that microbes played any beneficial role in the tissues of plants and animals. As Buchner correctly observed, biologists were more willing to accept the idea that algae could be symbionts in flatworms, but they were most reluctant to believe that bacteria and fungi could be of benefit to organisms ([4], p. 23). Indeed, both Portier and von Schanderl had attempted to demonstrate that bacteria were in healthy tissue, and had failed to do so convincingly. For Buchner, it was important to emphasize that to cultivate such "germs" from healthy tissue as he himself could do, should not be taken as implying that they were mitochondria that had reverted to their original stage of life.

Second, there was the problem of discerning the relationship between microbe and host. Discussions over such issues would often underlie competing definitions of symbiosis: did it mean mutualistic relationships of equal benefit or did it also embrace parasitism [22]. Buchner considered questions about how the balanced relations and adaptations of host and symbiont had evolved to be problems of the future. But as he saw it, one issue was certain: the animal host was in charge of the microbes. Studies of the symbiotic sites, in the mycetome, methods of transmission, and embryonic phenomena, all "indicates with commanding clarity that with genuine endo-symbioses the host animals are in all respects master of the situation."..."The symbiotic host regulates in the same fashion the degree and special form of propagating for his guests; it may give them a certain shape, regulate their size, and it even has the capacity for getting rid of them on occasion." ([4], p. 684).

Although he dissociated his work from the elaborate and discredited theories about organelle origins, which had often confused speculation with observation, his own detailed work showing the prevalence of hereditary symbiosis was used extensively by those who did speculate. Lynn Margulis [13] read Buchner's book closely when she revitalised the idea that cell organelles had emerged as bacterial symbionts, as had Lederberg when he sought to expand the mechanisms of heredity and evolution [12]. Buchner himself also recognized that symbiosis was a significant source of evolutionary novelty [1, 2, 3]. Wallin was particularly delighted to quote Buchner's comment that "If we refuse to create a completely new principle of cell structure through intracellular symbiosis, it does not necessarily follow that intimate symbiosis may not be the stimulus for the development of new animal forms. We have previously indicated such possibilities in the insects..." ([26], p. 146).

Wallin held symbiosis to be the cardinal factor in the origin of species, a source of new genes, as did Félix d'Herelle before him [21]. Although he stayed away from evolutionary speculation in his writings, as Ernst Mayr recalls, Buchner remained a neo-Lamarckian all his life – in the traditional sense of invoking environmentally induced adaptive changes to account for evolution [14]. His son Giorgio intimated that his father also believed that there was something else, an over-riding unknown principle that would account for directionality in evolution (interview, Porto d'Ischia, Italy, 12 April 1994).

Buchner saw symbiosis research to be an interdisciplinary field related to bacteriology, mycology and immunology. As he saw it, the phenomenon of intracellular symbiosis represented a new stage of knowledge for bacteriology and the theory of infection, comparable in importance with the discovery in the 1870s of the disease-causing capacities of bacteria and with the observations of Eli Metchnikoff on the process of phagocytosis as a defensive function. And, as he concluded in his book of 1965, he looked forward to the day "when professional bacteriologists will no longer be able to ignore the new findings brought to light by endosymbiosis research" ([4], p. 829).

It is ironic that evolutionists today accept the symbiotic origin of chloroplasts and mitochondria, which for so long was rejected as idle speculation, but ignore, and indeed deny, the scope and significance of the inheritance of symbionts through the eggs of animals. Thus, for example, John Maynard-Smith and Erös Száthmary assert that "transmission of symbionts

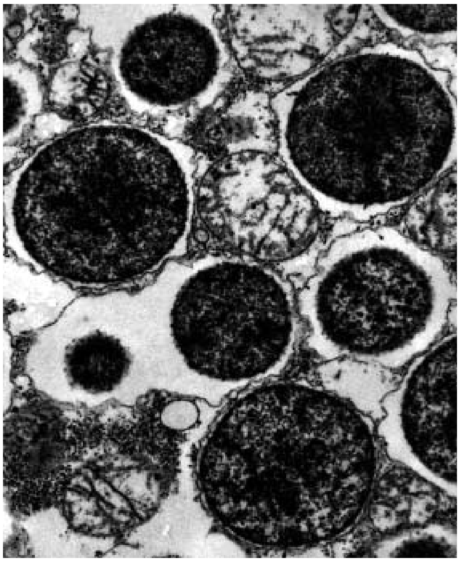

Fig. 2. Transmission electron micrograph of several cells of *Buchnera*, a bacterial symbiont of aphids (Insecta: Hemiptera: Aphidids), in a cell of their host. Courtesy of D. McLean, M. Kinsey and P. Baumann, University of California at Davis, Calif.

through the host egg is unusual" ([14], p.107). Buchner would have disagreed. Today it is estimated that at least 16% of all known insect species have bacteria of the genus *Wolbachia* inherited through the egg. *Wolbachia* manipulate the reproduction and development of their hosts: they cause parthenogenetic induction; they can convert genetic males into reproductive females, and they cause cytoplasmic incompatibility between strains and species of insects. Such bacteria have enormous implications for speciation in insects [27]. All aphids carry the bacteria of the genus *Buchnera* (Fig. 2) in their cells [15]. It is an older, indeed a 250 million-year-old, relationship that is obligate for both partners, and the symbionts are inherited through the host egg [7].

Acknowledgements The author wishes to thank the Social Sciences and Humanities Research Council and the Canada Research Chairs Program for support of this research.

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