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ESSAY REVIEW

Symbiosis in Evolution†

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Jan Sapp, *Evolution by Association: A History of Symbiosis* (New York and Oxford: Oxford University Press, 1994), xvii + 255 pp. ISBN 0-19-508820-4 Cloth; 0-19-508821-2 Paperback £19.95

The conventional neo-Darwinian interpretation of evolution assumes, with decreasing degrees of rigidity, that: (i) variations (through genetic mutation) arise at random, that is, with no correlation with induced fitness changes; (ii) natural selection is the dominant mechanism of evolutionary change; and (iii) individual evolutionary modifications are small—major evolutionary changes occur only through the accumulation of these minor modifications. Along with the standard models of inheritance (for instance, Mendelism or clonal reproduction), and a few subsidiary hypotheses, these three assumptions permit the reconstruction of the standard branching evolutionary tree from the fossil record. Much of this picture (though, of course, not the models of inheritance which were only constructed later) goes back to the early Darwin, in 1859, before his retreat in the face of criticisms by physicists.[1]

None of these assumptions is unchallenged. Punctuationists, such as Eldredge and Gould, challenge evolutionary gradualism (the third assumption).[2] They

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†Due to an absence of author corrections, this proof has been read by the Editor.

[1] See C. Darwin, *On the Origin of Species by Means of Natural Selection, or, The Preservation of Favoured Races in the Struggle for Life* (London: John Murray, 1859). For the physicists' criticism, see F. Jenkin, 'The Origin of Species', *North British Review* **46** (1867), 277–318. The thrust of this criticism was a thermodynamic argument (originally due to Kelvin) showing that the earth was simply not old enough for evolution to have proceeded along Darwinian lines. Darwin's retreat consisted of a modification of the principle of variation: he admitted Lamarckian mechanisms of use and disuse, along with some inheritance of acquired characteristics. For a detailed history, see J. D. Burchfield, *Lord Kelvin and the Age of the Earth* (Chicago: University of Chicago Press, 1990).

[2] N. Eldredge and S. J. Gould, 'Punctuated Equilibria: An Alternative to Phyletic Gradualism', in T. J. M. Schopf (ed.), *Models in Paleobiology* (San Francisco: Freeman, Cooper, 1972), pp. 82–115; S. J. Gould and N. Eldredge, 'Punctuated Equilibria: the Tempo and Mode of Evolution Reconsidered' *Paleobiology* **3** (1977), 115–151.

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claim that the paleontological record shows that evolution has consisted of long periods of stasis punctuated by short bursts of rapid change. However, it is far from clear that their challenge cannot be straightforwardly met within conventional neo-Darwinism: a mathematical analysis of the process of selection unearths many models which, at the macro-evolutionary level, would give rise to punctuated patterns in the paleontological record.[3] Neutralists, following Kimura[4] and King and Jukes,[5] urge that, at least at the molecular level (that is, the level of DNA and protein), most mutations are neutral with respect to fitness. Stochastic survival or extinction, rather than functional success or failure, determines what remains and what gets pruned from the evolutionary tree. At the bacterial level—and, perhaps, at the level of the simplest eukaryotes—there is ample evidence that some variation (that is, mutation) is not random but 'directional', that is, more prone to occur when they induce an increase in fitness.[6]

What is perhaps even more interesting—and reveals the extent to which the basic precepts of evolutionary theory are underdetermined by experimental evidence—is that at least the first two of these heresies have had significant adherents at every stage of the history of evolutionary theory. The punctuationists were preceded, for instance, by Goldschmidt who championed the existence of macromutations in the 1940s,[7] by de Vries and his 'mutation theory' during the early years of Mendelism[8] and, more than a century ago, by T. H. Huxley and the saltationists.[9] The neutralists were preceded by no less a figure than Wright, one of the founders of the modern theory of evolution. As early as 1931, Wright argued that population structure (for instance, breeding patterns) and stochastic factors in small populations may be more important than fitness differences in generating evolutionary change.[10] Even earlier, in 1921, Hagedoorn and Hagedoorn-Vorsheuvel la Brand argued for a pluralistic account of evolution in which natural selection was not given the dominant status that it has in the conventional interpretation of evolution.[11] Instead, stochastic (random) factors were emphasized, especially in the explanation of extinction.

[3] J. Maynard Smith, 'The Genetics of Stasis and Punctuation', *Annual Review of Genetics* **17** (1983), 11–25.

[4] M. Kimura, 'Evolutionary Rate at the Molecular Level', *Nature* **217** (1968), 624–626.

[5] J. L. King and T. H. Jukes, 'Non-Darwinian Evolution,' *Science* **164** (1969), 788–798.

[6] For reviews, see S. Sarkar, 'Lamarck *contre* Darwin, Reduction versus Statistics: Conceptual Issues in the Controversy over Directed Mutations in Bacteria', *Boston Studies in the Philosophy of Science* **129** (1991), 235–271, and P. Foster, 'Adaptive Mutation: the Uses of Adversity', *Annual Review of Microbiology* **47** (1993), 469–504.

[7] R. Goldschmidt, *The Material Basis of Evolution* (New Haven: Yale University Press, 1940).

[8] H. de Vries, *Die Mutationstheorie. Versuche und Beobachtungen über die Entstehung der Arten im Pflanzenreich. Vol. 1. Die Entstehung der Arten durch Mutation* (Leipzig: Veit, 1901).

[9] T. H. Huxley, 'Darwin on the Origin of Species', *Westminster Review* **17** (1860), 541–570.

[10] S. Wright, 'Evolution in Mendelian Populations', *Genetics* **16** (1931), 97–159.

[11] A. L. Hagedoorn and A. C. Hagedoorn-Vorstheuvel la Brand, *The Relative Value of the Processes Causing Evolution* (The Hague: Martinus Nijhoff, 1921).

These disputes by no means exhaust what has at least sometimes been found to be controversial in evolutionary theory. However, in the present context, what is most interesting about them is that, for all the passion, intellectual turmoil, and experimental work that they have generated, they do not question one very basic aspect of evolutionary theory, especially its reconstruction of evolutionary history.[12] This is the assumption that evolutionary change, besides extinctions, consists entirely of divergence from existing lineages (that is, evolutionary history can be represented by the familiar tree diagram which goes back to Darwin). Yet, almost throughout the history of evolutionary theory, there has been a heretical minority tradition that maintains that during the course of evolution there have occasionally been convergences, fusions of species (even from different taxa) to form new species. Such a possibility seems to have been first suggested in 1868 when Schwendener suggested that lichens were associations between algae and fungi (rather than being a distinct class of plants by themselves).[13] Other lichenologists were less than enthusiastic: to turn lichens into algae and fungi was to deny a reason for the existence of their research domain. Nevertheless, in 1877 Frank coined the term 'Symbiotismus' to describe the phenomenon; in 1878, de Bary, one of the most prominent of the early workers in the field, called it 'symbiose'.[14] A new natural phenomenon, 'symbiosis' had not only been discovered but also named. Those who believed it (that is, that it existed) and pursued it came from a variety of fields; most of them were so taken by the phenomenon that they urged that it was a central process of evolutionary change.

Jan Sapp's book, which is the subject of this notice, is a history of symbiosis from the 1870s to the 1980s, though he is willing to concede that the pursuit of symbiosis may only have been 'a dissenting footnote' to the history of orthodox evolutionary theory (p. xiv). This is the first extended history of symbiosis. It is an important and welcome addition to the history of biology especially because

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[12] Perhaps the only controversy which can be seen as truly threatening conventional theory is that about the non-randomness of variation (see, for example, R. E. Lenski and J. E. Mittler, 'The Directed Mutation Controversy and Neo-Darwinism', *Science* **259** (1993), 188–194). The main reason for the depth of the resistance to this possibility seems to be that an non-random variation must, in some sense, be induced by the environment. If such a variation is inherited, then one has the inheritance of an 'acquired' characteristic or Lamarckism as it is (inaccurately) called, which remains one of the taboos of modern evolutionary biology. The origins of this taboo are largely political (in a broad sense), from fraudulent reports by Lamarckians in the 1920s (see, e. g., P. Kammerer, *The Inheritance of Acquired Characteristics* (New York: Boni and Liveright, 1924)) to the persecution of orthodox geneticists by the Lamarckians in the Soviet Union during the Lysenko era. For a very interesting attempt to extend evolutionary theory to allow non-random variation and its inheritance, see E. Jablonka and M. Lamb, M., *Epigenetic Inheritance and Evolution: The Lamarckian Dimension* (New York: Oxford University Press, 1995).

[13] S. Schwendener, 'Untersuchungen über den Flechtenthallus', *Beiträge zur wissenschaftlichen Botanik* **6** (1868), 15–37. See J. Sapp, *Evolution by Association: A History of Symbiosis* (New York: Oxford University Press, 1994), pp. 4–6 for more detail.

[14] See Sapp, *op. cit.* in note 13, pp. 6–7.

most histories of evolutionary biology have ignored symbiosis altogether.[15] By focusing on experimental studies of symbiosis (rather than the sometimes mystical and often polemical writings of its adherents), Sapp constructs a history that emphasizes how relatively conventional biological concerns guided experimental work on symbiosis, that is, how this work fell squarely within the acceptable domains of biological investigation in spite of the researchers' theoretical heresies. It is a meticulous history, with just enough biological detail to be self-contained, and enough interpretive distance to be of general interest. The political contexts—e.g. how symbiosis as mutualism was incorporated into Kropotkin's social theories, or how it dominates the 'Gaia' responses to current environmental problems—are also treated, though only cursorily.

Sapp is sensitive to the nuances of the term 'symbiosis', the multiple meanings associated with it that continue to be used even today, and the vagueness of many discussions in which that term is invoked without any explicit delineation of its intended scope. As Sapp puts it:

> While many equate symbiosis with mutual benefit of associated species, others have continuously argued that this narrow meaning of the term is difficult, if not impossible to apply to real associations. Some have applied the term to relations between individuals; others insist that it be restricted to interspecies relations; still others have limited it further to apply only to relations between species which remain in contact throughout most or all of their life (p. xv).

Sapp does not attempt to adjudicate these disputes suggesting, somewhat unconvincingly, that the existence of multiple meanings of 'symbiosis' presents no worse problem than the existence of multiple meanings of other biological terms such as 'species', 'heredity' or 'gene'.[16] Rather, he navigates the disputed territories with care, paying attention to the differences but, nevertheless, presenting a unified history in the end.[17]

The early chapters of the book discuss the origins of symbiosis in lichenology and its career in various research institutes, particulary in France and Russia. This story is interesting because modern enthusiasts of symbiosis often invoke this 'prehistory' to remind the biological community of the allegedly undeserved neglect with which mainstream biologists had treated figures such as Schimper and Altman in Germany, and Famintsyn and Merezhovskii in

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[15] See, for example, E. Mayr, *The Growth of Biological Thought: Diversity, Evolution, and Inheritance* (Cambridge, MA: Harvard University Press, 1982).

[16] The reason why this is not fully convincing is that, whereas works using these other terms routinely do not explicitly define them, almost any modern treatment of symbiosis begins with an explicit attempt to define that term—see, for example, V. Ahmadjian and S. Paracer, *Symbiosis: An Introduction to Biological Associations* (Hanover, NH: University Press of New England, 1986).

[17] The reason that this unity can be maintained is that the alternative definitions and uses of 'symbiosis' are quite easily codified into a consistent unitary scheme—see, e.g. M. P. Starr, 'A Generalized Scheme for Classifying Organismic Associations', *Symposia of the Society for Experimental Biology* **29** (1975), 1–20. Sapp underestimates the importance of this factor—without it, a much more discordant story would have to be told.

Russia.[18] Such historical claims are often little more than ill-disguised ploys to demand ever more attention to the modern work on symbiosis. Though Sapp does not draw this conclusion, the story that he constructs undermines these claims. Symbiosis, though probably never at the forefront of evolutionary thought anywhere, was not neglected either. Symbiosis projects struggled along, especially in France, but progress was slow: the 1950 second edition of Caullery's *Le parastisme et symbiose* was almost identical to the 1922 edition.[19]

Though Sapp's account emphasizes continuity rather than abrupt change, it is at least arguable that attitudes towards symbiosis, especially about its relative importance in biology, underwent a radical transformation in the molecular era. In spite of the long history of studies of symbiosis, its real emergence as an important biological process was a result of the reconceptualization of cellular organization that was brought about by molecular biology. To simplify an interesting and complex story, for which Sapp could have provided much more detail without any loss of narrative balance, the problem that led to this transformation was the complexity of the relationship between bacteria and viruses. Lederberg, in particular, argued for an analogy between this relation (particularly in the case of lysogenic bacteria) and the relation between cells and their cytoplasmic hereditary components (the so-called 'plasmagenes').[20] He suggested that everything from what was conventionally called 'infection' to the association between cells and viruses or plasmagenes could be regarded as different degrees of symbiosis.[21] Lederberg's prominence as a geneticist and his continued advocacy of this position gave credence to a view of cells as consisting of integrated symbiotic units.

Nevertheless, this resurrection of symbiosis would probably have ended with the marginalization of the plasmagene models and the emergence of nuclear DNA as the sole arbiter of cellular fate but for startling developments in the 1960s. Beginning with the work of Ris and Plaut in 1962[22] and Nass and Nass in 1963[23] it was shown that chloroplasts and mitochondria had DNA and that there was undeniable homology between this DNA and that of blue–green algae (in the case of the chloroplasts) and bacteria (in the case of the

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[18] See L. Margulis, 'Symbiogenesis and Symbionticism', in L. Margulis and R. Fester (eds), *Symbiosis as a Source of Evolutionary Innovation* (Cambridge, MA: MIT Press, 1991), pp. 1–14.

[19] See M. Caullery, *Le parasitisme et symbiose* (Paris, Dion, 1922) and M. Caullery, *Le parasitisme et symbiose*, 2nd edn (Paris, Dion). It was actually the latter, not the former that was translated in to English in 1952: M. Caullery, *Parasitism and Symbiosis* (London: Sidgwick & Jackson, 1952), contrary to what Sapp implies (*op. cit.* in note 13, p. 106).

[20] J. Lederberg, 'Genetic Studies with Bacteria', in L. C. Dunn (ed.), *Genetics in the 20th Century: Essays on the Progress of Genetics during Its First 50 Years* (New York: Macmillan, 1951), pp. 263–289.

[21] J. Lederberg, 'Cell Genetics and Hereditary Symbiosis', *Physiological Reviews* **32** (1952), 403–430.

[22] H. Ris and W. Plaut, 'Ultrastructure of DNA-Containing Areas in the Chloroplast of *Chlamydomonas*', *Journal of Cell Biology* **19** (1962), 383–391.

[23] S. Nass and M. M. K. Nass, 'Intramitochondrial Fibers with DNA Characteristics', *Journal of Cell Biology* **19** (1963), 613–628.

mitochondria). By 1967 Margulis had synthesized the various suggestions; she argued forcefully that the origin of eukaryotic cells had to be regarded as a succession of endosymbioses.[24] Later experimental work has so far been consistent with this model. At least during that stage of evolution when the eukaryotic cells were first being formed, evolutionary history cannot be represented as a single branching tree. Different lineages merged to form the eukaryotes from which more complex organisms developed: it is only during the latter stage of evolutionary history that the conventional tree remains appropriate.

Margulis has since attempted to extend the domain of symbiosis well beyond this relatively circumscribed context. Since the early 1970s, along with Lovelock, she has argued that the entire biosphere should be regarded as a complex adaptive system, which Lovelock calls 'Gaia'.[25] The relations between many of the parts of this system are supposed to be symbiotic. Sapp's book ends with a brief account of this somewhat odd direction in which symbiosis research has lately gone. Unfortunately, his discussion of the religious and cultural determinants of this development leaves much to be desired. The critical question is whether the 'Gaia' hypothesis can at all be seen as a development largely motivated by 'internal' or intellectual concerns of the various research traditions of symbiosis. By emphasizing the alleged scientific basis of 'Gaia', Sapp seems to suggest that its origin can largely be attributed to intellectual factors but the case for this is far from plausible.

Meanwhile, the symbiosis story continues. Perhaps the most astonishing suggestion of recent years is that the evolution of some marine species is to be explained by the fusion of germinal cells from different species. As evidence, besides an interpretation of the life histories of several echinoderms, Williamson (the author of the new model) has offered apparently fertile offspring from sea urchin (*Echinus esculentus*) sperm and tunicate (*Ascidia mentula*) eggs.[26] Williamson's model will, of course, require much experimental testing. Though the requisite technologies are already available, its sheer novelty (and implausibility, from the orthodox point of view) will probably dissuade investigators from pursuing it seriously. A definitive answer does not appear to be immediately forthcoming. Nevertheless, it is whether such processes exist or not that will determine the ultimate fate of the conventional evolutionary trees, whether they can even be maintained for the period since the formation of the first eukaryotic cells.

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[24] L. Sagan, 'On the Origin of Mitosing Cells', *Journal of Theoretical Biology* **14** (1967), 225–274.

[25] J. Lovelock, *Gaia: A New Look at Life On Earth* (Oxford: Oxford University Press, 1979).

[26] D. I. Williamson, 'Incongruous Larvae and the Origin of Some Invertebrate Life-Histories', *Progress in Oceanography* **19** (1988), 87–116; D. I. Williamson, 'Sequential Chimeras', *Boston Studies in the Philosophy of Science* **129** (1991), 299–336; D. I. Williamson, *Larvae and Evolution: Toward a New Zoology* (New York: Chapman & Hall, 1992).

There are two intriguing questions that Sapp leaves partly unanswered: (i) how important could symbiosis have been in evolution, that is, beyond the critical role that it played in the genesis of eukaryotic cells, does the work that has been done so far suggest that it may have continued to be important in evolutionary processes?; and (ii) how important was the pursuit of symbiosis in the historical development of biology? It is, of course, unfair to demand that a historian answer the first question. (It is probably particularly unfair these days when methodologically sophisticated historians eschew any distinction between the truth and falsity of scientific claims.) Nevertheless, there is an unusual reason why a historian, especially one who has investigated the experimental record with as much attention to detail as Sapp has, might have some important insights to contribute on this problem.

Most historians and philosophers of biology now agree that the development of the life sciences in the 20th-century has routinely involved a narrowing of focus, casting aside from what is promulgated as the legitimate domain of inquiry all phenomena that did not adhere to the current orthodoxy. In genetics, Sapp's earlier (and very influential) work showed how phenomena that did not fit the nucleocentric model of heredity were relegated to the outskirts of genetics during the development of that model.[27] In evolutionary theory, Jablonka and Lamb have recently argued that phenomena indicating the inheritance of some acquired characteristics were similarly ignored.[28] One cannot help wondering whether similar displacements occurred during the history of symbiosis, that is, intriguing bits of data were summarily dismissed or not pursued because they were at odds with the orthodoxy. If so, then it is particularly important that radical new suggestions of symbiosis, such as that of Williamson, be pursued with vigor. Should such suggestions turn out to be true, symbiosis must form part of the general expansion of evolutionary theory beyond its orthodox confines that is going on at present.[29] Otherwise, symbiosis is still important, but its importance can be localized to the period of evolutionary history leading to the first eukaryotic cells. It is Sapp's misfortune that his earlier work raised so many questions, and set such high standards, that he is faced with such demands in what is certainly a much murkier context.

However, a historian can be expected to attempt some answer to the second question. Where did symbiosis fit into biological research, and how important was it? Was it really only a 'dissenting footnote' to the history of evolutionary theory, to be historically studied primarily as a curiosity? Sapp provides partial

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[27] J. Sapp, *Beyond the Gene: Cytoplasmic Inheritance and the Struggle for Authority in Genetics* (New York: Oxford University Press, 1987).

[28] Jablonka and Lamb, *op. cit.* in note 12, pp. 20–27.

[29] See, e.g. Jablonka and Lamb, *op. cit.* in note 12; M.-W. Ho and P. T. Saunders (eds), *Beyond Neo-Darwinism: An Introduction to the New Evolutionary Paradigm* (London, Academic Press, 1984); and S. J. Gould, 'Darwinism and the Expansion of Evolutionary Theory', *Science* **216** (1982), 380–387.

answers. His account suffices to rule out any truly important influence of symbiosis research on evolutionary biology (or in other biological sub-disciplines) in the (roughly) 1900–50 period, that is, after the full realization of the symbiotic nature of lichens but before the advent of molecular biology. It also shows (but this is well-known) that the work on the symbiotic origins of eukaryotic cells during the 1960s is of undeniable importance. But, what about the 1950s, for instance, the work of Lederberg that was already mentioned above? Should this early work at the molecular—or, at least, sub-cellular—level be regarded as setting the stage for the remarkable developments of the 1960s? Sapp largely avoids this question, presumably because of a reluctance (which is again standard among contemporary historians) to posit any linear progress.

However, an answer to this question is historiographically important. If there was such a direct influence from the 1950s, then symbiosis owes its revival as an important evolutionary process precisely to those differences in the conceptualization of biology that the molecular era induced. Molecular biology, in this case, rejuvenated an older biological sub-discipline, rather than marginalized it. Thus, symbiosis research may provide a striking counter-example to the thesis that molecularization has constricted biological research which is currently fashionable among many historians of biology.[30] Rather, to the extent that work on symbiosis has led to an expansion of evolutionary theory in very interesting ways, the credit for that must go to the advent of the molecular era. Sapp's book provides the background for pursuing this rather intriguing prospect.

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[30] See, e.g. S. Gilbert, 'Enzymatic Adaptation and the Entrance of Molecular Biology in Embryology', in S. Sarkar (ed.), *The Philosophy and History of Molecular Biology: New Perspectives* (Dordrecht: Kluwer, 1995).