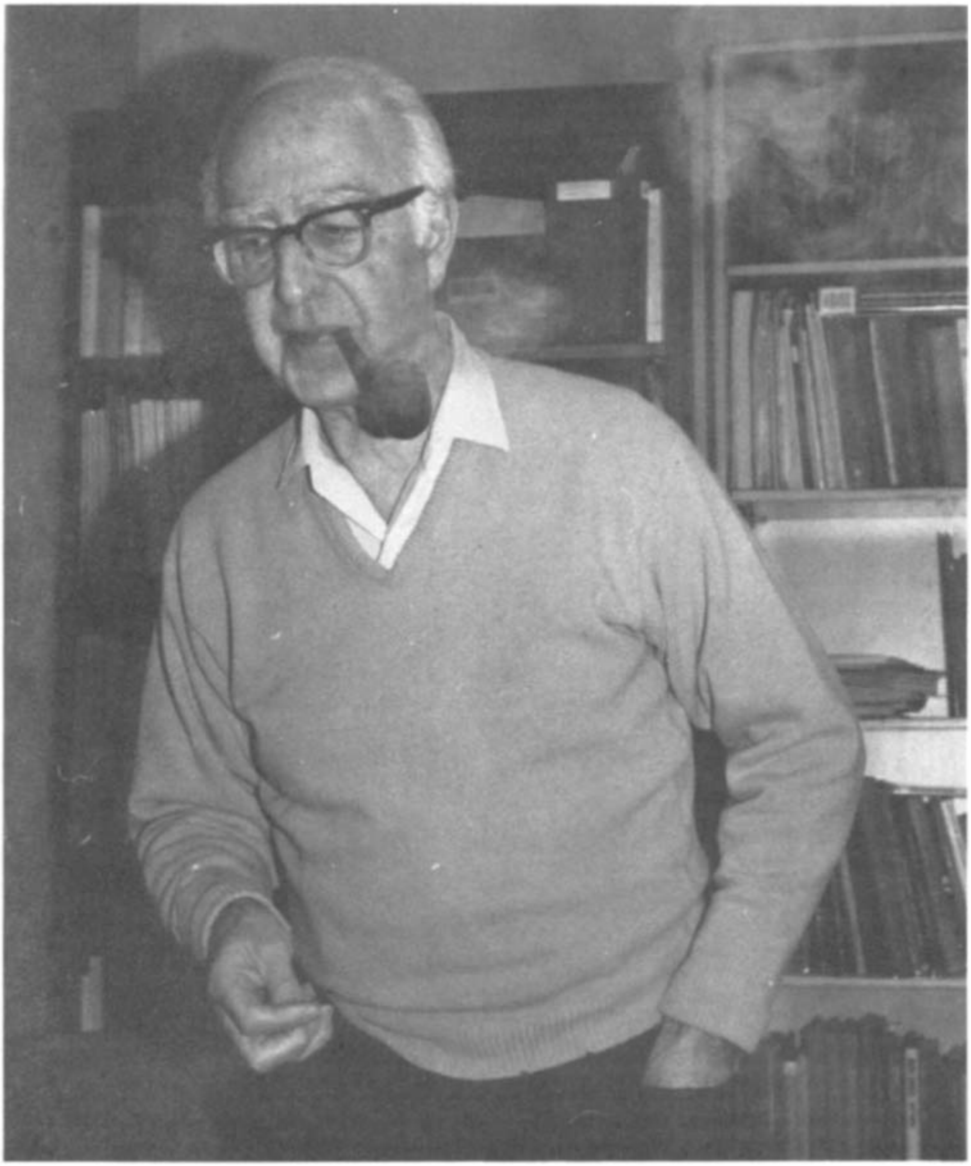

T. M. Sonneborn

1904–1981

Ann. Rev. Genet. 1981. 15:1–9

T. M. SONNEBORN: AN INTERPRETATION

◆3177

D. L. Nanney

Department of Genetics and Development, University of Illinois, Urbana, Illinois 61801

Tracy Morton Sonneborn was born October 19, 1904 in Baltimore, Maryland. His undergraduate (1925) and graduate (1928) degrees were earned in the same city, at Johns Hopkins University, where he was a student and long-time associate of Herbert Spencer Jennings. Sonneborn remained at Hopkins as an investigator until 1939, when he went to Indiana University as an associate professor of Zoology. The remainder of his career, except for brief excursions, was spent in Bloomington. There he was appointed to a professorship in 1943 and to a Distinguished Professorship in 1953. He became Distinguished Professor Emeritus in 1975 but continued to be active in research until near the time of his death, on January 26, 1981.

Sonneborn's career was long and productive. His bibliography lists over 230 titles published between 1928 and 1980, an average of over four contributions per year for over a half a century. About half of these are abstracts, short notes, or reviews. These shorter writings were not, however, trivial or duplicative. Sonneborn considered all forms of publication to be permanent records worthy of utmost care; he considered work published in abstract to have been truly published. Because he had difficulty in satisfying his own high standards of exposition, several of his important discoveries were never published *in extenso.* At the other end of the scale, some of his published works are long, meticulously documented, and closely argued treatises that summarized and crystallized all the evidence available on a subject. Examples are his 1947 review "Recent advances in the genetics of Paramecium and Euplotes" and his 1957 work on "Breeding systems, reproductive methods and species problems in protozoa." Sonneborn long dreamed of writing a masterwork on the biology of the cell, bringing up to date in a sense E. B. Wilson's masterwork (1925) and interpreting all cellular phenomena in the light of modern research. But he was frustrated by his own

0066-4197/81/1215-0001$01.00

inability to discard anything of potential significance; he was fascinated by the details, and could sense in them latent meanings not yet fully developed. Sonneborn's *Cell* would have rivaled the *Britannica,* could it have been completed.

Sonneborn's absorption with, and delight in, factual details made him a skillful observer, a superb natural historian. Perhaps his most obvious contributions were the problems he discovered, the phenomena he first described or focused concentrated attention on. He was remarkably persuasive in making connections between the things he found in Paramecium and the preoccupations of biologists working with other organisms. These connections are responsible for much of the visibility of ciliates. Nearly all geneticists and protozoologists are aware of the killer trait; they know that interesting things happen in serotype and mating type transmission, that the ciliate cortex has unexpected properties. Whether the awareness of the ciliates is supported by a genuine understanding of their special features is another matter, to which we must return.

Another area of major contributions was with methods. Sonneborn was always deeply involved in methodology, quick to develop and exploit new techniques, critical of the execution as well as the interpretation of experiments. His interest in methods yielded the works most often cited by other authors. His 1950 "Methods in the general biology and genetics of *Paramecium aurelia*" and his 1970 "Methods in Paramecium research" are permanent resources for investigators. The methodological matters of his central concern, however, were cellular, genetic, or organismic methods. Sonneborn never considered himself a molecular biologist, and never employed biochemical techniques, yet he maintained an intense interest in molecular advances, and became engaged with them occasionally at the theoretical level, as in his speculations on the evolution of the genetic code (1964).

After his thesis work on a microscopic worm, *Stenostomum incaudatum* (1930), Sonneborn focused most of his attention on the ciliated protozoa, and particularly on the *Paramecium aurelia* species complex. He adopted these organisms, accepting any biological constraints that went with them. The choice of organisms gave him a broad field of inquiry, and his studies ranged widely, following the organisms wherever they led. He was a cytologist and developmentalist, a physiologist and an immunologist, an evolutionist and a gerontologist, as well as a geneticist. His was a comprehensive concern with a whole organism.

Although he rarely worked with nonciliates, his interests and his competence were not correspondingly limited. He continually grafted the ciliate results into the phenomenological and theoretical corpus of general biological thought. A notable example is provided by his extension of his observations on aging in Paramecium (1954) to the mechanisms of human aging (1960). He was always, like his predecessor Jennings, concerned not only with the progress of science, but with its applications in the service of mankind. He was one of the original members of the Committee on Science and Public Policy of the National Academy of Science. He often participated in discussions concerning the use of genetic knowlege and was always respected for his knowledge, integrity, and humanity. One of his proudest achievements in this realm was the organization of the earliest public forum on the social effects of molecular genetics, convened in 1963 and published in book form in 1965.

For a crude indication of the impact of Sonneborn's work, we may glance at his citation record. The Science Citation Index lists some 1350 citations in the decade from 1970–1979. In the first five years of that decade, his citation rate was about 105 per year; in the second half-decade, it had risen to 165. At the time of his death, Sonneborn's influence, as measured by his citation history, was continuing to grow. In comparison with the citation rates of workers in heavily populated areas, Sonneborn's impact is not extraordinary; within his own field of ciliate genetics, however, it is unique, unmatched by that of predecessors, contemporaries, or younger workers.

Sonneborn's rising citation rate reflects not so much a rising influence within ciliate genetics, as a rising influence of ciliate genetics in modern biology. More interested biologists are now available to cite Sonneborn than were around a few years ago. He must be given credit for this phenomenon also. Sonneborn did not invent ciliate genetics; H. S. Jennings was there first (1929), and was a powerful force in drawing attention to the possibilities of genetic analyses with these organisms. But Sonneborn was the investigator who converted the possibilities into realities, with his discovery (1937) of how to regulate the breeding behavior of Paramecium. He was also responsible for training, directly or indirectly, many of the workers who now cite his publications. Sonneborn's connections with the other ciliate workers are not always apparent, because he maintained with few exceptions a policy of requiring graduate students (over three dozen) and postdoctoral associates (a couple of dozen) to publish their work on their own responsibility. His disengagement from publications coming out of his laboratory certainly was not because of a disengagement from the work or the worker; in fact, it left Sonneborn free to interact and criticize in a magisterial relationship of remarkable intensity, that persisted long after the end of formal training in his laboratory.

The impact of Sonneborn's life in science is reflected in a different way by the honors that were accorded him. In 1946, he was awarded the Newcomb Cleveland Research Prize of the American Association for the Advancement of Science and was elected to membership in the National

Academy of Sciences. Three years later, in 1949, he was elected to the American Academy of Arts and Sciences and became president of two major biological organizations: the Genetics Society of America and the American Society of Naturalists. In another three years (1952) he was elected to membership in the American Philosophical Society, thus completing the "triple crown" of high professional recognition available to an American scientist. He was subsequently honored by election to high office in other scientific societies: the American Society of Zoologists (1956), the Society for the Study of Evolution (1958), and the American Institute of Biological Sciences (1960). He won the Kimber Genetics Award of the National Academy of Sciences (1959) and the Mendel Medal of the Czechoslovakian Academy of Science (1965). He was elected a foreign member of the Royal Society of London (1964), and an honorary member of the French Society of Protozoologists, of the Genetics Society of Japan, and of the Faculty of the University of Chile. Other evidence for approval of his contributions came through honorary degrees he received from his alma mater, Johns Hopkins (1957), from Northwestern University (1975), from the University of Geneva, Switzerland (1975), from Indiana University (1979), where he served so long as professor, and from the University of Münster, West Germany (1979).

This catalog of honors demonstrates that this man was one of the most highly honored American geneticists of his generation. But we have not explained why Sonneborn was so honored. What were the achievements recognized by his colleagues across several academic disciplines, in his home country and in other lands? This question is not as easily answered as it is asked.

One might try to answer it by looking at current textbooks of genetics. The cult of personality is strong in this area of biology, and geneticists delight in calling the roll of their heroes. Contemporary textbooks of genetics provide a useful guide to geneticists' evaluation of the contributions of research workers. Nearly all of them mention Sonneborn and describe the genetic control of the killer character in Paramecium (Sonneborn, 1943); some make reference to the heritability of cortical patterns (Sonneborn, 1962). The appearance of this work in textbooks suggests that it is considered central to modern genetics. But its actual use in genetics courses reflects an ambivalence. It is located in optional chapters with other phenomena that the instructor usually chooses to ignore. Teachers have enough difficulty transmitting materials of clear immediate importance, without being distracted by observations on systems with some possible but as yet imperfectly perceived future significance. Few students in basic genetics courses are held responsible for the behavior of the nuclei in autogamy, for the roles of genes in the transmission of kappa, and for the mechanism of maintaining inverted ciliary rows.

One of the reasons that teachers do not insist on mastery of these matters is that they are considered difficult or complicated. The concepts of "difficulty" and "complexity" are, however, almost meaningless when separated from the concept of "significance." The sex life of *E. coli,* the structure of the *lac* operon, and the genetic control of immunoglobulins are complex subjects involving many detailed and interrelated bits of information. But students are required to master these "complicated" subjects, because the phenomena are believed essential to an understanding of recognized genetic mechanisms. Sonneborn's work is neglected in genetics courses not because it is complex, but because its connections with well-established general mechanisms are yet uncertain.

This judgment is supported by an examination of attempts to interpret the history of modern genetic analysis. *The Eighth Day of Creation: The Makers of the Revolution in Biology,* by H. F. Judson (1979), is one of the most recent and authoritative interpretations of the founding of modern genetics; it names nearly 400 contributors, but T. M. Sonneborn is not mentioned in that work. An earlier book, *A Century of DNA,* by F. H. Portugal and J. S. Cohen (1977), was recommended to me by Sonneborn as the best account he had read of the history of recent genetics. He does appear in this book, but as a T. *S.* Sonneborn, who was supposedly working "in Bloomington on phage genetics." J. D. Watson, who in his literary persona of "Honest Jim" (*The Double Helix,* 1968), gave what some have called the most honest account of the critical events in the genetic advances of the 1950s, makes no mention of Sonneborn, even though Watson was a regular and intimate associate of Sonneborn over a period of some three years prior to his move to Cambridge to collaborate with Crick. These evidences suggest that Sonneborn's discoveries were not central to the mainstream of modern genetics.

We have then something of a paradox: a person who was repeatedly honored for scientific achievement, but who seems to have left little permanent trace of those achievements in some of the places where they might be expected. The paradox requires explication.

Of course, I've marked the cards and stacked the deck. E. B. Wilson's name doesn't appear in *The Eighth Day of Creation* either, but we don't dismiss his genetic contributions lightly. The book does not pretend to be a comprehensive account of genetic studies, even of the middle quartiles of the century. What I am emphasizing is that Sonneborn's contributions lie outside the river of molecular genetics that has run at flood-tide in the modern era and that has swamped beyond notice some other genetic streams. A remarkable feature of Sonneborn's career is that high honors continued to punctuate it, despite the fact that the products have not yet been significantly integrated into the discipline but have remained a somewhat private, largely unassimilated corpus of enquiry.

Connections certainly do exist between ciliate genetics and the main body of modern genetics, but those connections are mainly in the past and perhaps in the future rather than in presently recognized realities. Sonneborn was one of the first to perceive the promise of microbial genetics, at a time when the only genetically domesticated organisms were *Drosophila melanogaster* and *Zea mays*. With other pioneers he began to explore the genetic utility of unicellular organisms, choosing perhaps circumstantially to work with the large complex ciliated protozoa. His first major step in the domestication of Paramecium was the discovery of mating types in 1937 and he moved quickly to investigate several heritable variations. As studies on other microbiol systems developed, especially on *Neurospora sitophila* and on *Escherichia coli* and its phages, Sonneborn recognized the necessity of gaining complete nutritional control over his organism and of making molecular connections. In this effort he was frustrated. The greater organizational and nutritional complexity of Paramecium prevented during a critical time the use of defined media and biochemically defined traits. The decisive genetic advances that were ready to be made were accomplished with other organismic tools. Neurospora became the first precision instrument for identifying the physiological function of the genes; *E. coli* first taught us about the organization and regulation of genetic elements. Beadle and Tatum, Lederberg, Luria and Delbruck, Hershey, Monod and Jacob took the highest prizes.

Sonneborn did not abandon Paramecium, of course, or his scientific focus. Very early he had discovered as his special level of concern "the interaction of genes, cytoplasm and the environment in the control of cellular heredity" (1948). Although to do so excluded him from full participation in the advances in molecular genetics, he remained faithful to his concern with the systemic properties of cells and with developmental mechanisms, and to his commitment to domesticate ciliates as instruments of genetic analysis. In the last half of his career he applied with increasing precision his continually improving instrument to problems of cellular patterning, nuclear organization, and nucleo-cytoplasmic integration. Both the problem and the organismic technology have matured greatly in the last quarter century. Whether Sonneborn's ciliates will now justify his persistent faith and provide the basis for major generalizable advances, only time will tell. But his faith was undimmed. After a recent conference on ciliate genetics, he said sadly, but with pride, "I feel like Moses must have felt, privileged to look into the promised land, but not allowed to go in myself."

Where is this promised land that Sonneborn thought he saw? He was not referring just to work on the ciliated protozoa; his vision encompassed the whole range of life manifestations. Almost certainly he considered our current preoccupation with a narrow range of molecular problems to be a necessary wilderness experience from which we will eventually emerge. I recall his unexpected reaction to the first edition of Jim Watson's other book, *The Molecular Biology of the Gene* (1965). "It is an absolutely brilliant synthesis. But I'm not sure that we should allow it to fall into the hands of students." When asked to expand on these remarks, he said something like the following, "It is a book written about the answered questions; it suggests that the story is told, and not just well begun." I also recall Sol Spiegelman's response to a demand from his students for a rigorous course in the biology of the cell. He agreed to teach such a course but, unexpectedly, he required that the students read E. B. Wilson's *Cell* (1925). He explained that most of the phenomena confronted by Wilson are still unexplained, and that their descriptions have been crowded out of the newer books. We may be so dazzled by our success with one scientific paradigm as to lose sight of the boundless mysteries of life awaiting exploration. Sonneborn's intimate familiarity with live things preserved him from an unreal sense of limitation, and led him, in a poignant fragment of a manuscript he was working on as he died, to anticipate "the next truly great push forward." He expected that, when the walls come tumbling down, the third- and fourth-dimensional phenomena with which he worked would be exposed and explained.

I have tried to be objective in this account of a life, focusing on measurable quantities, on official honors, on strategic evaluations. I am too close to the subject, however, to be more than superficially objective. And the objective considerations fail to convey important personal qualities manifested in that life. Those who experienced Tracy Sonneborn need not be reminded of these qualities and, unfortunately, those who never knew him will scarcely be truly informed by verbal descriptions. I must, nevertheless, call attention to Sonneborn's remarkable impact on those who saw him and worked with him. Few could resist his platform presence, the Groucho stalk, the orchestrated crescendo, the hypnotic intensity that often called forth spontaneous applause from classroom captives and public audiences alike. The intense focused energy was not, however, reserved for public displays, but was typical of his relationships with students and colleagues. He was not particularly vigorous physically but his intellectual vitality was immense, characteristically leaving his interactants both emotionally drained and intellectually charged.

Sonneborn's personal and intellectual gifts were always disciplined and kept in check by a ruthless dedication to the Truth. He had schooled himself to mistrust the easy answer, the expected solution. He would not allow himself to find in the laboratory what he had discovered in the air or in his own mind. He was fascinated by, riveted upon, Nature, unwilling to project upon Her his own constructs or to use Her for base purposes. For this reason he was a harsh critic, both of himself and of others. But for this reason he was also a source of confidence and inspiration to those with whom he shared his rigor.

A major determinant of the course of Sonneborn's career was what might be called his "scientific idealism." One of my first memorable experiences with research science was an address in 1946 by H. J. Muller, delivered in Bloomington at a banquet celebrating his Nobel Prize. On this occasion Muller proclaimed that high prizes should not be the goal of the scientist, that these are an unpredictable and unimportant by-product of a scientific career. This view of prizes seems strangely naive in the shadow of *The Double Helix,* and recent developments in scientific hagiography. But Sonneborn was not only a proponent of the view that science is its own reward, his career was its exposition. Sonneborn refused to run races with anyone. He would not do an experiment that someone else was likely to do, or could be prompted to do. Too much needed to be done to duplicate efforts in doing the obvious. Fortunately for the prosperity of the scientific enterprise, Sonneborn was not alone in his naive idealism. Quite beyond a narrow application of serendipity, the steady progress of science depends upon the stubborn persistence of dedicated individuals, who refuse to turn away from possibly unprofitable explorations, who will not flock to the racetrack to run for a prize.

I do not suggest that Sonneborn's labors were unprofitable, or that they have been permanently bypassed by the flow of history. I cannot even claim that he has been denied the prizes that celebrate a distinguished career. I do suggest that his prizes, particularly in the later years, may have been directed as much to the person, and to his scientific integrity, as to the product of his efforts. I do not assert this possibility as a reflection on Sonneborn's achievements, but rather to claim this occasion to celebrate the host of scientific investigators who mine their own claims, often far from busy highways, assiduously, intelligently, critically, ever hopeful for a special nugget of understanding, though often disappointed. Every scientist is a part of a trialogue with the natural world, and with human culture; fortunately for all of us, in some of the trialogues the voice of society is dampened, and the intercourse between a mind and Nature achieves a special intimacy. The consequences are individually unpredictable, but in the aggregate, they are essential. I believe that Tracy Sonneborn's career exemplifies one of those special relationships.

Literature Cited

Jennings, H. S. 1929. Genetics of the Protozoa. *Bibliogr. Genet.* 5:105–330

Judson, H. F. 1979. *The Eighth Day of Creation: Makers of the Revolution in Biology.* New York: Simon & Schuster. 686 pp.

Portugal, F. H., Cohen, J. S. 1977. *A Century of DNA: A History of the Discovery of the Structure and Function of the Genetic Substance.* Cambridge, Mass/London: MIT Press. 384 pp.

Sonneborn, T. M. 1930. Genetic studies on *Stenostomum incaudatum* (nov. spec.). *J. Exp. Zool.* 57:57–108, 409–49

Sonneborn, T. M. 1937. Sex, sex inheritance and sex determination in *Paramecium aurelia. Proc. Natl. Acad. Sci. USA* 23:471–502

Sonneborn, T. M. 1943. Gene and cytoplasm. I. The determination and inheritance of the killer character in variety 4 of *P. aurelia. Proc. Natl. Acad. Sci. USA* 29:329–38

Sonneborn, T. M. 1947. Recent advances in the genetics of Paramecium and Euplotes. *Adv. Genet.* 1:263–358

Sonneborn, T. M. 1948. Genes, cytoplasm, and environment in the control of cellular heredity. *Science* 107:459

Sonneborn, T. M. 1950. Methods in the general biology and genetics of *Paramecium aurelia. J. Exp. Zool.* 113:87–148

Sonneborn, T. M. 1954. The relation of autogamy to senescence and rejuvenescence in *P. aurelia. J. Protozool.* 1: 36–53

Sonneborn, T. M. 1957. Breeding systems, reproductive methods, and species problems in Protozoa. In *The Species Problem,* ed. E. Mayr, pp. 155–324. Washington D.C: Am. Assoc. Adv. Sci. 395 pp.

Sonneborn, T. M. 1960. The human early foetal death rate in relation to age of father. In *The Biology of Aging,* ed. B. L. Strehler, p. 288. Washington D.C: Am. Inst. Biol. Sci. 364 pp.

Sonneborn, T. M. 1962. Does preformed cell structure play an essential role in cell heredity? In *The Nature of Biological Diversity,* ed. J. M. Allen, pp. 165–221. New York: McGraw-Hill 304 pp.

Sonneborn, T. M. 1964. Degeneracy of the genetic code: Extent, nature and genetic implication. In *Evolving Genes and Proteins,* ed. V. Bryson, H. Vogel, pp. 377–97 New York: Academic 629 pp.

Sonneborn, T. M., ed. 1965. *The Control of Human Heredity and Evolution.* New York: Macmillan. 127 pp.

Sonneborn, T. M. 1970. Methods in Paramecium research. *Methods Cell Physiol.* 4:241–339.

Watson, J. D. 1965. *The Molecular Biology of the Gene.* Menlo Park: Benjamin. 494 pp.

Watson, J. D. 1968. *The Double Helix: A Personal Account of the Discovery of the Structure of DNA.* New York: Atheneum. 233 pp.

Wilson, E. B. 1925. *The Cell in Development and Heredity.* New York: MacMillan. 1232 pp. 3rd ed.