# T. M. Sonneborn: Reluctant Protozoologist

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# T. M. Sonneborn: Reluctant Protozoologist

Tracy Morton Sonneborn died January 26, 1981, at the age of 75 years, leaving an indelible impression on the biological sciences in his time. The organizing committee of the VI International Congress of Protozoology has designated this session of contributed papers on genetics and morphogenesis as a tribute to Professor Sonneborn's memory. The committee has honored me by asking that I make a few remarks concerning Sonneborn's life and his contributions to protozoology.

The public record of Sonneborn's achievements is provided by his bibliography, a list of some 230 titles published over a period of half a century. Such a list documents a long, disciplined and productive career. It does not explain itself entirely, however, particularly with respect to our immediate concerns. What did Sonneborn contribute to protozoology, and what did protozoa contribute to Sonneborn's career? In order to provide a framework for a brief survey of Sonneborn's life in science, I propose a thesis that contains a mild paradox: Sonneborn's substantial scientific contributions were achieved almost exclusively through his studies of the ciliated protozoa, yet Sonneborn was reluctant to consider himself a protozoologist. As a further aid to structure, I divide Sonneborn's career into four somewhat arbitrary phases.

## Phase I: The Lean Years

The first of these phases is the Hopkins phase. Sonneborn did both his undergraduate and graduate work at Johns Hopkins University in Baltimore, Maryland, the city in which he was born. His thesis advisor, Herbert Spencer Jennings, was well-known for his experimental work on protozoa. Jennings is remembered today primarily for his definitive work on protozoan behavior; you may recall that he described the "avoiding reaction" in Paramecium even before the turn of the century. Yet Sonneborn did not do his thesis work on protozoa, but concerned himself instead with the inheritance of form in an invertebrate metazoan, *Stenostomum incaudatum* (Sonneborn, 1930a, 1930b).

Sonneborn's international reputation, of course, is founded on his work with *Paramecium aurelia*, and the work on Stenostomum is virtually forgotten. Yet Sonneborn may have undertaken the protozoan work somewhat under duress. The "Great Depression" of the 1930's provided few opportunities for young scientists. New jobs were rare and research funds were difficult to obtain. Fortunately, Jennings' prominence as a scientist and as a spokesman for science had brought him strong and continuous research support through the Rockefeller Foundation. Because of his grant support, Jennings was able to offer a haven to Sonneborn during the lean years, provided only that he direct his efforts to the organisms specified by the Rockefeller benefactors.

I cannot know Sonneborn's feelings about these circumstances, but his postdoctoral years at Hopkins were idyllic in many ways. He had a sympathetic and supportive supervisor; he had a devoted and understanding wife; he was free from teaching responsibilities and much of the normal administrative clutter of academic life. Most importantly, he was free to investigate phenomena he found interesting, constrained only by the organismic prescription of his supporting agency. He had to work on protozoa.

Although the Hopkins years gave Sonneborn freedom, and time for his exploratory studies, they were nevertheless lean years in several ways. Sonneborn received his Ph.D. in 1928. Thereafter he worked thoughtfully and tenaciously for many years, attempting to bring Paramecium under experimental control. Year after year he worked with only moderate results for his efforts. Only in 1937, twelve years after beginning his graduate career, and nine years after receiving his Ph.D., did he make a really notable discovery - the discovery of "mating types" in Paramecium aurelia (Sonneborn, 1937).

I mention the circumstances of this important event for the illumination it provides, both to Sonneborn's work and more generally to the process of discovery. Many of Sonneborn's later achievements have their origins in this early latent period. And perhaps some of the discipline and patience that harnessed Sonneborn's enormous enthusiasm were gained through these early days of difficulties and false starts.

In this case, fortunately, the time was available, and the tempered investigator emerged. The moment of understanding came, and with it the opportunity to open many doors. What was Sonneborn up to in these days, and why were mating types so critical for achieving his purpose? Sonneborn was above all else an experimentalist, and he was determined to bring his organism under experimental control. And by "experimental control", he meant not just growth in the laboratory, but that most subtle manipulation of biological influences - breeding analysis. Sonneborn, like Jennings, was fascinated by the enigmas of heredity. He had also grasped the strategic significance of the scientifically domesticated organism. The technological foundation for the first great surge of genetic understanding in this century was the domesticated fruit fly - *Drosophilia melanogaster*. The parallel domestication of *Zea mays* provided an essential auxilliary resource.

Sonneborn and Jennings, however, perceived that genetic analysis with large complicated organisms had its limitations. They dreamed of bringing genetic studies to a deeper level of analysis using miniaturized genetic systems of simpler design, capable of being handled in larger numbers at a cheaper cost. From one perspective, Sonneborn's career can be viewed as an heroic effort to make Paramecium a protistan Drosophila. His discovery of mating types gave him the kind of control over reproductive processes necessary to that end. It gave him opportunities he exploited the rest of his life.

Phase II: Paramecium Goes Public

The discovery of mating types brought recognition to Sonneborn. It also brought mobility and the end of the Hopkins era. Jennings had retired at Johns Hopkins, and Sonneborn was ready to make a new start on his own. In 1939 he moved to Indiana University at Bloomington, which became his home base for the rest of his days.

The first years at Indiana, until about 1950, I will refer to as Phase II of his career. These were the days during which Sonneborn and his associates first used the tool of controlled mating to explore the basis of differences among individuals of this species. After the end of World War II, his research group grew, with many graduate students and postdoctoral fellows joining him in exciting studies.

The first organismic variations that Sonneborn subjected to breeding analysis were the mating types themselves (Sonneborn, 1939). These studies were quickly followed by others on the killer characteristic (Sonneborn, 1943). Still other breeding studies were carried out on the inheritance of antigenic traits (Sonneborn, 1948). The basic cultural methods and genetic technologies were summarized (Sonneborn, 1947, 1950a) and the first, descriptive phase of their application was essentially complete by the early 1950's. This work was meticulously documented and effectively presented to the scientific public (Sonneborn, 1950b, 1950c). The results were unexpected and excited wide discussion. Sonneborn was himself repeatedly recognized for highly regarded discoveries.

Nevertheless, the studies also generated some dissonance in theoretical biology and genetics. The overwhelming conclusion of classical genetic studies was that hereditary differences between individuals are controlled by chromosomal differences. Much of the work on Paramecium, though providing abundant evidence of Mendelian control of organismic capabilities, revealed complicated relationships between the genes, the cytoplasm and the environment in the expression and perpetuation of cellular differences. In particular, although each of the systems studied in Paramecium is different, they all manifest in some circumstances the phenomenon of "cytoplasmic inheritance" or "uniparental transmission."

The Paramecium work challenged geneticists to a more comprehensive understanding of the functional interactions of the components of the cell. Unfortunately, the time for that challenge was not ripe, and it has not yet been fully met. To understand what happened to Paramecium genetics, we need to take a broader view of what was happening in biology. The dream of a microbial genetics was not the sole property of Jennings and Sonneborn. Beadle and Tatum, and Luria and Delbruck also undertook the domestication of microbes as scientific instruments. And they chose organisms even smaller and simpler than Paramecium, organisms more congenial to the biochemical technologies available. Using these organismic tools, the genetic community developed a driving preoccupation to dissect the nuclear apparatus. Escherichia coli and its phages became the workhorses of genetics. The complicated and confusing ciliates and the problems they raised were set aside for later consideration.

Phase III: Paramecium as an Organism

I think that Sonneborn recognized something of these complex sociological events of the 1950's. He joined fully in the excitement of discoveries concerning the structure of DNA, the synthesis of proteins, the regulation of primary gene activity. But even though his area was by-passed in a sense, he did not abandon his efforts to domesticate Paramecium more completely or to use it in sophisticated analyses. Moreover, he must have been caused to wonder why the ciliates gave such unexpected answers to simple questions. In any case, for the next few years, until about 1960, Sonneborn gave a lot of thought to the ciliates as real organisms in Darwinian time and space. This period I refer to as Phase III, and its most characteristic expression was his long review in 1957 on the species problem in protozoa (Sonneborn, 1957).

This period is the one most productive of what one is inclined to designate as "protozoological" contributions, as opposed to "genetic" contributions. And perhaps this is as good a place as any to recognize Sonneborn's ambivalence toward "protozoology." Sonneborn did not work on protozoa for his doctoral thesis, and he may have begun to work with Paramecium at least in part through economic necessity. He taught protozoan genetics, but only as a periodic subject, alternating it with bacterial genetics, fungal genetics, and algal genetics. The one time he tried to teach protozoology, he became fascinated with a sample of pond water and manged to spend the whole semester working with the class on a few particular species. In the 1940's, he was opposed to the formation of a Society of Protozoologists, and in the 1950's he thought a journal devoted exclusively to the protozoa was an unfortunate conception. He never held high office in the Society of Protozoologists, though his curriculum vitae is loaded with services to other scientific societies.

I suspect that Sonneborn's attitude toward protozoology was connected with his hope that Paramecium would be recognized as a generalized cell and not as a ciliate, just as Drosophila was recognized in some sense as a generalized organism and not as an insect. He did not want his organism to be limited by its association with some peculiar, atypical, aberrant group. He did not want his discoveries published in a parochial journal read only by a partisan readership. Moreover, he refused to limit his own interests according to taxonomic criteria. He wasn't interested in Paramecium <u>because</u> it was a protozoan, but because it was alive.

The fundamental issue here probably lies in the diversity of the commitments of biologists. Some biologists become fixed on a particular phenomenon or structure, and pursue it through a multiplicity of organisms and with a variety of techniques. Others master a methodology and adhere to it while varying the objects to which it is applied. And, of course, some biologists make a primary organismic investment. And organismic biologists differ, not only with respect to the groups that attract their attention, but also with respect to the sizes of the groups. Some biologists direct concentrated attention to one species or to a small group of species; others give more diffuse attention to a much larger group. I am not entirely sure how a "protozoologist" is defined, but the term almost certainly implies a special interest in all the organisms classified as protozoa, and also a diminished interest in the organisms excluded from the category. If so, Sonneborn was not a protozoologist. He was never interested in any organism simply because it was a protozoan, and he refused to have his interests in other organisms restricted. I suspect he would have been amused by the confusion and diversity of opinion manifested in these meetings concerning what, if anything, a protozoan is. The debate would not have affected his identity. He was unequivocally a biologist, a geneticist, and a parameciologist.

I suspect that his achievement of the status of parameciologist came belatedly. I remember being startled by his opinion that only <u>specialized</u> mechanisms are <u>truly</u> interesting. This opinion of the 1960's would have been intolerable in 1950, and it indicated a revision of values. I believe that Sonneborn was converted when he accepted the challenge to explain the discrepancy between the studies on Paramecium and those on fungi and bacteria. Why should ciliates give such different results in breeding studies? What kind of an organism is a Paramecium anyway? The search for the universal principles would have to wait for a deeper understanding of the particular.

During the 1950's Sonneborn set about assembling, in his systematic way, all the information available on the biological characteristics of the beasts that circumstances had brought to be his companions. He wanted to know about their life histories, their distributions, their mating habits, their evolutionary relationships. The observations go back to the time that mating types were discovered, but their use in systematic comparative study was new.

I cannot adequately summarize here the masterly multi-dimensional synthesis of paramecium biology that Sonneborn produced at this time, but I must recall a few isolated elements. First, let me mention the phenomenon of cryptic species. The strains of Paramecium aurelia do not constitute a single large gene pool, but are broken up into many completely isolated non-interbreeding Mendelian populations. Using the techniques Sonneborn developed, other workers have shown that many "named" species of ciliates have the same kind of cryptic genetic complexity: genetically isolated populations of remarkably similar phenotypes, yet of great diversity of genetic structure and evolutionary history. This observation has not endeared Sonneborn to systematic protozoologists, or to ecologists forced to deal as best they can with manifest variation instead of cryptic genetic differences. Sonneborn's work strongly supports the biases of the "splitters" in their conflicts with the "lumpers", at least for many species of ciliated protozoa. The cryptic species of ciliates, on the other hand, are an unexpected gift to comparative biochemists, and a powerful instrument for studying the evolution of cellular structures.

A second protozoological insight came from asking about how the persistent cryptic species maintain their places in nature over extravagantly long periods of time. Their large phenotypic and distributional overlap leads one to expect some subtle micro-ecological distinctions. In fact, Sonneborn found the clue to their distinctiveness in what may be referred to as their "ecogenetic strategies." At the simplest level, sibling species are distinguished by different positions on an inbreeding-outbreeding scale. Some species are inbreeders, committed to mutational variety as a way to meet environmental challenges; others are outbreeders and rely importantly on recombinational variety. These generalizations are imbedded in a rich tapestry of relationships involving many facets of the life history, the aging process (Sonneborn, 1954), the mating system.

This synthesis preceded the recognition and study of ecogenetic systems in other organisms by many years. Sonneborn's work was not fully appreciated, however, either by protozoologists or by population biologists who should have been aware of what he was attempting. I am pleased to see the modern resurgence of ciliate work in this mode, particularly by the Italian school.

## Phase IV: Paramecium as an Instrument

The fourth stage of Sonneborn's career I am inclined to view as his mature phase. By 1960, Sonneborn had a firm grasp of the experimental capabilities of P. aurelia, and also of its limitations. He had faced and accepted its pecularities, and could choose for experimental analysis phenomena he considered interesting and important, with a realistic understanding of what could and could not be achieved.

It was during this time that I first became fully aware of his policy not to do an experiment that someone else was likely to do. Certainly it was implicit in his earlier practices, particularly in turning over to students and associates major projects that he had initiated. But I think that his mature phase was characterized by a fuller appreciation of the multitude of natural phenomena begging for analysis, and with the limited number of workers available to carry out those analyses. More than ever he encouraged students and colleagues to do their own things, to respond directly to their own observations and to determine their own priorities.

He was always marvelously perceptive of deep issues in trivial manifestations. I remember being surprised by his determination to study the hereditary basis of doublet paramecia. He asked me what I thought would happen if he crossed a singlet with a doublet. I replied that certainly one exconjugant would remain a singlet and the other would remain a doublet. He agreed, but he also asserted that therein resides a mystery for which conventional genetic wisdom has no explanation. And he announced that he would do that experiment with such sophisticated controls that no one could ever again doubt that the continuity of form in cellular lineages involved some new and important principles (Sonneborn, 1963; Beisson and Sonneborn, 1965).

I must admit to thinking in 1960 that Sonneborn was not entering his mature phase, but rather passing beyond it into his senile phase.

Nothing seemed duller to me at that point that cortical morphogenesis. Yet within a few years Sonneborn's doublet work had recruited a new array of talented experimentalists into ciliate work. And even I, who had earlier refused to look at a silver--stained specimen, found myself caught up in the excitement of "cytotaxis", " structural guidance", and "positional information." Sonneborn's demonstration of the role of cellular fabrics in directing the assembly of organelles was a major contribution to biological thought, with applications far beyond the limits of the ciliates (Sonneborn, 1967, 1970a).

Leaving Paramecium morphogenesis in good hands, Sonneborn took up as his last major experimental project, the understanding of yet another apparently trivial phenomenon - the failure of certain long-maintained strains to express an hereditary characteristic they had once manifested. This difference concerned the ability of the cells to discharge their trichocysts. In a characteristically elegant study, Sonneborn demonstrated that these hereditary differences arise as consequences of developmental events in growing new macronuclei (Sonneborn and Schneller, 1979). He connected this phenomenon with the earlier studies on mating type determination, and pointed to editorial alterations of the macronuclear chromatin as the basic mechanism. This work brought Sonneborn back into convergence with a major stream of inquiry. Similar phenomena are now being recognized in many other organisms, in mice and maize and Drosophila, in yeast and Salmonella. The difference is that the phenomena once considered special and confusing, are now considered general and capable of resolution (1977).

After a recent conference on experimental ciliatology, Sonneborn remarked that he felt a little like Moses must have felt, privileged to look into the Promised Land, but not allowed to go in himself.

The more complex systemic properties of cells, and the interactive roles of cell components in cellular heredity, are at last receiving attention; powerful new technologies are resolving mysteries that Sonneborn helped define. The ciliated protozoa will play a role in future advances primarily because T.M. Sonneborn prepared them for such a role (Sonneborn, 1970b). Not just protozoology, but all biology is indebted to him.

## Conclusion

One cannot in half an hour do justice to half a hundred years of distinguished science. I have tried to focus attention on Sonneborn's scientific, and particularly protozoological achievements, but these can scarcely be considered in isolation from his personal characteristics. Sonneborn's personal qualities attracted to experimental ciliatology an international community of superlative investigators, who have in concert achieved far more than he alone could have accomplished.

I recently asked a friend of mine who is a distinguished historian of science, why the concept of "catastrophism" went into eclipse in the early 19th century. It was an exciting idea; it was supported by the simplest reading of the record in the rocks and by the mythologies of many cultures; it was promoted by the brilliant and charismatic Cuvier. Yet the dull but sophisticated concept of "gradualism" won out for a time in favor over catastrophism. A century and a half later were are returning to a serious consideration of saltatory and catastrophic events in the history of life. Why were Cuvier and his ideas passed over? The answer, according to Burkhardt, probably lies in recruitment. Cuvier was unable to attract and sustain vigorous students and colleagues. The uniformitarians, on the other hand, were not dominated by an inhibitory genius, but consisted of a diversified collection of independent and mutually supporting scientists.

Perhaps Sonneborn's most lasting contribution to protozoology has been his recruitment to the protozoa of an exceptional crop of tough-minded, if warm-hearted, experimentalists. He contributed to these recruits a commitment to rigor coupled with an excitement concerning both the organismic particularities and their general extrapolations. Moreover, he established a tradition of mutual respect and cooperation among the workers that is distinctive in a time of personal, professional and national insecurity. The sense of community among ciliate experimentalists is a rare and precious legacy.

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Editor: The material below is probably too personal to be included in the published version. Please use your own best judgement.

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Those of you who knew Tracy Sonneborn realize that the fostering of a sense of community was not Tracy's work alone. He was aided and abetted every step of the way by his companion through the years. When Ruth Sonneborn heard that this session was to be dedicated as a memorial to Tracy, she asked if she could send a brief message, which I hereby transmit:

June 26, 1981

Dear Friends of Tracy and of mine --

Your letters to him while he was ill and to me during these past weeks made us realize how much you are part of our lives, and the scientific quest which you shared with him; as well as the affection and concern which you have given. I hope soon to write to you individually and I do read and reread your messages. I am busy trying

trying to get Tracy's files ready for the library so that some of his life may be available if any of you want reprints or manuscripts. Many of you are represented with correspondence and your own reprints among these papers.

What fortunate people we have been and what a fine spirit of "give and take" has existed among us, from so many different countries, so many different undertakings. Tracy ended his Camerino remarks:

"I think that the future holds promise for ciliate work at every level-from populations to cells, and on down -- but the generation of opportunities and advances, especially the unpredictable ones, depends also on individuals who follow their own curiosities and interests. Good Hunting and Much Joy in the Search."

I hope that this meeting brings you new understandings of your own work and that of your colleagues, and some new vistas.

My gratitude and affection,

Ruth Sonneborn

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