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LEMUEL ROSCOE CLEVELAND

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A Biographical Memoir by

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PROFESSOR CLEVELAND'S scientific work was his life, or so it seemed to his students and colleagues. Always ready to talk science, he rarely revealed anything of his private life. This is unfortunate, since he had an unusual background. Born November 12, 1892 in Newton County, Mississippi, he grew up in this rural area with Indian children as his playmates. He worked on the farm and once remarked that in three years with the same mule he had gotten to know it better than most of his human friends. After two years of high school in Union, Mississippi, he entered the University of Mississippi where he received a B.S. in 1917 and then spent a year as a graduate student and Instructor in zoology. After a brief period of military service he taught at Emory University for two years and at Kansas State College for one year. He then entered Johns Hopkins University where he began the career of highly productive scientific research that terminated only shortly before his death in 1969. After receiving his Ph.D. in 1923 he stayed on at the Hopkins School of Hygiene and Public Health as a National Research Council Fellow until 1925 when he went to the Department of Tropical Medicine at the Harvard Medical School.

It was at Harvard that I had the good fortune to meet L. R. Cleveland and to become his first graduate student. In

the fall of 1930 Cleveland's laboratory was an exciting place. He was just finishing his studies on cultivation of the human dysentery amoeba, *Entamoeba histolytica*. He and his associates had developed a much improved medium in which the entire life cycle of this important parasite could be propagated. They had also made initial attempts at bacteria-free cultivation of amoebae. With characteristic insight, Cleveland recognized the importance of what we now call axenic cultivation, but his efforts toward this end with *E. histolytica* were not successful. (Success in this was not achieved until many years later, with L. S. Diamond's work in 1961.)

Most exciting, however, was the new material Cleveland had brought back from the mountains of Virginia. He had discovered that the large wood-dwelling roach *Cryptocercus punctulatus* contains a seething mass of protozoa in an enlarged portion of its hindgut. All were new species, many representing new genera and new families. But what was especially significant and particularly fascinating to Cleveland was the fact that these protozoa were obviously closely related to the symbiotic intestinal flagellates of termites. The protozoa of termites had been known for many years, but it was Cleveland who first discovered their symbiotic nature. In a series of elegant experiments, done while he was a fellow of the National Research Council at the Johns Hopkins University School of Hygiene, Cleveland showed that the ability of termites to live on a diet of wood or cellulose depends on the digestive capacities of their intestinal flagellates. Termites deprived of these protozoa, but still infected with intestinal bacteria and spirochetes, would die of starvation if fed only wood or cellulose, but they could be saved if reinfected with the protozoa. This was the first instance in which a mutualistic relationship between internal microorganisms and their metazoan host was clearly proved. It was pioneering work

(published in 1923–1928) that paved the way for many later studies on symbiotic microorganisms.

One can easily imagine Cleveland's delight at finding in a different kind of insect, the wood-feeding roach, the same types of protozoa with which he had already been so successful in termites. It did not take him long to establish that the roach *Cryptocercus,* like termites, depends on its intestinal flagellates for its ability to utilize cellulose as its principal food. He then embarked on a detailed study of all the new species of protozoa living in the hindgut of *Cryptocercus.* With the aid of a devoted research assistant, Miss Jane Collier, and of two postdoctoral fellows, Dr. Elizabeth Sanders Hobbs and Dr. S. R. Hall, he soon published a classic monograph (see bibliography, 1934).

Cleveland worked for the rest of his life mainly on taxonomic and experimental studies with the protozoa of *Cryptocercus*. Early in these studies he was the first to see and photograph in a living cell the fibers of the mitotic apparatus. In part because of their large size, certain of the flagellates of *Cryptocercus* provided exceptionally favorable material, but it was Cleveland's exacting microscopy and his application of the then newly available phase contrast methods that led to his beautiful results. He also gave much thought to the role of the centriole and its attendant organelles in cellular division. He produced two monographs (*Trans. Am. Philos. Soc.,* 1949 and 1953) on behavior and structure of chromosomes.

Far exceeding all these observations in general biological importance was Cleveland's discovery of the effect of molting of the host insect on sexual reproduction in its intestinal protozoa. Soon after he began working with *Cryptocercus* he noted cyst formation and various anomalous reproductive stages among the protozoa. There was a period of over five years during which Cleveland published hardly any papers

while he was trying to determine what was really going on. Then came a long series of papers on the sexual cycles of the flagellates of *Cryptocercus* (summarized in a paper in *J. Protozool.*, 3[1956]:161–80). Sex had been unknown in these families of protozoa. Cleveland now showed that the sexual cycle was in all cases related to the molting cycle of the host insect. Some of the protozoa underwent only autogamy, others formed male and female gametes which fused and then underwent zygotic meiosis. Though the timing of these events also differed from species to species, it could always be correlated with molting in the roach. Furthermore, Cleveland showed that injection of an adult roach with a dose of the molting hormone ecdysone too small to induce molting in the insect, nevertheless did induce the sexual cycles of the protozoa. The effect seems to be a direct one by the host hormone on the symbiotic protozoa. In the later stages of his scientific career Dr. Cleveland prepared several excellent cinemicrographs dealing with the sexual cycles of flagellates of *Cryptocercus* and with the structure and movement of these protozoa as well as of protozoa in termites.

Since *Cryptocercus* occurs, in the eastern United States, only in the Blue Ridge Mountains, Cleveland regularly spent his summers at the Biological Station at Mountain Lake, Virginia, and, late in his career, at the Biological Station at Highlands, North Carolina. Here his rural youth surely served him well as he swung his ax to break up logs in the search for colonies of *Cryptocercus.*

Cleveland was elected to the National Academy of Sciences in 1952. He was President of the Society of Protozoologists in 1955 and was an honorary member of the Society. At Harvard, he moved in 1936 from the Medical School to the Biology Department where he was advanced to Professor of Biology in 1946. He became Emeritus Professor in 1959 and, at the invitation of R. B. McGhee, went to the University of

Georgia at Athens. Here he continued his active research. In 1965 he was among the protozoologists who were particularly honored at the Second International Congress on Protozoology in London.

Unlike his triumphant scientific career, Cleveland's personal life was marked with sadness. His first wife, Mabel Bush, whom he married in 1925, died of cancer in 1936, when their daughter, Margaret Elaine, was three years old. Margaret died when only twenty-five.

Cleveland's second marriage, to Dorothy Eleanor Colby, was more fortunate. She, and their son, Bruce Taylor Cleveland, a physicist, survive.

Cleve, as we called him, was dearly loved by his friends and family. He was sometimes difficult, but only because completely honest men are likely to be difficult. He will be remembered mainly, however, for his great body of scientific achievement, and this is surely the way he would want it to be.

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