Chapter 9

The Life Cycle, Longevity, and Aging

A. BACKGROUND

Over a century ago, Ehrengerg (1838) came to the conclusion that the protozoa are potentially immortal. Later, Weismann (1891) stated that the protoplasm or cells of a metazoan animal could be classified into two groups, namely, the body or somatic protoplasm and the germinal protoplasm. He proposed the idea that the former is mortal but the germinal protoplasm is potentially immortal. Weismann contended that old age and natural death are penalties demanded of the metazoa, including man, because of their specialization and differentiation into somatic and germinal protoplasm, whereas the protozoa, without this protoplasmic specialization, are potentially immortal like the germ cells.

An examination of the many different species that make up this large, diverse division, the protozoa, shows a wide range of well-defined differences among them. Some groups, like flagellates and especially amebas, are far less structurally complex than are ciliates as exemplified by Paramecium. In addition, some, like Paramecium, have extremely complex sexual stages (autogamy, cytogamy, conjugation) that are lacking in the former groups. There is evidence that certain flagellates and amebas do indeed have the capacity to multiply indefinitely provided they have a sufficient food supply and their other physiological needs are met.

For the amebas, I cite two excellent examples of potential immortality adduced by a former associate, the late Professor A. A. Schaeffer (1883–1981), long an outstanding student of amebas. He maintained a clone of Chaos diffluens (also called Amoeba proteus) in continuous cultivation for over 58 years and clones of the giant multinucleate ameba, Chaos chaos (also called Chaos carolinensis), for more than 30 years, after which the cultures were discontinued (Wichterman, 1976). This is very likely a record in biology whereby clonal cultures of single species of protozoa have been maintained continuously and personally by one researcher. It may also be considered a long-term experiment in clonal longevity that proves unequivocally that there is no fixed life-span for these common, asexually reproducing amebas.

That amebas can multiply indefinitely when maintained in culture
with a food supply that permits logarithmic vegetative multiplication was also reported by Danielli and Muggleton (1959), Muggleton and Danielli (1968), and Muggleton-Harris (1979). However, they reported that if the amebas are kept for a time on a limited food supply and then transferred to the optimum diet, their life-span is variable, extending from 30 days to 30 weeks. This life-span was said to be dependent on the conditions of exposure to the deficient food source. It occurs to me that when the amebas were placed on the restricted or limited food source, an artificial, unnatural situation was created. Also, to test for longevity and life-spans in animals, optimum nutritional needs must be provided.

While potential immortality may be demonstrated with amebas, many early workers questioned this concept as applied to the structurally complex ciliates like *Paramecium*. Hertwig (1888 a,b, 1889a,b, 1892), Maupas (1888, 1889), Joukowsky (1898), Simpson (1901a,b, 1902), Calkins (1902c, 1904, 1906a), and others maintained that ciliates in isolation cultures passed through several hundred or more generations over a period of 3 or more months in which the fission rate ultimately decreased until the animals died. It was therefore concluded that the ciliates completed their life cycle or life-span, then died a natural death. Calkins (1913–1933) believed that youth, adolescence, and old age are characteristic stages in the ciliate’s life history, with conjugation being a part of adolescence. It was his opinion that conjugation or autogamy (which he called endomixis) may postpone old age. In light of our present knowledge of aging in some species of *Paramecium*, this is a most precocious concept. Calkins reported that old specimens of *P. caudatum* that had not conjugated for a long period of time were characterized by hypertrophy of the macronucleus, loss of trichocysts in the cortex, and abnormal division stages leading to monster formation. Takagi and Yoshida (1980) found somewhat similar abnormalities in their study of carefully controlled isolation cultures of *P. caudatum* (Figure 9.1). Later investigators, including Sonneborn (1938, 1954), Nanney (1974, 1980), and Smith-Sonneborn (1976, 1981), reported that clones of the *P. aurelia* complex are incapable of multiplying indefinitely by asexual reproduction. Accordingly, it was claimed that old age, a natural condition of protoplasm, was applicable to ciliate protoplasm as well as metazoan, both following the same physiological laws of aging.

**B. ISOLATION CULTURES AND CLONAL AGING**

To study clonal aging, single paramecia—usually following a sexual process—are isolated and placed in a favorable growth medium. This may be a buffered lettuce medium with a bacterial food source (*Klebsiella aerogenes*) or an axenic medium. The isolated paramecia are allowed to