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This Week's Citation Classic®

Schuster F. An electron microscope study of the amoebo-flagellate, *Naegleria gruberi* (Schardinger). I. The amoeboid and flagellate stages. *J. Protozoology* 10:297-313, 1963.
[Langley Porter Neuropsychiatric Institute, San Francisco, CA]

The ultrastructure of the ameboid and flagellate stages in the *Naegleria gruberi* life cycle is described in this paper, as are the events involved in formation of the flagellar apparatus and its constituent parts. [The *SCI*® indicates that this paper has been cited in over 145 publications.]

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This *Citation Classic* resulted from my doctoral dissertation in zoology at the University of California, Berkeley. My mentor, the late Bill Balamuth, was interested in the ameboflagellate protozoa, of which *Naegleria gruberi* is an example. Although basically amebas, they transform into flagellates upon appropriate induction. Balamuth suggested that I work on the *Naegleria* transformation. After first getting the organism into axenic cultivation, I began a study of the flagellation response using the transmission electron microscope.

In other cell types where flagella form, basal bodies (or kinetosomes) arise from preexisting centrioles (as in sperm cells) or from preexisting basal bodies that may function either as kinetosomes or as centrioles (as in some flagellated protozoa). The prevailing dogma held that flagellar basal bodies formed *only* from preexisting units present in the cell. This view was reinforced by earlier studies on ciliated protozoa where new kinetosomes were reported to arise from preexisting kinetosomes by division.

It was evident from microscopy of transforming amebas that neither basal bodies, centrioles, nor any portion of the flagellar apparatus were present at the onset of the transformation. Thus, it appeared that basal body origin in *Naegleria* differed markedly from the generally accepted sequence in not having the obligatory precursor.

This apostasy did not pass unnoticed. A recurring criticism was that precursors were present in the ameba, but I just hadn't found them. Having read somewhere that one couldn't fully understand an electron microscope problem without having taken at least 2,000 micrographs, I dutifully achieved that number, and then, feeling reasonably confident that conventional precursors were not present, I wrote up my thesis. For fellow graduate students and my mentor, whose eyes would glaze as I approached with yet another pile of electron micrographs, this was probably a profound relief.

At face value, the study was just another ultrastructural description of an organism. What saved it from neglect and made it a *Citation Classic* was, in all likelihood, the link between morphogenesis and the *de novo* origin of flagellar basal bodies. This came at a time when interest was shifting from purely descriptive studies of organelles to concern about their origins and development. Other papers appeared over the next several years redefining the origins of basal bodies in protozoa as well as in ciliated epithelial cells. Bradbury and Pitelka, for example, repeated at the electron microscope level one of the earlier studies on kinetosome origin in ciliates, and they showed that new basal bodies did indeed arise alongside of preexisting units, but not by division.[1] A 1979 review updates research on the ameboflagellate transformation.[2] Recent studies by Fulton[3] and Walsh[4] have focused on the molecular events involved. I still work with *Naegleria*; it continues to surprise, and occasionally delights.

1. **Bradbury P & Pitelka D R.** Observations on kinetosome formation in an apostome ciliate. *J. Microscopie* 4:805-10, 1965.
2. **Schuster F L.** Small amebas and ameboflagellates. (Levandowsky M & Hutner S, eds.) *Biochemistry and physiology of protozoa.* New York: Academic Press, 1979. Vol. 1. p. 215-85.
3. **Fulton C.** Macromolecular syntheses during the quick-change act of *Naegleria. J. Protozoology* 30:192-8, 1983.
4. **Walsh C.** Synthesis and assembly of the cytoskeleton of *Naegleria gruberi* flagellates. *J. Cell Biol.* 98:449-56, 1984.