

The Uses of Apoptosis

Apoptosis, programmed cell death, is a mechanism often used to remove cells that are superfluous, dangerous (as is the case of lymphocytes that would destroy body tissues), or no longer needed. Here, we discuss two cases of apoptosis where the cells are no longer needed either developmentally or evolutionarily.

I. The case of the dead sisters

One of the principles of biology (and Western literature, for that matter) is that some die so that others may live. (Try that for your next term paper: "Sacrificial death in the works of Dickens, Tolstoy, David Kirk, and Hermann Steller.") McCall and Steller (1998) have shown that apoptosis of the nurse cells is a critical component of oocyte development in *Drosophila*.

The *Drosophila* ovary consists of egg chambers, each of which contains 16 sister germline cells. These cells have a common precursor cell and remain interconnected through cytoplasmic bridges, the ring canals. One of these 16 cells becomes the oocyte, while the others develop into nurse cells that are linked to the oocyte by these ring canals. The nurse cells become polyploid and synthesize mRNA, ribosomes, and proteins, all of which become actively transported through the ring canals and into the oocyte. Several hours later, the oocyte, now full of yolk, ribosomes, proteins, and mRNAs from the nurse cells, finishes its meiotic divisions. The nuclei of the nurse cells, no longer needed after the marathon of transcription, decompose, and the nurse cells die.

The cells die from apoptosis, and McCall and Steller have shown this by making mutations for a gene necessary for apoptosis, the caspase gene *dcp-1*. Those flies whose germlines were deficient in *dcp-1* were found to be sterile. The egg chambers of these sterile females turned out to be extremely interesting. First, they did not all undergo the normal apoptosis, and second, they did not transfer their contents to the oocyte. It appears that these cells transfer their contents as they die. If they do not die, their membranes do not contract, and their cytoskeleton does not reorganize for transport.

It appears, then, that the apoptosis process is critical for the transport of material from the nurse cells into the oocyte. As the authors of this paper conclude, "Finally, this process is a clear example of how a single cell, the oocyte, uses the death of its sister cells to develop properly."

II. The case of the blind fish

In the cases of salamanders, crabs, and fish that live in dark caves, eyes are not needed. Indeed, most cave dwelling animals whose ancestors had been on land lose their eyes and their pigmentation, while all other features of their body remain the same. It appears that another principle of biology (and physics and politics, for that matter) is illustrated here: if you don't select for the maintenance of a structure, that structure will be lost. Eyes are "expensive" to make and maintain. The body has to construct different cell types and the borders distinguishing them. If eyes are not required--that is to say, if they are not adaptive to the individual having them--then they will be lost by random mutation. Jeffery and Martasian (1998) have looked at eyed (surface dwelling) and eyeless (cave-dwelling) populations of the fish *Astyanax mexicanus*. This species is unusual in that it has a surface-dwelling form with large eyes and also several isolated cave populations of *eyeless*

members the same species (Cahn, 1958; Avise and Selander, 1972). Thus, one can directly compare the eye development of the surface and cave members of the species (Figure 1).

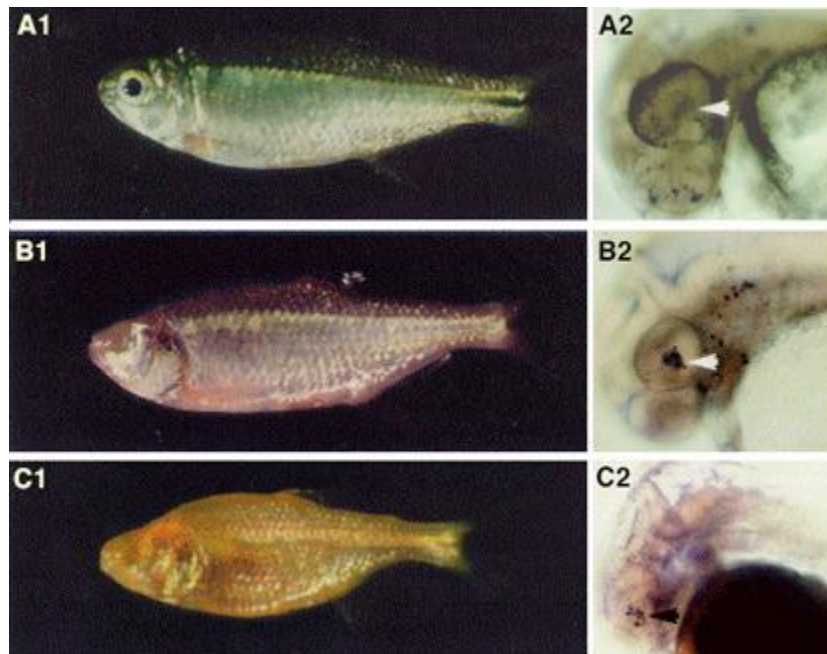


Figure 1 Surface dwelling (eyed) and cave-dwelling (eyeless) forms of *Astyanax mexicanus*. Adjacent to them are sections of the embryonic eyes, stained with a reagent (TUNEL) that binds to and stains DNA fragments produced by apoptosis. A1. Surface form with eyes and pigmentation. A2. 25 hour embryo of surface form, showing very little apoptosis in the lens. B1. Cavefish from La Cueva Chica with reduced eyes and reduced pigmentation. B2. 25 hour embryo of the Chica cave-dwelling form, showing severe apoptosis in the lens vesicle (arrowhead). C1. Cavefish from Cueva de El Pachón showing neither eye nor pigmentation. C2. Apoptosis in lens and corneal epithelium in the 25 hour embryo of the Cueva de El Pachón cavefish. (After Jeffery and Martasian, 1998.)

Molecular data show that some of the eyed surface members of *Astyanax* entered caves during the Pleistocene period. *Astyanax* populations with absent or reduced eyes have been found in 29 different caves in eastern Mexico, and surface populations still exist in ponds in the vicinity of these caves. Jeffery and Martasian found that the cavefish embryos begin forming eyes, developing an optic primordium consisting of a lens vesicle and optic cup. However, this is as far as the eye gets, and instead of developing into lens and retina, the tissues undergo apoptosis (Figure 2).

There is still controversy over what forces (or lack of them) cause the loss of structures in the evolution of cave animals (see Culver, 1982). However, knowledge of the proximate causes by which these changes occur might provide us with clues as to what factors are important and what factors are not.

Literature Cited

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