The Evolution of Developmental Patterns in Unicellular Protists

Every living organism develops. Development can be seen even among the unicellular organisms. Moreover, by studying the development of unicellular protists, we can see the simplest forms of cell differentiation and sexual reproduction.

Control of developmental morphogenesis: The role of the nucleus

A century ago, it had not yet been proved that the nucleus contained hereditary or developmental information. Some of the best evidence for this theory came from studies in which unicellular organisms were fragmented into nucleate and anucleate pieces (reviewed in Wilson 1896). When various protists were cut into fragments, nearly all the pieces died. However, the fragments containing nuclei were able to live and to regenerate entire complex cellular structures.

Nuclear control of cell morphogenesis and the interaction of nucleus and cytoplasm are beautifully demonstrated in studies of Acetabularia. This enormous single cell (2-4 cm long) consists of three parts: a cap, a stalk, and a rhizoid (Figure 2.5A; Mandoli 1998). The rhizoid is located at the base of the cell and holds it to the substrate. The single nucleus of the cell resides within the rhizoid. The size of Acetabularia and the location of its nucleus allow investigators to remove the nucleus from one cell and replace it with a nucleus from another cell. In the 1930s, J. Hammarling took advantage of these unique features and exchanged nuclei between two morphologically distinct species, A. mediterranea* and A. crenulata. As Figure 2.5A shows, these two species have very different cap structures. Hammarling found that when he transferred the nucleus from one species into the stalk of another species, the newly formed cap eventually assumed the form associated with the donor nucleus (Figure 2.5B). Thus, the nucleus was seen to control Acetabularia development.

The formation of a cap is a complex morphogenetic event involving the synthesis of numerous proteins, which must be accumulated in a certain portion of the cell and then assembled into complex, species-specific structures. The transplanted nucleus does indeed direct the synthesis of its species-specific cap, but it takes several weeks to do so. Moreover, if the nucleus is removed from an Acetabularia cell early in development, before it first forms a cap, a normal cap is formed weeks later, even though the organism will eventually die. These studies suggest that (1) the nucleus contains information specifying the type of cap produced (i.e., it contains the genetic information that specifies the proteins required for the pro-

*After a recent formal name change, this species is now called Acetabularia acetabulum. For the sake of simplicity, however, we will use Hammarling’s designations here.

Figure 2.5

(A) Acetabularia crenulata (left) and A. mediterranea (right). Each individual is a single cell. The rhizoid contains the nucleus. (B) Effect of exchanging nuclei between two species of Acetabularia. Nuclei were transplanted into enucleated rhizoid fragments. A. crenulata structures are darker, A. mediterranea structures lighter green. (Photographs courtesy of S. Berger.)
duction of a certain type of cap), and (2) material containing this information enters the cytoplasm long before cap production occurs. This information in the cytoplasm is not used for several weeks.

One current hypothesis proposed to explain these observations is that the nucleus synthesizes a stable mRNA that lies dormant in the cytoplasm until the time of cap formation. This hypothesis is supported by an observation that Hämmerling published in 1934. Hämmerling fractionated young *Acetabularia* into several parts (Figure 2.6). The portion with the nucleus eventually formed a new cap, as expected; so did the apical tip of the stalk. However, the intermediate portion of the stalk did not form a cap. Thus, Hämmerling postulated (nearly 30 years before the existence of mRNA was known) that the instructions for cap formation originated in the nucleus and were somehow stored in a dormant form near the tip of the stalk. Many years later, researchers established that nucleus-derived mRNA does accumulate in the tip of the stalk, and that the destruction of this mRNA or the inhibition of protein synthesis in this region prevents cap formation (Kloppstech and Schweiger 1975; Garcia and Dazy 1986).

It is clear from the preceding discussion that nuclear transcription plays an important role in the formation of the *Acetabularia* cap. But note that the cytoplasm also plays an essential role in cap formation. The mRNAs are not translated for weeks, even though they are in the cytoplasm. Something in the cytoplasm controls when the message is utilized. Hence, the expression of the cap is controlled not only by nuclear transcription, but also by the translation of the cytoplasmic RNA. In this unicellular organism, “development” is controlled at both the transcriptional and translational levels.

**WEBSITE 2.3 Protist differentiation.** Three of the most remarkable areas of protist development concern the control of sex type in fission yeast, the transformation of *Naegleria* amoebae into streamlined, flagellated cells, and the cortical inheritance of the cell surface in paramecia.

**Unicellular protists and the origins of sexual reproduction**

Sexual reproduction is another invention of the protists that has had a profound effect on more complex organisms. It should be noted that sex and reproduction are two distinct and separable processes. Reproduction involves the creation of new individuals. Sex involves the combining of genes from two different individuals into new arrangements. Reproduction in the absence of sex is characteristic of organisms that reproduce by fission (i.e., splitting into two); there is no sorting of genes when an amoeba divides or when a hydra buds off cells to form a new colony.

Sex without reproduction is also common among unicellular organisms. Bacteria are able to transmit genes from one individual to another by means of sex pili. This transmission is separate from reproduction. Protists are also able to reassort genes without reproduction. Paramecia, for instance, reproduce by fission, but sex is accomplished by conjugation. When two paramecia join together, they link their oral apparatuses and form a cytoplasmic connection through which they can exchange genetic material (Figure 2.7). Each macronucleus (which controls the metabolism of the organism) degenerates, while each micronucleus undergoes meiosis to produce eight haploid micronuclei, of which all but one degenerate. The remaining micronucleus divides once more to form a stationary micronucleus and a migratory micronucleus. Each migratory micronucleus crosses the cytoplasmic bridge and fuses with (“fertilizes”) the stationary micronucleus, thereby creating a new diploid nucleus in each cell. This diploid nucleus then divides mitotically to give rise to a new micronucleus and a new macronucleus as the two partners disengage. Therefore, no reproduction has occurred, only sex.

The union of these two distinct processes, sex and reproduction, into sexual reproduction is seen in unicellular eukaryotes. Figure 2.8 shows the life cycle of *Chlamydomonas*. This organism is usually haploid, having just one copy of each chromosome (like a mammalian gamete). The individuals of each species, however, are divided into two mating types: plus and minus. When a plus and a minus meet, they join their cytoplasmic nuclei to form a diploid zygote.