A. CILIARY MOVEMENT AND LOCOMOTION

From the time of the discovery of cilia by Leeuwenhoek three centuries ago, many investigators have been fascinated with cilia and how they move. As a result, an enormous amount of research has been done in an effort to explain ciliary movement and locomotion in Paramecium. (For detailed information on the structure, organization, and distribution of cilia on the body of Paramecium, refer to Chapter 2.)

When analyzed, the movement of a cilium is observed to consist of two parts: first, a power or effective stroke; second, a recovery stroke (Figure 6.1). In an actively swimming Paramecium, the cilium, during its power stroke, moves as a fairly rigid rod, though it bends throughout its length and strikes the water in such a manner that the organism tends to move in a direction opposite to that of the power beat. In the faster recovery stroke, the cilium moves in a greatly flexed condition, thereby exposing considerably less surface to the resistance of the water.

The cilia are arranged in longitudinal or oblique rows, or kineties, on the body of Paramecium, and although these locomotor structures move at the same rate, they do not beat in the same phase. If the behavior of a single cilium in a single row of cilia is studied, it will be noted that the cilium is in a slightly advanced stage of beating relative to the one just behind it and in a slightly retarded stage relative to the one just in front of it, so that taken collectively, the cilia, moving in a characteristic wave-like manner, are said to beat metachronally (see Figures 6.1e, 6.2, 6.3, and 2.11). This appearance is generally likened to the wavelike motion of a field of grain or tall grass on a windy day. The crests of the ciliary waves moving in this metachronal manner are cilia at the peak of their power stroke, while the troughs are cilia at or near the beginning of their recovery stroke. However, cilia in the same transverse row beat synchronously or almost so.

Why does the explanation of ciliary motion present such a complex problem to investigators? A number of obstacles are present: (1) Size—
They are extremely thin (≈0.3 μm in diameter) and relatively small. (2) **Number**—They are compactly arranged in a circumscribed area. (3) **Visibility**—Being clear and optically homogeneous in the living condition, they lack sharp contrast against the animal’s background and are best observed in profile. (4) **Movement**—The greatest difficulty of all is that the three-dimensional ciliary beat is too rapid for detailed study and analysis with the naked eye.

This last problem has been attacked in recent years by investigators using a variety of methods and instruments that have resulted in important discoveries in ciliary beating and metachronal wave systems. The studies involved a “rapid fixation technique” (Párducz, 1955), the use of the scanning electron microscope (SEM) (Tamm, 1972), and the use of ultra-high-speed cinematography (Kúznicki et al., 1970) and flash photography of living paramecia (Machemer, 1974a). In the important technique of rapid fixation, swimming animals are fixed (killed) instantaneously and their ciliary beat pattern and metachronal wave system then studied and analyzed. In this manner, both a profile and a surface view can be obtained that reveal cilia “stopped” in motion not shown by previous methods (Figures 6.3 and 6.4).

Almost identical to the findings of Párducz are the more detailed studies of Tamm, who employed the SEM, which is ideally suited for observing the three-dimensional surface of cells. Also using the instantaneous fixation method with *P. multimicronucleatum* and utilizing special procedures, he was able to faithfully preserve and study the ciliary beat. By analyzing the micrographs, Tamm reconstructed the positions of successive cilia in a forward-swimming paramecium through a single

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**Figure 6.1.** Diagrams illustrating ciliary movements. (A–D) Movement of a single cilium showing the recovery or preparatory stroke (A) and the beginning of the power or effective stroke (B) for more rapid movement than shown in (C) and (D). (E) A longitudinal row, or kinety, of cilia showing metachronous movement. From Kudo (1966).