CHAPTER 14
GLIDING MOTILITY, PROTONMOTIVE FORCE MOTOR, AND FLAGELLAR ROTATION

1. MODELS FOR GLIDING MOTILITY
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Key ideas

The isolated sacculus of *Escherichia coli* can be expanded from its minimum surface area by lowering or raising the pH. The chemiosmotic process can lower the pH by several units just outside of the cytoplasmic membrane. These facts suggest a model for gliding motility of Gram-negative microorganisms based on the assumption that the volume enclosed by the sacculus is normally enlarged by chemiosmotic extrusion of protons. It is postulated here that a gliding cell is able to control special shunts that allow protons to return freely to neutralize the excess negative charges remaining inside the cell and it does so in local regions at controlled intervals. When these shunts are activated, a series of physical processes occur which result in the shrinkage of the regions where the special shunts are functional, and slight expansion where they are not functioning. This expansion wedges the cell in the substratum by favoring hydrogen bonds between the cell surface and the environmental surface or slime layers. When the shunts are periodically turned off, the volume changes are reversed, and the cell inches forward. This murein expansion/contraction could be a prokaryotic mechanoenzymes substitute. It could be also the basis of rotation of the motor mechanism for motility in flagellar organisms.
1. MODELS FOR GLIDING MOTILITY

Various bacteria move by gliding motility. The prokaryotes that do this come from a wide variety of morphological and taxonomic classes. Four characteristics seem to unify the process (see Burchard, 1981; Pate, 1988); (i) the organisms are all Gram-negative; (ii) gliding motility requires a suitable surface; (iii) slime may be an essential component of that surface; and (iv) the process is powered by chemiosmosis. There appear to be no other common elements. When these Gram-negative bacteria are viewed microscopically, the means of motion are not evident since flagella are undetectable and their presumed sinusoidal movements are not detected. These observations have increased, rather than decreased, the number of proposed mechanisms. Earlier models, reviewed by Burchard (1981), have invoked forces such as osmotic pressure, surface tension, slime secretion, and contractile cell-surface waves. Other models involve the retraction of fimbriae (MacRae and McCurdy, 1976), make-and-break of envelope interactions with the substrate (Dickson et al., 1986), and "electrokinetic" phenomena. Dworkin and associates (Dworkin et al., 1983; Keller et al., 1983) introduced a model of surfactant release, Pate and Chang (1979) have suggested rotary motors, and Lapidus and Berg (1982) have imagined that gliding cells have continuous tracks under the outer membrane that revolve around the cell. A variant has been proposed by Ridgway and Lewin (1988) in which the limited motion of many mechanically independent domains is functionally coordinated.

I have proposed one more mechanism (Koch, 1990), based on observations of the elasticity of the peptidoglycan of a Gram-negative cell (Woeste and Koch, 1992; see Chapter 10) and the change in size of the isolated sacculus when the net charge is altered. Mainly the model is applied to organisms like Myxococcus and Cytophaga. But variation can be applied to other cases of gliding motility and the mechanism may power the more common flagellar motility typical of E. coli (see below).

2. MODELS FOR GLIDING MOTILITY

The extrusion of protons by the chemiosmotic mechanism is known to be the source of energy for gliding motility as it is for flagellar motility. See Pate (1988) and Khan (1988) for reviews of flagellar motility. Proton extrusion coupled to photosynthetic and non-photosynthetic electron transport lowers the pH immediately outside the membrane relative with the pH in the medium (Koch, 1986). In the first several nanometers inside the membrane, it also raises the pH relative to the bulk of the cytoplasm of the cell. The pH changes are calculated to be several pH-units different than the nearby bulk phases. The effect on the