Prokaryotic Locomotion

It transpires that the flagellar mechanisms used for propulsion by prokaryotic organisms (bacteria) are fundamentally different from those used by the larger eukaryotic organisms even though they may superficially appear similar. We begin with a description of the propulsive structure and function of prokaryotic cells. The flagella of bacteria are composed of a helical protein, flagellin. From one to eleven strands of flagellin coil together to form a single flagellum sheath (Gerber 1975) which has an amorphous core and a radius of $1.2 - 2.0 \times 10^{-6} cm$. Both motile and fixed-and-stained flagella form a helix that has a pitch range of $1.5 - 2.5 \times 10^{-4} cm$ (Lowy & Spencer 1968). Each flagellum is attached to the cell at its base; the attachment site, called the "hook-basal body complex" (DePamphilis & Adler 1971), consists of four rings around the flagellar cylinder, each $2.25 \times 10^{-6} cm$ in diameter as shown in Figure 1. The most important of these rings are apparently the S and M rings, which are located at the base of the hook.
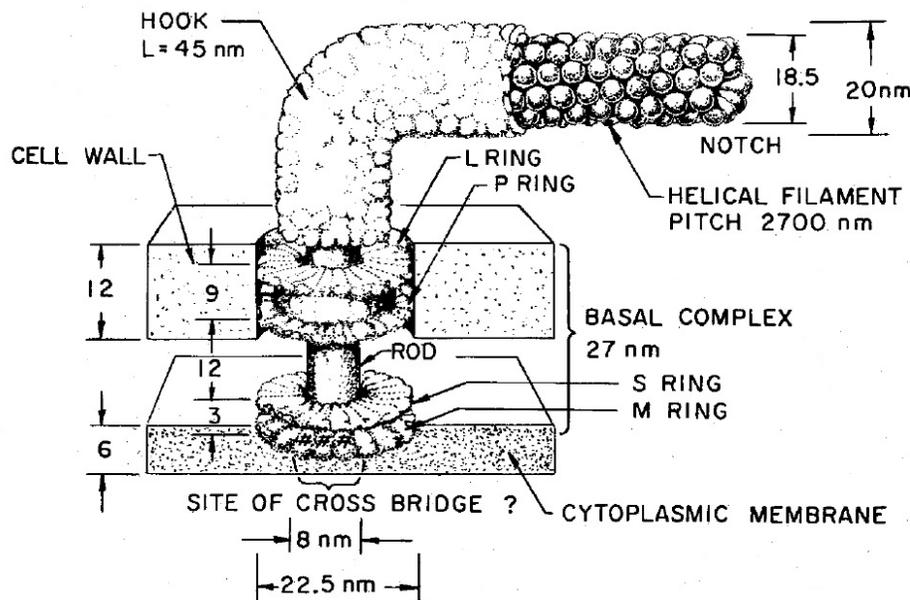

Figure 1: The hook-basal body complex at the junction of a prokaryotic cell and its flagellum. In the rotating-shaft models motion is presumed generated between the M and S position of the hook and the cytoplasmic membrane. Possible sites of cross-bridges for a model analogous to the muscle-sliding mechanism have been indicated. Adapted from Routledge (1975).

The contractile mechanism for bacterial flagella has been a subject of recent controversy (Routledge 1975). Doetsch (1966) first proposed the rather startling hypothesis that the material of the flagellum rotates relative to the cell body, indeed that the hook rotates in the cell wall, thus providing a unique example in nature of continuous rotational deformation. Berg & Anderson (1973) and Berg (1974, 1975) have further examined the evidence for, and apparent quantitative features of, this bacterial motor system. The motor seems to consist of rotation of the S and M rings with the flagellum that they carry being driven by some mechano-chemical process, presumably akin to the cross-bridge-stepping of heavy meromyosin on actin in striated muscle (Berg & Anderson 1973). However, some recent evidence (Larsen *et al.* 1974) indicates that ATP is not the energy source for this process, so cross-bridge models may be premature. Nevertheless, the basic model of a bacterial flagellar motion appears to be gaining acceptance (Silverman & Simon 1974) at the expense of alternative hypotheses that the contraction consists of a helical wave passing along the
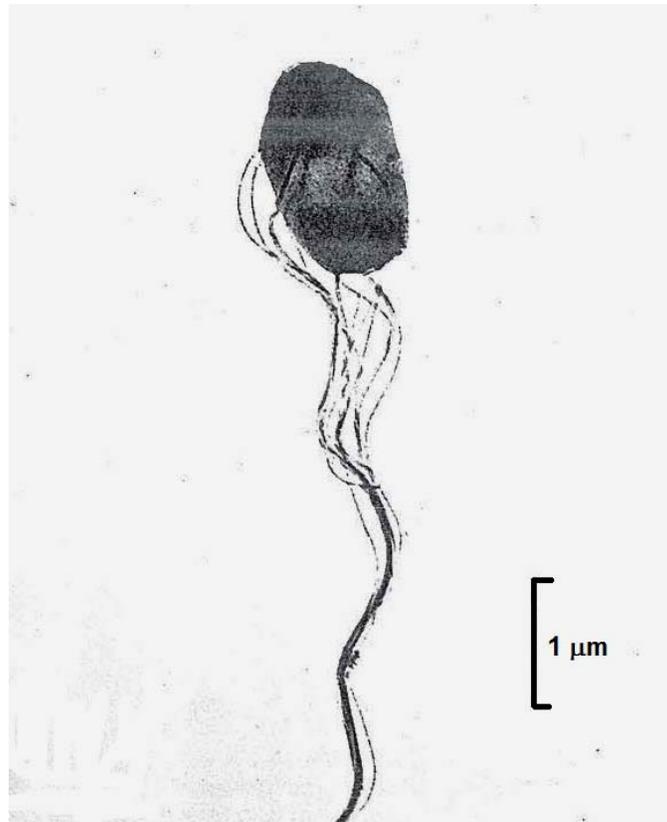
Figure 2: The flagellated bacterium *Salmonella abortus-equi* with its flagella bent aftward and associated in a flagellar bundle (Routledge 1975). This is a fixed specimen. The swimming organism would show less clearance between flagella. Adapted from Routledge (1975).

flagellum due to propagation of dislocations in the molecular structure of the outer sheath (Harris 1973, Calladine 1974). In terms of the external hydromechanics of the helical flagellum the two models differ only in the material motion of the surface of the flagellum. In the basal motor hypothesis the flagellum is basically like a rigid corkscrew rotating relative to the head; in the wave-propagation model the material of the flagellum does not rotate relative to the material of the cell body, but the helix is formed by the helical conformation of the propagated wave. Unless one can observe the material rotation of the flagellum, the two motions appear identical and thus it is difficult to distinguish between them.

Many bacteria (e.g. *Escherichia coli*, *Salmonella*) have several flagella attached at points distributed over the surface of the cell (see Figure 2). When such bacteria are swimming, the separate flagella come together in a synchronous flagellar bundle, which propels the cell (Iino & Mitani 1966). In some strains, periods of concerted swimming are interrupted by brief periods of erratic wobbling ("twiddling"), which may be caused by the fact that the bundle has come apart and each flagellum is acting independently (Macnab & Koshland 1972, Adler 1976). Anderson (1975) discusses the qualitative hydromechanical features of the formation of flagellar bundles.

The close association of rotating flagella in the bundle clearly implies the presence of lubricating layers of fluid between the individual flagella and thus a significant fluid resistance internal to the bundle, especially in the basal motor model; to our knowledge the hydromechanics of this situation has not as yet been closely examined quantitatively, although Berg & Anderson (1973) discount it. Viewed from the exterior fluid the flagellar bundle could be considered as a single slender body whose mean surface rotates relative to the head if the basal motor model is assumed. Thus, whether the principal propulsive unit is a single flagellum or a bundle, will have relatively minor effects on the external hydromechanics within the context of a

particular contractile process. Finally, it is noteworthy that many bacteria exhibit an increased motility with small increases in viscosity of the surrounding medium and a subsequent decrease with larger increases in viscosity (Schneider & Doetsch 1974 and Shoesmith 1960).

The rotation of the prokaryotic flagellum relative to the cell body, as illustrated in Figure 3, gives rise to
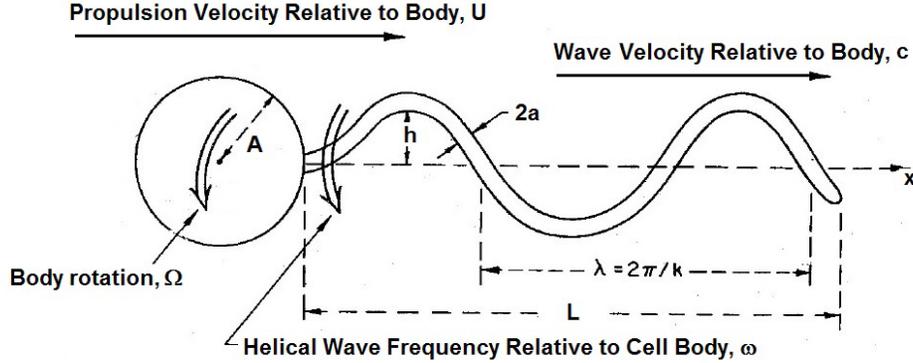

Figure 3: Flagellar propulsion with a helical waveform.

a torque about the longitudinal axis of the organism; this causes the cell body to rotate so that an equal and opposite torque on the cell body is generated and the total torque on the organism is zero as it must be from mechanical first principles. Therefore a complete solution for the mechanics in which both the condition of zero total longitudinal force and the condition of zero total torque are satisfied yields both the ratio of the forward speed, U, to a speed associated with the relative rotation at the cell/flagellum junction, but also the ratio of the angular velocity of spin of the cell body, Ω, to the angular velocity of rotation of the flagellum relative to cell body, ω: λ is the wave length of the helical wave). These interconnected results are

$$\frac{c}{U} = \frac{1 + 2k^2h^2 + A^*}{k^2h^2}\left\{1 + \frac{2(1+k^2h^2)^2 + (2+k^2h^2)A^*}{(1+2k^2h^2+A^*)B^*}\right\} \tag{Dff1}$$

$$-\frac{\omega}{\Omega} = 1 + \frac{(1+2k^2h^2+A^*)B^*}{2(1+k^2h^2)^2 + (2+k^2h^2)A^*} \tag{Dff2}$$

where we have changed the sign of the second expression by defining values of ω and Ω to be positive in the same rotational sense in order to highlight the fact that, as a result of the torque balance, ω and Ω are naturally of opposite sign. In the above expressions h is the radius of the flagellum helix, λ is the pitch of the helix (see figure 3 and note that $k = 2\pi/\lambda$) and

$$A^* = \frac{3\mu A(1+k^2h^2)^{1/2}}{2\pi LC_s} \quad \text{and} \quad B^* = 4\mu\frac{\pi a^2 + A^3(1+k^2h^2)^{1/2}/2\pi L}{h^2 C_s} \tag{Dff3}$$

where A is the radius of the cell body (assumed spherical), L is the distance from the cell body to the end of the flagellum, a is the radius of the circular cross-section of the flagellum, and C_s is the tangential resistive coefficient. It has been assumed that $\gamma = C_n/C_s$ was equal to $1/2$.

It is valuable to take note of the difference between this analysis and that for a eukaryotic organism propagating a helical wave along its flagellum (see next section). The analysis (and therefore the results presented here and in the next section are essentially identical. The only difference in the mechanics is the rotation of the material of the surface of the flagellum about the longitudinal axis down the center of the flagellum. This material rotation generates a torque which differentiates the two analyses. However this torque is minor compared with the torque arising from the lateral motion of the flagellum which is

the same in both cases. The former is proportional to the velocity ωa (or Ωa) whereas the major torque is proportional to the velocity ωh (or Ωh) and since $a \ll h$ the minor is much smaller than the major torque. Therefore the minor torque has been neglected in both analyses and, consequently, the analyses are identical.

These above results, (Dff1) and (Dff2), exhibit interesting asymptotic limits; with a vanishingly small head $(A \to 0)$ the forward propulsion given by U/c will become small and the material tends to rotate with a velocity, Ω, almost equal and opposite to the angular wave velocity, ω. On the other hand, for a large cell body Ω tends to zero, but the propulsive velocity again becomes small due to the large drag on the cell body.

Shimada, Yoshida & Asakura (1975) made a complete set of measurements for the bacteria *Salmonella* (many flagella forming a bundle) and *Pseudomonas* (single flagellum) and compared their observations with the expressions (Dfc8) and (Dfc9). The proper comparison might be with the expressions modified as suggested above; nevertheless, it is of interest to observe that while the agreement in the case of *Pseudomonas* appeared reasonable, the theory gave significantly lower values for U/c than those observed for the multiflagellated *Salmonella*. Although other explanations are possible, these results suggest that the effective γ for a flagellar bundle may be significantly less than $1/2$, a not unreasonable possibility.