

The Junctional Pore Complex and the Propulsion of Bacterial Cells

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Key Words

Gliding motility · Cyanobacteria · Myxobacteria · Junctional pore complex

Abstract

Gliding motility is defined as translocation in the direction of the long axis of the bacterium while in contact with a surface. This definition leaves unspecified any mechanism and, indeed, it appears that there is more than one physiological system underlying the same type of motion. Currently, two distinct mechanisms have been discovered in myxobacteria. One requires the extension, attachment, and retraction of type IV pili to pull the cell forwards. Recent experimental evidence suggests that a second mechanism for gliding motility involves the extrusion of slime from an organelle called the 'junctional pore complex'. This review discusses the role of slime extrusion and the junctional pore complex in the gliding motility of both cyanobacteria and myxobacteria.

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Introduction

Prokaryote propulsion is bewilderingly diverse. Many bacteria swim through fluids by rotating a long helical flagellum driven by a rotary motor [Namba and Vonderviszt, 1997; Berg, 2003]. Other bacteria, such as *Synechococcus* [Waterbury et al., 1985] and *Spiroplasma* [Gilad et

al., 2003], are themselves helical and swim using mechanochemical filaments [Trachtenberg et al., 2003; Wolgemuth et al., 2003]. Cells that move on solid surfaces use other mechanisms. One such motion, generically called 'gliding motility', refers to translocation in the absence of any visible propulsive organelle. This led Reichenbach [1981] to propose the deliberately vague definition as 'translocation in the direction of the long axis of the bacterium while in contact with a surface'. Many different bacterial species glide, including cyanobacteria, myxobacteria, flexibacteria, mycoplasmas, Chloroflexaceae, and Beggiatoaceae [Burchard, 1981]. Gliding is slow compared to swimming, with average speeds ranging from micrometers per second in *Mycoplasma mobile*, down to micrometers per minute in *Myxococcus xanthus* [Spormann and Kaiser, 1995; Hoiczky, 2000].

Gliding motility exhibits a number of different characteristics [see recent reviews: McBride, 2000, 2001]. For example, some species rotate during translocation [Ladipus and Berg, 1982], others do not; myxobacteria leave telltale slime 'tracks' in an agar substratum on which they glide, but mycoplasmas neither secrete slime nor leave any detectable tracks. *M. xanthus* has been shown to have two genetically distinct mechanisms for gliding. Social (S)-motility requires the extension and retraction of type IV pili [Wall and Kaiser, 1999; Kaiser, 2000]. This type of motility is similar to so-called 'twitching motility' observed in many other species. The second type of locomotion, so-called Adventurous (A)-motility, depends on the secretion of slime. Recent experimental evidence strongly suggests that, in both cyanobacteria and myxobacteria, slime extrusion from a sur-

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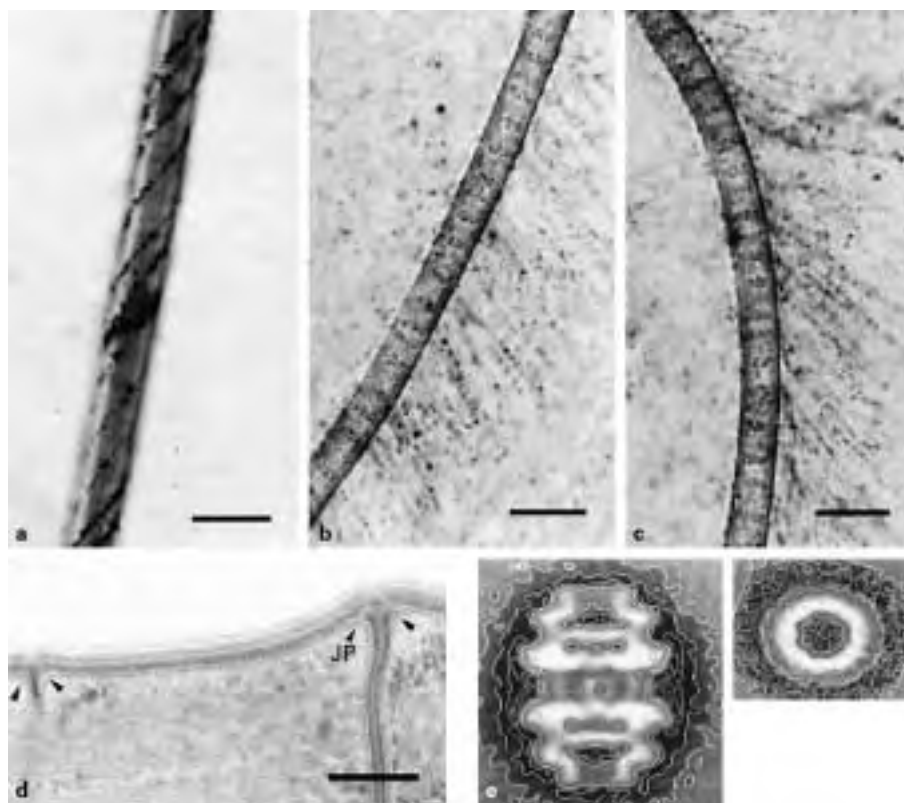
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Fig. 1. Slime extrusion and nozzles in cyanobacteria. **a–c** Show secreted slime stained with India ink in *P. uncinatum*. **a** Immobilized filament showing helically wrapped slime bands. **b, c** Slime bands shear off the surface when fluid flow is passed over the filaments. Slime emanates from points near septa and elongates at a rate comparable to the gliding rate. **a–c** The scale bar represents 10 μm . **d** Electron micrograph of a cross-section of *P. uncinatum*. JPC (arrowheads) are visible near the septum. The scale bar represents 200 nm. **e** Averages of the side- and top-view projections of the pore complex of *P. uncinatum*. Reprinted from Hoiczky and Baumeister [1998], with permission from Elsevier.



face organelle drives gliding locomotion. In the first section, we will discuss the experimental evidence related to slime secretion and the secreting organelle that supports this notion. In the second section, we will describe two recent models that describe this type of motility.

Experimental Findings

Cyanobacteria

Cyanobacteria are a morphologically diverse group of phototrophic, gram-negative bacteria. The cell walls of these bacteria are much thicker than the walls of other gram-negative bacteria, ranging from 30 to 700 nm [Hoiczky and Baumeister, 1995]. Many members of this group of bacteria can glide at speeds of up to 10 $\mu\text{m}/\text{s}$. The most efficient gliders among the cyanobacteria are found in the filamentous forms, such as *Oscillatoria*, *Spirulina*, *Phormidium*, and *Anabena* [Reichenbach, 1981]. Some species, such as *P. uncinatum* and *Oscillatoria*, rotate about their long axis while gliding; others, such as *A. variabilis*, translate laterally [Hoiczky and Baumeister, 1998]. Other cyanobacteria, such as *Synechocystis*, move by ‘twitching’, analogous to S-motility in myxobacteria [Bhaya et

al., 1999] which is also driven by type IV pili [Wall and Kaiser, 1999].

Cyanobacterial gliders secrete mucilage, or slime, while moving. Hoiczky and Baumeister [1998] discovered that diluted India ink particles stuck to the secreted mucus in *P. uncinatum* and *A. variabilis* filaments; this enabled them to visualize the secretion process using light microscopy (fig. 1a–c). In *P. uncinatum*, they observed that the cells were either covered in a tight-fitting slime tube or had a number of thin bands of slime that wrapped in a helical fashion over the surface (fig. 1a). Flowing fluid past the bacteria, sheared the slime bands off the surface of the cells except at fixed points located near the septa between cells from which the slime emerged (fig. 1b, c). In *A. variabilis*, slime was extruded in bands perpendicular to the long axis of the filaments, which also originated near the septa between cells. The slime bands elongated at $\sim 3 \mu\text{m}/\text{s}$, comparable to the speed at which *P. uncinatum* glides. This strongly suggests that slime extrusion plays an active, rather than passive, role in cyanobacterial gliding motility.

Electron microscopic studies on acid-treated, isolated cell walls from over two dozen species of cyanobacteria showed rows of fine pores, 14–16 nm in diameter, clustered circumferentially around the septa (fig. 1d) [Gugliel-

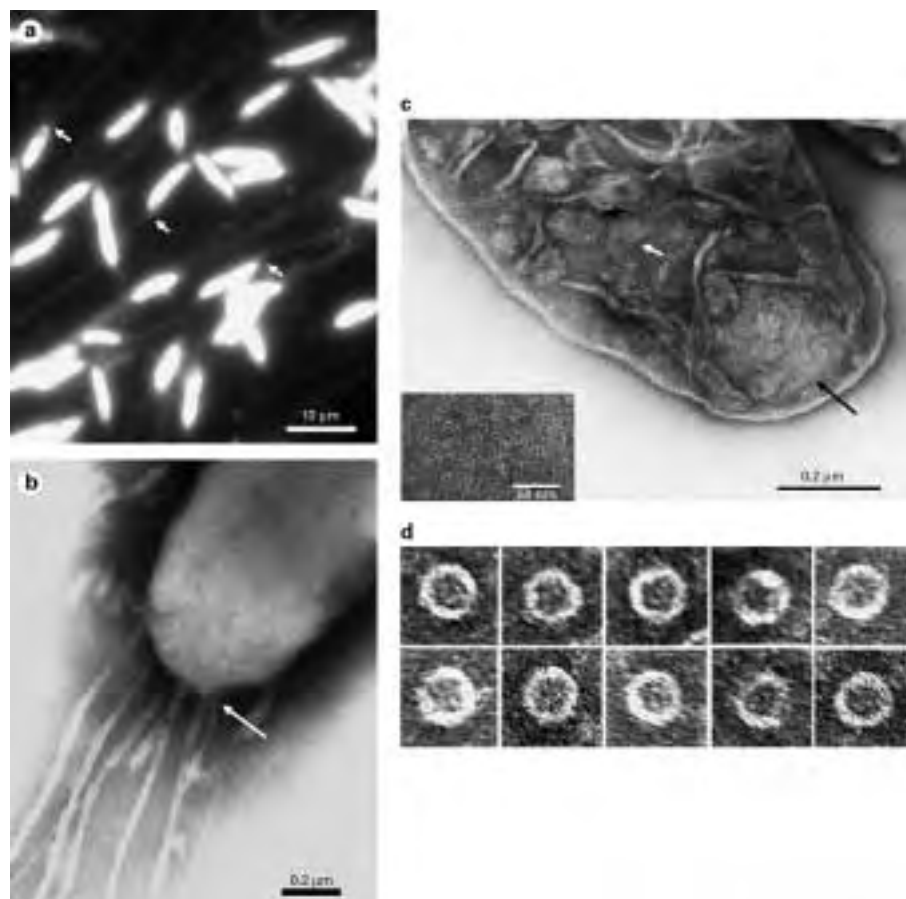


Fig. 2. Slime extrusion and nozzles in myxobacteria. **a** Fluorescent light micrograph of gliding wild-type *M. xanthus* DK1622 cell where the slime has been stained with acridine orange. **b** Electron micrograph of the cell pole of a gliding *M. xanthus* DK1622 cell showing several slime bands emanating from the cell pole. **c** Negatively stained electron micrograph of an isolated *M. xanthus* DK1622 cell envelope showing multiple ring-like structures located predominantly at the poles of the cell. **d** Gallery of electron micrographs of negatively stained isolated nozzles from *M. xanthus* DK1622. Reprinted from Wolgemuth et al. [2001], with permission from Elsevier.

mi and Cohen-Bazire, 1982]. However, these pores did not penetrate the entire cyanobacterial cell wall and so were initially disregarded as playing a role in gliding motility [Castenholtz, 1982]. Hoiczyk and Baumeister [1998] later discovered that these pores were actually part of a larger structure 70–80 nm in diameter, about 32 nm long, sufficient to span the entire cell wall. The entire structure is called the junctional pore complex (JPC). It consists of an outer membrane pore complex attached to a channel ~13 nm in diameter that spans the peptidoglycan layer. The pore is both mirror and cylindrically symmetric with a bulge in the center. The ends are roughly 8 and the center bulge 14 nm in diameter (fig. 1e). Ring-like structures encompass the pore near the central bulge. In both *P. uncinatum* and *A. variabilis*, the JPCs encircle the cell and are located near the septa. The channels formed by the JPCs are inclined at an angle of 30–40° relative to the cell axis, and are oppositely directed on either side of the septum. This angle provides directionality to the exuded slime that propels the cells forward. In *P. uncinatum*, the pores are aligned in a single row. In *A. variabilis*, several rows of pores

line both sides of the septum. In some circumstances, prolonged culture leads to the formation of filaments that are non-motile. These filaments do not secrete slime and the JPC organelles disappear leaving behind only the transpeptidoglycan channels [Hoiczyk and Baumeister, 1995].

The outer surface of four different gliding bacteria from the species Oscillatoriaceae consist of parallel, helically arranged protein fibrils [Hoiczyk and Baumeister, 1995]. In *Phormidium*, the protein that comprises this layer is oscillin, a Ca²⁺ binding protein that is required for motility [Hoiczyk and Baumeister, 1997]. Hoiczyk and Baumeister [1995, 1998] hypothesized that the surface striations formed by these proteins act as channels for the extruded slime to flow along. Therefore, if the filaments are helically arranged, the cell will rotate as it glides with the handedness of the rotation corresponding to the handedness of the wrapping. If the filaments are aligned radially, the cell will not rotate. In all species studied to date, this correlation is consistent, and provides a structural explanation for why some species rotate as they glide while others do not [Hoiczyk, 1998].

Myxobacteria

Myxobacteria are common, rod-shaped, gram-negative bacteria whose natural habitat is soil [Shimkets, 1990; Koch and White, 1998]. As mentioned above, myxobacteria have two propulsive motors. Retraction of type IV pili provides the force that propels S-motility [Wall and Kaiser, 1999; Kaiser, 2000; Merz et al., 2000; Sun et al., 2000; Skerker and Berg, 2001], and A-motility is associated with slime secretion. Gliding of A-motility mutants is quite different from that of S-motility mutants. For example, the gliding direction of wild-type (S+A+) *M. xanthus* can be altered by deforming the agar substratum, a property called 'elastocotaxis' [Stanier, 1942; Fontes and Kaiser, 1999]. However, A-motility mutants (S+A-) do not show such a response. A-motility and S-motility mutants also respond differently to the concentration of agar in the substrate. A-motility shows higher speeds on surfaces that are drier and firmer, whereas S-motility favors softer and wetter surfaces [Shi and Zusman, 1993]. Another marked difference between the two mechanisms is observed in filamentous mutants. A-motility gliding speed is not affected by cell elongation, but S-motility gliding speed is greatly reduced as filamentous cells lengthen [Sun et al., 1999].

If slime secretion from the JPC drives the motility of cyanobacteria, it is likely that the same mechanism provides thrust for A-motility in *M. xanthus*. Indeed, electron micrographs of whole cells and isolated cell envelopes from *M. xanthus* show ring-like structures in the cell wall nearly identical to the JPC in cyanobacteria [Wolgemuth et al., 2001] (fig. 2a). The *M. xanthus* rings have a central core roughly 6.5 nm in diameter with a less dense peripheral zone 12–14 nm in diameter. The rings are located predominantly at the ends of the cells with up to 250 nozzles at each end (fig. 2b). S-motility (S-A+) mutants still possess nozzles, as well as cells carrying a mutation in the *mgIA* gene, the only known gene required for both A-motility and S-motility. Side-view images of the nozzle have not yet been obtained so it is not possible to make a complete morphological comparison between the nozzles in *M. xanthus* and cyanobacteria.

Since S-motility is driven by the retraction of pili, might slime trails deposited by A- mutants be different from those left by S- mutants? Indeed, comparison of slime deposition by wild-type cells with that of A+S- and A-S+ motility mutants shows that both wild-type and the A+S- mutant cells leave slime trails, but an A-S+ mutant (Δ cglB) leaves 'puddles' of slime around each cell [Wolgemuth et al., 2001]. This suggests that slime is still secreted in this A-motility mutant, but without directionality. To

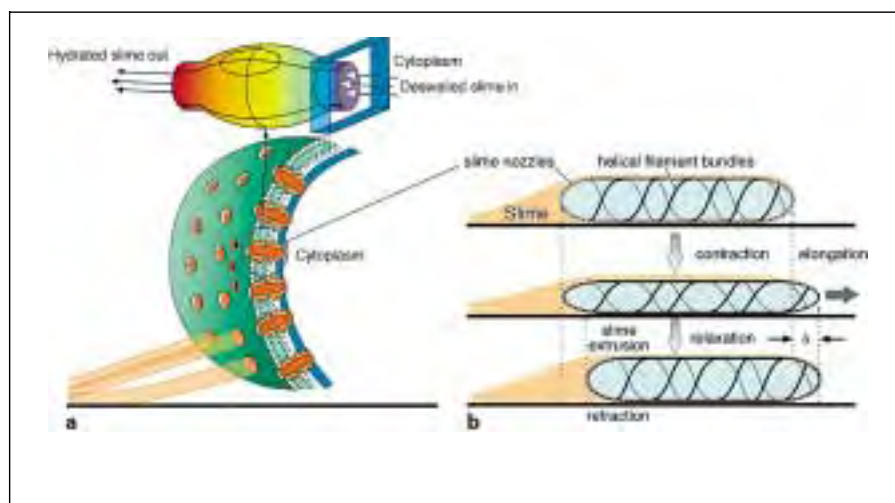
test whether slime secretion occurred at the nozzle sites, acridine orange was used to stain the secreted and deposited slime. As expected, slime trails originated at the rear of cells. *M. xanthus* cells were also induced to crawl over electron micrograph grids. High magnification visualization showed that slime trails originated from the rear of the cell in numerous small streams. These observations, combined with the location of the ring-like structures in *M. xanthus*, strongly implicate slime secretion from JPC organelles as the mechanism for A-motility in myxobacteria. This mechanism is also consistent with the observation that gliding speed in A+S- filamentous cells does not depend on the length of the filament. Since the number of cells increases in proportion to the length in filamentous cells, the number of nozzles, and therefore the propulsive force, will also increase in proportion with the length.

Models for A-Motility

The Slime Gun

Slime extrusion was proposed as a mechanism for thrust generation in gliding bacteria over 75 years ago [Jahn, 1924; Kuhlwein, 1953]. This model was largely discounted because it was unclear how slime excretion could produce sufficient thrust and directionality to propel the bacteria. Also, estimates of the energetic cost for slime production seemed excessively large. However, slime is a polyelectrolyte gel; that is, a charged, crosslinked polymer mesh embedded in a fluid solvent. Such gels can swell to many hundreds of times their dry volume, and generate enormous swelling forces. Recently, Wolgemuth et al. [2001] proposed a model for force generation based on the hydration of slime (fig. 3a). They proposed that the slime is introduced into the nozzle cavity in a deswelled state, perhaps (as in mucin granules) [Verdugo, 1991] by divalent cations. Fluid perfuses into the nozzle from outside of the cell and hydrates the slime, causing it to swell and extrude from the nozzle. As the gel stream leaves the nozzle it adheres to the substrate. This provides the swelling gel with a footing allowing it to push the cell forward. The mathematical model permitted calculating the force produced within a single nozzle as the slime hydrates and expands. By multiplying by the number of observed nozzles at a cell pole, and comparing this force with an estimate of the drag on a cell, Wolgemuth et al. [2001] were able to show that slime extrusion could produce a propulsive force sufficient to account for the observed gliding speed of both myxobacteria and cyanobacteria, and to predict how the velocity of the bacterium depends on resisting forces.

Fig. 3. a The slime gun. Top: Illustration of the JPC nozzle with deswelled slime being introduced near the inner membrane. The slime then swells and flows out of the pore. Bottom: Placement of the nozzles in *M. xanthus* near the end of the cell. Slime flows out of the nozzle, adheres to the surface and pushes the cell forward. **b** The slime ratchet. Cartoon of a possible mechanism for A-motility in myxobacteria. Helically wrapped filaments are able to contract and expand periodically changing the length of the bacterial cell. Slime is extruded from pores in the bacterial cell wall and adheres to the surface preventing the cell from moving backwards. The cell then expands, pushing itself forward against the adhered slime. Relaxation of the filaments returns the cell to its original size.



This slime propulsion mechanism is consistent with a number of the observed phenomena mentioned previously.

Slime Trail Following [Burchard, 1981]. If extruded slime adheres more strongly to itself than to the substratum, a cell that encounters a trail left by another cell will be pivoted into alignment with the existing slime trail and will continue moving along the direction of the trail.

Elasticotaxis [Burchard, 1981; Fontes and Kaiser, 1999]. If the slime adheres to the solid part of the agar substrate, alignment of the slime polymer with those of the strain-aligned agar provides more adhesive sites for traction, which favors propulsion along strain lines.

Velocity Dependence on the Volume Fraction of the Agar Substrate [Shi and Zusman, 1993]. That there is an optimal volume fraction for the agar substrate suggests two things. First, at low volume fractions, the agar gel is not sufficiently stiff to provide the necessary resistive force. Therefore, the slime pushes against a soft wall that yields, reducing the thrust and hence the cell velocity. At high agar volume fractions, the gliding velocity in *M. xanthus* also decreases [Shi and Zusman, 1993]. This can be understood since both the agar and the slime are gels, and when in contact, they will tend towards an osmotic equilibrium. If the agar is less hydrated than the slime, it will draw water out of the slime, causing the slime to dehydrate and so generate less propulsive thrust.

Etching of the Agar [Burchard, 1981]. Gliding cells 'etch' the agar substrate on which they move. This occurs because the osmotic pressure of the gel is greater than that of the agar, so water is drawn out of the agar gel, producing a local depression [Burchard, 1981].

The Slime Ratchet

Electron micrographs of *Mycococcus* cells reveal helical filamentous structures wrapping the periplasmic space [Burchard et al., 1977; Lunsdorf and Reichenbach, 1989; Freese et al., 1997; Lunsdorf and Schairer, 2001]. These filaments have been implicated in gliding motility, and recent experiments suggest that they are responsible for morphological changes, such as twisted forms, in actively gliding myxobacteria; these twisted morphologies are not observed in non-motile mutants [Lunsdorf and Schairer, 2001]. Dynamic oscillatory morphology changes have been shown to drive motility in wall-less mollicute bacteria [Miyata and Uenoyama, 2002; Gilad et al., 2003; Trachtenberg et al., 2003]. A similar mechanism could also drive motility in myxobacteria through a slime ratchet-type mechanism [Wolgemuth et al., 2003]. This model hypothesizes that the mechanochemical cycle of conformational changes in the helical filament subunits, coupled with the cell turgor pressure, cyclically changes the overall cell length. Slime secreted from the rear of the cell adheres to the substrate and holds the cell in place during lengthening of the cell and prevents the cell from moving backward during the contraction phase. Repetition of this process slowly ratchets the cell forward, as illustrated in figure 3b. This 'slime ratchet' mechanism can be experimentally distinguished from direct propulsion by slime extrusion by observing the correlations between the front and rear of gliding cells. Perfect correlation implies the cell is moving as a rigid body, and supports the slime nozzle model. Conversely, if the front and rear are cyclically correlated out of phase, then the slime ratchet model is more likely.

Open Questions

Experiments provide strong support for the idea that slime secretion from the JPC organelle is the force-driving motility in many cyanobacteria and A-type motility in myxobacteria. However, the details of the propulsive mechanism are still vague. Here we have suggested two models for slime-associated motility consistent with the available evidence. Experiments that can distinguish between these models are proposed, but remain undone [Wolgemuth et al., 2001; 2003]. A number of other questions also remain. The hydration model suggests specific material qualities for the slime; does the chemical composition of the slime conform to these values? How is slime

imported into the nozzles? How do myxobacteria alternate the active cell end during their periodic reversals? Are the nozzles of *M. xanthus* morphologically similar in side view to those observed in cyanobacteria? While the fog of mystery surrounding gliding motility is slowly lifting, much remains to be learned before we can declare the mystery solved.

Acknowledgments

C.W. was supported by NSF Grant MCB-0327716. G.O. was supported by NIH Grant GM59875-02. The authors would like to thank Dale Kaiser for his comments and insights.

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