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Helical growth and the curved shape of *Vibrio cholerae*

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Abstract

The curved, comma, or bent shape of *Vibrio cholerae* is attributed to, and explained by, the normal helical growth of the cell. The comma-like shape of *V. cholerae* is not due to an asymmetrical positioning of peptidoglycan such that some chains of peptidoglycan are placed so they are more spread out on one side of the cell and squeezed together on the other side.

Keywords: Shape; Peptidoglycan; *Vibrio cholerae*

At a seminar presented by Dr. John Mekalanos at the University of Michigan, a slide was shown of a filamentous strain of *Vibrio cholerae*. Dr. Mekalanos noted that the cell showed a helical growth pattern (N. Judson and J. Mekalanos, unpublished results). This helical pattern was obvious to all in the audience (This strain is described in a publication, [1]). This helical pattern can now explain the 'comma' shape of *V. cholerae*.

V. cholerae is described as a 'comma-shaped' bacterium. Unlike *Escherichia coli* and other bacilli, where the rod-shaped cell is described as a regular cylinder capped by two hemispheres, the *V. cholera* cell consists of a bent tubular shape capped by hemispheres.

The underlying peptidoglycan structure of Gram-negative bacteria is consistent with the linear cell shape of *E. coli*. The glycan chains of the net-like peptidoglycan encircle the cell as hoops encircle a barrel. Although the individual glycan chains are not long enough to completely encircle the cell, the effective length of the end-to-end chains does encircle the cell as illustrated in Fig. 1a. As the peptidoglycan is stretched, all of the adjacent distances between the glycan chains or hoops are equivalent. This is because of the internal pressure within the cell that stretches the peptidoglycan hoops apart and stresses the crosslinking amino acid chains [2].

A problem arises when the cell is not linear but curved. If there is a circumferential enclosing of the *V. cholerae* cell by glycan chains as in *E. coli*, then the chains must be viewed as in Fig. 1b where chains at the outer side of the curved cell are further apart than the chains at the inner part of the cell. This is difficult to envisage, as it is likely that the turgor pressure inside the *V. cholerae* cell is not very different from that in *E. coli*. This turgor pressure would tend to straighten out the cell. A possible solution to the inter-bond distance difference would be to have additional glycan chains between the separated glycan chains as in Fig. 1c. This rather inelegant solution has its own problems because it is difficult to know why or how the cell would maintain the curvature with the cell having a high interior turgor pressure.

I wish to suggest an alternative explanation for the comma or curved shape of *V. cholerae*. I propose that *V. cholerae* grows in a helical shape, as suggested by the helical growth of the filamentous strain. If one takes a helix, and cuts it into short pieces, the individual pieces retain the curvature of the helix. This can be seen in Fig. 2 where a model of helical shape, the helically wound telephone cord, has been photographed next to short cut pieces of the helical cord. The short pieces retain a curved structure.

This explanation of curvature of *V. cholerae* merely still leaves unanswered the deeper question, how does the helical growth of a rod-shaped bacterial cell come about? The mechanics of helical shape in bacteria has been the focus of a great deal of attention lately [3–6]. In particular, a pattern of helical growth has been described for *Bacillus subtilis* [7,8]. The origin of helical growth in *B. subtilis* appears to be based, in some unknown way, on something about the biosynthesis of peptidoglycan [9–17] and its pre-

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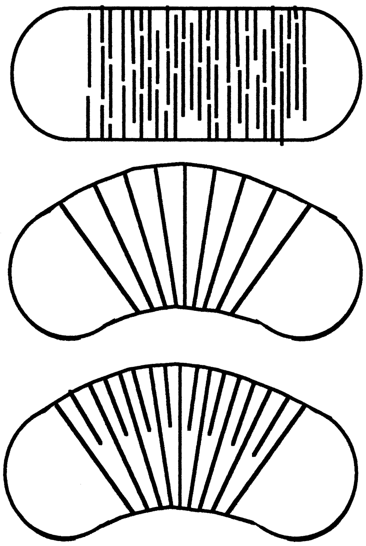

Fig. 1. Relationship of peptidoglycan arrangement and cell shape. (a) Parallel glycan strands in *E. coli*. (b) Peptidoglycan in *V. cholerae* illustrating the larger distances between glycan chains at the 'outer' regions of the cell and the shorter distances between glycan chains in the 'inner' regions of the cell. (c) One solution to the inter-glycan chain distance problem in *V. cholerae*: the insertion of additional chains between the spread out chains.

sumed interaction with other wall components such as the membrane.

Although one can now argue about how the peptidoglycan is arranged in the bacterial surface, and how it interacts with the membrane to produce helical growth, what emerges from the model for *V. cholerae* curvature presented here is the simple proposal that the comma shaped cells are merely parts or sections of a much longer helical mode of growth. The comma-like shape of *V. cholerae* is thus not due to asymmetric positioning of peptidoglycan at the inner and outer parts of the curved cell. Rather, the curvature is related to a constant and isotropic helicity of growth pattern that leads to a curved cell when only a short part of the helix is present.

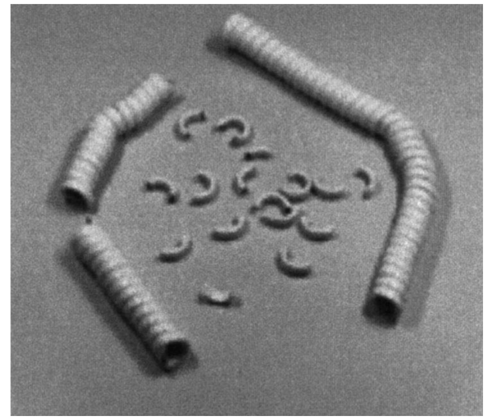

Fig. 2. Helical growth produces short comma-shaped cells. A telephone cord with a permanent helical shape is photographed along with short pieces cut from the longer wire. The short pieces have a comma-like shape.

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