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Mechanism of Attachment of Swarm Cells of *Thiothrix nivea*

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Swarm cells of *Thiothrix nivea* were found to possess a group of fimbriae at one pole. The other pole either was bare or possessed from one to three fimbriae. By using this polarity as a marker, it was found that the initial step in attachment of swarm cells involves the fimbriated pole and that this initial step is followed by the production of holdfast material.

*Thiothrix nivea* lives in a gradient in the environment, existing in flowing water in which the sulfide concentration is about 0.1 to 1.0 mg/liter, the oxygen concentration is about 10% or less of saturation, and the pH is near neutrality (1, 2, 5, 6, 9). In a suitable environment, *T. nivea* cells grow as long filaments attached to a substrate or as rosettes or filaments attached by their poles to objects or other organisms (including themselves). Single cells, called swarm cells, are released from the open end of the sheath and suitable environment and escapes being swept away by the current (9). The mechanism of this attachment is unknown and is the subject of this report.

*T. nivea* JP2, which was isolated (7) and described previously (8), was used in this study. Stock cultures were maintained on either MP or MY broth (8) over a plug of the corresponding agar in screw-cap tubes. For experimental cultures, the organism was grown in MY broth in which thiosulfate was substituted for sulfide.

![FIG. 1. Negative stain of a *T. nivea* JP2 swarm cell. The arrows point to fimbriae that are located on a single pole.](image)

Swarm cells exhibit gliding motility when on a solid surface (8). Swarm cells are responsible for dispersal of the colony; they may attach to a substrate and produce a multicellular filament, or they may attach to other swarm cells and produce a rosette. The attachment of *T. nivea* to a surface or to other cells, as in a rosette, is the mechanism by which it remains in a suitable environment.

Negative stains on Formvar-coated grids were prepared with phosphotungstic acid, pH 7.4. Cells for scanning electron microscopy were fixed in 1 M Veronal acetate buffer–3% glutaraldehyde, dehydrated in a graded ethanola series, dried to the critical point, and coated in a sputter coater as described previously (12).

Negatively stained preparations were scanned in the electron microscope until a well-isolated swarm cell was found, and each pole of the cell was examined. Only single cells

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were examined because they would be newly produced swarm cells from the pole of a *Thiotrix* filament (9). If both ends of the cell were not visible, the cell was not examined.

A total of 51 individual swarm cells were found in which both ends of each cell could be examined. Of these cells, 43 (84%) had many fimbriae at one end, while the other end was bare (Fig. 1). Four swarm cells (8%) had many fimbriae at one pole and only one to three fimbriae at the other pole. Four cells (8%) had no detectable fimbriae. Thus, 47 of 51 swarm cells (92%) exhibited an easily observed polarity, which could be detected by the location of their fimbriae. Neither pole of a swarm cell or unattached filament had an accumulation of holdfast material, which would have made observation difficult. At high magnification, the fimbriae consisted of single thin filaments or filaments which were aggregated into much larger filaments (Fig. 2). The polarity of the swarm cell was used as a marker to determine which end of a swarm cell harbored the attachment mechanism.

Swarm cells that were attached at their poles in groups of two to five cells were located on negatively stained preparations (Fig. 3). The presence and location of fimbriae on each cell of these developing rosettes were determined. Single cells that were attached to the sides of filaments were examined in the same way.

Frequently, it was not possible to see the fimbriae on cells that were attached because of the accumulation of holdfast material. However, because of the polarity of the swarm cells it was possible to determine whether attachment occurred at the fimbriated or nonfimbriated end by examining the free end of the cell, which had no holdfast material.

The distribution of fimbriae on the unattached ends of cells in developing rosettes is shown in Table 1. Of the poles away from the attachment sites, 91% had no fimbriae, 6% had one to three fimbriae, and 3% had a group of fimbriae. Thus, 97% of the swarm cells in a beginning rosette attached at the fimbriated pole. Of swarm cells that attached to the sides of a filament, 100% attached with the heavily fimbriated pole. Overall, 98% of all of the attached swarm cells attached with the end that had the tuft of fimbriae.

These data demonstrate that the fimbriated pole of the *T. nivea* swarm cell is always at the point of attachment. Additional evidence that fimbriae are involved in attachment was found when, after several years in culture, this strain of *T. nivea* simultaneously lost both the ability to produce fimbria and the ability to attach to a substrate.

Holdfast material was not seen on unattached swarm cells, making observation of the poles a simple matter. Fimbriae could sometimes be seen between the poles of the cells in newly attached pairs. As the number of swarm cells in a rosette increased, it became increasingly difficult to see the attachment area because of the accumulation of slimelike material. Thus, it appears that holdfast material is produced after the initial attachment by the fimbriae. In a scanning electron micrograph of the center of a rosette (Fig. 4), strands of slimelike material can be seen extending between cells, and they undoubtedly play some role in adherence.

The mechanism(s) used by bacteria to produce rosettes may differ among species, but several surface structures have been implicated. Moore and Marshall (11) examined rosette formation in a *Hyphomicrobium* sp. and suggested that the polar flagellum may be involved in attachment. An

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**TABLE 1. Distribution of fimbriae on the free ends of swarm cells that had attached to other cells**

<table>
<thead>
<tr>
<th>Type of free ends</th>
<th>No. of free ends&lt;sup&gt;a&lt;/sup&gt; in developing rosette having:</th>
<th>Total no. of free ends examined (% of total)</th>
<th>No. of single cells attached to a filament</th>
<th>Total no. of ends examined (% of total no.)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2 Attached cells</td>
<td>3 Attached cells</td>
<td>4 Attached cells</td>
<td>5 Attached cells</td>
</tr>
<tr>
<td>Observed</td>
<td>18</td>
<td>3</td>
<td>6</td>
<td>5</td>
</tr>
<tr>
<td>With 0 fimbriae</td>
<td>15</td>
<td>3</td>
<td>6</td>
<td>5</td>
</tr>
<tr>
<td>With 1 to 3 fimbriae</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>With tuft of fimbriae</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

<sup>a</sup> The end away from the attachment site.

<sup>b</sup> The ends of cells in some rosettes could not be seen and were not counted.
acidic polysaccharide was responsible, at least in part, for attachment and rosette formation in *Asticcacaulis biprosthecum*; fimbriae and flagella were not involved (13).

MacRae et al. (10) examined 22 gliding bacteria and found that 19 of them had a tuft of fimbriae at one pole, while the other pole was bare. In a follow-up study (3), they concluded that fimbriae are organelles which function to establish and maintain intercellular contact. The communal swarming behavior of myxobacteria requires the presence of fimbriae (3, 4).

Our results indicate that the swarm cells of *T. nivea* are similar to those of the gliding bacteria described by MacRae et al. (10) in that they have a tuft of fimbriae at one pole only and the fimbriae appear to act as structures used to establish intercellular contact.

**LITERATURE CITED**