

## A Capillarity Mechanism for Diatom Gliding Locomotion

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**Abstract.** It is proposed that the diatom raphe is a parallel-plate capillary containing a fluid which reacts at the trailing end, turning into a form which no longer "wets" the raphe walls, and which is left behind as a trail. More unreacted raphe fluid is drawn by capillary pressure from a source near the leading end of the raphe. This fluid sticks out from the raphe along its length, adhering to surfaces, thus causing gliding locomotion. Formulae are given for the maximum velocity and force of a moving diatom in terms of the raphe dimensions and the surface tension and viscosity of the fluid. An *a priori* estimate of the force exerted by a moving diatom, 1-50 millidynes, agrees with measured values. Five experimental tests of the theory are proposed.

Many bacteria and blue-green algae<sup>1-3</sup> (procaryotes) and diatoms<sup>3</sup> (eucaryotic algae) move in a smooth gliding motion when they are attached to a surface, with no apparent moving parts.<sup>4</sup> In all of these organisms the mechanism has remained a mystery, although it has been investigated and speculated about for well over a century.<sup>5</sup> We will present a new theory for the gliding locomotion of diatoms based on their fine-structural geometry and the physical chemistry of capillaries,<sup>6</sup> which seems to tie together most of the known facts, and is quantitatively testable. We suggest that diatoms move by an entirely new mechanochemical process.

**Basic Theory. The diatom motor:** Diatoms are single cells which reside within an ornate, species-characteristic, long, rigid box made of silica.<sup>7</sup> All *motile* diatoms possess slits or "raphes" in the silica shells,<sup>7</sup> which generally occur in two pairs on opposite faces of the box. The raphes in a pair are end to end along the long axis.

Contact between a raphe and a fixed substratum is required for locomotion.<sup>8,9</sup> The dimensions of the raphes vary roughly with the size of the diatom. A raphe is 10-100  $\mu\text{m}$  long, 200-2500  $\text{\AA}$  wide in its narrowest region, and 1-10  $\mu\text{m}$  deep, cutting all the way through the silica shell.<sup>8</sup> Thus, the walls of the raphe form a fine parallel-plate capillary.

Raphes exude a mucilaginous substance (raphe fluid) which the diatom leaves behind as a trail.<sup>3,5,8</sup> If we assume: (1) the raphe fluid undergoes a reaction at the trailing end of the raphe; (2) the raphe walls are "wet" preferentially by unreacted raphe fluid; (3) a source of fluid exists at the leading end of the raphe; then the reacted raphe fluid will be continuously removed from the trailing end,

and fluid will flow along the raphe, so long as the source holds out. (An analogy may be made with molten wax moving up the wick of a candle as it burns.)

When the internal source releases raphe fluid freely, and if the reaction at the trailing end of the raphe occurs as fast as fluid arrives, then the speed of the fluid will depend on the drag caused by the walls, and on the pressure gradient pushing the fluid. Under these conditions the unreacted raphe fluid moves at its maximum speed  $v_{max}$ , a function of the width  $w$  of the raphe, the viscosity  $\eta$  of the fluid, and the pressure gradient  $P/l$ , where  $l$  is the length of the raphe:

$$v_{max} = w^2P/(12\eta l). \quad (1)$$

Equation (1) is Poiseuille's equation for steady flow between parallel plates.<sup>10,11</sup>

It is unlikely that the internal pressure contributes to the driving pressure  $P$ , since plasmolyzed diatoms remain motile,<sup>3,8,12</sup> so long as the protoplast retains contact with a raphe: We suggest that the capillary pressure<sup>13</sup>

$$P = 2\gamma/w, \quad (2)$$

where  $\gamma$  is the surface tension of the unreacted raphe fluid, is responsible for the pressure gradient along the raphe.<sup>14</sup> This is the same pressure which causes the raphe to fill with fluid in the first place. We predict the maximum speed of a diatom is then

$$v_{max} = w\gamma/(6\eta l). \quad (3)$$

**How locomotion is achieved:** When Chinese ink is placed near a motile diatom on its side, ink particles can be seen moving along the raphes.<sup>8</sup> Thus the raphe fluid protrudes from the raphe. We need only assume that the protruding material binds to surfaces<sup>9</sup> to explain locomotion by our model.

**The pushing force of a diatom:** The force  $F$  which a diatom can exert is given by the capillary pressure  $P$  multiplied by the cross-sectional area of the raphe ( $wh$ ), where  $h$  is the portion of the depth of the raphe which has the narrowest width  $w$ . (Capillary pressure is highest in the narrowest parts of a capillary, and to a first approximation wider parts may be ignored in calculations.) Therefore

$$F = Pwh = 2\gamma h. \quad (4)$$

**A quantitative agreement:** Most pure liquids and aqueous solutions of sugars have surface tensions<sup>15</sup> between 20 and 80 dynes/cm, a remarkably narrow range. Thus we may make an *a priori* estimate that the surface tension  $\gamma$  of unreacted raphe fluid is also within this range. Since  $h = 0.3\text{--}3 \mu\text{m}$  in various diatoms, the capillary pressure  $P$  (Eq. 2) should be somewhere between 2 and 80 atm, and the force  $F$  a diatom exerts (Eq. 4) should be between 1 and 50 millidynes. Harper and Harper<sup>9</sup> have measured the adhesive and tractive forces of moving diatoms by the bending of fine glass fibers. Our predicted range falls *within* the range of their experimental data. The magnitude of this capillary force explains why a diatom is capable of lifting thousands of times its own weight.<sup>9</sup>

**Testing the theory quantitatively:** A variety of tests of our model is possible

