versal" of the surviving strain is predicted, not because of competition, but because the strain with the lower K_s and μ is washed out at the higher flow rate, whereas the strain with the higher μ is not. Consequently, it must be shown that both species grown alone can persist at the given flow rate to establish that competition was the agent of elimination. For a given D, this is equivalent to showing that $r > 0$ for both strains.

Reversals are not predicted by the theory for variation in the influent concentration of the limiting resource, S_0 (*5, 7*). If such reversals occur, it is probable that at higher levels of S_0 the culture has become limited by some other nutrient for which a strain different from the previous winner now has the lower J. The equations of mixed growth (Eq. 1) are then altered to describe the consumption of the new limiting resource, R, with concomitant changes in the growth parameters of each strain (K_s, μ, y) that are appropriate for the new resource. Accordingly, the number of strains potentially capable of winning in mixed-growth culture depends (i) on the number of potentially limiting resources in the culture medium and (ii) on the distribution of minimal J's for these resources among the competing strains. Thus, where there are more potentially limiting resources than strains, and all strains have at least one minimal J for some resource, then all strains are potential winners with appropriate choices of resources.

When limiting resources are known, resource-based competition theory represents a conceptual advance over classical theory because the outcomes of exploitative competition can be forecast from data taken on the rival species grown alone. Thus, for two competing species with similar death rates, the winner is expected to be the species whose half-saturation constant for the limiting resource is smaller in comparison to its intrinsic rate of increase. A good competitor is a species able to grow at low resource concentrations at a higher intrinsic rate than its rivals, an ability summarized in the parameter J. Classical competition theory asserts that two-species outcomes are independent of the intrinsic rates of increase of the two species (*15*), a claim that the more mechanistic resource-based approach shows to be incorrect.

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4. The elementary theory of pure-strain growth in continuous culture has been the subject of many experimental and theoretical investigations, as reviewed by S. J. Pirt, *J. Appl. Chem. Biotechnol.* **22**, 55 (1972).
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6. F. M. Stewart and B. R. Levin (*1*) have shown that the conclusions hold for a more general set of assumptions than those in Eq. 1, via linearized analysis near equilibrium points.
7. S. B. Hsu, *SIAM (Soc. Ind. Appl. Math.) J. Appl. Math.*, in press.
8. In classical competition theory, attributed to A. J. Lotka and V. Volterra, competitive outcomes depend on relationships between "carrying capacities" (equilibrium population sizes when each species is grown alone) and "competition coefficients" (per capita effects by each species on the growth rate and equilibrium population of rival species). This is a phenomenological theory in the sense that it seeks to describe how populations of competing species change without being specific about which resources are limiting and the focus of competition, nor about the relative abilities of the species to exploit these resources. Parameters such as S_0, K_s, μ, and y do not appear. Application of classical theory for prediction has been hampered by the difficulty of measuring the competition coefficients independently of actually growing the competitors together.
9. The most frequently expressed opinion is that the K_s values should be sufficient to explain the competitive outcomes between microorganisms [for example, R. W. Eppley and J. L. Coatsworth, *J. Phycol.* **4**, 151 (1968); P. Kilham, *Limnol. Oceanogr.* **16**, 10 (1971)]. D. Titman [*Science* **192**, 463 (1976); *Ecology* **58**, 338 (1977)] performed a direct test of resource-based competition theory between two diatom species, *Cyclotella* and *Asterionella*. In competition, *Cyclotella* wins under silicate limitation, and *Asterionella* wins under phosphate limitation. Titman's results are consistent with the J criterion.
10. A series of flasks containing different amounts of tryptophan in 100 ml of minimal medium was placed in a constant temperature shaker bath at 34°C. Initial cell density was kept very low (10^3 cell/ml); tests showed that no detectable alteration in batch tryptophan concentration occurred at these cell densities during the 8-hour determinations. Each hour for 8 hours, samples were removed, plated, and counted after 24 hours of incubation. Microscopic cell counts confirmed plate counts and a lack of cell clumping. Regression of ln (cells per milliliter) against time gave the log-phase growth rate at each concentration of tryptophan.
11. Competition experiments were carried out in autoclavable, continuous flow chemostats (VirTis) at a culture volume of 200 ml, in a constant temperature shaker bath at 34°C. To monitor growth of each strain, samples were withdrawn under conditions of sterility, diluted to a range of known concentrations of the original sample, and plated. Sequential serial dilution was necessary to ensure that accurate plate counts could be made, regardless of the cell density of the strain at the time of sampling (densities ranged over four to six orders of magnitude in the culture). Each strain was counted on two separate series of plates treated with an inhibitor to which one strain was resistant and the other sensitive. Microscopic cell counts confirmed that plate counts were accurate. No measurable wall growth or cell clumping occurred at the low cell densities reached in culture.
12. In both experiments 1 and 2, death rates of the losing strain were faster than predicted by Eq. 1. This was most likely due to the existence of a minimum threshold tryptophan concentration below which the losing strain experiences an increased death rate. Concentrations of tryptophan are driven below this threshold by the winning strain.
13. The cause of the fluctuations in the two strains at approximate steady state is not known, but occurred in all three replicate cultures at about the same time. The pumping rate may have been affected by fluctuations in line voltage.
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Motile Flagellum with a "3 + 0" Ultrastructure

Abstract. *The male gamete of the parasitic protozoan* Diplauxis hatti *has a flagellum consisting of three doublet microtubules. This flagellum exhibits a helicoidal waveform in which bends propagate toward the tip with a frequency of about 1.5 hertz. It is the simplest motile eukaryotic flagellum yet described.*

Most flagella and cilia of eukaryotic cells have a classical "9 + 2" axoneme in which a pair of single microtubules is surrounded by a ring of nine doublet microtubules (*1*). A number of exceptions to this general scheme have been found, but generally the motility of the cells has not been described (*2*). The simplest motile axoneme reported so far is the 6 + 0 flagellum of the male gamete of a parasitic protozoan, the gregarine *Lecudina tuzetae* (*3*). The existence of an axoneme consisting of only three doublets has been noted in the male gamete of another gregarine, *Diplauxis hatti* (*4*); we now report that this axoneme is motile, and describe its structure and motility.

The male gamete of *Diplauxis hatti* is a spherical cell about 4 μm in diameter (Fig. 1a), with a flagellum about 20 μm long. The diameter of the flagellum is only 0.11 to 0.13 μm, compared to the typical diameter of 0.2 μm for classical cilia and flagella (*1*). The flagellum runs along the nucleus for several micrometers before emerging from the cell body. The axoneme has a 3 + 0 microtubular structure both in the flagellum (Fig. 1b) and within the cell body (Fig. 1c).

The ultrastructure of the doublets is similar to that of the doublets from a 9 + 2 flagellum; they measure about 34 by 26 nm. If the doublets are oriented with the A-subfibers facing clockwise

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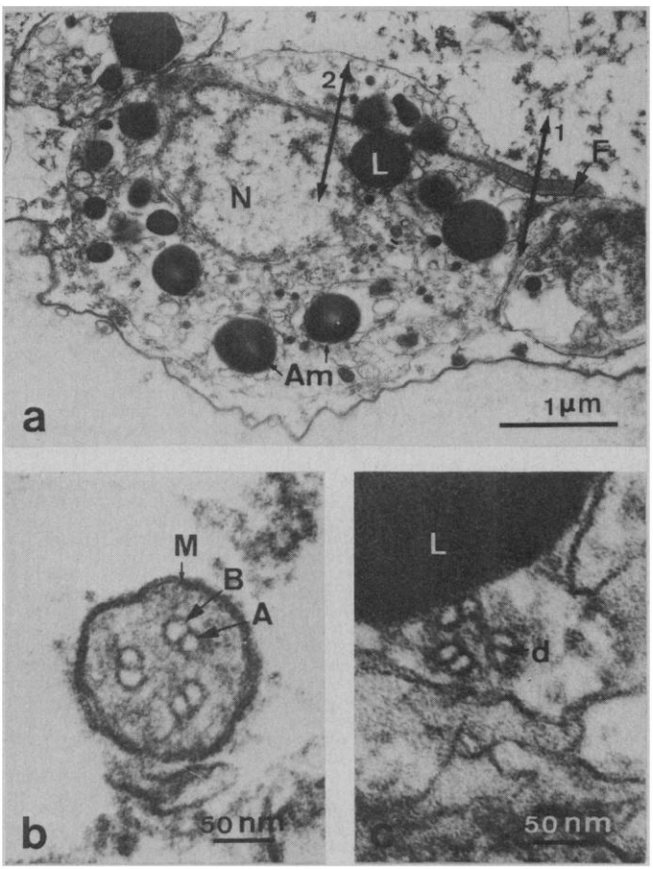

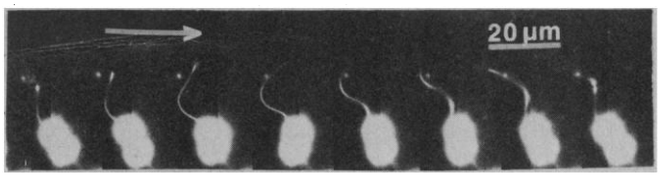

Fig. 1 (left). (a) Section of the male gamete of *Diplauxis hatti* Viv. Orm. Tuz., a coelomic gregarine of the polychaete worm *Perinereis cultrifera* Grübe, fixed with 6 percent glutaraldehyde in 0.1*M* phosphate buffer and postfixed with 2 percent osmium tetroxide in the same buffer. Ultrathin sections were stained with uranyl acetate and lead citrate. The flagellar axoneme (*F*) runs along the nucleus (*N*). Arrows 1 and 2 indicate levels of cross sections shown in (b) and (c), respectively; *Am*, amylopectin granule; *L*, lipid droplet (×16,000). (b) Cross section of free flagellum [section 1 of (a)]. The A-subfiber, *A*, corresponds to the complete microtubule of each doublet; *B*, B-subfiber; *M*, flagellar membrane (×165,000). (c) Cross section of flagellum within the cell body [section 2 of (a)]. The doublets (*d*) are surrounded by a dense material; *L*, lipid (×165,000). Fig. 2 (above). Dark-field multiple-exposure photograph of the male gamete of *D. hatti*, taken with the film moving to prevent overlap of images, as described previously (*5*). The first image is on the left and the cell body is attached to the slide. Interval between exposures, 0.1 second. Beat period, 0.7 to 0.8 second. Arrow indicates order of exposures (× 460).

and a triangle is constructed from the lines that bisect both subfibers, one of the angles of this triangle is larger than the other two.

Of the photographs available, eight were suitable for detailed analysis, and from these the largest angle measured 72° ± 2°; proceeding clockwise from that angle, the other two measured 53° ± 6° and 55° ± 7°, respectively. The doublets that form the largest angle are separated by a distance of 24 ± 2 nm and the distances that separate each of these doublets from the third are both about 20 ± 3 nm. These distances between the A- and B-subfibers of adjacent doublets are larger than the typical distance of 17.5 to 20 nm observed in a 9 + 2 flagellum (*1*). No interconnecting structures between doublets were seen clearly or consistently, but fixation of this flagellum is difficult: the presence of dynein arms cannot be excluded.

Movements of the cell bodies of the gametes can be observed through the cyst wall. For photography and analysis of motility, gametes were removed from the cyst by tearing the cyst wall with needles in a drop of seawater. The movements of the free cells appear similar to those observed within the cyst.

This flagellum, which can stop and start moving spontaneously, produces helicoidal bends (Fig. 2) that travel from the cell body toward the tip, with a frequency of about 1.5 Hz. Sometimes the sense of the helix appears to reverse when beating restarts. Occasionally, a low-amplitude oscillation is superimposed on the basic waveform; the frequency of this oscillation appears to be about two or three times the beat frequency. It is not clear whether these small oscillations are standing or traveling. The flagellar movement produces primarily a rotation of the cell body, with little forward movement.

This 3 + 0 flagellum demonstrates the ability of an axoneme with a very simple ultrastructure to produce regular beating and, to our knowledge, is the simplest motile flagellum yet described in eukaryotic cells. Bundles of a few doublets from the 9 + 2 flagellum of *Chlamydomonas* have been observed to produce oscillatory movements during separation from the rest of the axoneme (*6*). The beating of the 3 + 0 flagellum of *Diplauxis hatti* suggests that bends could be produced by groups of doublets from any flagellum under appropriate conditions.

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