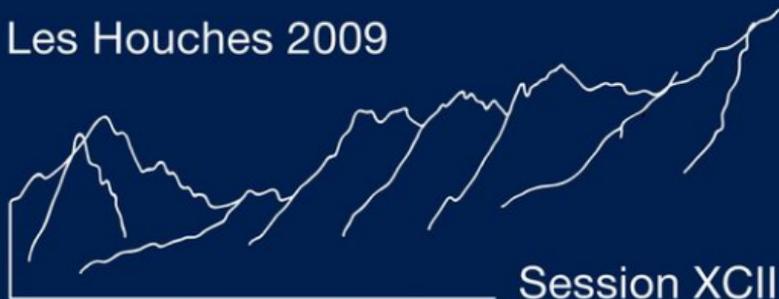


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Les Houches 2009



Session XCII

# New Trends in the Physics and Mechanics of Biological Systems

M. Ben Amar  
A. Goriely  
M. M. Müller  
L. F. Cugliandolo

Editors

# New Trends in the Physics and Mechanics of Biological Systems

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**École de Physique des Houches**

Session XCII, 6–31 July 2009

**New Trends in the Physics and  
Mechanics of Biological Systems**

Edited by

Martine Ben Amar, Alain Goriely, Martin Michael Müller,  
Leticia F. Cugliandolo

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XC	2008	Long-range interacting systems
XCI	2009	Ultracold gases and quantum information
XCII	2009	New trends in the physics and mechanics of biological systems
XCIII	2009	Modern perspectives in lattice QCD: quantum field theory and high performance computing

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- Sessions IX and X: Herman, Wiley
- Session XI: Gordon and Breach, Presses Universitaires
- Sessions XII–XXV: Gordon and Breach
- Sessions XXVI–LXVIII: North Holland
- Session LXIX–LXXVIII: EDP Sciences, Springer
- Session LXXIX–LXXXVIII: Elsevier
- Session LXXXIX– : Oxford University Press

# Preface

Over the last few decades, the life sciences have experienced a quiet but radical revolution. This revolution has transformed biology from a mostly observational and qualitative discipline into a fully quantitative science at all scales, ranging from the DNA code to proteins, cells, tissues, and organs. In the process, biology has become one of the ultimate scientific frontiers and exploded into many diverging sub-disciplines, all requiring the integration of mathematical, computational, and physical sciences. As such, biophysics and biomechanics is now an ever-growing branch of traditional physics. In particular, with the ability to measure forces, velocities, and displacements at the cellular and tissue levels, there is a clear need for mathematical theories and models that integrate the mechanical, chemical, and biological environments. For instance, it has now been understood that biological growth and development have an important mechanical component, playing a role in genetic programming, morphogenesis, and the regulation of physiological processes such as heart and artery remodeling. However, a unified theory of the growth of elastic tissues that addresses the fundamental coupling between geometric quantities and physical and chemical fields is still lacking. Theoretical progress on this problem will be needed both to answer basic scientific questions and to tackle fundamental challenges such as tumor growth. Similarly, the motion of biological organisms such as bacteria, sperm, and insects through fluids requires an understanding of fluid–solid interactions between self-propelled organisms and fluids that can have a gel-like or active response. With their training in mechanics, mathematics, and modeling, physicists have a unique opportunity to play a central role in the development of such modern biological theories. However, the classical training in the physical sciences does not introduce students to such problems, and fails to give them the proper state-of-the-art tools to address these challenges.

In July 2009, many experts in mathematical modeling in the biological sciences gathered in Les Houches for a four-week summer school on the mechanics and physics of biological systems. The goal of the school was to present to students and researchers an integrated view of the new trends and challenges in the physical and mathematical aspects of biomechanics. Although the scope of such a topic is very wide, we focused on problems where solid and fluid mechanics plays a central role. The school covered both the general mathematical theory of mechanical biology in the context of continuum mechanics and the specific modeling of particular systems in the biology of cells, plants, and microbes, and in physiology. The school was organized around five different main topics, all connected by the common theme of continuum modeling for biological systems. These collected lecture notes reflect the same organization, namely biofluidics, biogels, biomechanics, biomembranes, and morphogenesis. These lecture notes are not meant as a journal review of the topic but rather as a gentle tutorial introduction to

readers who want to understand the basic problems of modeling biological systems from a mechanical perspective.

It is with great pleasure that we acknowledge the financial support of various organizations: the Centre Nationale de la Recherche Scientifique through its Formation Permanente program; the newly established Fondation Pierre-Gilles de Gennes; the Réseau des Systèmes Complexes (Paris Fédération); the Université Pierre et Marie Curie; the École Doctorale systèmes complexes (Paris); and the European Union through its Marie Curie Intra-European Fellowship (EIF) grant 042069, CancerBio-Mechanics, under the 6th Framework Programme. It is also our pleasure to thank the staff of the École for their support.

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**Part I**

**Biofluidics**

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# 1

# Locomotion at low Reynolds numbers

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## 1.1 Introduction

The following three lectures are intended as an introduction to locomotion at low Reynolds numbers rather than as a comprehensive review. For students who desire a more in-depth treatment, I have included references throughout the text. These notes are written in an informal tone to match the lectures, which included a mix of chalk talks and PowerPoint presentations. Many of the PowerPoint slides have been reproduced here, although some copyrighted images have been omitted (deleted images have been replaced by references directing the reader to the original sources).

## 1.2 Lecture 1: Swimming

Over the three days of these lectures, we discussed various forms of low-Reynolds-number locomotion, including:

*Day 1:* overview & swimming;

*Day 2:* crawling (snails);

*Day 3:* burrowing (clams).

However, before we consider these specific forms of locomotion, it is useful to consider what types of biological organisms, generally speaking, operate in a low-Reynolds-number regime.

### 1.2.1 Reynolds numbers in biology

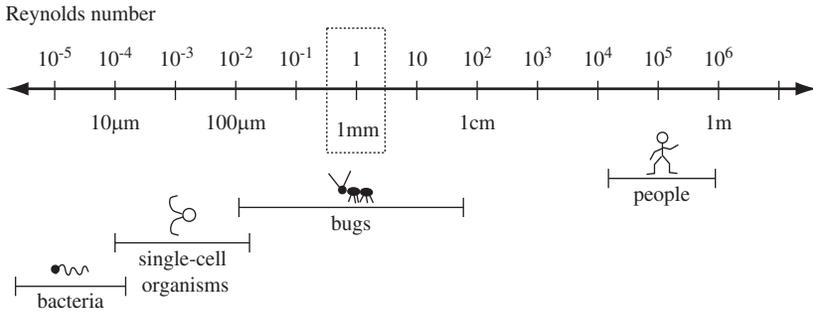
The Reynolds number is a dimensionless group that characterizes the ratio of inertial to viscous forces. It is defined as

$$Re = \frac{\rho UL}{\mu} = \frac{UL}{\nu},$$

where  $\rho$  is the density of the medium the organism is moving through,  $\mu$  is the dynamic viscosity of the medium,  $\nu$  is the kinematic viscosity,  $U$  is a characteristic velocity of the organism, and  $L$  is a characteristic length scale. When we discuss swimming *biological* organisms, we are usually referring to creatures that are moving through water (or through a fluid with material properties very close to those of water). This means that the material properties  $\mu$  and  $\rho$  are fixed<sup>1</sup> and the Reynolds number is roughly determined by the *size* of the organism.

In general, the characteristic size of the organism and the characteristic swimming velocity are related. As a rule of thumb, the characteristic locomotion velocity  $U$  in biological organisms is related to  $L$  by  $U \sim L/\text{second}$ ; for example for people,  $L \sim 1$  m and we move at  $U \sim 1$  m/s; bugs are about  $L \sim 1$  mm, and they move at about  $U \sim 1$  mm/s; for microorganisms,  $L \sim 100$   $\mu\text{m}$  and  $U \sim 100$   $\mu\text{m/s}$ . Obviously, this is a very, very, very rough estimate, and one does not have to think very hard to come up with exceptions (as is always the case in biology!). However, it serves as a good starting point for estimating the Reynolds numbers for various biological organisms

<sup>1</sup>For water,  $\nu \approx 10^{-2}$   $\text{cm}^2/\text{s}$  and  $\rho \approx 1$   $\text{g}/\text{cm}^3$ .



**Fig. 1.1** Typical Reynolds numbers for various biological organisms. Reynolds numbers are estimated using the length scales indicated, the “rule of thumb” in the text, and material properties of water.

as illustrated in the sketch in Fig. 1.1. Note that even for organisms as small as ants, the Reynolds number is still on the order of 1 (which is not very low). In this lecture, we will focus on  $Re \ll 1$ , which is relevant to single-cell organisms and bacteria.

At this point it is worth mentioning a few biological details about single-celled organisms. A good place to start is the well-known image sketched by the fluid dynamist James Lighthill (made in the days before PowerPoint). I haven’t included the image here, for fear of copyright infringement, but it is worth looking up and readily available in Lighthill (1976). Lighthill’s figure represents a fluid dynamicist’s view of biology as he has classified the organisms first and foremost not by any biological metric, but by how they swim. Organisms within the central circle all consist of a head (which is generally modeled as a sphere) propelled by  $N$  tails, where  $N$  is a small number (generally 1, 2, or 3). Organisms outside the circle use some other mechanism or don’t locomote at all.

On top of this division, there is a second (more traditional) biological classification. The semicircle dividing the top of the image from the bottom marks the dividing line between eukaryotic cells and prokaryotic cells. Roughly speaking, prokaryotic cells are bacteria and eukaryotic cells are everything else (people, fungi, grasshoppers, elephants, algae, ...). This distinction between eukaryotic and prokaryotic swimmers is quite important, because the structure of the tails (which determines the mechanics of swimming) is different in the two groups. For eukaryotes, the tail is made of flagellin and has a characteristic 9+2 microtubule structure. This has two important consequences:

1. By sliding the microtubules relative to one another, the organism can exert a local bending moment anywhere along the length of the tail, which means that eukaryotic organisms can *select the shape of the tail as a function of time* (i.e. they can control the kinematics). This is in contrast to prokaryotic organisms, which have a single motor that connects the tail to the head and hence can only apply a localized torque at the base of the tail.

**Table 1.1** The structure of tails

<b>Eukaryotes</b>	<b>Prokaryotes</b>
Flagellin	Tubulin
Distributed torque	Concentrated torque
9+2 microtubule structure	
Diameter of tail $\sim 300$ nm	

2. Since all eukaryotic tails have the same 9+2 microtubule structure, they all have roughly the same cross-sectional diameter. The length of the tail may vary from organism to organism, but the diameter is approximately 250–400 nm for all species (this includes the cilia in our lungs, the tails of green algae, the tails of spermatozoa, etc.).

These differences between prokaryotic and eukaryotic tails are summarized in Tabel 1.1

### 1.2.2 The physics of low-*Re* swimming

At this point we need to introduce our next reference, Purcell (1977). This is one of the most well-known papers on swimming at low Reynolds numbers and I highly recommend it for anyone who is looking for a gentle introduction to the topic. For the purposes of this lecture, we will define swimming as follows:

**Swimming:** To undergo cyclic deformations that result in a net translation and/or rotation (with no externally applied forces or torques).

The governing equations for low-Reynolds-number flow around an organism undergoing such deformations are the Stokes equations:

$$\nabla p = \mu \nabla^2 \mathbf{u}, \nabla \cdot \mathbf{u} = 0.$$

In addition, the forces and torques on the organism must balance (since we are considering an inertialess world, there is no acceleration, and hence  $m\mathbf{a} = 0$ ):

$$\mathbf{F} = \mathbf{0}, \mathbf{M} = \mathbf{0}.$$

A few features of swimming at low Reynolds number are readily apparent from these equations:

1. Usually when we balance forces in locomotion studies, we balance some propulsive force against drag (e.g. vortex shedding or inertia). However, at low Reynolds numbers the only thing that can balance drag is . . . drag! Hence propulsion comes from the *anisotropy* in the drag force. At low Reynolds numbers, the drag force on an object moving through a fluid is linearly proportional to the velocity:  $\mathbf{F} \propto \mathbf{U}$ , or

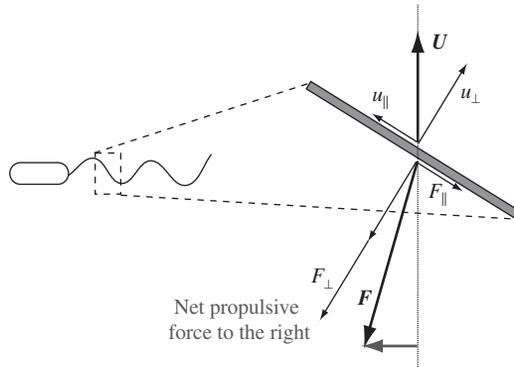


Fig. 1.2 Net propulsive force generated by a deforming tail.

$$F_{\perp} = C_{D\perp} u_{\perp}, \quad F_{\parallel} = C_{D\parallel} u_{\parallel},$$

where the subscripts indicate directions parallel to and perpendicular to the surface of the object (as shown in Fig 1.2), and  $C_D$  is the drag coefficient. For a slender object,  $C_{D\perp} \approx 2C_{D\parallel}$ . This difference in the magnitude of the parallel and perpendicular drag coefficients can result in a net propulsive force as illustrated in the figure.

**Challenge to students:** Can you think of “objects” for which  $C_{D\perp}/C_{D\parallel} > 2$ ? Or examples of slender objects for which the drag coefficient in the “thin” direction is greater than the drag coefficient in the “thick” direction? (For a sphere,  $C_{D\perp}/C_{D\parallel} = 1$ .)

- Time does not appear explicitly in the Stokes equations (which are linear), and, consequently, they are time-reversible. This reversibility is beautifully demonstrated in G. I. Taylor’s movie on low-Reynolds-number flows, which is now available online at

[web.mit.edu/fluids/ww.shapiro/ncfmf.html](http://web.mit.edu/fluids/ww.shapiro/ncfmf.html).

(The demonstration of reversibility begins approximately 27 minutes into the film). Reversibility implies that a swimmer that undergoes a reciprocal deformation (i.e. a sequence of deformations that is symmetric when time is reversed) can never generate a net translation. This inability of reciprocal “swimmers” to swim at low Reynolds number is commonly known as the *Scallop Theorem* (since, as in Purcell’s paper, scallops are often used as the canonical example of a swimmer that can only undergo reciprocal deformations). In “Life at low Reynolds number,” Purcell (1977) suggests a number of ways to beat the Scallop Theorem that are *intrinsic* to the swimmer (e.g. by introducing chirality into the swimmer or by additional degrees of freedom).

**Challenge to students** (originally posed by Purcell): A three-link swimmer consists of three rigid pieces (two “arms” and a “body”) connected by hinges; time-varying torques can be independently applied at each of the hinges.

Imagine that the swimmer is activated in the following sequence (starting with both arms up): (1) arm 1 moves down, (2) arm 2 moves down, (3) arm 1 moves up, (4) arm 2 moves up. Which direction does this three-link swimmer go? (See Purcell (1977) for an illustration of the swimmer; see Becker *et al.* (2003) for the solution.)

However, in addition to *intrinsic* solutions, there has been a recent surge in interest in developing strategies to beat the Scallop Theorem that are *extrinsic* to the swimmer. The key idea here is to make things *soft*. For example, one can:

- (a) Put the swimmer near a “soft” interface (e.g. a free surface, membrane, or elastic solid). The flow around the swimmer induces deformations in the interface, and the resulting change in geometry introduces a source of nonlinearity that can break the symmetry (Troulloud *et al.* 2008).
- (b) Give the surrounding fluid a “soft microstructure” which leads to a viscoelastic constitutive relationship. (Other people will talk about this at this summer school, so I will not discuss swimming in viscoelastic fluids here.)

In addition to making things soft, one can also beat the Scallop Theorem by *swimming with friends*. See, for example, Lauga and Bartolo (2008).

3. In optimization calculations, we need to choose a metric to quantify what is being optimized. Common goals in locomotion studies include:

- (a) maximize speed for a given power (“sprinter”) or
- (b) maximize efficiency for a given speed (“endurance”).

Since time does not appear explicitly in the Stokes equations (which are linear), *speed and efficiency are equivalent measures of performance at low Reynolds numbers* The efficiency is generally defined as

$$\eta = \frac{\text{Rate of useful work}}{\text{Rate of viscous dissipation}} = \frac{\text{Force} \cdot \text{Velocity}}{\Phi} = \frac{\alpha V^2}{\Phi}.$$

The second criterion, maximizing efficiency for a given speed, corresponds to maximizing  $\eta$ . Likewise, maximizing the speed for a given power (fix  $\Phi$  and maximize  $V$ ) also corresponds to maximizing  $\eta$ . These two criteria, associated with speed and endurance, are equivalent at low Reynolds numbers because time can be scaled out of the equations and the performance of the stroke is determined purely by geometric considerations. Typical efficiencies for low-Reynolds-number swimmers are 1–2%; I would consider 10% to be a fantastically good efficiency for a low-Reynolds-number swimmer. In general, if authors cite numbers that are as high as (or higher than) 10%, they have used a different definition of  $\eta$ .

As an aside, Purcell worried about these low efficiencies (why would nature select organisms that are so inefficient?). To understand this, he calculated the power *per unit mass* for microorganisms, which he found to be on the order of 0.5 W/kg, which is lowish relative to larger organisms. Purcell likened this to “driving a Datsun in Saudi Arabia”: it’s not a great car, but it’s cheap to fill up the tank.

### 1.2.3 Simple swimmers

In the next part of the lecture we will review a simple model for a specific low-Reynolds-number swimmer, the 2D swimming sheet as analyzed by Taylor (1951).

For his swimmer, Taylor considered an infinite, inextensible sheet undergoing small-amplitude sinusoidal deformations. The vertical displacement of the sheet is prescribed by a traveling wave  $y_0 = b \sin(kx - \sigma t)$  (Fig.1.3) moving with a wave speed  $c = \sigma/k$ . Recall that the Stokes equations can be rewritten using the stream function as

$$\nabla^4 \psi = 0, \quad (1.1)$$

where  $\psi$  is the stream function and is related to the velocity field  $\mathbf{u} = (u, v)$  by  $u = -\partial\psi/\partial y$ ,  $v = \partial\psi/\partial x$ . This equation must be solved subject to the following boundary conditions:

- no slip at the sheet:  $\mathbf{u} = \mathbf{u}_{\text{sheet}}$  at  $y_0 = b \sin(kx - \sigma t)$ ; and
- $\mathbf{u} = \mathbf{0}$  as  $x \rightarrow \infty$  or  $\mathbf{u} = (-V, 0)$  in a frame moving with the sheet, where  $V$  is the swimming velocity.

The general solution to eqn (1.1) is given by

$$\frac{1}{\sigma} \psi = \sum_{n \text{ odd}}^{\alpha} (A_n y + B_n) e^{-ny} \sin nz + \sum_{n \text{ even}}^{\alpha} (C_n y + D_n) e^{-ny} \cos nz - \frac{Vy}{\sigma},$$

where  $z \equiv kx - \sigma t$ . (Note that in addition to  $A_n$ ,  $B_n$ ,  $C_n$ , and  $D_n$ ,  $V$  is also unknown and must be found by applying the boundary conditions.) Taylor then assumed  $bk \ll 1$ , expanded in powers of  $bk$ , and, half a page of algebra later, found  $V = 0$  at lowest order (i.e. no swimming). The next-order correction is found many, many, many pages of algebra later (which I will not write out here) to be

$$\frac{V}{C} = \frac{2\pi^2 b^2}{\lambda^2} \left( 1 - \frac{19}{4} \frac{\pi^2 b^2}{\lambda^2} \right).$$

Thus the sheet travels  $\approx \lambda/84$  in one cycle (which is consistent with what is observed in live microorganisms).

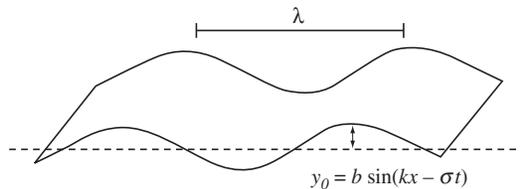


Fig. 1.3 2D swimming sheet.

1.2.4 Slightly less simple swimmers

In the final part of this lecture, I will discuss recent work from our group (primarily done by Daniel Tam) on slightly more realistic microswimmers. This part of the lecture was given in PowerPoint format and the slides have been included here as figures. We consider a swimmer that consists of a spherical head attached to a slender tail. The swimmer is allowed to select the kinematics of the tail (as is the case with eukaryotic flagella), and we seek the optimal curvature of the tail as a function of  $s$ , the distance along the flagellum, and of  $t$ , the time. The tail is modeled using slender-body theory and the head is modeled as a singularity distribution (for details, see the references in the slide shown in Fig. 1.4).

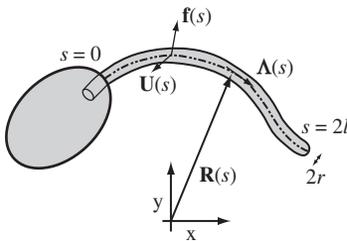
To test the model, we first consider an organism with no head. The optimal wave form is found numerically to be a sawtooth, consistent with the analytic optimal solution found by Lighthill for an infinitely long swimming snake (see the table in Fig. 1.4 for a quantitative comparison).

Next we consider an organism with a spherical head, and find that the optimal strokes have several characteristics that are consistent with what is observed in nature:

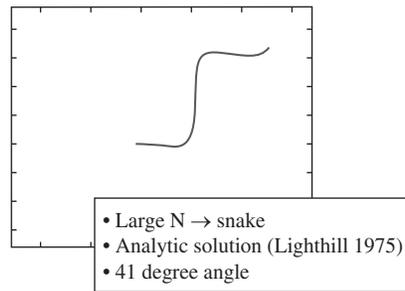
- The optimal strokes contain approximately one wavelength.
- The optimal wave shapes are *not* sinusoidal; rather, they consist of localized regions of high curvature connected by segments of low (approximately zero) curvature.
- The optimal curvature gradually decreases from head to tail.

Swimmer model

- Flagellum: Slender-body theory - find Stokeslet distribution (Keller and Rubinow 1976)
- Head: Exact singularity distribution (Chwang and Wu 1975)
- Head–flagellum interaction: Faxen’s laws (Happel and Brenner 1973)
- Find optimal curvature along the tail

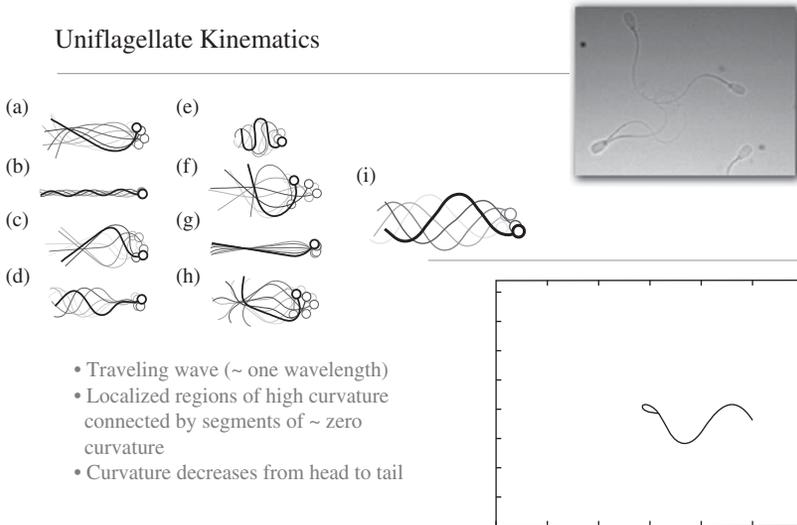


No head:



	$\Psi$	$\epsilon$	$U/V$
Analytical solution	$40^\circ$	0.0857	0.29
Computed solution	$\sim 41^\circ$	$\sim 0.08$	$\sim 0.25$

Fig. 1.4 Single-tail swimmer model.

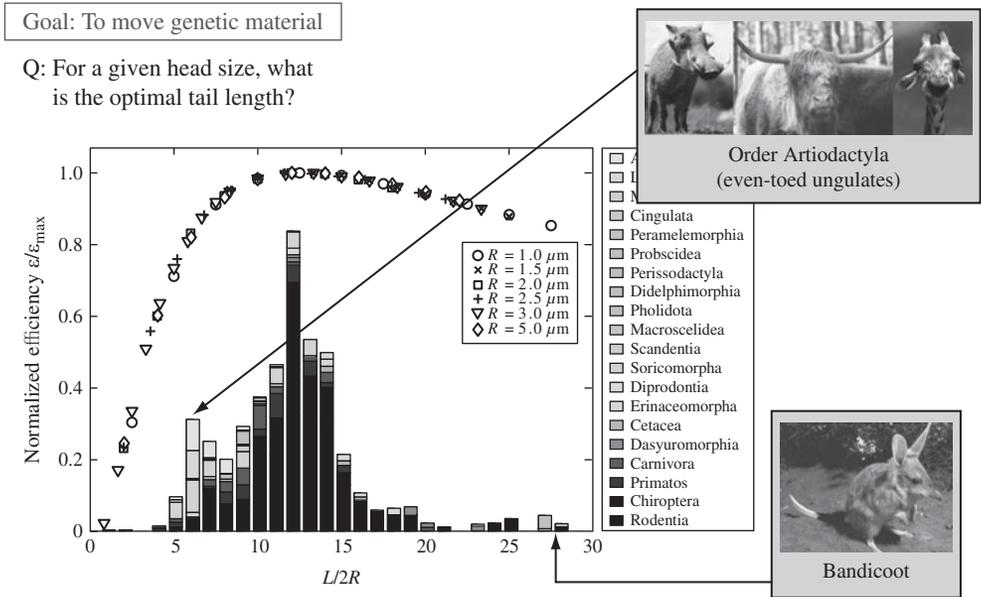


**Fig. 1.5** Initial guesses for the optimal stroke pattern. All initial conditions converge to (i).

These optimal strokes, along with sample initial guesses used in the optimization routine, are shown in Fig 1.5. While this qualitative comparison with live organisms is promising, it is difficult to make quantitative comparisons with biological data, as finding high-resolution kinematic data is challenging. However, although detailed kinematic data is lacking, there is quite a bit of data available on *morphology*.

To determine whether optimal morphologies for swimming have evolved in nature, we consider a specific microorganism with a well-defined objective function, the spermatozoon. It can be argued that spermatozoa have one primary objective: to deliver a package of genetic material to the egg. Hence we consider the following question: For a given head size (containing the genetic cargo), what is the optimal length of the tail for propulsion? One can argue that such an optimal length should exist by considering two extreme tail lengths  $L$ . As  $L \rightarrow 0$ , the organism cannot move and the swimming efficiency goes to zero. As  $L \rightarrow \infty$ , all of the energy goes into moving the infinitely long tail rather than the precious genetic payload, and again the efficiency goes to zero. Since there are tail lengths for which the efficiency is not zero (and the optimal efficiencies appear to vary smoothly with  $L$ ), there must be at least one optimal value between these two extremes. Figure 1.6 shows computed optimal efficiencies for various values of head-to-tail length ratio. Note that every point on this curve corresponds to an optimization calculation, and the optimal kinematics for short tails may not be the same as the optimal kinematics for long tails. Our computations indicate that the optimal value of  $L/2R$  is approximately 12, which corresponds to the peak in the histogram, containing data from over 400 mammalian species! We can now postulate that the morphologies of spermatozoa have evolved into optimal geometries for low-Reynolds-number swimming.

### Optimal Tail Length



**Fig. 1.6** The data points show the optimal efficiency as a function of head-to-tail length ratio,  $L/2R$ ; the histogram represents the number of mammalian species that exhibit a given value of  $L/2R$ .

However, one could argue that the most interesting data points in the histogram are the ones that are *far* from optimal, as those points represent species that either are suboptimal or have been subject to unique evolutionary pressures and constraints. In our data set, the organisms at the far right (long-tailed sperm) correspond to several species of bandicoot and other mammals where the sperm have unusually thick tails. These organisms violate our assumption that the radius of the tail is set by the 9+2 microtubule structure discussed earlier, as the flagellum is encased in a thick sheath, which adds mechanical toughness. At the other end of the spectrum (short tails), the outliers correspond to monotremes, the egg-laying mammals. In these species, the head of the sperm has a helical shape, far from our spherical approximation, so again it is not surprising that they fall far from the computed optimum.

The set of outliers that is more difficult to explain corresponds to the peak in the histogram for the even-toed ungulates (pigs, sheep, goats, cows, ...). These points deviate consistently from the optimal value of tail length by about a factor of two. We have been unable to rationalize this discrepancy, and we leave it as a puzzle for the students. For further details, see Tam and Hosoi (2010).

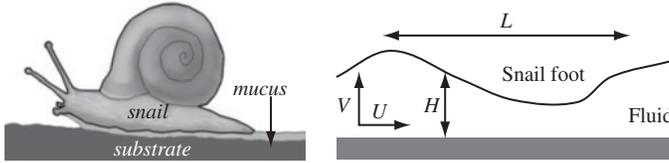


Fig. 1.7 Schematic illustration of snail and thin film. The characteristic velocities in the vertical and horizontal directions are denoted by  $V$  and  $U$ , respectively.

### 1.3 Lecture 2: Crawling

Our studies of crawling on fluid begin with snails. It is well known that snails crawl on top of a thin film of viscous fluid (pedal mucus), as shown in Fig. 1.7. The foot is not in direct contact with the substrate, and the only way that the snail's foot can interact with the substrate is by generating stresses within this thin film.

At this point we should ask: Does this qualify as low-Reynolds-number locomotion? Recall that I told you last time that in order to qualify as a low-Reynolds-number swimmer,  $L_{\text{organism}} \lesssim 1$  mm, and most snails are bigger than that (some, such as the giant African land snail, can grow to up to 30 cm in length!). However, we are saved because there are *two* characteristic length scales in a thin film,  $H$  and  $L$  (see Fig. 1.7). Comparing viscous and inertial forces, we find that we are allowed to neglect inertial terms in the equations of motion provided

$$\rho \frac{U^2}{L} \ll \mu \frac{U}{H^2} \Rightarrow \frac{\rho U H^2}{\mu L} \ll 1 \Rightarrow \left(\frac{H}{L}\right)^2 Re_L \ll 1.$$

In snails,  $H \sim 10 - 20 \mu\text{m}$  and  $L \sim 1$  mm, and hence  $(H/L)^2 \sim 10^{-4}$ . Combining this with the chart shown in Fig. 1.1, we find that even snails with sizes on the order of 10 cm still qualify as low-Reynolds-number locomotors.

#### 1.3.1 Locomotion on thin films: Out-of-plane waves (see Chan *et al.* 2005)

In this lecture, we begin by considering a waving sheet near a wall (analogous to Taylor's sheet in the previous lecture). This is a naively simple model for a snail, but we will later see that even though snails do not use this method for propulsion, we can glean useful information from this simple approximation. Before we calculate anything, we can argue that we expect this configuration to generate propulsion. As fluid is squeezed beneath constrictions between the foot and the substrate, high-pressure regions develop in front of the wave (See Fig. 1.9 later). This high pressure acts on the tilted foot surface, resulting in a net propulsive force opposite to the direction in which the wave travels. We model the sheet as inextensible and assume that the wave amplitude is small, limited by the presence of the rigid substrate. Again, the goal is to prescribe the kinematics, i.e. the shape of the foot as a function of time  $h(x, t)$ , and find the crawling velocity  $V_s$  associated with a given deformation. As with Taylor's sheet, we will work in a frame moving with the wave to eliminate the time dependence in the problem. Rescaling the equations of motion using  $\hat{u} = u \hat{V}_w$ ,

$\hat{v} = v(\hat{H}/\hat{L})\hat{V}_w$ ,  $\hat{y} = y\hat{H}$ ,  $\hat{x} = x\hat{L}$ , and  $\hat{p} = p\mu\hat{V}w\hat{L}/\hat{H}^2$ , the dimensionless lubrication equations become to lowest order

$$\frac{\partial p}{\partial x} = \frac{\partial^2 u}{\partial y^2}, \quad \frac{\partial p}{\partial y} = 0.$$

Solving for the velocity with the boundary conditions given in Fig.1.8, we find

$$u = \frac{\partial p}{\partial x} \frac{1}{2} y(y-h) + V_s \left( \frac{y}{h} - 1 \right) + 1. \quad (1.2)$$

If we consider steady-state crawling, the volumetric flux  $Q$  in the  $x$  direction must be a constant (i.e. not a function of  $x$  or  $t$ ), and hence

$$Q = \int_0^h u \, dy = \text{constant}.$$

Combining this with the expression for  $u$  yields

$$\frac{\partial p}{\partial x} = \frac{12}{h^3} \left[ h \left( 1 - \frac{V_s}{2} \right) - Q \right]. \quad (1.3)$$

Next we assume periodic boundary conditions in  $x$ ; in particular,  $p(0) = p(1)$ . This implies

$$\int_0^1 \frac{\partial p}{\partial x} dx = 0 = \int_0^1 \frac{12}{h^3} \left[ h \left( 1 - \frac{V_s}{2} \right) - Q \right] dx = \left( 1 - \frac{V_s}{2} \right) \underbrace{\int_0^1 \frac{dx}{h^2}}_{I_2} - Q \underbrace{\int_0^1 \frac{dx}{h^3}}_{I_3}.$$

Solving for  $Q$ , we find

$$Q = \left( 1 - \frac{V_s}{2} \right) \frac{I_2}{I_3},$$

where we have defined the integrals  $I_n = \int_0^1 dx/h^n$ .

So far we have invoked *conservation of momentum*, *conservation of mass*, and *periodicity*. The last step is to enforce *force balance*. The traction acting on the bottom of the foot of the snail is defined as

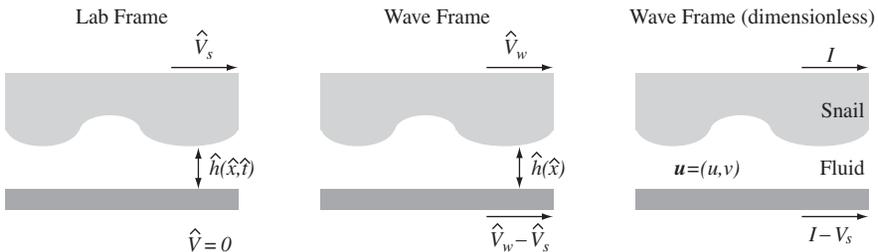


Fig. 1.8 Snail boundary conditions in stationary and moving frames.

$$\text{Force/length} = \text{traction} = \mathbf{f} = \boldsymbol{\sigma} \cdot \mathbf{n}.$$

In the  $y$ -direction, the weight of the crawler is balanced by the pressure in the thin film (which doesn't tell us anything about the crawling velocity). Force balance in the  $x$ -direction is more useful:

$$f_x = p \frac{dh}{dx} + \frac{\partial u}{\partial y}.$$

Integrating over one wavelength, we find

$$F_x = \int_0^1 \left( p \frac{dh}{dx} + \frac{\partial u}{\partial y} \right) \Big|_{y=h} dx = 0 \quad (1.4)$$

$$= ph|_0^1 - \int_0^1 h \frac{\partial p}{\partial x} \Big|_{y=h} + \int_0^1 \frac{\partial u}{\partial y} \Big|_{y=h} dx = 0. \quad (1.5)$$

Solving for  $V_s$ , we find

$$V_s = \frac{6(1-A)}{4-3A}, \text{ where } A = \frac{I_2^2}{I_1 I_3} \text{ and } I_n = \int_0^1 \frac{dx}{I_n^n}, \quad (1.6)$$

which tells us how to find the crawling speed given the shape of the foot. A demonstration of the effectiveness of this crawling strategy is illustrated in Fig. 1.10, which shows a robotic crawler using out-of-plane waves.

We can now use eqn (1.6) to select optimal wave shapes for crawling. First, consider the properties of the shape function  $A$ . Using the Cauchy–Schwartz inequality, we can find upper and lower bounds for  $A$ :

$$I_2^2 = \left( \int h^{-1/2} h^{-2/3} dx \right)^2 \leq \int h^{-3} dx \int h^{-1} dx = I_3 I_1.$$

Hence  $0 < A < 1$ . Combining this with eqn (1.2), we find that the maximum crawling velocity (Fig. 1.9) is achieved when  $A \rightarrow 0$ , which corresponds to “sharp” profiles. This

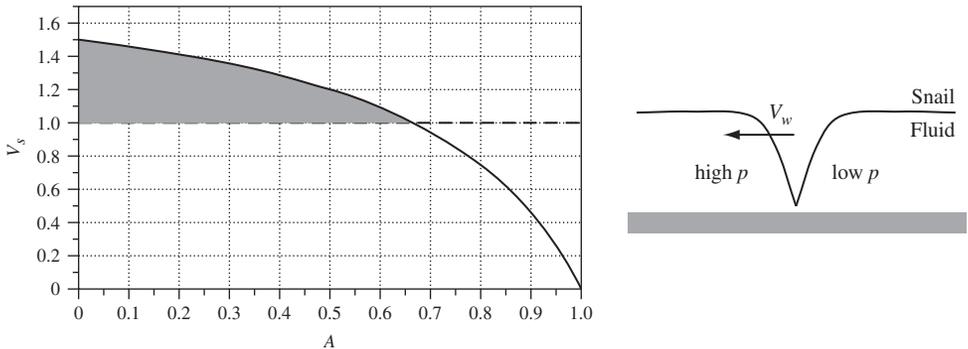


Fig. 1.9 Crawling velocity as a function of the shape function  $A$ .