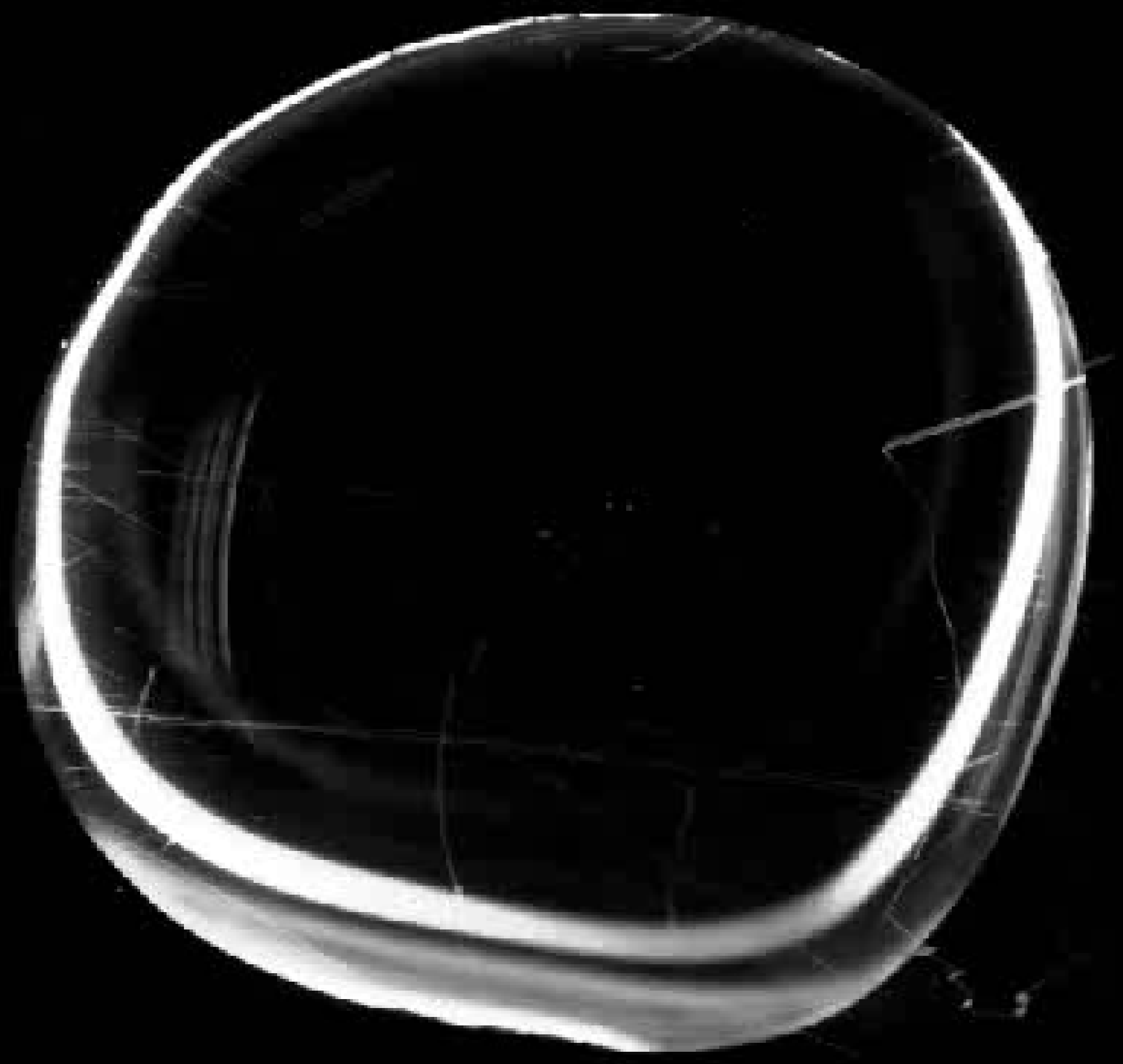
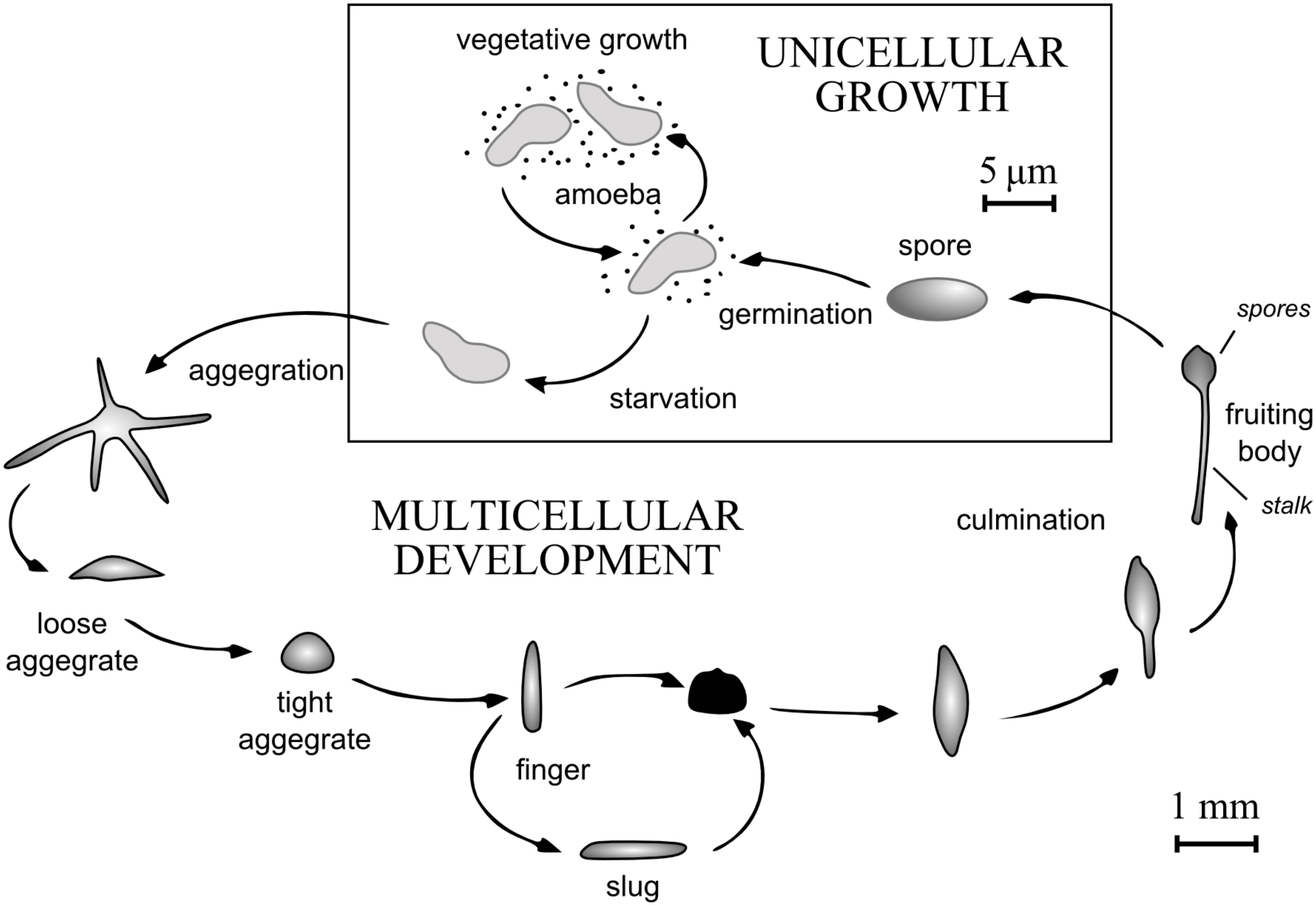
Bioconvection

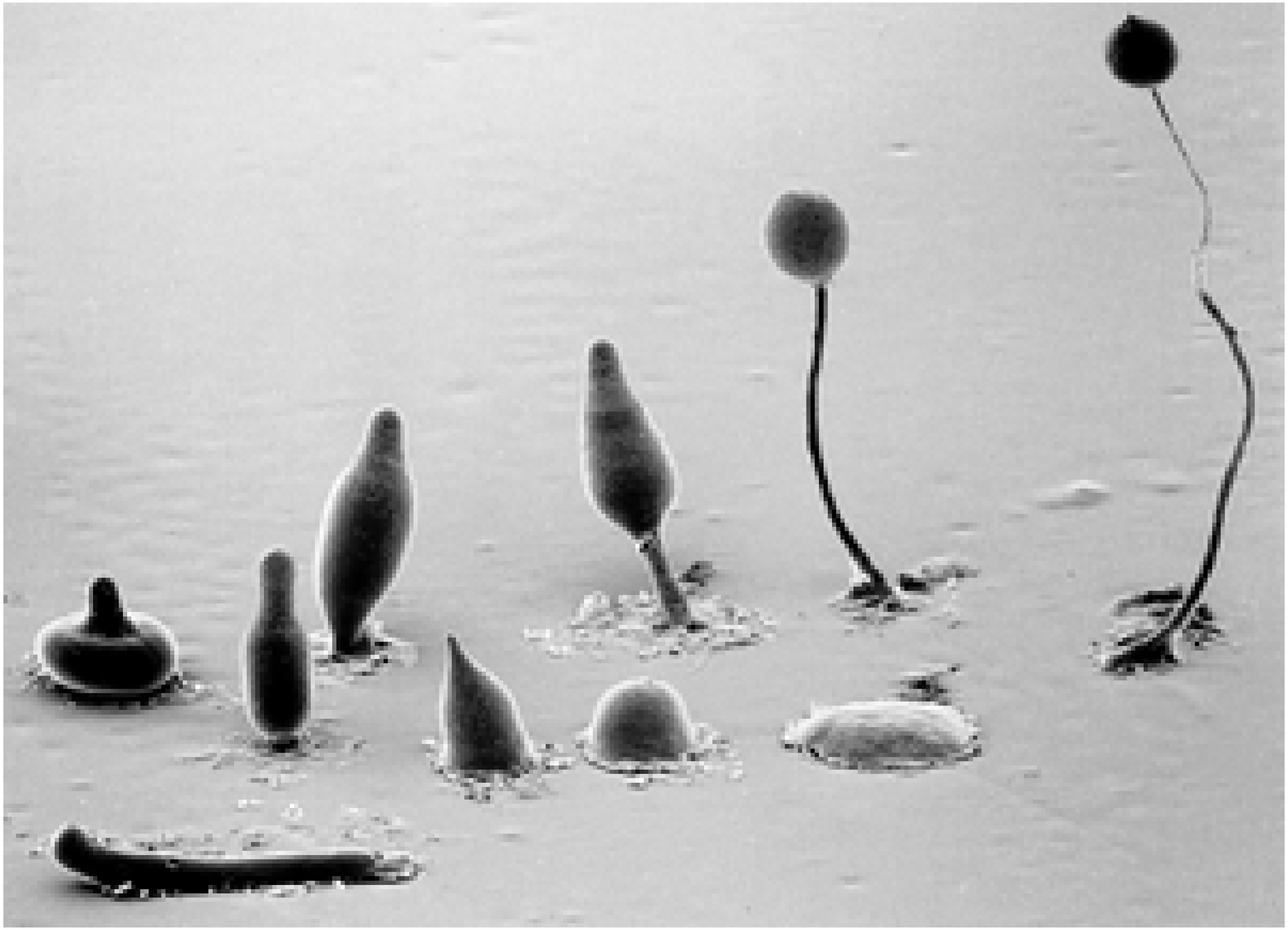


Dictyostelium discoideum

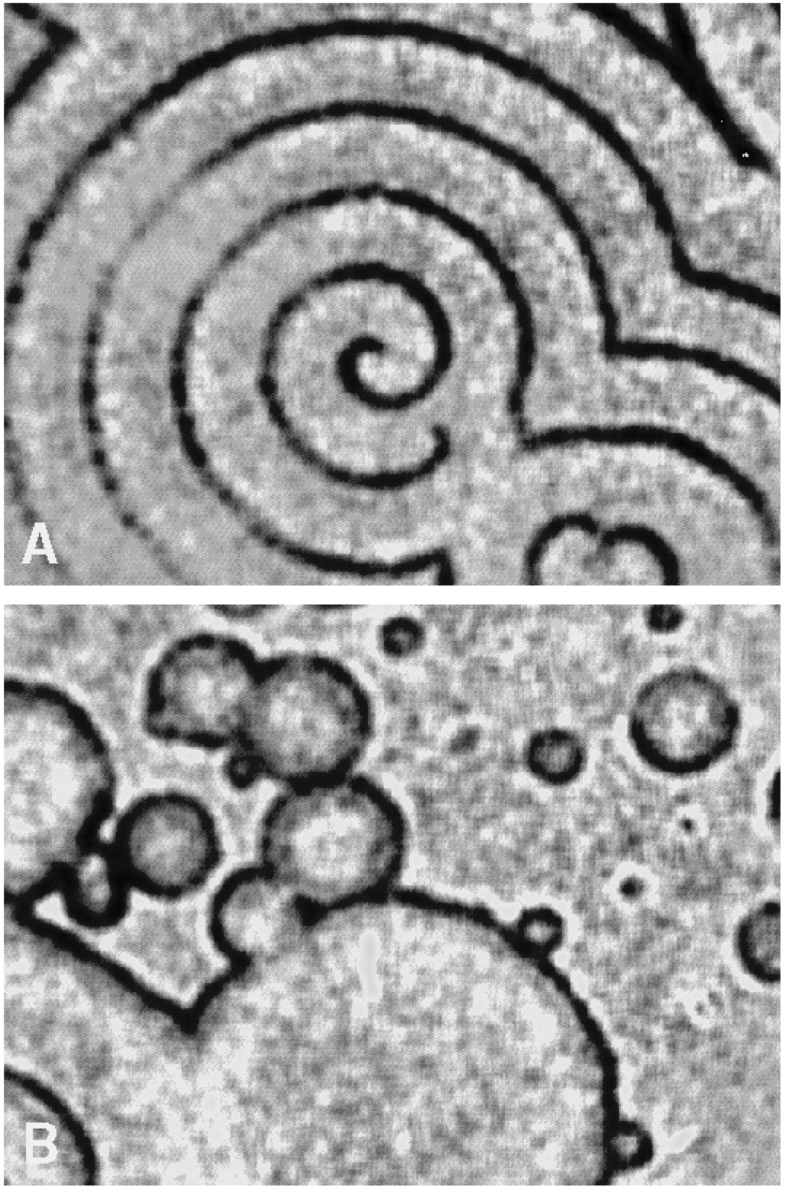


Wikipedia

Dictyostelium discoideum



Chemical Waves



Dictyostelium – the movie

Keller-Segel Model of Chemotaxis/Instability

This is a model with two variables: n, the cell concentration, and c the chemoattractant concentration. In the absence of cell division, n must obey a conservation law of the form

$$n_t = -\boldsymbol{\nabla} \cdot \mathbf{J} \ ,$$

where the cell current has diffusive and chemotactic contributions,

$$\mathbf{J} = -D_n \boldsymbol{\nabla} n + rn \boldsymbol{\nabla} c \ .$$

Here, the response coefficient r might be a function of the chemoattractant concentration c, as in oxygentaxis. For run-and-tumble locomotion, we expect $D_n \sim \ell^2/\tau$, with $\ell \sim u\tau$, where u is the swimming speed. Accounting for release and degredation of c the KS eqns are

$$\begin{aligned} n_t &= D_n \nabla^2 n - \boldsymbol{\nabla} \left(rn \boldsymbol{\nabla} c \right) \\ c_t &= D_c \nabla^2 c + fn - kc \ . \end{aligned}$$

Clearly there is a steady state with $n = n_0$ and $fn_0 = kc_0$, so $c_0 = fn_0/k$.

KS Model - continued

We perform a linear stability analysis in one spatial dimension by setting

$$n = n_0 + \eta \ , \qquad c = c_0 + \chi \ .$$

which yields

$$\begin{aligned} \eta_t &= D_n \eta_{xx} - r n_0 \chi_{xx} \\ \chi_t &= D_c \chi_{xx} + f\eta - k\chi \ . \end{aligned}$$

The linear stability problem for perturbations of the form $e^{iqx+\sigma t}$ is just

$$\begin{vmatrix} -D_n q^2 - \sigma & r n_0 q^2 \\ f & -D_c q^2 - k - \sigma \end{vmatrix} = 0 \ .$$

If we write this as $\sigma^2 + b\sigma + c = 0$, with $b = k + (D_n + D_c)q^2$ and $c = D_n q^2 (D_c q^2 + k) - f r n_0 q^2$, then $\sigma_\pm = (-b \pm \sqrt{b^2 - 4c})/2$, and we require $b^2 - 4c > 0$ for real roots. The stability condition is $c > 0$, or

$$D_n \left(D_c q^2 + k \right) > f r n_0 \ .$$

Thus, as $q \to 0$ an instability is possible if

$$\frac{f r n_0}{D_n k} > 1 \ .$$

Diffusion and Advection

Let us return to the competition between advection and diffusion discussed at the beginning of the course to understand the important concept of *boundary layers*. If a concentration field is subject to transport by a fluid flow field $\mathbf{u}$ in addition to diffusion, then

$$\frac{\partial c}{\partial t} + \mathbf{u} \cdot \boldsymbol{\nabla} c = D \nabla^2 c \ .$$

By the usual scaling arguments we suppose there exists a characteristic speed U and length scale L, implying a time scale L/U. Then if we introduce

$$t' = t/(L/U) \ , \quad \mathbf{x}' = \mathbf{x}/L \ , \quad \mathbf{u}' = \mathbf{u}/U \ ,$$

the advection-diffusion equation becomes

$$\frac{U}{L}\frac{\partial c}{\partial t'} + U\mathbf{u} \cdot \frac{1}{L}\boldsymbol{\nabla}' c = D\frac{1}{L^2}\nabla'^2 c \ ,$$

or

$$Pe\left(\frac{\partial c}{\partial t'} + \mathbf{u} \cdot \boldsymbol{\nabla}' c\right) = \nabla'^2 c$$

Diffusion and Advection - continued

Consider now a two-dimensional example in which a uniform fluid velocity field moves from left to right, $\mathbf{u} = (U, 0)$, so

$$\frac{\partial c}{\partial t} + U\frac{\partial c}{\partial x} = D\nabla^2 c \ .$$

This might be flow sweeping past a small pointlike source in the plane or, as we consider here, parallel to a surface at $y = 0$ held at c_0. In the steady state, the only length scale in the problem is D/U, so if we scale space by that we have

$$\frac{\partial c}{\partial x} = \nabla^2 c \ ,$$

with $c = c_0$ at $y = 0$ and $c \to 0$ as $y \to \infty$.

The key point is that if a region in which $c \neq 0$ remains *thin* then

$$\left|\frac{\partial^2 c}{\partial y^2}\right| \gg \left|\frac{\partial^2 c}{\partial x^2}\right|$$

Then,

$$\frac{\partial c}{\partial x} \simeq \frac{\partial^2 c}{\partial y^2}$$

Diffusion and Advection - continued

The problem

$$\frac{\partial c}{\partial x} \simeq \frac{\partial^2 c}{\partial y^2}$$

is just a disguised version of the previously-solved time-dependent diffusion equation ($t \to x, x \to y$), so we read off the answer as:

$$c = c_0 \mathrm{erfc}\left[\frac{y}{\sqrt{4x}}\right] = c_0 \mathrm{erfc}\left[\frac{y}{\sqrt{4Dx/U}}\right] = c_0 f(\eta)$$

which we recognize as a similarity solution with a length scale $\delta \sim (Dx/U)^{1/2}$.

Is the original assumption justified?

$$c_x \sim c_0 \frac{\eta f'(\eta)}{x}\,, \qquad c_y \sim c_0 \left(\frac{U}{4Dx}\right)^{1/2} f'(\eta)\,,$$

so $|c_y| \gg |c_x|$ if

$$\left(\frac{U}{Dx}\right)^{1/2} \gg \frac{1}{x}\,, \qquad \text{or} \qquad x \gg D/U\,.$$

Nonlinear Diffusion I.

There are many examples in biological physics (and elsewhere) in which the diffusion constant depends on the concentration C. Consider the case $D = kC$ in one spatial dimension. The diffusion equation is then

$$C_t = k\left(CC_x\right)_x \ .$$

Suppose we start with a finite amount of solute at $x = 0$:

$$C(x,0) = S\delta(x) \ ,$$

with $C \to 0$ as $|x| \to \infty$, $t \geq 0$. Then for all time $\int_{-\infty}^{\infty} dx C(x,t) = S$. Once more, we can do a lot with dimensional analysis. For $C = F(S,k,x,t)$, but with $[Sk] = L^3/T$, the only way to get a dimensionless number is via

$$\xi = \frac{x}{(Skt)^{1/3}} \ ,$$

obviously suggesting that $(Skt)^{1/3}$ is the proper scaling for x. The conservation of S suggests that the proper scaling of C is $S/(Skt)^{1/3}$ (that is, S/length). Hence, we surmise that there is an interesting similarity solution of the form

$$C(x,t) = \frac{S^{2/3}}{(kt)^{1/3}} F(\xi) \ .$$

Nonlinear Diffusion II.

If we substitute this back into the nonlinear diffusion equation we obtain the ODE

$$(FF_\xi)_\xi = -\frac{1}{3}(F + \xi F_\xi) \ .$$

This has the form of a total derivative: $(FF_\xi + (1/3)\xi F)_\xi = 0$. With boundary condition $F \to 0$ as $|\xi| \to \infty$ and $\int_{-\infty}^{\infty} d\xi F = 1$ we obtain

$$F\left(F_\xi + \frac{1}{3}\xi\right) = \text{const} = 0 \ .$$

Thus, either $F = 0$ or $F_\xi + (1/3)\xi = 0$. Hence $F = A - (1/6)\xi^2$ for some $A > 0$. But, wait a minute: $F = 0$ at $\xi = \sqrt{6A}$ and we cannot have $F < 0$. We conclude that the solution stops at $\xi = \xi_0 = \sqrt{6A}$ and $F = 0$ beyond. The integral constraint then yields $A = (3/32)^{1/2}$ and so $\xi_0 = (9/2)^{1/3}$. In original units, $x_0 = \xi_0(SDt)^{1/3}$. A solution with compact support!

See Matlab file nonlindiffusion.m

Fisher Equation (1937)

The Fisher equation describes diffusion in a system with so-called logistic kinetics:

$$u_t = u_{xx} + u(1-u) \ .$$

Note that $u(1-u) = -\partial_u[-(1/2)u^2 + (1/3)u^3]$, so we can see that the state $u = 0$ is an unstable maximum and $u = 1$ is a stable minimum of the effective potential.
Suppose we start with a finite blob of stuff. As shown in the matlab solution, at large times we get travelling waves of fixed shape (and speed $\gamma = 2$). The initial state is no longer remembered.

See Matlab file fisher.m

Let's try to analyze a travelling wave of fixed shape, $u = f(\xi)$, where $\xi = x - \gamma t$.

Fisher Equation (1937)

Then

$$-\gamma f_\xi = f_{\xi\xi} + f(1-f) \ ,$$

and for the rightward travelling wave, $f \to 0$ as $\xi \to \infty$ and $f \to 1$ as $\xi \to -\infty$. Can we predict $\gamma = 2$? Not easily, but consider the wave front, where $f \ll 1$. Then

$$-\gamma f_\xi \simeq f_{\xi\xi} + f \ ,$$

so $f \sim exp(-\alpha\xi$ where $\gamma\alpha = 1 + \alpha^2$, or

$$\gamma = \frac{1}{\alpha} + \alpha \ .$$

So, a solution appears to be possible for all α and $\gamma \geq 2$. Kolmogorov (1937) proved that is the initial data have compact support (i.e. $u(x,0) = 0$ for $|x| > x_0$), then at large times the wave speed is 2 (hard). But if the initial data $\to 0$ as $|x| \to \infty$ as $\exp(-ax)$, say, then the wave speed depends critically on a. If $a < 1$ then γ cannot be 2 because $\mathrm{e}^{-ax} > \mathrm{e}^{-x}$. Then $\gamma = a + 1/a$.