## MATHEMATICAL TRIPOS Part III

Friday, 2 June, 2023 9:00 am to 12:00 pm

## PAPER 355

## BIOLOGICAL PHYSICS AND FLUID DYNAMICS

## Before you begin please read these instructions carefully

Candidates have THREE HOURS to complete the written examination.
Attempt ALL questions.
There are THREE questions in total.
The questions carry equal weight.

| STATIONERY REQUIREMENTS | SPECIAL REQUIREMENTS |
| :--- | :--- |
| Cover sheet | None |
| Treasury tag |  |
| Script paper |  |
| Rough paper |  |

You may not start to read the questions printed on the subsequent pages until instructed to do so by the Invigilator.

1 Two nearby spherical colonies of the alga Volvox of radius $R$ swim up to the airwater interface and hover so their centres are a distance $R$ below the surface, and their initial lateral separation is $x_{0}$. Each has a density $\rho$ greater than the density $\rho_{w}$ of water, with $\epsilon \equiv\left(\rho-\rho_{w}\right) / \rho_{w} \ll 1$ and keeps itself from sinking under the action of the gravitational acceleration $g$ by constant up-swimming.

Treating each organism's effect on the fluid as a downwardly directed point force due to gravity, and the air-water interface as a stress-free surface, find the equation of motion for the separation $x$ between the particles as they are each advected laterally by their mutual flows, recalling that the velocity components for a Stokeslet in free space are

$$
u_{j}=\frac{F_{k}}{8 \pi \mu}\left(\frac{\delta_{j k}}{r}+\frac{r_{j} r_{k}}{r^{3}}\right)
$$

where $F_{k}$ are the components of the force. Express the equation of motion in suitably rescaled units of space and time so that no material parameters appear explicitly. Show that the equation of motion for the scaled separation $\xi$ as a function of scaled time $\tau$ has the form of a gradient flow,

$$
\begin{equation*}
\frac{d \xi}{d \tau}=-\frac{d V(\xi)}{d \xi} \tag{1}
\end{equation*}
$$

for an effective potential $V(\xi)$ that you should find and sketch. Using the far-field behavior of $V(\xi)$, estimate the time $T$ for the particles to collide, starting from the initial separation $x_{0}$. Estimate that time using the values $\epsilon=0.03, R=200 \mu \mathrm{~m}$ and $x_{0}=5 R$.

2 An elastic filament of length $L$, radius $a$ and bending modulus $A$ lies along the $x$-axis with its left end at the origin, surrounded by a fluid of viscosity $\mu$ at temperature $T$. Thermal fluctuations cause small deviations $h(x)$ from its equilibrium straight configuration. Assuming that the filament is clamped at $x=0$ such that $h(0)=h_{x}(0)=0$, find the mean squared displacement of the filament's tip, and the autocorrelation function of the tip displacement using resistive force theory to describe its motion in the fluid. Simplify your answers based on the dominant mode. Estimate the scale of the fluctuations and the time constant that appears in the autocorrelation function for microtubules, assuming $L=10 \mu \mathrm{~m}, a=0.5 \mu \mathrm{~m}$, and the persistence length is $L_{p}=3 \mathrm{~mm}$.

3 A simple model for the dynamics of biological filaments driven by motor proteins involves two rigid links of length $\ell$ joined together at point $A$, the left link fixed at the origin $O$, constrained to lie in the plane $z=0$, as in the figure. A follower force $\boldsymbol{\Gamma}=-\Gamma \hat{\mathbf{t}}$ acts at the tip of the second link, always parallel to the tangent vector $\hat{\mathbf{t}}$ of the second link. The two degrees of freedom in the system are the angles $\theta_{1}(t)$ and $\theta_{2}(t)$ with respect to the $x$ axis. Elasticity is included by introducing two torsional springs, each with spring constant $k$, such that the restoring moments acting on the two rods are $-k \theta_{1}$ at point $O$ and $-k\left(\theta_{2}-\theta_{1}\right)$ at $A$. The system moves in Stokes flow, and the drag forces are assumed to be concentrated at points $A$ and $B$ only, characterized by a drag coefficient $\zeta$.


Figure 1: Two-link model.

Use the principle of virtual work in the form

$$
\begin{equation*}
\boldsymbol{\Gamma} \cdot \delta \mathbf{r}_{B}+\mathbf{F}_{B} \cdot \delta \mathbf{r}_{B}+\mathbf{F}_{A} \cdot \delta \mathbf{r}_{A}-k \theta_{1} \delta \theta_{1}-k\left(\theta_{2}-\theta_{1}\right)\left(\delta \theta_{2}-\delta \theta_{1}\right)=0 \tag{1}
\end{equation*}
$$

to obtain the equations of motion for the two angles $\theta_{1}$ and $\theta_{2}$. Show by suitable rescaling of time that the quantity $\Sigma=\Gamma \ell / k$ is the only parameter in the problem, and that the coupled dynamics takes the form

$$
\begin{align*}
2 \theta_{1}^{\prime} & +\cos \left(\theta_{1}-\theta_{2}\right) \theta_{2}^{\prime}+2 \theta_{1}-\theta_{2}-\Sigma \sin \left(\theta_{1}-\theta_{2}\right)=0 \\
\theta_{2}^{\prime} & +\cos \left(\theta_{1}-\theta_{2}\right) \theta_{1}^{\prime}-\theta_{1}+\theta_{2}=0 \tag{2}
\end{align*}
$$

where ${ }^{\prime}$ denotes differentiation with respect to the rescaled time. Find the the filament dynamics in the special case $\theta_{1}=\theta_{2}=\theta$ and give a physical explanation for its form. Perform a linear stability analysis of the full dynamics around the straight configuration $\theta_{1}=\theta_{2}=0$ and show that the system has a Hopf bifurcation beyond a critical value of $\Sigma$ that you should find. Sketch the trajectory in the complex plane of the growth rate of the unstable modes as a function of $\Sigma$. Explain the existence of the oscillatory unstable modes in terms of the variational structure of the dynamics.

## END OF PAPER

