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Bifurcation Analysis in the Follower Force Model

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CONTACT ME!

1. MOTIVATION

Microtubules (MTs) are long, slender polymers, which drive fluid flow at the microscopic scale. Their dynamics are driven by molecular motors which translocate along the filament length, applying compressive forces. Collectively, MTs can lead to phenomena like cytoplasmic streaming and metachronal waves in ciliary arrays, making MT-motor systems essential in understanding fluid transport and cell motility.

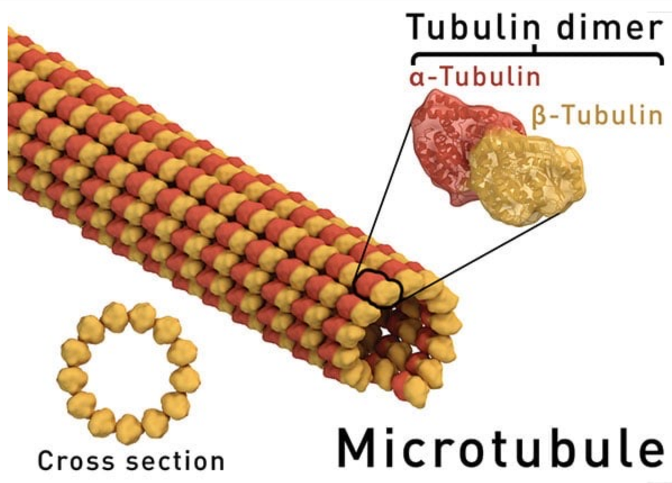


Figure 1 (above): A schematic of a microtubule from [1].

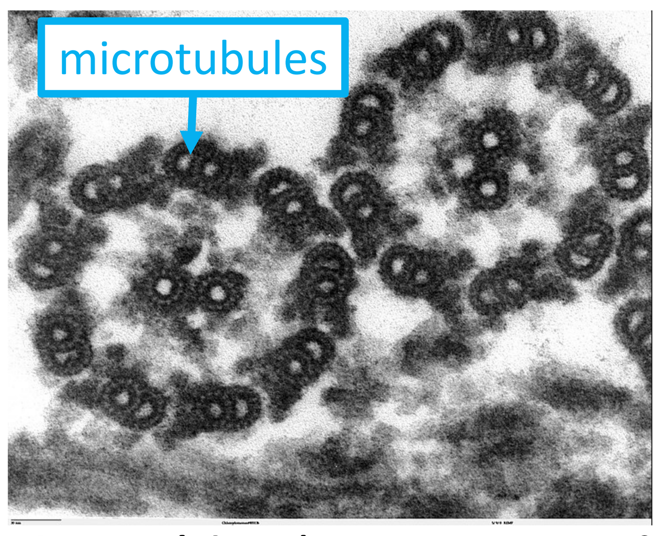


Figure 2 (above): A cross-section of two cilia from [2]. The small circular rings shown are microtubules.

GOAL: to develop a complete understanding of the fundamental microtubule-motor protein model.

2. THE MODEL

- To represent a single molecular motor, we impose a **compressive force** at the filament tip (see ***Figure 3***).

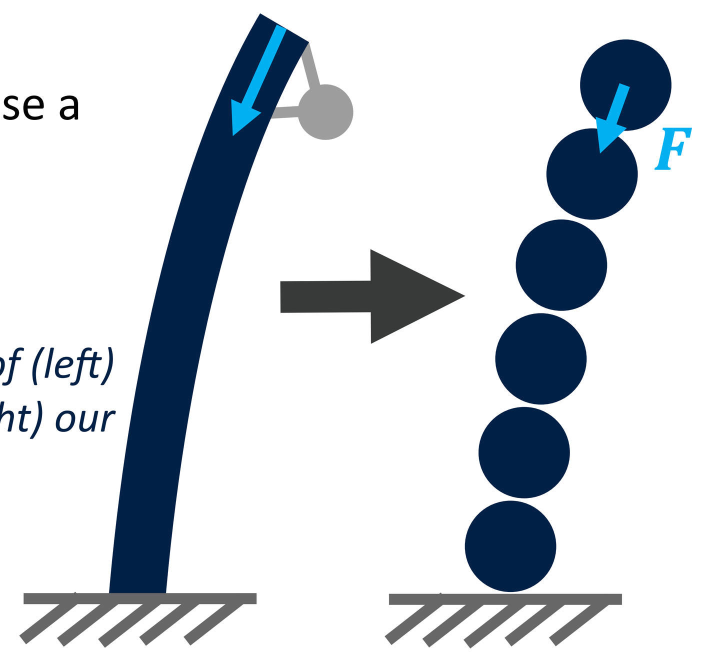


Figure 3 (right): *A schematic of (left) the physical problem, and (right) our model in the discrete setting.*

- Filament model from [3]:
- Model filament as N segments, radius a.
- Segment n has position vector $\boldsymbol{Y}_n$ and tangent $\hat{t}_n$.
- For each segment we have force and torque balances:

$$F_C - F_H = 0$$
$$T_E + T_C - T_H = 0$$

where F_C/T_C are the constraint forces/torques to enforce inextensibility of the filament, T_E are the elastic torques and F_H/T_H are the hydrodynamic forces/torques, accounting for the effect of the fluid.

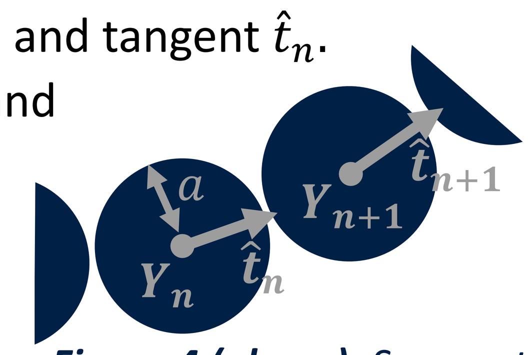


Figure 4 (above): *Segments n and $n+1$ in our discretisation.*

- In Stokes flow, velocity and angular velocity of each segment are then found through the relation:

$$\begin{bmatrix} V \\ \Omega \end{bmatrix} = M \begin{bmatrix} F_H \\ T_H \end{bmatrix}$$

- Explicit approximations of M can be found.
- Integrate the system forward in time to progress the simulation, using unit quaternions to describe the rotation of the local frame over time.
- $f = C||\boldsymbol{F}||$ is the nondimensional follower force, controlling the **strength of the force**, where C is a constant depending on the bending rigidity and filament length.
- $\alpha = length/radius$ is the **aspect ratio** affecting the ratio of viscous forces to elastic bending forces.

We vary f and α and observe the corresponding behaviours.

3. OVERVIEW OF BEHAVIOURS – INITIAL VALUE PROBLEM

- Using the **initial value problem** (IVP) we can vary α and f to generate the solution space
- Initial condition: vertically upright filament.
- We find a variety of behaviours, characterized into **6 regions**.

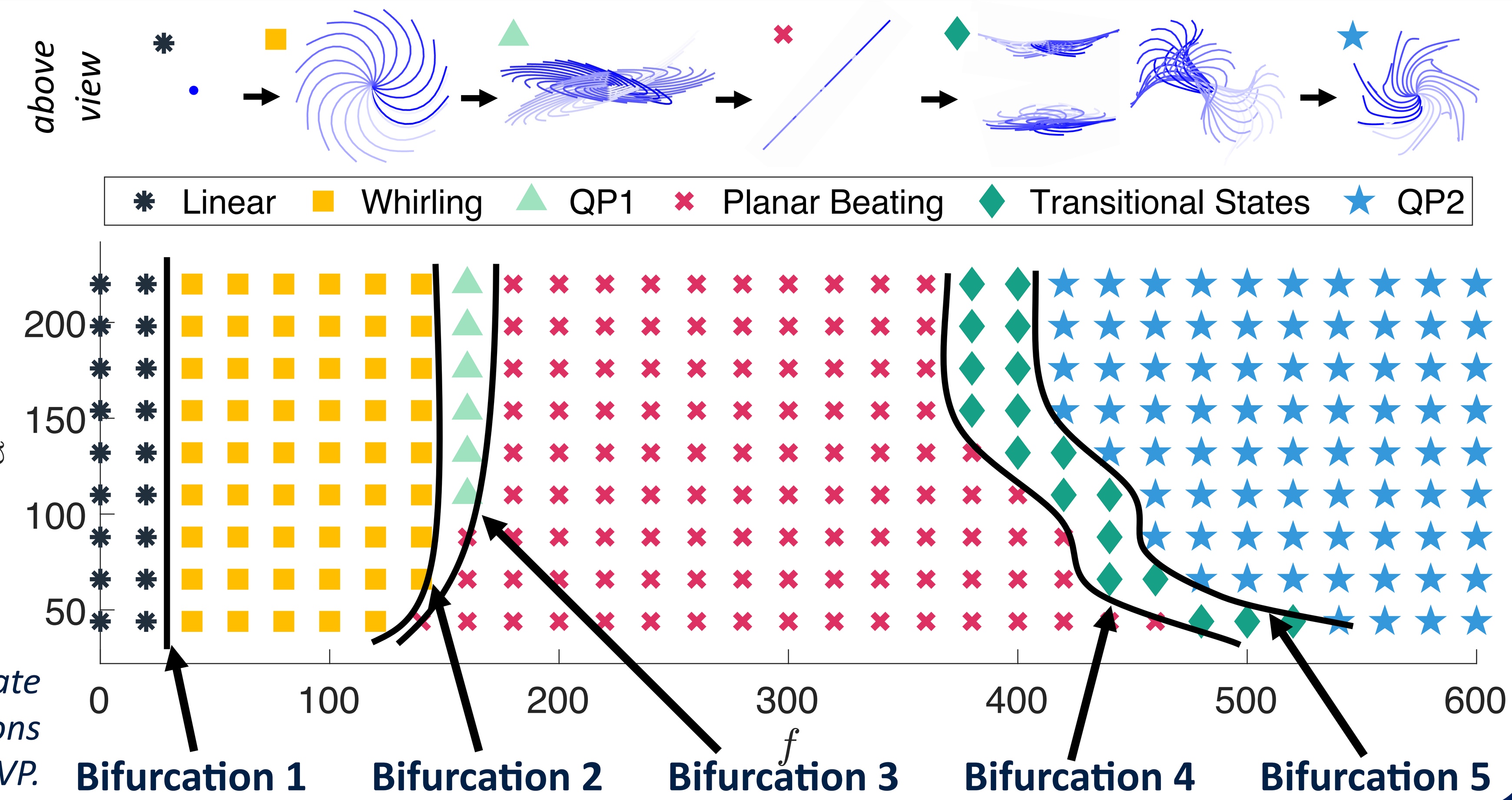


Figure 5 (right): *State space of solutions obtained via the IVP.*

4. BIFURCATION ANALYSIS

Bifurcation 1: Buckling

- **Linear stability analysis** shows the steady state becomes unstable at $f \approx 35.3$, regardless of the aspect ratio.
- At bifurcation, $\lambda \in \mathbb{C} \Rightarrow$ **Hopf bifurcation**.
- Two complex conjugate pairs of eigenmodes become positive at the same time $\Rightarrow$ Double Hopf Bifurcation.
- Consistent with weakly nonlinear analysis (growth of solution scales like $\sim O(\sqrt{f-f^*})$).

CONCLUSION: Double Hopf Bifurcation

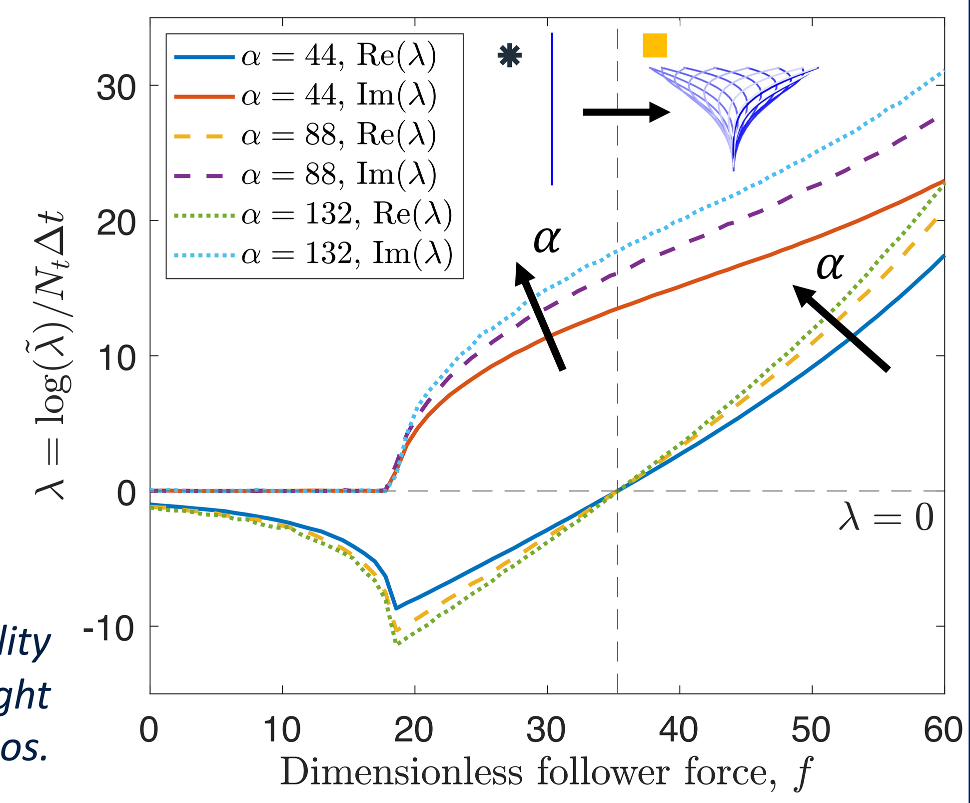


Figure 6 (right): *Linear stability analysis on the vertically upright filament for various aspect ratios.*

Bifurcation 2: Whirling to QP1

- **Floquet analysis** on whirling $\Rightarrow$ bifurcation at $f \approx 137.2$.
- IVP shows stable behaviour is then QP1.
- $\lambda \in \mathbb{C} \Rightarrow$ period doubling or **Hopf**.
- QP1 is quasiperiodic $\Rightarrow$ not period doubling.

CONCLUSION: Supercritical Hopf Bifurcation

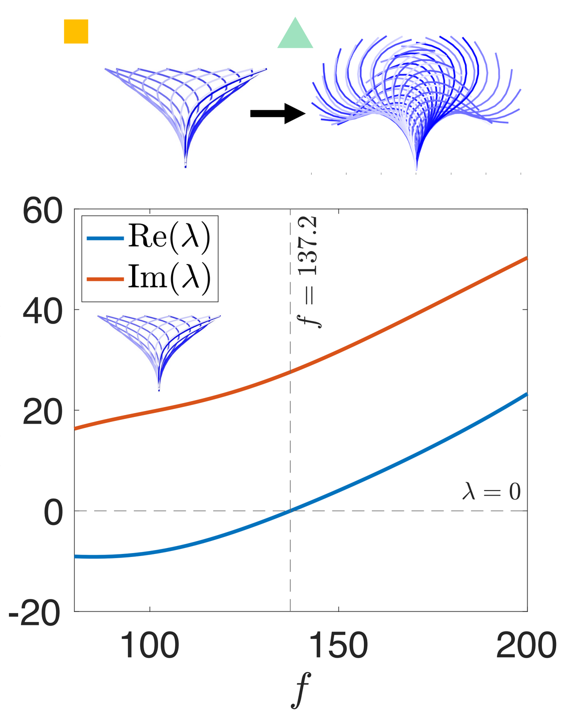


Figure 7 (above): *Floquet analysis on the time-periodic whirling solution.*

Bifurcation 3: QP1 to Beating

- **Floquet analysis** on beating $\Rightarrow$ bifurcation at $f \approx 140.2$.
- IVP confirms this is where QP1 becomes unstable.
- $\lambda \in \mathbb{R} \Rightarrow$ saddle node, **pitchfork** or transcritical.
- IVP $\Rightarrow$ pitchfork.

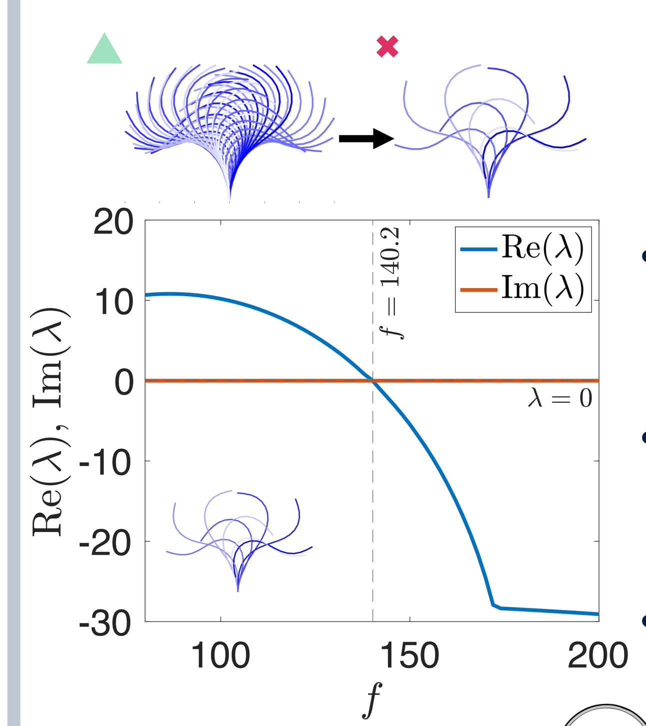


Figure 8 (above): *Floquet analysis on the time-periodic beating solution.*

CONCLUSION: Pitchfork Bifurcation

Bifurcations 4/5: Beating Onwards

- Floquet analysis on beating ***(Figure 9)*** $\Rightarrow$ bifurcation 4 at $f^* \approx 460$ for $\alpha = 44$ ($f^* \downarrow$ as $\alpha \uparrow$).
- $\lambda \in \mathbb{C} \Rightarrow$ period doubling or Hopf.
- IVP $\Rightarrow$ enter a transitory region with chaotic intermittent (T1) and periodic (T2,T3) behaviours depending on f and α – bifurcation classification depends on α!
- Increasing f we recover another solution (QP2) - quasiperiodic, so can't use Floquet analysis!

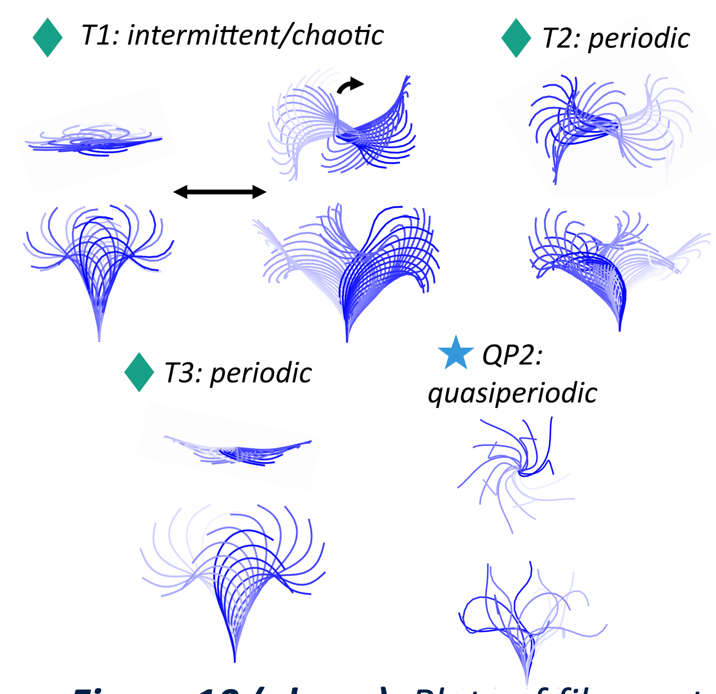
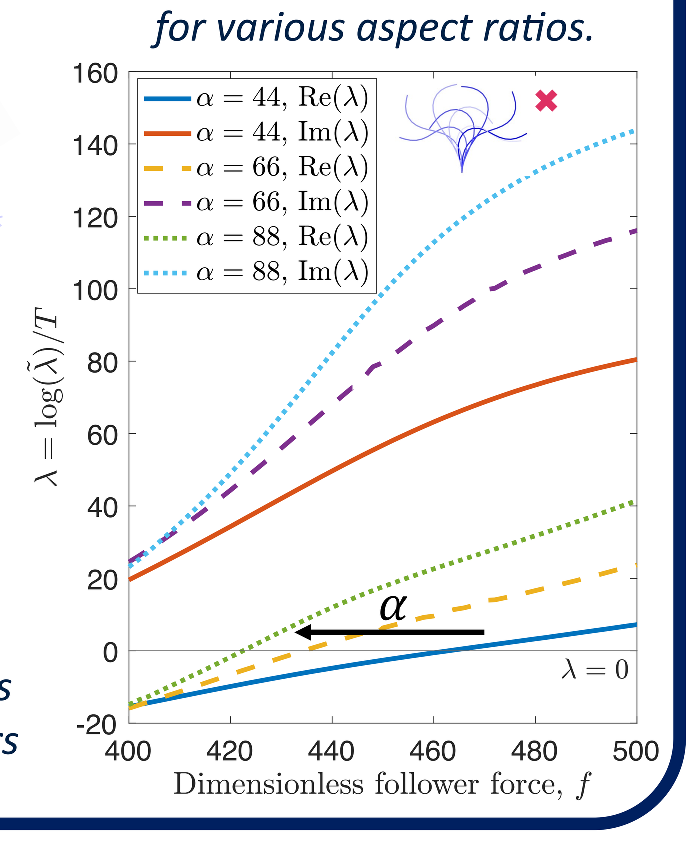


Figure 10 (above): *Plots of filaments over several timesteps for behaviours in transition/QP2 regimes.*

CONCLUSION: Depends on α!

Figure 9 (below): *Floquet analysis on the beating solution for various aspect ratios.*



REFERENCES

[1] Biology Dictionary "Microtubule – Definition, Function Structure" https://biologydictionary.net/microtubule/ [31/5/23]

[2] Dartmouth electron Microscope Facility, Dartmouth College, https://www.dartmouth.edu/emlab/

[3] S. F. Schoeller, A. K. Townsend, T. A Westwood and E. E. Keaveny, 'Methods for suspensions of passive and active filaments', *Journal of Computational Physics*, 2021

CONCLUSIONS/FURTHER WORK

- We have evaluated the state space for the follower force model, uncovering new quasiperiodic behaviours and identifying bifurcations using tools such as Floquet analysis.
- In future work, we plan to investigate more complex microtubule motor protein models to see how they affect the state space – for instance accounting for a density of motors along the filament (1), the slip flows generated by the motors (2), or the dynamics of collections of filaments to see whether synchronisation occurs.

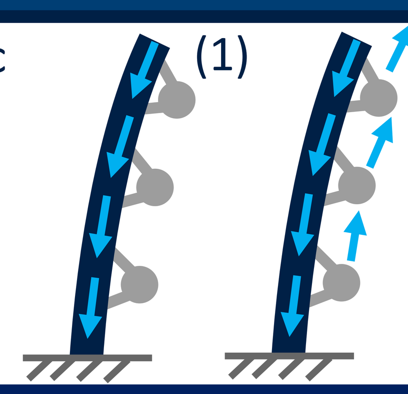


Figure 11: *The two model modifications discussed in the conclusion.*

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