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Ciliate Biology: The Graceful Hunt of a Shape-Shifting Predator

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Even single-celled eukaryotes are capable of highly complex behaviors. A new study reveals how one unicellular predator actively manipulates and remodels its unique cytoskeletal morphology to achieve rapid shape changes and a remarkable hunting strategy.

Under the scrutiny of a well-aimed lens, the microscopic world contained within a single droplet of pond water can be brought sharply into focus. Assorted tiny creatures, small and motile, dart backwards and forwards with complex movements, driven by an incessant need to feed or to reproduce. Many are in fact single cells — among the very simplest forms of living matter.

One of the strangest organisms you might hope to encounter is *Lacrymaria olor* (Figure 1A), a predatory ciliate occasionally found concealed among decaying aquatic plants and other organic matter [1]. Aptly named for their peculiar morphology (from the Latin *lacryma* = ‘tear’, and *olor* = ‘swan’), these cells have a teardrop-shaped cell body ($\sim$ 100 μm) attached to an elongated neck that can easily extend up to 2 mm within seconds. *Lacrymaria* is a formidable hunter, able to stretch out its neck in any direction with astonishing agility to locate and capture its prey — often first paralyzing them with discharged toxicysts [2]. How these organisms enact fast morphological changes has fascinated and confounded scientists for decades. In a new study published in this issue of *Current Biology* by Coyle *et al.* [3], high-speed imaging and state-of-the-art computer vision shed new light on this remarkable behavior.

Lacrymaria is the ultimate shape-shifter (Figure 1B). Observing the purposeful writhing movements of its impossibly long neck, it is hard to believe that this is a single cell. Early researchers [1,2] have already noted that cells can be found either in a dormant state in which the neck is fully retracted, or in a highly active hunting state with an extended neck. The entire organism is ciliated, exhibiting a dense covering of short body cilia. At the apical end is a dome-like structure containing the oral apparatus, through which food particles and prey are routinely engulfed and passaged to the cell body for digestion. Meanwhile, the dome is encircled by a ring of longer oral cilia that beat vigorously during neck extensions but are quiescent during retractions [3,4].

Culturing ciliates in the lab is notoriously difficult. Based on protocols established in a previous study [4], Coyle *et al.* [3] were able to maintain stable populations of *L. olor* in the lab, by co-culturing with a prey ciliate called *Cyclidium*. These cultures successfully recapitulated native behaviors observed in the field, allowing for detailed, long-term behavioral studies to take place in controlled laboratory conditions. The authors imaged *Lacrymaria* activity at rates of 1,000 frames per second and developed automated software to segment and digitize a comprehensive 300,000 subcellular postures. They found that hunting occurred in short, episodic bursts separated by longer periods of inactivity lasting tens of minutes. During ‘hunting events’, the cell body itself remains surprisingly motionless (Figure 1B).

By aligning tracked shapes to the reference frame of the rigid cell body and studying the neck morphodynamics, the authors explain *Lacrymaria*’s unique hunting strategy [3]. The neck and head region sweep out a radius of influence about a suitably chosen pivot, defining a ‘strike zone’ for each hunting event. In prey-free conditions, neck sampling is rapid, uniform (reaches all directions), and dense (shows a high percentage of coverage). This means that the head can access all locations within the strike zone, independently of the initial cell body position. It is likely that, in the presence of prey (a condition not studied here), a more biased sampling strategy would enhance prey encounter or capture efficiency.

Analysis of the neck shape modes revealed that this scrambling, or randomization, of the initial position is achieved mechanically. The authors tracked hundreds of thousands of neck shapes and projected these onto a basis set of shapes called eigenmodes [5]. They found that the neck motion occurs on two distinct timescales: a short timescale (seconds) over which compressive buckling locally rescrambled trajectories, and a longer timescale (minutes) over which the fundamental length of the neck region can also change. The short timescale behavior fits well to a phenomenological model of a slender filament under load. In this way, *Lacrymaria* activates different buckling modes to realise small reorientations or localized steering.

The cytoskeleton of *Lacrymaria* harbors further clues into this shape regulation [4,6]. Coyle *et al.* [3] also imaged the protein scaffolding in whole organisms by immunostaining for both tubulin and the abundant calcium-sensitive protein centrin [3]. They showed that the helical microtubule scaffold is coupled to a network of centrin fibers. Centrin mediates fast contractility in diverse eukaryotes, including other pond organisms, such as *Vorticella* [7] and *Stentor* [8,9], and is also found in the basal apparatuses of algal flagellates [10].

Closer inspection of the scaffold revealed something intriguing. The

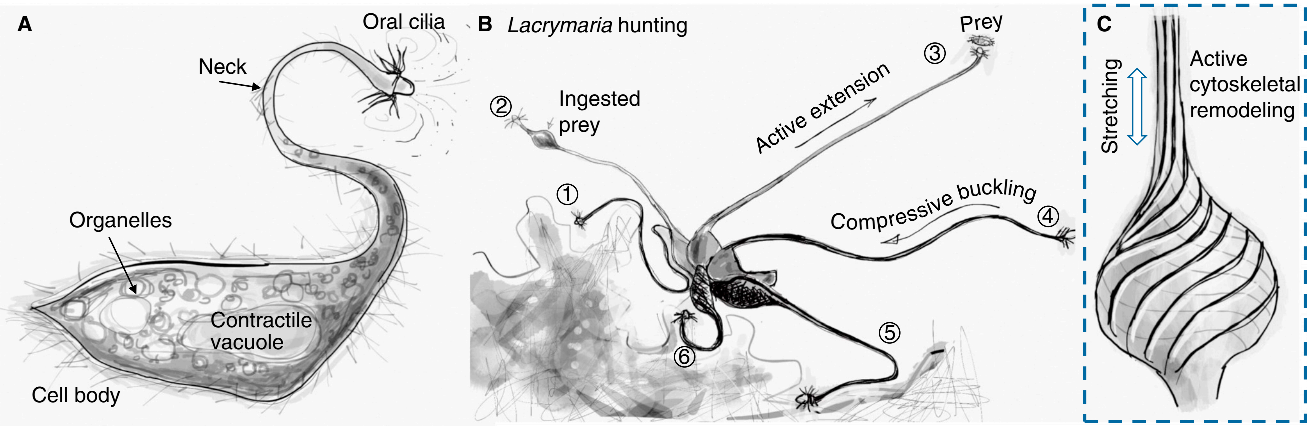

Figure 1. Active shape control in a unicellular hunter.
(A) *Lacrymaria olor* is a unicellular predatory ciliate with a flexibility reminiscent of a swan's neck (or perhaps a microscopic version of the mythical Loch Ness monster if you are of a more imaginative disposition).
(B) Coyle *et al.* [3] found that when *L. olor* hunts, the cell body is often concealed and anchored, relying upon the stochastic and episodic extension and retraction of the neck to sample the environment (snapshots of this behavior are represented by the circled numbers 1–6). The neck protuberance can stretch tens of body lengths, undergo tortuous movements, and even warp around encountered obstacles. Mast [1] writes of its feeding action: "*The (prey) ciliate was engulfed in less than a second, but it required fully fifteen seconds to pass down through the neck which was bulged out much like the neck of an ostrich in swallowing an orange*".
(C) How does *L. olor* engineer such extreme changes in shape? The cytoskeleton could be key. Turns out that there is a marked transition in the helical pitch of the microtubular network going from the cell body to the neck region — where it becomes almost parallel. Dynamic shape-shifting can then be achieved by active stretching along coordinate directions.

meshwork of microtubules undergoes a transition from a small helical pitch in the body, to a much larger pitch in the neck region (Figure 1C). This led the authors to hypothesize that the cell accesses extensile modes by rearranging its cytoskeleton to increase the proportion in the neck geometry where the filaments are nearly parallel. Activation of short timescale modes, on the other hand, requires only minimal remodeling of the existing cytoskeleton already present in the neck region.

One possible mathematical explanation for this shape-shifting process appears in a recent study that suggests a new paradigm known as Gaussian morphing [11]. In this view, cells actively modulate their surface geometry (as defined by Gaussian curvature) by prescribing the metric tensor for how distances are measured in curved space [12]. Cells can then control their shape by changing this metric. This can be done in two main ways: either by shearing or sliding of neighboring pellicle strips around the cell in the case of metaboly (dynamic changes in cell shape) in *Euglena* [13]; or by an active stretching mechanism, which seems applicable to *Lacrymaria*. Future studies could aim to visualize cytoskeletal rearrangements in real time and compare this with the proposed model.

What drives the neck extension? Could it be the beating of the oral cilia? There is some evidence to suggest this is the case. The neck extends to extraordinary lengths only during feeding when the body is anchored, but the neck is much less extended during free swimming. This can be interpreted as a consequence of both force-free and torque-free swimming at low Reynolds number [14]. Coyle *et al.* [3] also showed that calcium signaling — a main regulator of ciliary beating and cytoskeletal contractility — also affects *Lacrymaria*'s hunting dynamics. But how exactly is ciliary activity coupled to a shape-shifting cytoskeleton to trigger the fast and slow dynamics?

One idea could be to decouple the head cilia and body contributions. After all, the assignment of 'head' and 'body' is a somewhat anthropomorphic notion. In *Lacrymaria*, and in many other ciliates, the head, which contains the oral apparatus, can be removed and regenerated [15]. Reputedly, "detached heads" can "do everything except the backward movement" [1]. It would be interesting to study the morphodynamics of the body and neck changes while a new head is regenerated and investigate how this depends on ciliary hydrodynamics.

From a bioengineering perspective, the *Lacrymaria* neck allows an impressive freedom of movement that is somehow unconstrained by detailed ultrastructure (in contrast to joint actuation in vertebrates, for example). These differences reflect a deeper trade-off: at the smallest scales, microorganisms have had to evolve diverse strategies to exploit noisy sensing and response. In *Lacrymaria* this manifests as alternating active hunting vs dormant states; in other species this takes the form of stochastic motility strategies exhibiting separation between fast and slow timescales, with examples including run-and-tumble [16,17], run–stop–shock [18], or more complex navigation mechanisms [19]. Indeed, the tendency for stochastic sampling could be a universal mechanism for detecting low concentrations in noisy environments [20].

In this new study, Coyle *et al.* [3] showcase the resolution that is now achievable with modern imaging and tracking technologies. Combining computational methods with data-driven biophysical models, they have offered new insights into an age-old fascination over how a protist can manipulate its shape so dynamically. (How cells actually compute Gaussian curvature remains an open question...) It is time to renew our appreciation for the remarkable feats of the unicellular organism.

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Chronobiology: The Circadian Clock under Extreme Photoperiods

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Circadian clocks are time-measuring devices found in a majority of organisms synchronizing their behavior and metabolism with the day–light cycle. What happens in extreme latitudes, where the environmental conditions can be harsh at any time of day?

The circadian clock keeps track of the time in organisms, which is important for avoiding predators, eclosing from pupa at the right time of day, or arriving at a particular plant when nectar is being produced. The spectacular long-distance migration of monarch butterflies and the everyday harvesting activity of honey bees require a precise orientation to time and the position of the sun for accurate navigation. Our internal clock wakes us up in the morning to be fresh and ready, which is often not the case, given the self-imposed social jet lag that the majority of the modern population experiences.

If the circadian clock is so important for orchestrating daily activity and physiology, what happens under extreme geographical latitudes where winter corresponds to complete darkness (DD), summer is characterized by constant light and temperatures can unpredictably drop even on a warm spring or summer day? A new study reported in this issue of *Current Biology* from Bertolini *et al.* addresses this question in insects [1].

A few reports on arctic reindeer demonstrate that their clock completely stops under the extreme environment of the northern tundra [2,3]. But there are not only reindeers and polar bears living up in the north, or penguins in Antarctica. Though unable to warm up their bodies, some insects are found in these remarkably extreme environments. And, their abilities are often amazing — for instance, the fully-grown larva of *Chymomyza costata*, a drosophilid fly related and superficially very similar to the