Quick guide
Mesodinium

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What is Mesodinium? The Mesodinium genus is a group of globally distributed marine and freshwater ciliates — single-celled protists that propel themselves with tiny, hair-like projections or ‘cilia’. In Mesodinium, the cilia are arranged in a distinctive double band around the midsection of the bilobate cell, like a double hula skirt (Figure 1A,C,E). The first Mesodinium species to be described (by H. Lohmann, in 1908) was Mesodinium rubrum, which recurrently drew attention (and several name changes) over the next century because of its ability to form red tides. When the ciliate grows rapidly and forms dense populations, its pigmentation makes the surface of the water turn red (Figure 1G,H). These non-toxic blooms are biogeochemical hotspots and have some of the highest rates of primary production ever observed in aquatic systems. M. rubrum blooms have been observed all over the world, from estuaries like Chesapeake Bay, to upwelling zones off the coast of South America, to fjords in Scandinavia. Even Darwin himself described sailing through a red water bloom while aboard The Beagle off the coast of Chile.

Although scientists quickly realized that M. rubrum’s ability to form blooms came from rapid photosynthetic growth, the origin of this ability was enigmatic. Transmission electron microscopy revealed that the ciliates were always found with plastids, appeared to have unusually small cytostomes (mouths), and did not have food vacuoles, but prey nuclei were not always observed. The structural variability in prey organelles led to a debate about whether M. rubrum had a permanent symbiont (much like Dinotoms) or only transiently acquired prey organelles. Only when M. rubrum and their preferred prey were successfully isolated from Antarctica did it become apparent that the ciliate’s light-harvesting abilities come from stolen photosynthetic machinery, rather than a true symbiosis. M. rubrum is ‘kleptoplastidic’ or ‘chloroplast-stealing’. When it encounters cryptophyte algae from the Teleaulax or Geminigera genera, it ingests them and retains their functional plastids and other organelles. In fact, M. rubrum’s red color (and species name) actually come from the red phycobiliproteins used as accessory pigments in these stolen chloroplasts. Since the first descriptions of M. rubrum, a half dozen other members of the genus have been identified. These species form distinct phylogenetic lineages, but can also be grouped by how they handle their prey: M. rubrum and M. major get most of their energy by photosynthesizing with stolen chloroplasts, whereas M. pulex and M. pupula do not steal plastids at all and are entirely heterotrophic; two other lineages, M. chamaeleon and M. coatsi, are intermediate.

Why are Mesodinium cells so colorful? Mesodinium species range in coloration because of differences in how they retain prey plastids. The heterotrophic M. pulex and M. pupula are generally colorless, whereas M. rubrum and M. major are red because they retain plastids from a very specific group of red cryptophytes. In contrast, as its species name suggests, M. chamaeleon (and M. coatsi) can be multicolored. These Mesodinium species can retain plastids from multiple genera of cryptophyte algae, including blue-green (phycocyanin-containing) and red (phycoerythrin-containing) species. Thus, M. chamaeleon can take on a rainbow of colors from turquoise to rose to dark red depending upon its feeding history. The coloration of Mesodinium cells also depends upon the environment.

Figure 1. Mesodinium ciliates and their red water blooms. (A,B) Lateral and apical view of M. pulex with ingested prey. (C,D) Lateral and apical view of M. chamaeleon with phycocyanin plastids. (E,F) Lateral and apical view of M. rubrum with phycoerythrin plastids. (G) An M. rubrum bloom in the Columbia River Estuary. (H) A bloom of M. rubrum off the outer banks of North Carolina, near Oregon Inlet. Photo credits: (A,B) Oliver Skibbe (FU Berlin); (C,D) Paul Hargraves (URI, FAU); (E,F) Audrey Duval (IFREMIR); (G) Alex Derr; and (H) Pat Tester.
The phycobiliproteins that give *Mesodinium* cells their color are accessory pigments. This means that they harvest additional wavelengths of light that are not already captured by chlorophyll for photosynthesis. But when overall light levels are high, a chloroplast can harvest all the light it needs with chlorophyll alone. Thus, in bright light, cryptophyte algae (and the *Mesodinium* cells that steal their plastids) stop investing in phycobiliproteins and turn straw-colored rather than red or blue-green.

**How do stolen chloroplasts work?** In order to maintain function, chloroplasts need instructions for the synthesis of pigments and repair of photosynthetic machinery. In photosynthetic eukaryotes, some of these instructions are encoded in a small DNA plasmid inside the chloroplast itself, and others are encoded in the eukaryotic nucleus. Thus, when a *Mesodinium* cell steals a chloroplast, it faces a challenge: How can it keep the chloroplasts functional without its own copy of the nuclear-encoded owner’s manual? *Mesodinium* species have solved this problem in at least two ways. In the case of *M. chamaeleon*, stolen chloroplasts are housed in vacuoles that include largely intact cryptophyte cells. While prey flagella are missing, the prey’s membrane structures are intact, and the prey nucleus remains transcriptionally active. Although *M. chamaeleon* cells seem unable to synthesize new photosynthetic machinery, they can prolong photosynthetic function for up to two weeks after feeding. The stolen prey machinery is diluted by growth, with new daughter cells receiving a smaller and smaller portion of prey organelles over time. The photosynthetic machinery also wears down; thus, *M. chamaeleon* cells need to capture new prey regularly to continue to grow. *M. rubrum* has a more elaborate approach. Its vacuoles contain only prey chloroplasts, mitochondria, cytoplasm, and endomembrane; the other organelles have been egested or digested away. However, the prey nucleus is extracted from the vacuole and placed in the ciliate’s cytoplasm adjacent to the ciliate’s own nuclei. This ‘kleptokaryon’ is transcriptionally active, though how signals and gene products are targeted back to the kleptoplastids remains unclear. The kleptokaryon allows *M. rubrum* to maintain photosynthetic machinery, photoacclimate to new light levels, and even divide its complement of kleptoplastids alongside its own cell division. Ultimately, *M. rubrum*’s growth is limited by the availability of the kleptokaryon, which does not appear able to divide. Thus, *M. rubrum* must feed periodically to obtain fresh genetic instructions from its prey.

**Why do Mesodinium cells swim so fast?** *Mesodinium* ciliates are recognizable for their ‘jumping’ behavior. By synchronously beating the double-band of cilia around its midsection, a *Mesodinium* cell can abruptly jump at rates of up to 9.6 mm per second. For a large cell of 45 µm in size, this represents a speed of more than 200 body lengths in a single second. (By comparison, a cheetah running at full speed travels only about 100 body lengths per second.) Although *Mesodinium* cells are predators, they do not appear to use this jumping behavior to pursue and capture prey. Instead, *Mesodinium* cells are sit-and-wait predators that wait for prey to swim by before stunning and capturing them with Y-forked feeding tentacles. However, jumping may enable *Mesodinium* cells to escape their own predators and quickly move to new regions of the water column when local nutrient supplies have been depleted. High motility also supports *M. rubrum*’s photosynthetic ecology. In stratified systems, populations of *M. rubrum* can perform diel migrations of tens of meters. Traveling together in a thin layer, the ciliates swim to deeper water during darkness to mine nutrients that are depleted in surface waters, and then rise to the surface during daytime to photosynthesize. They also move to avoid currents that may flush them out of estuaries.

**What can Mesodinium teach us about acquired metabolism?** Because its members span a gradient of reliance on stolen organelles, the *Mesodinium* genus is a model system for studying acquired metabolism. Acquisitions of metabolic machinery (such as kleptoplasty) or instructions (for example, horizontal gene transfer) can transform an organism’s ecological role. For example, in *Mesodinium* species, kleptoplasty instantaneously transforms a genotypically heterotrophic species into a primary producer. This can also shape a lineage’s evolutionary trajectory, sometimes leading to permanent incorporation of the acquired metabolism (as in eukaryotic phytoplankton, via endosymbiosis) or increased prey specialization and reliance on stolen organelles (as in *Mesodinium*). Because *Mesodinium* has extant heterotrophic, highly photosynthetic, and intermediate lineages, we can compare the ecology and physiology of different species to identify the possible key evolutionary transitions that underlie the acquisition of photosynthesis.

**Where can I find out more?**


**DECLARATION OF INTERESTS**

The authors declare no competing interests.

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