

obstacles can ablate possibility as effectively as physical obstacles. There are no physical obstacles to creating a society in which goods, capital and services are distributed ‘from each according to their ability, to each according to their needs,’ but that should not make us think that a socialist utopia is currently within reach. Mann seems to dismiss the entire field of philosophical ethics by quoting an article<sup>4</sup> from *Quillette*, an Australian online magazine. In this article the writer reports his impression from attending an international conference that “philosophical ethics remains obsessed with individual responsibility” and does not appreciate “that all the really serious moral problems of our time are collective action problems.” There are more reliable ways of learning about the field (see <sup>5</sup>, for example) than reading *Quillette*, a magazine which Mann does not otherwise seem to hold in high regard (he harshly criticizes its primary contributor on climate change, as a “soft denialist” (p. 228)).

Given how much of the book is devoted to vigorously criticizing apparent allies, it is surprising that Mann writes that it is important that we do not become “enabler[s]” of “a divide-and-conquer strategy against climate advocates” (p. 96) ... “Don’t let yourself get dragged into divisive spats with those who are on the same side as you” (p. 97).

Perhaps the fact that he sees himself as engaged in a war helps to explain this apparent discrepancy. Indeed, Mann has been treated like an enemy combatant by climate change deniers. Still, the accuracy and utility of thinking of climate change as a war is far from self-evident. It is not always clear who the parties are to this war; for example, when Mann writes that “we” are at war (p. 1), but “the planet is losing” (p. 3). Is the planet collateral damage or itself a party to the war? Many scholars think of climate change as, at its heart, a collective action problem (the insight that is supposedly missed by philosophical ethicists). Insofar as this is true, it provides a quite different way of thinking about climate change than the martial one that Mann endorses.

My own view is that climate change gives rise to a vast array of problems (including energy, justice, security, etc.), but itself is more productively thought

of as an early manifestation of an epoch in which no earthly place, form, entity, process, or system escapes the reach of human action. We are likely to arrive at a carbon-free energy system sometime in this century, while at the same time finding ourselves even deeper in the Anthropocene. Our fundamental challenge will be to grow our ability to live with abrupt change across all the physical and social systems that condition and control our lives. This will require new thinking about how we organize ourselves politically, how we relate to each other as individuals and members of collectives and how to find meaning in our lives, as well as new ways of doing and narrating science<sup>6</sup>. What we need is to think constructively about these challenges, and in my opinion the language of war is not conducive to this.

Still, as I have said, there are many ways to think about climate change and no single one is undeniably correct. Although this book has its problems, almost anyone will benefit from reading it. Whether or not we should think of ourselves as involved in a climate war, there is no doubt that Michael Mann has fought the good fight for all of his professional life. For this he should be thanked, and we should learn from his experience.

#### DECLARATION OF INTERESTS

The author declares no competing interests.

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Center for Environmental and Animal Protection, New York University, New York, NY 10003-6653, USA.  
E-mail: [dale.jamieson@nyu.edu](mailto:dale.jamieson@nyu.edu)

## Quick guide

# Purple photosymbioses

Sergio A. Muñoz-Gómez<sup>1,\*</sup>, and Sebastian Hess<sup>2</sup>

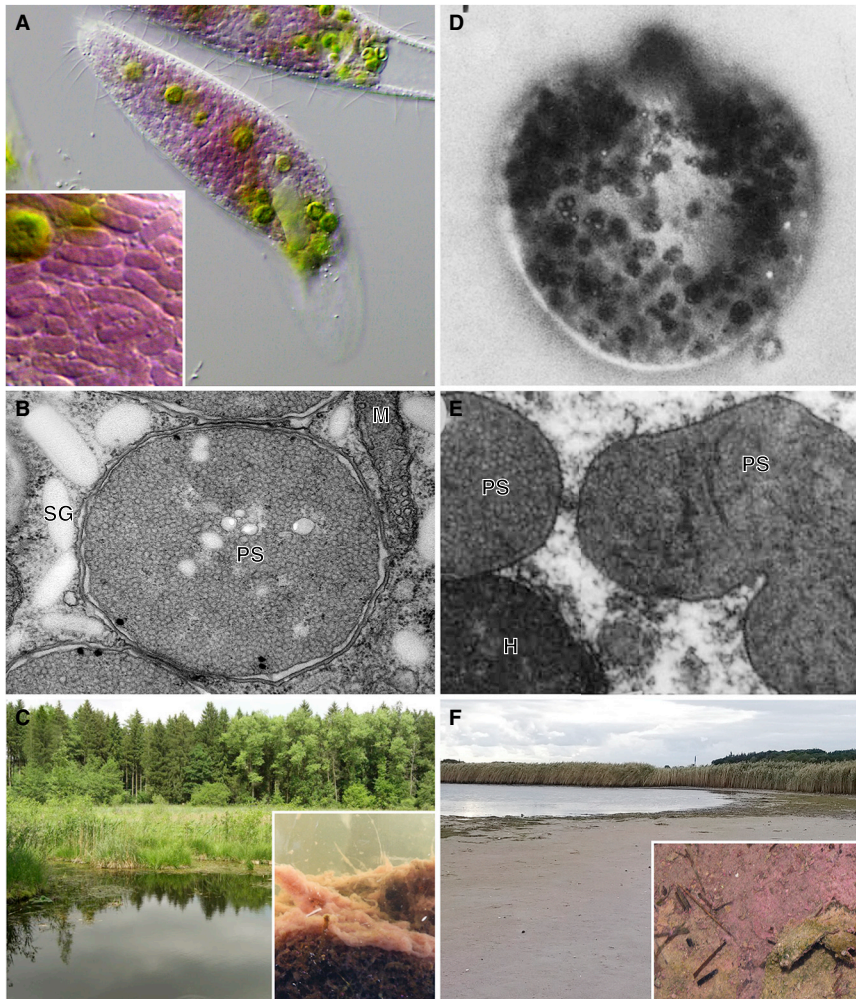
#### What are purple photosymbioses?

Purple photosymbioses are associations between a heterotrophic eukaryote and intracellular purple bacteria. These associations constitute a type of photosymbiosis as they involve photosynthetic symbionts that use light as an energy source and fix atmospheric carbon dioxide into biomass. However, purple bacteria are anoxygenic photosynthesizers, which means that they do not release oxygen as a byproduct of photosynthesis. This property distinguishes them from oxygen-releasing algae and cyanobacteria, which are part of the much more common and widespread ‘classical’ photosymbioses. Although many purple bacteria are purple, purple-red, or purple-violet in color, they can also be orange, brown, yellow, or green by combining diverse accessory photosynthetic pigments such as carotenoids. Out of the few bacterial groups that contain anoxygenic phototrophs (for example *Proteobacteria*, *Chloroflexi*, *Gemmatimonadetes*, *Chloroacidobacteria*, *Chlorobi*, *Heliobacteria*, and “*Candidatus Eremiobacterota*”), only purple bacteria (found within the *Proteobacteria*) are known to be intracellular photosynthetic symbionts of eukaryotes.

#### What are purple bacteria?

Purple bacteria is an informal term that refers to anaerobic and anoxygenic photosynthetic (or photoautotrophic) bacteria that are phylogenetically scattered in the phylum *Proteobacteria*. As such, purple bacteria do not represent a distinct phylogenetic group. Their main defining property, anoxygenic photosynthesis, has been lost repeatedly or transferred to species found in primarily non-photosynthetic (that is, chemotrophic) groups. Purple





**Figure 1. The two purple photosymbioses known, their purple symbionts, and habitats.** (A) The heterotrich ciliate *P. tenue*. Cell-body length is about 200  $\mu\text{m}$ . Inset shows a close-up of its purple bacterial and green algal symbionts. (B) TEM micrograph of a purple symbiont of *P. tenue* (~1.75  $\mu\text{m}$  in diameter) neighboring a cristate mitochondrion and cytoplasmic storage granules. (C) A pond in the Simmelried moorland in Germany where Martin Kreutz rediscovered *P. tenue*. Inset shows the loose organic-matter-rich sediments covered by a layer of purple bacteria. Image credit: Martin Kreutz. (D) The spirotrich ciliate *S. purpureum*. Cell-body length is 40–50  $\mu\text{m}$ . Image from Fenchel and Bernard (1993b) and reprinted with permission from Oxford University Press. (E) TEM micrograph of the purple symbionts of *S. purpureum* (~1  $\mu\text{m}$  in diameter) next to a hydrogenosome-like organelle. Image from Fenchel and Bernard (1993b) and reprinted with permission from Oxford University Press. (F) Purple sand beach in Nivå bay in Denmark where Fenchel and Bernard found *S. purpureum*. Inset shows the layered microbial mats that develop in these sands. Image credit: Tom Fenchel. PS, purple symbionts; M, mitochondria; SG, storage granules; H, hydrogenosomes.

bacteria have further been traditionally classified as ‘sulfur’ or ‘non-sulfur’ based on their tolerance for hydrogen sulfide and the presence of sulfur globules in their periplasm.

Purple bacteria serve as primary producers in ecosystems, but, in contrast to algae and plants, do so in anoxic or suboxic environments. Due to the relative paucity of grazers in these environments, it is still unknown

to what extent the carbon fixed by purple bacteria contributes to higher trophic levels. There are several important physiological and ecological differences between purple bacteria and oxygenic photosynthesizers. For example, purple bacteria exclusively photosynthesize in the absence of oxygen and can use hydrogen sulfide, hydrogen, or low-molecular-weight organic compounds as photosynthetic

electron donors. They absorb infrared light (>780 nm) for photosynthesis by possessing bacteriochlorophyll *a* or *b* as their primary photosynthetic pigments. As these longer wavebands penetrate deeper into sediments and microbial mats, due to less diffraction and scattering or absorption by algal photosynthetic pigments, purple bacteria can colonize habitats that are otherwise unfavorable to cyanobacteria and algae. Purple bacteria are found in various environments (for example, marine microbial mats and freshwater lakes), where some of them can engage in syntrophic extracellular symbioses with other prokaryotes. However, they are extraordinarily rare as intracellular symbionts of eukaryotes.

**What examples of purple photosymbioses are known?** There are currently only two examples of eukaryotes that are known to harbor purple bacteria as intracellular symbionts. Both are free-living and ciliated protists (Ciliophora, Alveolata) and were first described by the German schoolteacher and naturalist Alfred D.F. Kahl about a century ago. However, these two species are not very closely related to each other and even belong to different taxonomic classes in the Ciliophora. One of them, *Pseudoblepharisma tenue* (Figure 1A), was observed a few times by Kahl in the sapropel or organic-matter-rich sediments of unspecified freshwater ponds in Germany. *P. tenue* was described as pinkish due to the presence of purple bacteria (or ‘rhodobacteria’ in Kahl’s terms; Figure 1B) in its cytoplasm, and also contained a few sparse green-algal symbionts (‘zoochlorellae’). To this day, *P. tenue* still represents the only eukaryote known to combine two contrasting photosynthetic symbionts in a heterotrophic host. Due to morphological similarities to species belonging to the genera *Blepharisma* and *Spirostomum*, *P. tenue* was originally classified by Kahl as a heterotrich ciliate. More recently, Martin Kreutz rediscovered *P. tenue* in the Simmelried moorland in Germany. Here, the ciliate lives in the loose and organic-matter-rich sediments of shallow and slightly acidic freshwater ponds (Figure 1C). In these freshwater

sediments, *P. tenue* often co-occurs with free-living purple bacteria and a few other eukaryotic microbes such as euglenids. Although early attempts to establish laboratory cultures of *P. tenue* were not successful, single-cell genomics confirmed the affiliation of *P. tenue* to the class Heterotrichea and hinted at the metabolic interactions that sustain this unique symbiotic consortium.

The other ciliate that represents a purple photosymbiosis was originally described from the brackish waters (~1–2% salinity) of the Brenner Moor salt marshes in Oldesloe, Germany. Kahl reported a red or reddish-brown ciliate, *Strombidium purpureum* (class Spirotrichea), the cytoplasm of which was largely occupied by purple bacteria (Figure 1D,E). More than 60 years later, Catherine Bernard and Tom Fenchel isolated *S. purpureum* from sandy sediments in Nivå bay (~3.5% salinity) in Denmark (Figure 1F). These sands contain stratified microbial mats characterized by steep oxygen and sulfide gradients that change throughout day and night. Bernard and Fenchel managed to cultivate *S. purpureum* and concluded that the behavior of the symbiotic consortium was largely dictated by the metabolic activity of their purple-bacterial symbionts. So far, purple photosymbioses have only been reported from a few locations in Germany and Denmark, but it is likely that both *P. tenue* and *S. purpureum* have much more widespread distributions, as is the case for many rare microbes. Their rarity, as evident by sparse reports in the literature, may be a consequence of some very peculiar environmental conditions required for purple photosymbioses to thrive.

**How do purple photosymbioses function?** Both purple photosymbioses represent examples of mixotrophy because the host ciliates have been observed feeding on bacteria — there is evidence of food vacuoles with partially digested prey in both *P. tenue* and *S. purpureum*. This is similar to many classical photosymbioses in protists such as ciliates that harbor green symbionts, including the well-known *Paramecium bursaria*. However, phagotrophy might play a

minor role in purple photosymbioses; food vacuoles are generally sparse and *S. purpureum* even displays a reduced oral apparatus compared to other *Strombidium* species (as reported by Kahl in 1932). As in other (oxygenic) photosymbioses, purple symbionts are very likely to provide photosynthetic products in the form of small organic compounds, such as maltose, glucose, or glycerol, to the host cell. In exchange, the host may provide the symbionts with a source of nitrogen, probably amino acids or ammonium — intact genes for these transporters have been retained in the reduced genome of the purple symbionts of *P. tenue*. Unlike classical photosymbioses, in which the photosynthetic partner uses water as a source of electrons, the purple symbionts derive electrons from either hydrogen or small organic compounds (for example, acetate) that likely stem from fermentations within the symbiotic consortia. In the dark, the purple symbionts rely on (micro) aerobic respiration.

**How do the two known purple photosymbioses differ?** Because of their independent evolutionary origins, *P. tenue* (Heterotrichea) and *S. purpureum* (Spirotrichea) are expected to differ in several aspects. Indeed, the purple symbionts of *P. tenue* are bound by a host-derived vacuolar membrane (symbiosome) and belong to the Chromatiaceae (Gammaproteobacteria), whereas those of *S. purpureum* are free in the host cytoplasm and arguably belong to the Rhizobiales (Alphaproteobacteria), given that they possess bacteriochlorophyll *a* and appear to multiply by budding. Furthermore, it is conceivable that *S. purpureum* possesses more than a single type of intracellular bacterium because its symbionts are considerably variable in ultrastructure. In contrast, *P. tenue* harbors a single species of purple bacteria (“*Ca. Thiodictyon intracellulare*”) and green algae of the genus *Chlorella*. The presence of two contrasting photosynthetic symbionts (anoxygenic bacteria and oxygenic algae) in *P. tenue* is one of the most fundamental differences that distinguishes it from *S. purpureum*.

Another major difference between *P. tenue* and *S. purpureum* concerns their host mitochondria and energy metabolism. *P. tenue* has *bona fide* mitochondria with well-developed tubular cristae capable of aerobic respiration (Figure 1B). Moreover, *P. tenue*'s mitochondria are facultatively anaerobic: as predicted from genome data, they possess the set of enzymes required for anaerobic fumarate respiration (or fumarate reduction). In contrast, *S. purpureum* has hydrogenosome-like organelles, sometimes found closely associated with the purple symbionts, that are acristate and presumably incapable of aerobic respiration (Figure 1E). Instead, they may perform a type of hydrogen-releasing fermentation.

The *S. purpureum* symbiotic consortium is strictly anaerobic in the light (that is, it avoids even traces of oxygen) and is thought to rely on the (syntrophic) exchange of hydrogen between hydrogenosome-like organelles and purple symbionts. In the dark, *S. purpureum* becomes temporarily microaerobic and can survive partial oxygen pressures of <5% atmospheric saturation by means of respiration of its purple symbionts. At atmospheric partial oxygen pressures, *S. purpureum* dies within 30 minutes of exposure. The behavior of *S. purpureum* has been shown to accommodate the physiology of its purple symbionts because the ciliates swim away from oxygen pressures >1% atmospheric saturation and accumulate under infrared light. In contrast, *P. tenue* tolerates much higher oxygen tensions and can survive in open Petri dishes for days. This is not surprising considering that *P. tenue* has aerobically respiring mitochondria as well as oxygenically photosynthesizing green symbionts. We thus hypothesized that *P. tenue* is a physiologically flexible symbiotic consortium that can transiently survive in a relatively broad spectrum of environmental conditions. Despite this potential physiological flexibility, *P. tenue* appears to be specialized as a mixotroph that combines anoxygenic photosynthesis and predation.

**When and how did the purple photosymbioses originate?** Although detailed analyses have yet

to be carried out, both *S. purpureum* and *P. tenue* are considerably derived within the Ciliophora, suggesting a relatively recent origin for their symbioses. Both ciliates have relatively close non-photosynthetic relatives with similar morphologies (genetic divergence in the 18S rRNA gene sequences >95%). Published, dated phylogenetic trees (chronograms) for the Ciliophora suggest that the *Spirostomum*-like ciliates, to which *P. tenue* belongs, diversified ~200 Ma ago, and the Oligotrichea, which contains the genus *Strombidium*, is ~300 Ma old. The purple photosymbioses of *P. tenue* and *S. purpureum* must thus be much more recent than these conservative estimates for the age of their respective groups. For context, the photosymbiosis with a cyanobacterium that gave rise to all plants (Archaeplastida) is estimated to be ~1.9 Ga old, whereas that which led to photosynthetic *Paulinella* species is thought to have occurred ~90–140 Ma ago.

Compared to classical photosymbioses, purple photosymbioses are extraordinarily rare in nature. One may speculate on the reasons why they have not evolved more than twice, as far as we know. One possibility is that there have been much fewer opportunities for the evolution of purple photosymbioses. During times of higher atmospheric partial oxygen pressures (for example after the Proterozoic eon), anaerobic purple bacteria have been restricted to fewer environments than oxygenic photosynthesizers, such as anoxic habitats that provide the right electron donors and light for anoxygenic photosynthesis. This limits their overall abundance. Moreover, purple bacteria require a host that is adapted to anoxic environments to remain photosynthetically competent. However, anaerobic grazers that could serve as hosts are comparatively less diverse and abundant than their aerobic counterparts. Another reason might be that the physiology of many eukaryotes is incompatible with that of purple bacteria. For example, hydrogen sulfide, a photosynthetic

electron donor used by many purple bacteria, inhibits the aerobic respiratory chain of (facultatively) aerobic eukaryotes. Finally, it is possible that purple bacteria are less productive, for example due to shorter photosynthetic electron transport chains, than oxygenic photosynthesizers. Purple photosymbioses might thus face a competitive disadvantage relative to classical photosymbioses in most environments. Future comparative studies of the physiology and ecology of *P. tenue* and *S. purpureum* may shed some light on the causes for the improbable evolutionary origin and persistence of purple photosymbioses.

#### Where can I find out more?

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<sup>1</sup>Department of Biological Sciences, Lilly Hall of Life Sciences, Purdue University, 915 W State Street, West Lafayette, IN 47907, USA. <sup>2</sup>Institute for Zoology, Cologne Biocenter, University of Cologne, Zùlpicher Strasse 47b, 50674 Cologne, Germany.

\*E-mail: [samunozg@purdue.edu](mailto:samunozg@purdue.edu)

## Primer

# Specification and evolution of lateral roots

Abdellah Lakehal<sup>1,2</sup>, Asma Dob<sup>1,2</sup>, and Tom Beekman<sup>1,2,\*</sup>

Plants have evolved a remarkable capacity to develop new organs post-embryonically throughout their lifespan. A prime example of this is root branching. Root branching occurs in two ways: dichotomous and lateral branching. The dichotomous branching is the result of the division of the root apical meristem into two daughter meristems, likely through symmetric cell divisions of the root apical cell, as has recently been illustrated in the extant lycophyte *Selaginella moellendorffii* (Figure 1). Lateral root branching relies on the *de novo* specification of a subset of founder cells (hereinafter referred to as lateral root stem cells) located in the internal tissues of an existing root. This step is followed by initiation, in which the specified cells re-enter the cell cycle, and subsequently by primordium formation and emergence. In this primer, we summarize recent advances describing the molecular bases underlying lateral root stem cell specification in angiosperms and highlight the important positional signals that fine tune this process. By delving into the evolutionary origins of root branching, we point out that positional control of lateral root stem cell specification has not been the prevailing mechanism among all plants and discuss the process in ferns (i.e., a sister group of seed plants), where it seems to be under the control of lineage-dependent mechanisms.

### Auxin signaling and homeostasis control lateral root stem cell specification

In seed plants, lateral roots initiate acropetally from the pericycle, which is a single cell layer surrounding vascular tissues along the primary root axis. More precisely, lateral roots initiate from xylem pole pericycle (XPP) cells in eudicot species (e.g., *Arabidopsis thaliana* (*Arabidopsis*)),

