


## PERSPECTIVE

# The diatom *Fragilariopsis cylindrus*: A model alga to understand cold-adapted life

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## Abstract

Diatoms are significant primary producers especially in cold, turbulent, and nutrient-rich surface oceans. Hence, they are abundant in polar oceans, but also underpin most of the polar food webs and related biogeochemical cycles. The cold-adapted pennate diatom *Fragilariopsis cylindrus* is considered a keystone species in polar oceans and sea ice because it can thrive under different environmental conditions if temperatures are low. In this perspective paper, we provide insights into the latest molecular work that has been done on *F. cylindrus* and discuss its role as a model alga to understand cold-adapted life.

## KEYWORDS

cold adaptation, diatom, evolution, *Fragilariopsis*, genome, phytoplankton

Conducting research in polar regions is still a significant challenge because of issues with access and working at subfreezing temperatures. Yet, polar environments are home to significant biological diversity, including diverse primary producers. As photosynthesis on land is limited by permafrost and glaciers, marine phytoplankton groups and, especially, diatoms underpin most of the polar food web (Boyd, 2002; Horner et al., 1992; Smetacek, 1999). Diatoms can cope well with low temperatures and significant seasonality, including the long and dark polar winter (McMinn & Martin, 2013). Although global warming appears to diminish the dominance of diatoms in polar oceans (Ardyna & Arrigo, 2020), diatoms are still a significant driving force in terms of underpinning polar food webs and global biogeochemical cycles (Hop et al., 2020).

*Fragilariopsis cylindrus* is an obligately cold-adapted (psychrophilic) pennate diatom found in Arctic and Antarctic seawater and sea ice (Figure 1). It is

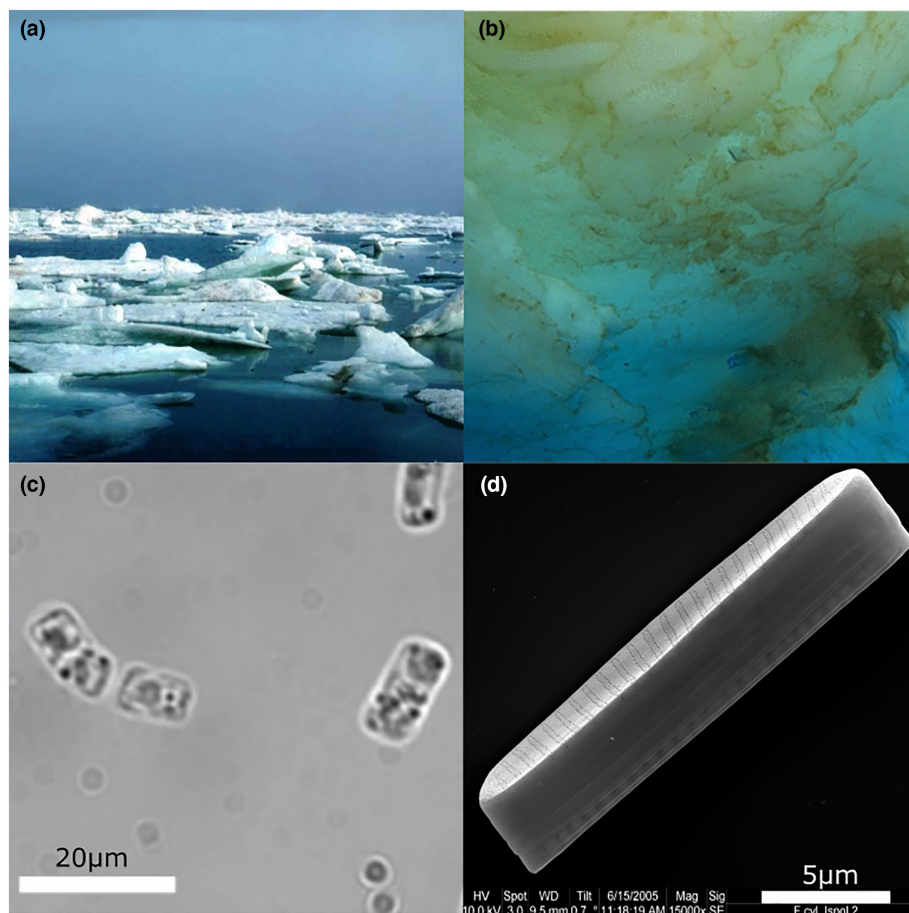
considered a keystone species for polar waters, thriving under diverse polar conditions and forming blooms in sea ice and at the sea-ice edge (Hop et al., 2020). As a polar indicator species, *F. cylindrus* actively thrives under high salinity, low temperatures, and semi-enclosed sea-ice systems (Kang & Fryxell, 1992). In this perspective paper, we provide a brief overview on the work that has been done so far on *F. cylindrus* and discuss its role as a model alga to understand cold-adapted life.

The genome of *Fragilariopsis cylindrus*, published in 2017 (Mock et al., 2017), was the first sequence of a cold-adapted eukaryote. In recent years, whole genome sequences of several additional polar algal species have followed suit, such as genomes from dinoflagellates, chlorophytes, and prasinophytes (Joli et al., 2017; Stephens et al., 2020; Ye et al., 2022; Zhang et al., 2021). Those sequences laid the foundation for studying the molecular adaptation of algae to polar

**Abbreviations:** CRISPR, Clustered Regularly Interspaced Short Palindromic Repeats; HGT, Horizontal gene transfer; IBPs, Ice-binding proteins; MOSAiC, Multidisciplinary Drifting Observatory for the Study of Arctic Climate.

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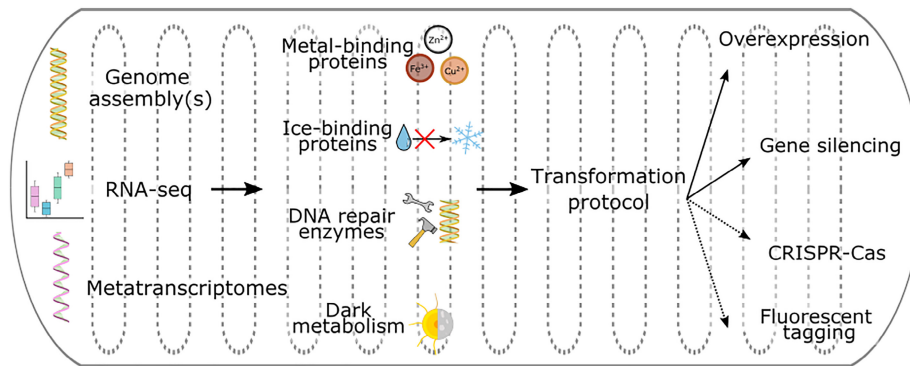
**FIGURE 1** *Fragilariopsis cylindrus* is a psychrophilic pennate diatom found in polar oceans and sea ice. (a) Arctic sea ice. (b) Photosynthetic communities on the underside of sea ice. (c) Bright-field microscope image of *F. cylindrus*; scale bar represents 20  $\mu\text{m}$ . (d) Scanning electron micrograph of a single cell of *F. cylindrus*; scale bar represents 5  $\mu\text{m}$ . In order (a), (b), (c), (d), these images were obtained from: the United States Fish and Wildlife Service (USFWS) under a Free to use CC0 license, Castellani et al. (2022), Faktorová et al. (2020), and Mock et al. (2017) under their respective CC BY 4.0 licenses.

oceans (Jabre & Bertrand, 2020; Kennedy et al., 2019; Morin et al., 2020; Petrou et al., 2012). This work focused on the response of polar algae to low temperatures including freezing, light–dark cycles, complete darkness, and scarcity of essential nutrients such as dissolved iron and other trace metals.

Even though molecular research into *Fragilariopsis cylindrus* has only begun recently, it has resulted in several resources that support both a growing set of additional genome sequences from Arctic/Antarctic *F. cylindrus* isolates and molecular genetic toolkits (Figure 2). Instrumental for these efforts is a high-quality reference genome that improves on the draft sequence published in 2017. By applying a combination of Oxford Nanopore and Illumina sequencing, an additional haplotype-specific assembly was developed in 2022 using a novel assembly pipeline, the SDG-Threader (Hodgkinson et al., 2022). This work, which included a k-mer-based analysis, suggested that the *F. cylindrus* strain CCMP1102 was in fact triploid with two cases of aneuploidy and several truncations. However, for most of the 11 assembled chromosomes,

the three copies merged into two distinct haplotypes, likely caused by their high sequence similarity, like the initial assembly published in 2017 (Mock et al., 2017). An attempt was made to split the assembly into three haplotypes by first mapping a set of primary transcripts to the assembly using BLAT (Kent, 2002; parameters: -noHead -extendThroughN -q = rna -t = dna). However, because of the high sequence similarity (>98%) between these two haplotypes compared with the much more diverged third haplotype, the vast majority of genes in the genome of *F. cylindrus* CCMP1102 fall in the two-copy category with only a small set of 81 genes mapping three times. The assembly was then partitioned into two haplotypes selecting a set of genes that occur in exactly two locations and used them to pair contigs. Contigs were then partitioned into two haplotypes, such that the gene overlap between the two haplotypes was minimal.

As there is evidence that *Fragilariopsis cylindrus* reproduces sexually (Hodgkinson et al., 2022), the genome of the strain CCMP1102 may be the result of meiotic nondisjunction of homologous chromosomes,



**FIGURE 2** Resources and genetic tools to explore diverse features of the polar diatom *Fragilariopsis cylindrus*.

which could have led to diploid gametes. If the latter combined with a haploid gamete, the result would be a trisomic zygote leading to a triploid cell line as observed for *F. cylindrus* CCMP1102 with three copies in two distinct haplotypes, each parental line and a recombinant.

Polyploidy is a significant driving force in the evolution of diatom species (Parks et al., 2018). Due to its significant haplotype divergence, *Fragilariopsis cylindrus* CCMP1102 might also be an appropriate candidate for testing how the potential variation in the expression levels of alleles contributes to fitness effects and, therefore, the adaptive evolution of diatoms. To address this question will require confirmation of the new triploid assembly using highly accurate PACBIO HIFI sequencing for DNA and the generation of full-length cDNAs based on single HIFI reads. Both sequencing approaches are being applied as part of the “100 Diatom Genomes Project” (<https://jgi.doe.gov/csp-2021-100-diatom-genomes/>), which is addressing the above-mentioned question on a larger scale.

Although forward and reverse genetics in diatoms recently have made significant leaps (e.g., Belshaw et al., 2022; Faktorová et al., 2020; Serif et al., 2018), generating recombinant cell lines in *Fragilariopsis cylindrus* is still challenging (Hopes, 2017). Yet, to the best of our knowledge, it remains the only cold-adapted eukaryote that is genetically tractable. A transformation protocol was established in 2013 (Faktorová et al., 2020; Hopes, 2017). The protocol utilizes microparticle bombardment with tungsten particles to introduce genetic material into the cell, similar to the established protocols for diverse temperate diatoms such as *Phaeodactylum tricornutum* and *Thalassiosira pseudonana* (Apt et al., 1996; Poulsen et al., 2006). However, the cells of *F. cylindrus* must always be kept cold during the transformation procedure. In order to obtain homozygous (biallelic) colonies, subsequent restreaking on agar plates is necessary to reduce the mosaicism of colonies. The establishment of knock-in reporter genes (e.g., GFP) and marker genes has therefore been key to successful transformation and selection in this species (Faktorová et al., 2020; Hopes, 2017).

Genome editing using CRISPR/Cas is under development for *Fragilariopsis cylindrus*; however, preliminary results are inconclusive. This may be due either to the level of ploidy in this species or to the low activity of all currently available Cas enzymes under low temperatures (e.g., Abudayyeh & Gootenberg, 2021; Kim et al., 2018; Shan et al., 2018). Although LbCas12a is still active at temperatures below 10°C, as tested by an in vitro temperature assay (*OmicronCr* Research Service), its activity might still be too low for efficient genome editing at 4–8°C. Future work therefore aims to isolate a psychrophilic CRISPR/Cas system from either psychrophilic prokaryotes or novel genome-resolved metagenomes from permanently cold environments. Preliminary data based on a first set of sequenced samples from the MOSAIC (Multidisciplinary drifting Observatory for the Study of Arctic Climate) expedition (2019–2020) in the central Arctic Ocean likely will have already increased the number of CRISPR/Cas systems from cold-adapted prokaryotes (Mock et al., 2022). Taken together, reverse genetics of *F. cylindrus* is still in its infancy, but the availability of novel genomic resources from permanently cold environments will advance this field and will help to shed light on the hidden life of cold-adapted organisms.

Once CRISPR/Cas-based genome editing becomes available for polar organisms and algae in particular, many hypotheses generated by descriptive research can be tested in vivo. This may reveal novel and likely unexpected insights as, currently, our knowledge about the fitness advantages imparted by individual genes under polar conditions is limited. However, certain gene families involved in freezing tolerance have been more extensively studied. In diatoms, this trait has likely been acquired through horizontal gene transfer (HGT) and domain shuffling of ice-binding proteins (Sorhannus, 2011; Vance et al., 2019; Winder et al., 2023), of which *Fragilariopsis cylindrus* encodes >47 (Mock et al., 2017). Another trait that appears to be equally essential for algae in polar oceans is the adaptive expansion and neo-functionalization of regulatory zinc-binding proteins such as from the MYND

(Myeloid, Nervy, and DEAF-1) and C3HC4 ring-type families (Mock et al., 2017; Ye et al., 2022). However, once CRISPR/Cas-based genome editing (e.g., Hopes et al., 2016) or at least gene silencing (De Riso et al., 2009) becomes available for *F. cylindrus*, the in vivo roles of any of these proteins will likely be revealed.

Insights from the most recent “omics” projects with polar algae suggest that functional redundancy might be under selection to thrive under the highly variable environmental conditions of polar environments (Hüner et al., 2022). In order to identify unifying evolutionary concepts underpinning algal life in polar environments, mechanisms of evolution and maintenance of this redundancy should be explored. Drivers might include polyploidization, local differences in copy number variations caused by aneuploidy, and transposon-driven genetic diversity. If and how a temperature dependence of spontaneous mutation rate contributes to these drivers as shown in multicellular and heterothermic organisms (Waldvogel & Pfenninger, 2021) remains to be seen. Equally unknown is the role of DNA repair in contributing to the genome evolution (e.g., recombination) of polar algae and microbes in general (e.g., Bulankova et al., 2021; Krasovec et al., 2019). However, current research addresses the gap in this fundamental knowledge and, therefore, will contribute to understanding how warming affects algal life in polar environments.

An important consideration when choosing a model organism is the transferability and generalizability of conclusions to other organisms. The parallel evolution of IBPs and regulatory zinc-binding proteins in diverged and therefore distant algal lineages (Ye et al., 2022) provides evidence that convergent evolution and HGT, or a combination of both, shape life in the extreme conditions of polar ecosystems. Thus, fundamental adaptations are likely transferrable. However, taxon-specific differences in functional redundancies (e.g., taxon-specific domain shuffling of IBPs) suggest that “ecological vacancies” are filled by diverse genotypes (Winder et al., 2023). This could reflect adaptations to diverse and highly variable local environments such as those present in the central Arctic Ocean. Consequently, extending the set of polar model organisms according to their biogeography may reveal how diversity has evolved and is maintained within polar ecosystems. In this context, *Fragilariopsis cylindrus* is the first of a generation of polar model organisms for understanding cold-adapted life and the potential consequences of global warming in these regions.

## AUTHOR CONTRIBUTIONS


**Antonia Otte:** Conceptualization (equal); data curation (equal); investigation (equal); writing – original draft (equal); writing – review and editing (equal). **Johanna Winder:** Conceptualization (equal); data curation (equal); investigation (equal); writing – original draft (equal); writing – review and editing (equal). **Longji**

**Deng:** Conceptualization (equal); formal analysis (equal); investigation (equal); methodology (equal); writing – original draft (equal); writing – review and editing (equal). **Jeremy Schmutz:** Conceptualization (equal); data curation (equal); methodology (equal); writing – original draft (equal); writing – review and editing (equal). **Jerry Jenkins:** Conceptualization (equal); data curation (equal); methodology (equal); writing – original draft (equal); writing – review and editing (equal). **Igor V. Grigoriev:** Conceptualization (equal); data curation (equal); methodology (equal); writing – original draft (equal); writing – review and editing (equal). **Amanda Hopes:** Conceptualization (equal); data curation (equal); methodology (equal); writing – original draft (equal); writing – review and editing (equal). **Thomas Mock:** Conceptualization (equal); data curation (equal); investigation (equal); writing – original draft (equal); writing – review and editing (equal).

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