



Big evolutionary fireworks in tiny glass houses

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The global ubiquity and ecological centrality of diatom algae make them difficult to overlook in any discussion of microbial eukaryote (protist) evolution or ecology. Whether you sample a drop of seawater, scrape a rock from freshwater, or swab a damp terrestrial surface, if it has access to sunlight, you are likely to find a biofilm composed of these shimmering siliceous microalgae. With an estimated 200,000 species inhabiting marine, freshwater, and even terrestrial ecosystems (1), diatoms are among the most speciose and ecologically impactful microeukaryotes (protists) on Earth. Alverson et al. (2) present a comprehensive phylogenomic analysis that integrates fossil calibrations with newly sequenced transcriptomes from a broad range of diatom species to help illuminate the genomic backdrop of key evolutionary transitions. Their findings significantly advance our understanding of diatom evolution, revealing how an extended period of stasis preceded a rapid burst of diversification.

Encased in intricate silica frustules (like tiny glass Petri dishes), diatom cells are enclosed in a rigid, unmalleable wall produced through tightly regulated biosilicification pathways (3). These walls, formed exocytotically from silica deposition vesicles when fused with the plasma membrane (4), exhibit astonishing architectural diversity, with pores, spines, and ridges arranged in radial or bilateral symmetry (5). Upon death, the frustules accumulate to form diatomaceous earth (diatomite), a substance with numerous applications in agriculture, paleontology, bioremediation, and even used in the original recipe for dynamite, making it more stable and safer. However, diatoms' contributions are far more encompassing. As primary producers, they are responsible for approximately 20% of Earth's oxygen production and play critical roles in the global cycling of carbon, nitrogen, and silica (5, 6).

Understanding how diatoms respond to environmental pressures is essential for predicting ecological shifts, especially as climate change alters aquatic systems worldwide. Some taxa, such as *Pseudo-nitzschia*, form ecologically and economically devastating harmful algal blooms (HABs) that produce domoic acid, a neurotoxin that causes amnesic shellfish poisoning in humans, kills marine wildlife, and disrupts fisheries (7). Recently, domoic acid poisoning has been linked to erratic, aggressive behavior in California sea lions, some of which have attacked surfers (8). These recent episodes have eerie echoes of Alfred Hitchcock's iconic film, *The Birds*, itself reportedly inspired by a 1961 avian poisoning event by *Pseudo-nitzschia*'s toxin (9).

Diatoms belong to the ochrophytes, a subgroup of Stramenopiles (within the SAR clade) (10) that acquired photosynthesis via secondary endosymbiosis with a red alga (11). While other ochrophytes, such as the kelps, chrysophytes, and xanthophytes, contribute significantly to ecosystem productivity, none match the ecological reach or evolutionary success of the diatoms. Despite their importance, major evolutionary transitions within the group have remained murky

(e.g., refs. 12 and 13). Alverson et al. (2) address this gap by presenting a taxonomically dense, fossil-calibrated phylogenomic framework based on transcriptomes from 181 diatom species combined with 15 genomes and 88 other transcriptomes. Their results reveal that much of diatom diversity traces back to a burst of diversification following more than 100 My of evolutionary constraint, thus a "slow-burning fuse" followed by a mid-Mesozoic explosion in form, function, and ecological range (Fig. 1).

The silica frustules of diatoms can be fossilized and are uniquely characteristic to diatoms, resulting in a relatively rich but patchy fossil record (14). Using 18 validated fossil calibration points and more than 1,000 orthologs, Alverson et al. estimate the crown group origin of diatoms at around 271 Mya. For nearly 100 My, diatom evolution was restricted to a relatively conserved phenotypic (morphological and ecological) traits with oogamous (i.e., sperm and egg) sexual life cycle, radial symmetry, and marine planktonic lifestyles. Then, in the middle Jurassic to early Cretaceous, a flurry of evolutionary innovations emerged, including the evolution of bilateral symmetry, isogamy, and the raphe system, which permits incredible speeds of locomotion through excretion of slime. These innovations culminated in the pennate diatoms that dominate benthic ecosystems today. This event mirrors other well-known macroevolutionary pulses such as the Cambrian Explosion in animals (15) or the Cretaceous diversification of angiosperms (16). The closest known relatives of diatoms, the Parmales, share a common ancestor roughly 270 Mya but remained species-poor and morphologically conservative (17), making diatoms a striking exception.

Modern diatoms exhibit two main frustule morphologies, centric diatoms with radial symmetry and pennate diatoms with bilateral symmetry. These silica shells consist of two overlapping halves, like a shoebox with a lid larger than the bottom. Through mitotic binary fission, each cell inherits one half during division, generating a smaller half *de novo*. Over generations, this leads to a gradual size reduction in daughter cells, necessitating episodic sexual cycles and auxospore formation to restore maximal cell size (18, 19).

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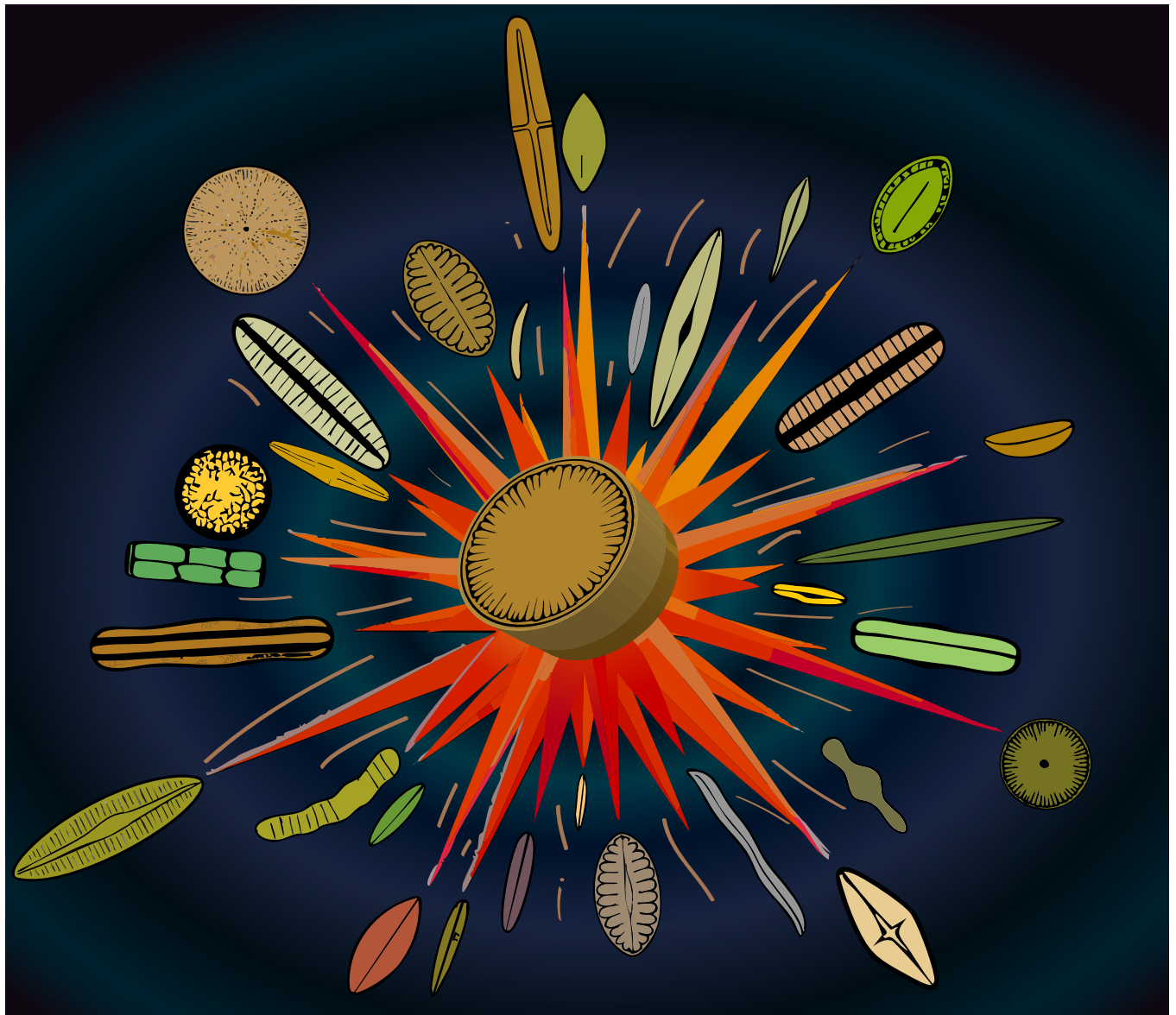


Fig. 1. Alverson et al. (2) show that the diatoms exploded in a period of rapid diversification roughly 170 Mya following a period of 100 My of evolutionary dormancy.

Among pennates, the evolution of the raphe (a slit in the cell wall enabling substrate gliding via extracellular mucilage) represents a key innovation (20). This trait not only allows for active motility but also facilitates biofilm formation and microbial trapping, with implications for both ecology and materials science (21). The development of bioadhesive coatings based on diatom mucilage is already underway, offering ecofriendly alternatives to antifouling marine paints.

Molecular phylogenomic studies have revealed deep and persistent conflicts in diatom evolutionary history (13). One of the most intriguing aspects of the Alverson et al. study is its focus on phylogenetic discordance, highlighting the difficulty in resolving the tree of diatoms. Despite analyzing over 1,000 orthologs across hundreds of taxa, some relationships in the diatom tree remain difficult to resolve or unresolvable given the data. The authors directly test for incomplete lineage sorting (ILS), a common cause of gene tree discordance in animals and plants, arising when rapidly diverging lineages inherit different subsets of ancestral

alleles before those alleles have had time to sort into distinct lineages. However, they find that ILS is unlikely to be the primary cause in diatoms. Due to their short generation times and large effective population sizes, diatoms experience more rapid coalescence of alleles between speciation events, minimizing the impact of ILS. Instead, the authors identify low phylogenetic signal and severe sequence saturation as the likely culprits. Their simulations demonstrate that even with thousands of genes, short internal branches at key nodes remain refractory to resolution. They suggest that these conflicts may reflect the true evolutionary difficulty of recovering rapid, successive divergences especially when combined with genome duplications, as suspected in early polar centric and pennate lineages (22).

Among the major macroevolutionary patterns identified are three diversification rate shifts, two of which are associated with ecological transitions, the invasion of polar ice habitats by *Fragilariopsis* (aided by antifreeze proteins) and the planktonic recolonization by the toxin-producing genus

Pseudo-nitzschia. A third diversification shift was observed in *Thalassiosira*, a centric genus with buoyancy adaptations and wide marine distribution. Importantly, net diversification was found to be lowest in radial centrals and highest in pennates, hinting at a possible connection between ecological flexibility and evolutionary tempo. Although Alverson et al. do not identify a single underlying cause for diatom diversification, their findings point to a complex interplay of morphological innovation, ecological opportunity, and developmental plasticity as key contributors to the evolutionary success of the group. One particularly intriguing hypothesis is that structural constraints imposed by frustule morphology may have influenced predation dynamics. Fracture mechanics suggest that pennate frustules, being more elongated and asymmetric, are more susceptible to shearing and predation at their poles, possibly creating selective pressure for rapid diversification (23).

Currently, two model diatoms dominate genomic research, *Thalassiosira pseudonana* and *Phaeodactylum tricornutum*. While these have been foundational to protistan research, they represent only narrow ecological and evolutionary slivers of diatom diversity. Emerging model systems such as *Fragilariopsis cylindrus* (polar) and *Pseudo-nitzschia multistriata* (toxic) are helping to close this gap, but more broadly distributed genomic resources are urgently needed (24). The field is poised for a surge in protist genomics, and the

Alverson et al. study underscores the value of transcriptomic and genomic-scale data for tackling deep phylogenetic questions. With continued investment, we may soon gain a clearer view of the genomic correlates of innovation in this remarkable lineage.

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Diatoms are architects of aquatic ecosystems, masters of microscopic engineering, and agents of global biogeochemical cycles. The phylogenomic framework developed by Alverson et al. represents a milestone in our understanding of their deep history. By highlighting both the power and the limits of large-scale molecular data, this study not only clarifies longstanding questions in diatom evolution but sets the stage for future discoveries. Diatoms have much more to teach us, from the origins of morphological innovation to the constraints imposed by being housed in glass.

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