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World Without Eukaryotes: Alternative Evolution of Complex Life from Giant Sulfur Bacteria

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Abstract

The emergence of the eukaryotic cell is regarded as a pivotal transition in the history of life on Earth. However, mounting evidence suggests eukaryogenesis was a specific, accidental event sparked by a syntrophic symbiosis between an Asgard archaeon and a bacterial endosymbiont. This prompts a fundamental counterfactual question: what if this symbiosis never occurred? The prevailing assumption is that life would remain perpetually microbial, constrained by the bioenergetic limits of prokaryotic cells. This article challenges that view by exploring the evolutionary potential of a unique group of bacteria: giant sulfur bacteria. These bacteria, driven by powerful selection pressure to bridge spatially separated pools of hydrogen sulfide and oxygen, have independently evolved remarkable sizes and different forms of complexity, including a form of eukaryote-like compartmentalization in *Thiomargarita magnifica*. Through the analysis of their novel bioenergetic solutions and conceptual modelling of an alternative evolutionary history, I propose that in an eukaryote-free world, giant sulfur bacteria represent a plausible starting point for the *de novo* evolution of complex, multicellular life. This thought experiment, albeit extremely speculative, offers new understanding of mechanisms of gaining complexity and could be useful for the analysis of the actual eukaryogenesis event, as well for the modelling of life complexity in astrobiological settings.

Keywords: eukaryogenesis; giant sulfur bacteria; *Thiomargarita magnifica*; multicellularity; alternative evolution; bioenergetics; complexity; syntrophy

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The origin of the eukaryotic cell remains one of the most profound unanswered questions in biology. For decades, the dominant narrative framed compartmentalized, organelle-rich eukaryotic architecture as a deterministic, progressive step in evolution — an inevitable leap forward in complexity from a simpler prokaryotic state. This view, however, is being supplanted by one emphasizing profound evolutionary contingency. The discovery of Asgard archaea, a superphylum harboring a suite of eukaryotic signature proteins (ESPs), provided compelling evidence for a two-domain tree of life, wherein eukaryotes emerged from within the archaeal domain through a specific endosymbiotic event (Spang et al., 2015; Zaremba-Niedzwiedzka et al., 2017). The leading "syntrophy hypothesis" postulates that this partnership was powered by a metabolic coupling between a hydrogen-dependent Asgard archaeon and a sulfate-reducing bacterial partner, which eventually became the mitochondrion (López-García & Moreira, 2020). This model suggests that eukaryogenesis was not a biological inevitability but a singular, colossally improbable "black swan" event.

This perspective invites a rigorous, albeit counterfactual, scientific thought experiment: what trajectory would life have taken if this single symbiosis had failed to occur? The conventional answer is that life would have remained stuck in a prokaryotic rut, forever limited by the fundamental bioenergetic constraints of the bacterial cell plan (Lane & Martin, 2010). The surface-area-to-volume ratio is restricted by a bacterium's energy demands; in turn, the size limitations might cap genome size, protein inventory, and ultimately, morphological and regulatory complexity. This article challenges this deterministic view of prokaryotic limitation by examining a group of microorganisms that have already shattered these constraints: the giant sulfur-oxidizing bacteria. These bacteria, driven by a unique geochemical selection pressure, have evolved giant sizes, striking intracellular complexity, and multiple independent forms of multicellularity. By analyzing their biology as a real-world evolutionary “what-if” experiment, I propose that in a world without the Asgard-bacterial chimera, these giant sulfur bacteria might have evolved to fill the void of complex life, leading to an alternative, sulfur-fueled living world.

Sulfur-Oxygen Paradox: Geochemical Crucible for Gigantism

The term “giant sulfur bacteria” is usually applied to the representatives of the genus Thiotrichales that are remarkable by their giant sizes and include the most forms discussed below. However, cable bacteria from the order Desulfobulbales (with the most remarkable representatives Electrothrix and *Electronema*) live in the similar ecological niche, extend up to 3-7 cm in length and have similar morphology (Meysman, 2018; Trojan et al., 2016). Cable bacteria and Thiotrichales have different taxonomic placement and phylogenetic origin; however, they can be called giant sulfur bacteria in terms of their ecology, morphology and physiology. Thus, “giant sulfur bacteria” will be here used as the term for a specific peculiar life form, not the specific taxonomical group.

The driving force behind the evolution of giant sulfur bacteria is a deceptively simple physico-chemical dilemma. These chemolithotrophs derive energy from the oxidation of hydrogen sulfide (H_2S) with an electron acceptor, typically oxygen (O_2) or sometimes nitrate (NO_3^-):

$$\mathbf{H_2S + 2O_2 \rightarrow SO_4^{2-} + 2H^+}$$

In stratified aquatic environments, such as coastal upwelling zones or cold seeps, these two vital substrates exist in a spatial paradox. Hydrogen sulfide is generated in the anoxic sediment layers through the decomposition of organic matter by sulfate-reducing bacteria or is supplied from geological sources. In contrast, oxygen is supplied from the atmosphere and saturates the upper water column. This creates a vertical counter-gradient, where the oxidant and reductant are separated by a considerable distance (Larkin & Henk, 1996; Schulz & Jørgensen, 2001).

A typical micrometer-scale bacterium would be confined to a single zone and thus starved of one substrate. The fundamental solution to this paradox is to physically bridge the gap. This creates a direct and intense positive selection pressure for extreme lengths, which allows the cell to span the chemocline, simultaneously accessing sulfide from the anoxic sediment with its base and oxygen from the overlying water with its apex. This lifestyle, anchoring into the sulfide-rich sediment while stretching into the oxidized zone, is the primary catalyst for the evolution of gigantism in this lineage, pushing them to sizes visible to the naked eye and making them veritable giants of the microbial world (Schulz et al., 1999; Salman et al., 2015). An indirect confirmation of the existence of such selection pressure is the independent emergence of similar giant forms in two orders — Thiotrichales and Desulfobulbales. Facing the same biochemical challenges, they have elaborated similar evolutionary solutions and achieved similar grades of complexity.

Solving the Bioenergetic Bottleneck: Two Routes to Complexity

The drive for gigantism immediately encounters the core bioenergetic constraint of the prokaryotic cell. In all living cells, the primary energy currency, ATP, is generated by membrane-bound ATP synthases powered by a transmembrane proton gradient. Because this energy-producing complex is confined to the cell membrane, energy supply scales with the square of a cell’s linear dimensions. Energy consumption, however, is a function of the total volume of metabolically active cytoplasm, scaling with the cube of its dimensions. As a cell grows larger, it faces a catastrophic energy deficiency (Lane & Martin, 2010). To achieve their massive sizes, giant sulfur bacteria have not circumvented this constraint but have evolved two distinct structural solutions that prefigure the fundamental pathways to biological complexity.

The first strategy is **multicellularization**, epitomized by the genera *Beggiatoa* and *Thioploca* in the order Thiotrichales and also by cable bacteria in the order Desulfobulbales (**Figure 1**). These bacteria form long, segmented trichomes composed of stacked, disk-like cells. Each cell maintains a small, energetically favorable volume, and the total length of the filament is achieved by integrating many simple units. The total energy-producing membrane area of the entire filament grows in lockstep with its total volume, circumventing the single-cell bottleneck. This is a direct evolutionary solution where the metric of complexity is the number of cells, and it mirrors classic experiments where unicellular organisms evolve multicellular clusters under selection for larger size (Ratcliff et al., 2012; Kurakin, 2023).

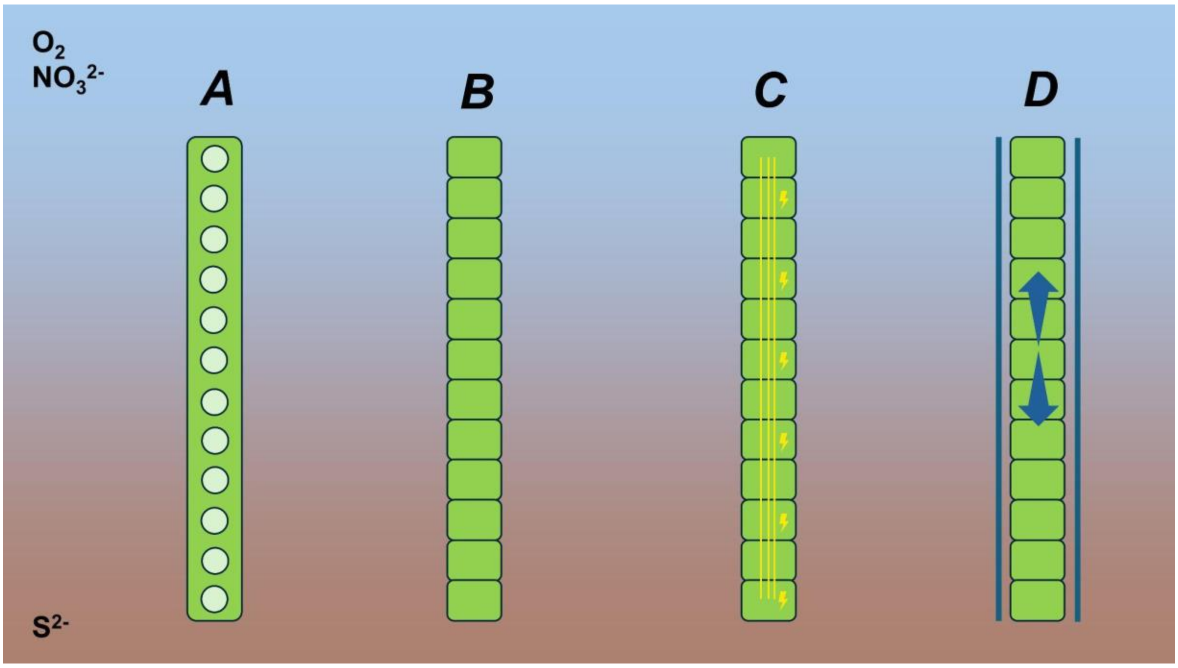

Figure 1. Schematic representation of different strategies of giant sulfur bacteria to achieve sufficient length for spanning sulfide-oxidant gradient: **A** — eukaryotization (*Thiomargarita magnifica*), **B** — multicellularization (*Beggiatoa spp.*); **C** — multicellularization + electroactivity (cable bacteria); **D** — multicellularization + motility (*Thioploca spp.*).

The second, more radical, strategy is **eukaryotization** (or **internal eukaryote-like compartmentalization**). This path is astonishingly demonstrated by the recently discovered *Thiomargarita magnifica* (Volland et al., 2022). Instead of forming a chain of separate cells, *T. magnifica* becomes a single, macroscopic, filamentous cell that grows up to 2 centimeters in length. It overcomes the surface-area-to-volume bioenergetic bottleneck by packing its cytoplasm with thousands of membrane-bound, ATP-generating "organelles" termed pepins that also contain its DNA and ribosomes, creating primitive compartments that combine the roles of nuclei and mitochondria (Volland et al., 2022; Kurakin, 2023). This strategy is conceptually identical to the eukaryotic solution: increasing complexity not by adding more cells, but by multiplying the energy-producing membrane systems *within* a single cell (**Figure 1**). This discovery represents a stunning case of convergent evolution, where a bacterium, under the selective pressure towards larger size, has "reinvented" a core tenet of the eukaryotic blueprint.

Both examples show that, when the demand for larger size meets the restriction of the surface-to-volume ratio of a single cell, **increasing complexity** becomes the only way of **increasing size**. Technically, giant sulfur bacteria are a perfect example of natural selection for larger complexity proxied by natural selection for larger size.

The case of cable bacteria confirms this assumption: they have one more layer of integration between different parts of their filaments. All cells in the filament are connected by conductive metal-organic fibers which provide electrical coupling between oxidation and reduction reactions at the opposite ends of the filament; these fibers show meta-like conductivity without any signs of redox or semiconductor-like conductance (Pankratov et al., 2024; Meysman et al., 2025). Such an **electrical connection** of the cells in a multicellular organism represents an additional level of complexity developed above multicellularity (**Figure 1**). Taken together, all these facts show that oxygen-sulfide (or nitrate-sulfide) interfaces are hotspots for bacterial complexity evolution.

"Giant Sulfur World": An Alternative Biosphere

With this biological foundation, we can construct a scientifically grounded model of an alternative evolutionary history. Let us set the initial condition: approximately 2 billion years ago, the nascent syntrophic partnership between an Asgard archaeon and a sulfate-reducing bacterium fails to establish and stabilize into endosymbiosis. The Great Oxidation Event, driven by cyanobacterial photosynthesis, still proceeds, resulting in a fully oxygenated atmosphere and upper oceans. Continuing sulfate-reducing activity in the deep ocean and sediment pores ensures persistent, extensive sulfidic zones.

In these conditions, giant sulfur bacteria might go further in the complexity evolution that we observe now. We could assume a scenario where there were more living forms of giant sulfur bacteria and more combinations of different strategies. If the combination "**multicellularization + electroactivity**" created cable bacteria, the combination "**multicellularization + eukaryotization**" might give rise to organisms with much higher gene regulation and cell-to-cell signalling systems that we see in real sulfur bacteria.

In this "giant sulfur world," the ecological roles we associate with complex eukaryotes would be filled by the diverse descendants of the giant sulfur bacteria, leveraging their two pre-existing complexity strategies.

Fungal and plant analogues are the most expected: multicellular, filamentous forms like *Beggiatoa* and *Electrothrix* would be pre-adapted to evolve into vast, interconnected mycelial networks penetrating the sediment (**Figure 2**). Their growth form, a long, branched filament, perfectly mirrors that of fungal hyphae, allowing them to efficiently explore a 3D volume for patchy sulfide resources. In our real world, mycelial forms emerged multiple times in bacteria and eukaryotes (in actinobacteria, water moulds, and fungi), which shows the efficiency of these life forms in the real earthly settings. We might expect that this form would be a promising strategy for giant sulfur bacteria in an alternative world with greater availability of sulfide.

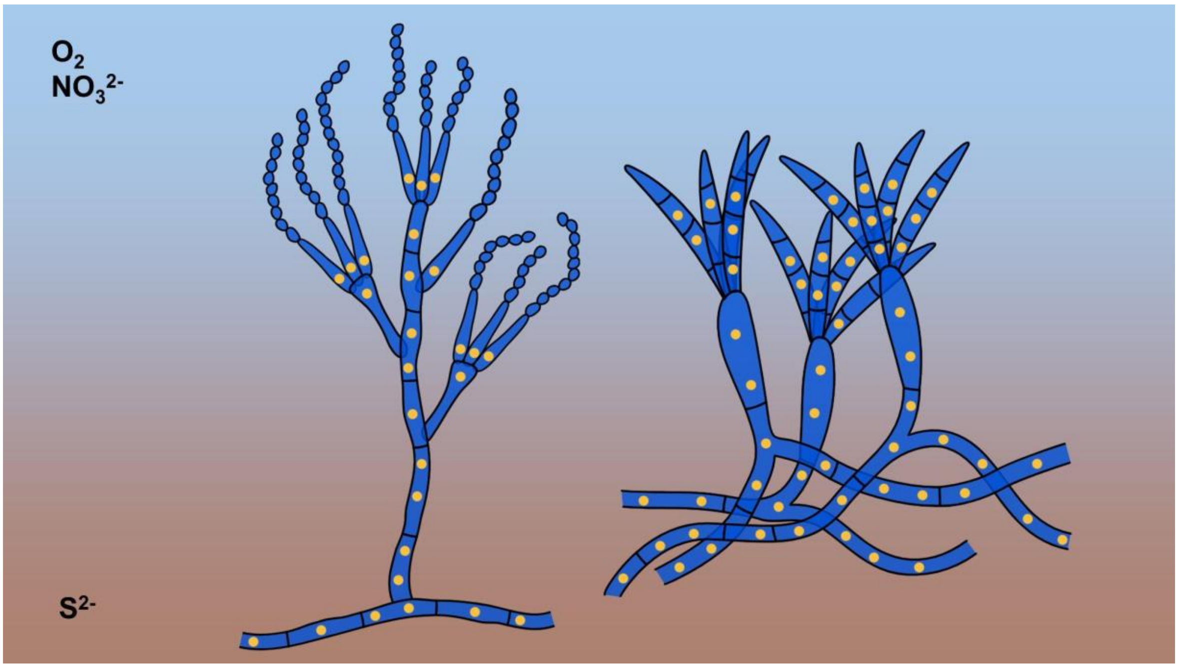

Figure 2. Mycelial organisms that could evolve from giant sulfur bacteria might differ from the extant fungi and water moulds solely by yellow sulfur granules inside — which are also present in some extant giant sulfur bacteria. *Created with Mind the Graph.*

Like some extant giant sulfur bacteria, some lineages could evolve to accumulate elemental sulfur (S^0) as a solid intermediate and energy storage compound within their cells. This would lead to organisms similar to extant fungi and water moulds, but with yellow crystalline inclusions. With a further evolutionary step, some could evolve an upright, branched "tree-like" morphology, anchoring deeply into the sulfidic sediment with root-analogs while exposing their oxidizing, sulfur-laden "crowns" to the atmosphere, creating a kind of forest.

The possibility of emergence of **animal analogues** is more disputable. The pathway to motile, heterotrophic "animals" is less direct: even in our real world, clonal motile multicellular organism is the most uncommon type of multicellularity which emerged only once and is considered as an evolutionary "black swan" event. However, some extant giant sulfur bacteria developed motility as one more life strategy driven by the same geochemical dilemma. Some species, like *Thiomargarita namibiensis*, survive by "holding their breath," storing nitrate reserves in a massive central vacuole, and then migrating or being transported to the sulfidic zone (Schulz, 2002). Such species evade selection for complexity completely due to their motility. However, representatives of the genus *Thioploca* (**Figure 1**) combine multicellular morphology with vertical motility (Kurakin, 2023), and such forms could technically evolve in simple animal-like motile organisms.

The diversity of evolution strategies within giant sulfur bacteria could potentially result in a wide range of clonal multicellularity types. In contrast, aggregative multicellularity (like in slime moulds) seems implausible for giant sulfur bacteria, but could have evolved in other bacterial lineages. In the real conditions, myxobacteria independently developed the living form of a slime mould; in the absence of eukaryotic slime moulds, more bacterial taxa might explore this way.

This alternative biosphere would be sustained by a fundamentally different energy circuit. Primary production in the deep, dark sediment would not depend on photosynthetically fixed carbon raining down from the surface, but on the direct chemolithoautotrophic oxidation of geologically sourced sulfide. The giant "plants" and "corals" would be the primary producers, directly converting inorganic chemical energy into complex biomass.

Actually, fossil data show that giant sulfur bacteria might have existed about 2 billions years ago (this means they could be contemporaries of the eukaryogenic archaeo-bacterial symbiosis), but remained unchanged after all this time (Schopf et al., 2015). They are the best confirmation of the null hypothesis of Darwinian evolution: their sulfidic habitats have been stable for billions of years — and the absence of any selection pressure rendered them living fossils.

Comparison Between Giant Sulfur Bacteria and Syntrophic Associations

The biological potential of giant sulfur bacteria remained unfulfilled due to the same geochemistry that has driven them to unique forms of complexity. But this thought experiment has direct implications for our understanding of the actual eukaryogenesis event. The discovery that extant anaerobic methanotrophic (ANME) archaea and their sulfate-reducing bacterial partners form direct electrically conductive consortia (**Figure 3**) adds a new dimension to the syntrophy hypothesis (Yu et al., 2025).

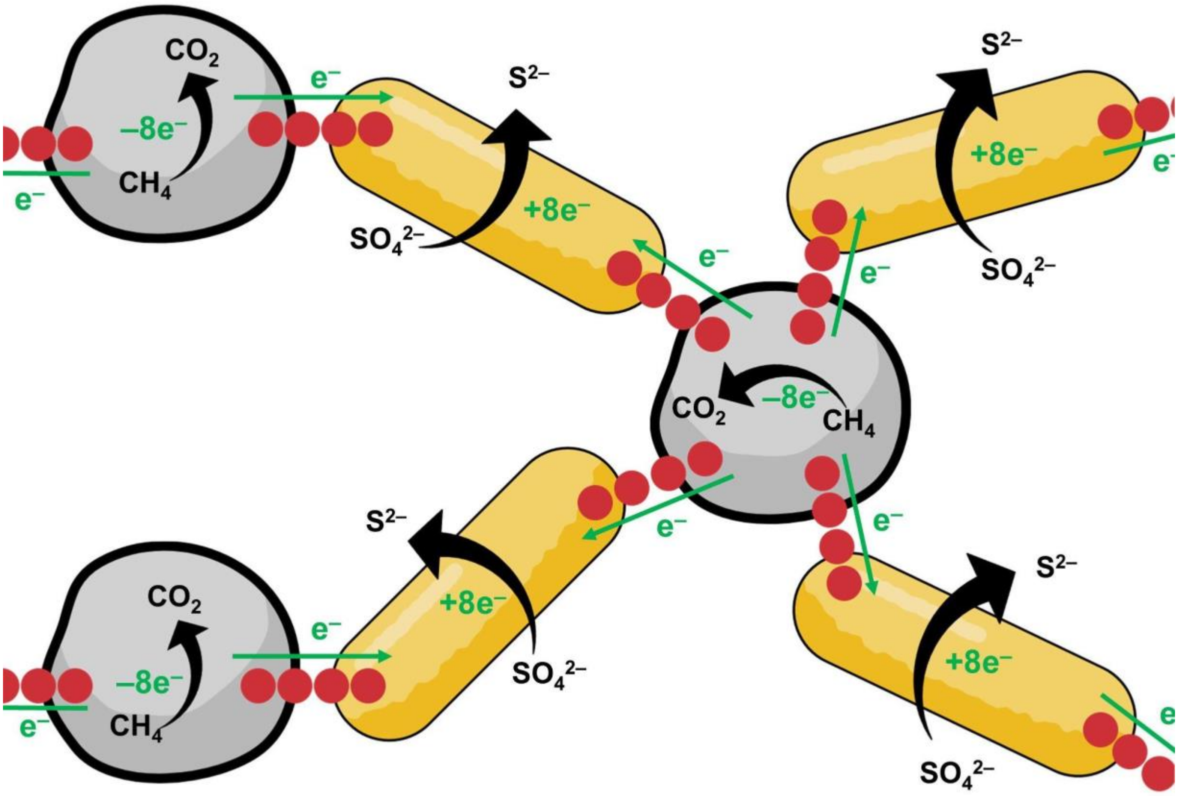

Figure 3. Structure of a syntrophic association of anaerobic methanotrophic archaea (ANME) and sulfate-reducing bacteria (SRB). Gray cells represent ANME, yellow rod-shaped cells represent SRB, red circles represent multi-heme cytochrome c, a putative conduction protein which connects these cells into a single large “power grid”. *Created with Mind the Graph.*

This looks like an alternative solution to the “joining forces” problem for syntrophic association, allowing them to achieve similar metabolic integration without endosymbiosis. In contrast to cable bacteria with metal-like conductivity, this association uses cytochrome chains with redox conductivity — but they still allow the integration of individual cells to a living electric network with electron transfers for distances much larger than the size of an individual cell. Thus, syntrophic associations and giant sulfur bacteria explored 2 of 3 shared complexity scenarios — only multicellularity is unique to giant sulfur bacteria since true multicellularity is impossible in multispecies consortium (**Table 1**). However, multicellularity further evolved multiple times in the eukaryotic domain and achieved more complex form than bacterial multicellularity — showing that in different settings, life has a limited variety of the pathways to complexity.

Table 1. Comparison of implementation of different complexity strategies in giant sulfur bacteria and archaeal-bacterial syntrophic associations.

Complexity strategy	**Giant sulfur bacteria**	**Archaeal-bacterial syntrophic associations**
Multicellularity	Clonal, filamentous	*(not applicable)*
Eukaryotization	Endogenous	Endosymbiotic

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Electric conductivity	Metal-like, metal-organic	Redox, cytochrome-based

Conclusion

This thought experiment, while speculative, serves as a powerful tool for dissecting the principles of major evolutionary transitions. It challenges the assumption that the eukaryotic cell is the unique, inevitable product of a drive towards complexity. The simultaneous existence of multicellular and "eukaryote-like" forms within a single ecological group of bacteria strongly implies that the eukaryotic innovations of compartmentalization and multicellularity are not magic keys, but repeatable, convergent solutions to the universal biochemical problems. This can not only reframe our understanding of multicellularity and complexity, but also provide interesting insights for astrobiology.

By interrogating the biology of giant sulfur bacteria, we can formulate a coherent alternative history for complex life on Earth, one that does not depend on the endosymbiotic origin of the mitochondrion. The powerful selection pressure to bridge oxygen-sulfide gradients forced these bacteria to independently solve the fundamental bioenergetic constraints on cell size, producing two parallel solutions — multicellularity and intracellular compartmentalization — that define biological complexity. This thought experiment reframes eukaryogenesis not as a unique ladder to complexity, but as one outcome among multiple potential solutions, championed by a specific kind of syntrophic partnership. It powerfully demonstrates that to understand life's true potential, we must sometimes look beyond the singular history we have and learn to imagine the ones that never were.

Supplementary information: This thought experiment and the related considerations were first proposed in my blog post titled *"Alternative history of life on Earth: complex life evolving from giant sulfur bacteria"* on *Springer Nature Research Communities*: https://communities.springernature.com/posts/alternative-history-of-life-on-earth-complex-life-evolving-from-giant-sulfur-bacteria. It contains some additional details such as AI visualizations of the possible life forms in this alternative evolution scenario, which were not included in the main text to make it more scientifically rigorous..

Generative AI statement: I used **DeepSeek** for the initial rewriting of the blog article mentioned above in the scientific article style; then the resulting article underwent major manual rework to include additional considerations, images, and references, as well as to align it with my key ideas. I also used **Perplexity** as an "AI reviewer" of the initial blog article, which helped me identify the key article about Darwinian "null hypothesis" applied to giant sulfur bacteria (Schopf et al., 2015) and include it into the current article. I hereby declare that this article is the product of my creativity, and the role of AI tools was predominantly technical.

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