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Significance of Endosymbiosis in Photosynthetic Organisms

1. Introduction

A world devoid of endosymbiosis would be a world without biomass– or more precisely a world without multicellular biomass (McFadden and van Dooren, 2004). Though it occurred in the Proterozoic eon, the first primary endosymbiotic event peopled the oceans with a panoply of algae, and the land a stunning array of flora (McFadden and van Dooren, 2004; Falkowski, 2008, p.3; Lhee *et al.*, 2019). This incredible fusion of two cell lineages, in which a heterotrophic protist consumed and retained a proto-cyanobacteria, was arguably the most significant event in early evolutionary history (Reyes-Prieto, Weber and Bhattacharya, 2007; Keeling, 2013). Brought to prominence by the female scientist Lynn Margulis in 1967 (Sagan, 1967), endosymbiotic theory offers a solution to a core question in biology: how did multicellular life evolve and what were its consequences? This essay explores the profound significance of endosymbiosis, beginning briefly the plastid, before moving on to the green algal (Viridiplantae) and red algal (Rhodophyta) lineages, which formed the foundation of the trophic web (Bhattacharya, Yoon and Hackett, 2003; Lhee *et al.*, 2019).

2. Primary endosymbiosis: significance of the plastid

2.1. Significance of the plastid

With the engulfment and retention of a tiny cyanobacteria into a Proterozoic protist came complexity: specialized multicellularity (organelles), novel gene replacement, autotrophy in eukaryotes and vast phenotypic diversity. With the new genes obtained from the proto-cyanobacteria, eukaryotes were able to adapt to new environments (Keeling, 2010). This led to a flush of eukaryotic life, laying the groundwork for the evolution of complex marine, freshwater and terrestrial organisms (Falkowski, 2008, p.114; Keeling, 2013). From primary symbiosis came two main lineages, which subsequently underwent further endosymbiosis as displayed in figure 1.

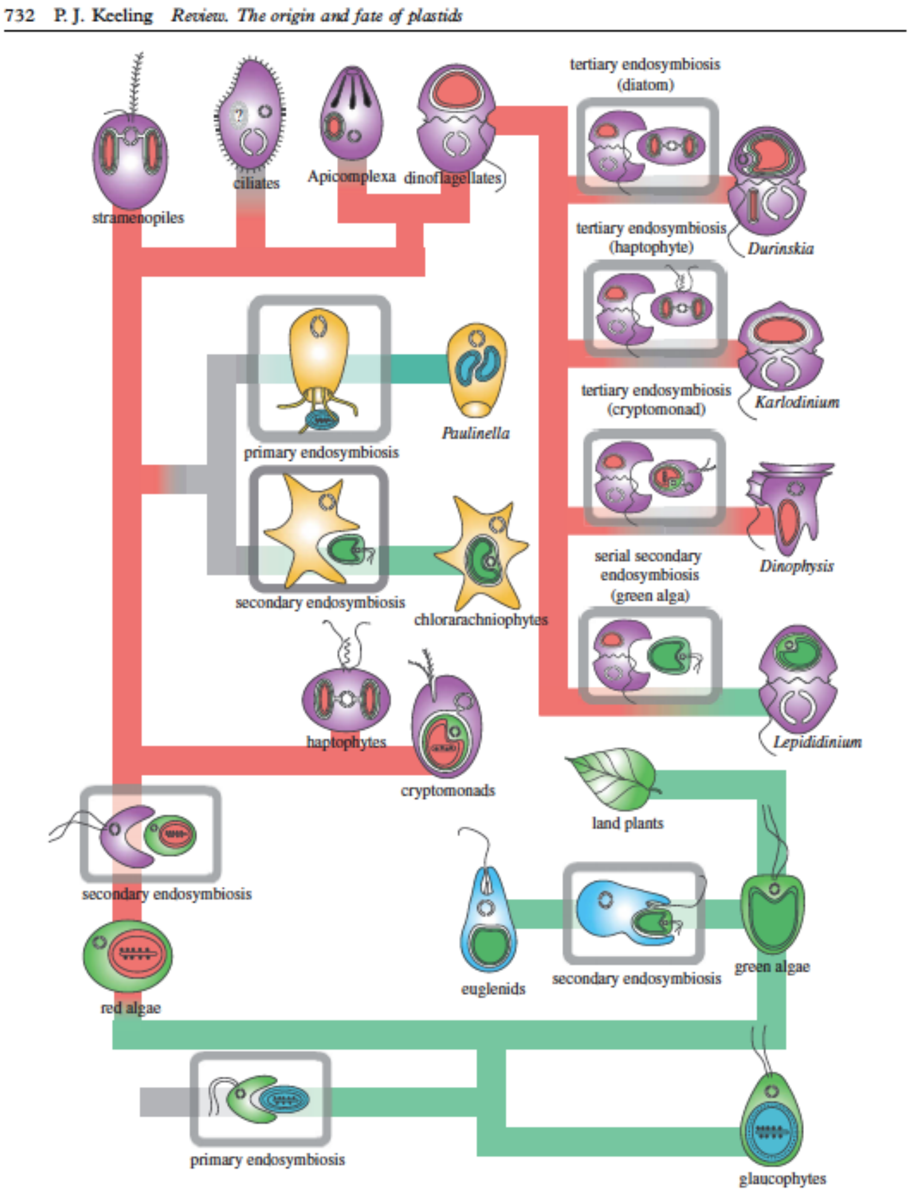

Figure 1: Three lineages of endosymbiosis. In green, on the right-hand side of the figure, are the two produced from primary endosymbiosis, the glaucophytes and green algae (Viridiplantae). While on the left, and scrolling around to the top right, the red algal lineage (Rhodophyta) can be seen. The only other occurrence of primary endosymbiosis is the case of *Paulinella,* which appears to have broken off more recently (Adapted from Keeling, 2010).

3. **Glaucophytes**

Glaucophytes are one of the earliest lineages stemming from endosymbiosis, but remain relatively small with just ~25 species, and producing no further lineage (Keeling, 2010). Their evolutionary significance is, therefore, insignificant. However, because they retained a relict peptidoglycan wall– the smoking gun of the cyanobacteria– they contributed to endosymbiotic theory (Keeling, 2010). Geen algae, by contrast, went on to colonize an extraordinary range of habitats, including, for the first time in evolutionary history, terrestrial environments (Lewis and McCourt, 2004).

4. Green algal lineage (Viridiplantae)

In terms of evolutionary success, the primary endosymbiotic event that initiated Viridiplantae is truly remarkable. Perhaps the most familiar of these descendants are the Embryophytes, or land plants. However, as seen in figure 1, these Charophytes were relatively late comers, compared to the earlier lineage, Chlorophyta. Viridiplantae boasts over half a million species and are characterized by the plastid bearing a double thick membrane, as well as thylacoids containing chlorophyll a (*Chla)*, chlorophyll b *(Chlb)* and intraplastidial starch, as displayed in figure 2 (Bachy *et al.*, 2022).

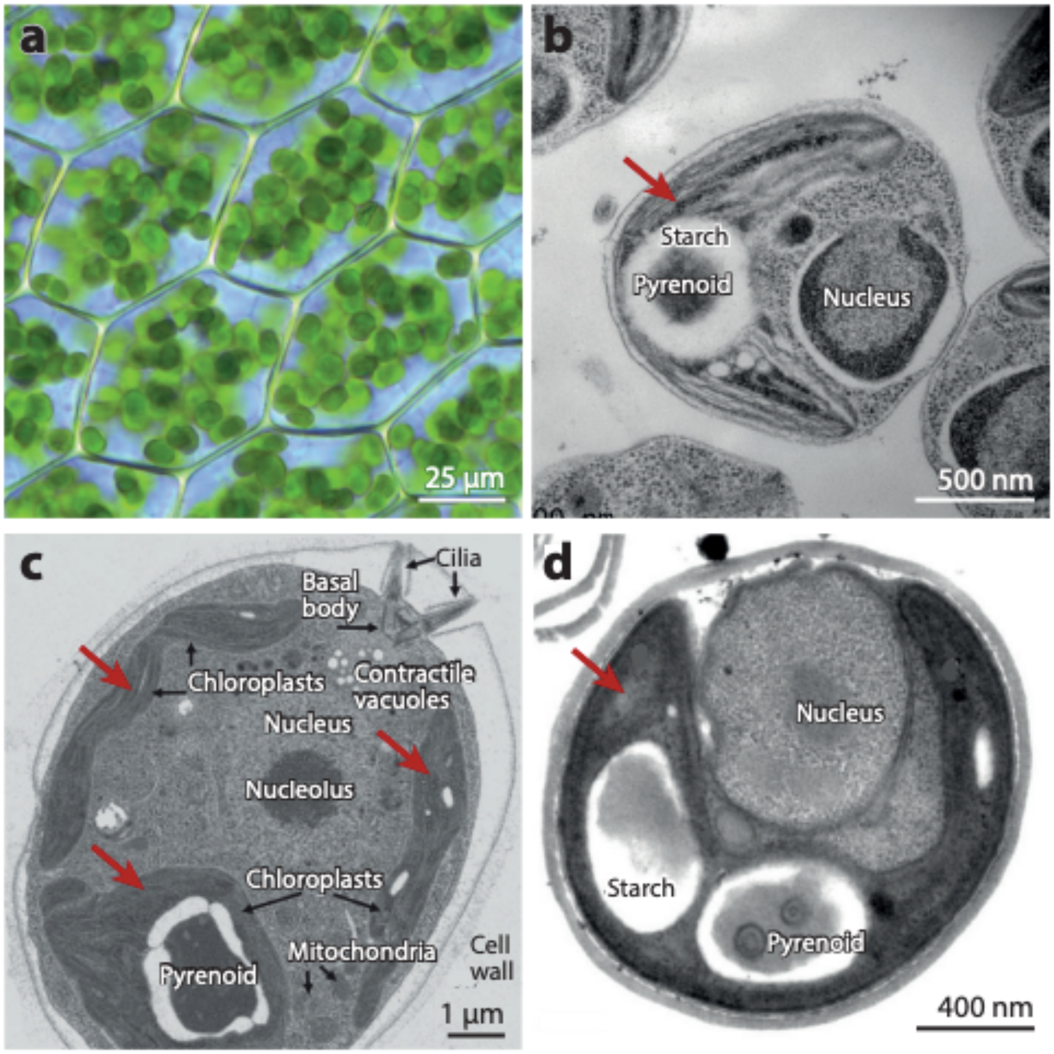

Figure 2: Four images of from Viridiplantae, displaying the core evolutionary advancements, notably the plastids, most prominently seen in (a) and (c), which gave Eukayotes the power of autotrophy.

4.1. Chlorophytes (Chlorophyta):

The first of the two green algal lineages were the Chlorophytes, found in both marine and freshwater ecosystems and produced a diverse array of taxa (Delwiche and Cooper, 2015). In terms of significance, these green microalgae such as *Micromonas* and *Ostreococcus* became foundational in the marine trophic web, providing a food source for bivalves and other invertebrates (Bachy *et al.,* 2022).

4.2. Charophytes (Charophyta):

As aforementioned, all Embryophytes evolved from green algae, phylogenetically from Charophyta (Delwiche and Cooper, 2015). Because this clade evolved in freshwater, their adaptation to terrestrial habitats became possible (Bachy *et al.*, 2022). Though they never underwent secondary endosymbiosis, Charophytes colonized an incredible range of freshwater and terrestrial habitats and underwent diverse morphological changes. They began occupying novel ecological niches, gradually forming the trophic base for terrestrial hetrotrophes, which, eventually included *Homo sapiens* (Lewis and McCourt, 2004). Although Viridiplantae underwent secondary endosymbiosis, such as the freshwater Euglenids (Euglenophyceae), important players in freshwater phytoplankton communities, further endosymbiotic belonged almost exclusively to Rhodophyta.

5. Red algal lineage (Rhodophyta)

If there was a prize for most endosymbiotic events in a photosynthetic taxon, red algae, Rhodophyta, would win that prize. Although with 5000-6000 species, it less phylogonectially diverse than Viridiplantae, it holds far more endosymbiotic events. Not only does this taxa sport two secondary endosymbiotic clades– the Stramenopiles and the Alveolates– it also contains tertiary endosymbiosis, occurring almost exclusively in the dinoflagellates (Archibald and Keeling, 2002). The significance of these events for marine life cannot be understated. In addition to forming the vegetal base of oceans– from communities of microscopic flagellates to giant kelp forests– they also underwent further endosymbiosis.

5.1. Further endosymbiosis: secondary and tertiary

During each subsequent endosymbiotic event, the plastid gains a membrane (Douglas *et al.*, 2001). Dinoflagellates, a product of secondary endosymbiosis, for example, contain plastids with three membranes (Archibald and Keeling, 2002), as illustrated in figure 3.

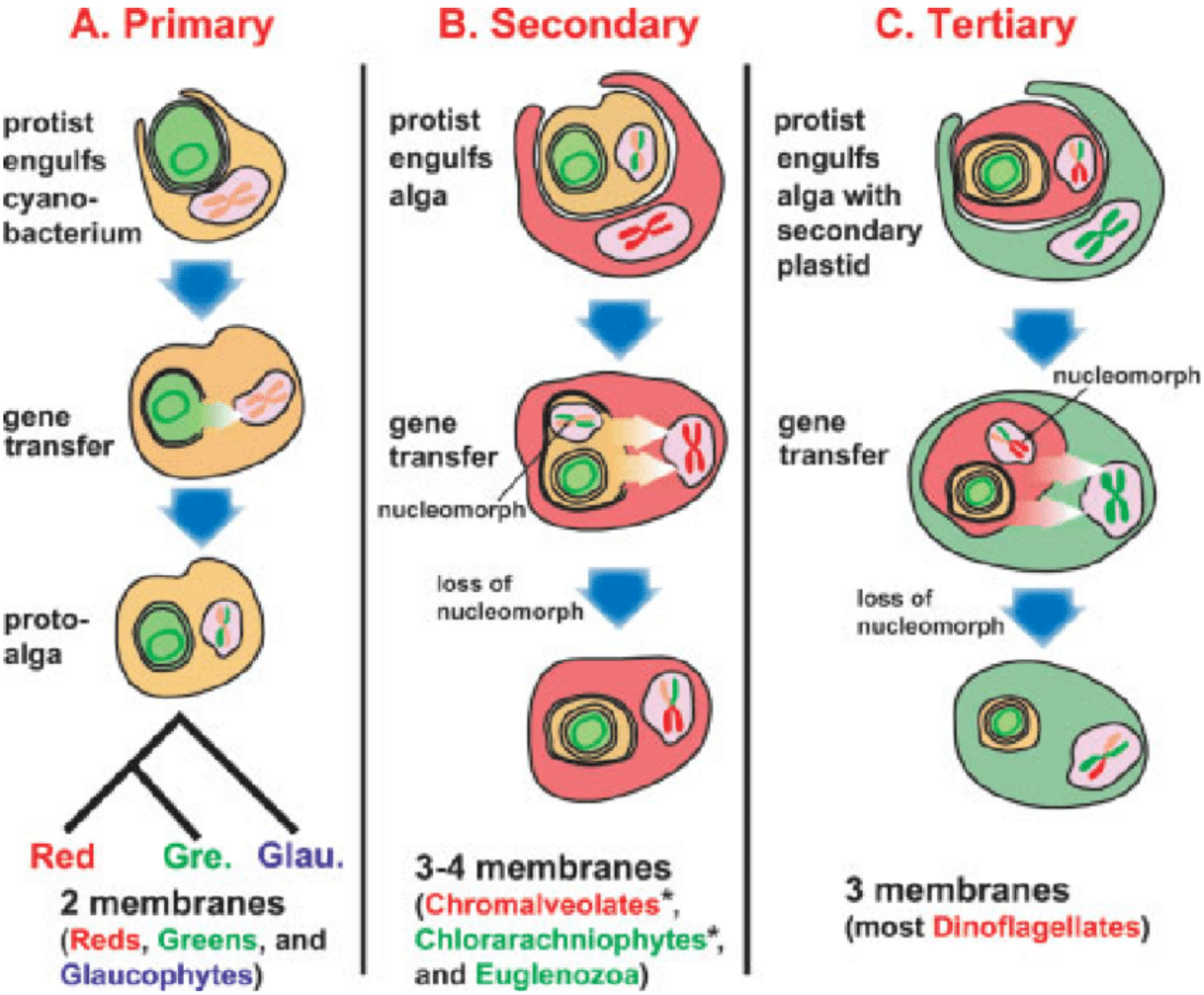

Figure 3. Illustration of primary, secondary and tertiary endosymbiosis, including gene transfer from the endosymbiont, loss of the nucleomorph and gain of an additional membrane around the plastid. (Adapted from Bhattacharya, Yoon and Hackett, 2003)

A good example of tertiary endosymbiosis is ‘dinotoms,’ dinoflagellates that have consumed a diatom (Bachy *et al.*, 2022). But why is this significant? Because these groups would become primary producers in marine habitats as well as major drivers of evolution around the globe (Bhattacharya, Yoon and Hackett, 2003).

5.2. Haptophytes, Stramenopiles and Alveolates

Not only did photosynthetic life first evolve in marine environments, but complex organisms, such as giant kelp forests and edible red algae, also arose in marine environment. Even molecular Rhodophyta play a crucial role in the global processes, such as the carbon cycle (Bhattacharya, Yoon and Hackett, 2003). Haptophytes, for example form great blooms that produce coccolith scales, which then act as carbon sinks; while dinoflagellates (Alveolates) can cause massive ‘red tides,’ resulting in mass sickness in human communities due to shellfish poisoning (Bhattacharya, Yoon and Hackett, 2003). Elsewhere in the oceans, Stramenopiles such as diatoms and giant kelp play crucial roles in driving trophic cascades, acting as both the base of the food chain as well as marine breeding grounds for many marine chordates (Douglas *et al.*, 2001).

6. **Conclusion**

The extraordinary diversity and evolutionary success of photosynthetic organisms is truly astounding. Yet, it is even more astounding that none of these adaptations could have evolved were it not for a single event dating back, perhaps one billion years (Keeling, 2013). But of all the subsequent of evolutionary developments gained from endosymbiosis, perhaps the most consequential was photosynthesis which unlocked the potential of autotrophy in Eukaryotes. Without the succession of endosymbiotic events which formed the plastid and other endosymbionts, none of the spectacularly diverse photosynthetic organisms— nor the heterotrophs which depend upon them— could exist.

Word Count: 997

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