

Diversity and Evolution of Plastids and Their Genomes

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Abstract Plastids, the light-harvesting organelles of plants and algae, are the descendants of cyanobacterial endosymbionts that became permanent fixtures inside nonphotosynthetic eukaryotic host cells. This chapter provides an overview of the structural, functional and molecular diversity of plastids in the context of current views on the evolutionary relationships among the eukaryotic hosts in which they reside. Green algae, land plants, red algae and glaucophyte algae harbor double-membrane-bound plastids whose ancestry is generally believed to trace directly to the original cyanobacterial endosymbiont. In contrast, the plastids of many other algae, such as dinoflagellates, diatoms and euglenids, are usually bound by more than two membranes, suggesting that these were acquired indirectly via endosymbiotic mergers between nonphotosynthetic eukaryotic hosts and eukaryotic algal endosymbionts. An increasing amount of genomic data from diverse photosynthetic taxa has made it possible to test specific hypotheses about the evolution of photosynthesis in eukaryotes and, consequently, improve our understanding of the genomic and biochemical diversity of modern-day eukaryotic phototrophs.

1 Introduction

The origin and evolution of plastids,¹ the light-gathering organelles of photosynthetic eukaryotes, is a subject that has intrigued biologists for more than a century. Since the original musings of Schimper (1885) and Mereschkowsky (1905), a wealth of structural, biochemical and, most recently, molecular sequence data

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¹The term “chloroplast” is sometimes used to refer to all photosynthetic plastids among eukaryotic phototrophs and, occasionally, only in reference to the photosynthetic organelle of green algae and land plants.

has accumulated and shown convincingly that these important cellular structures are of endosymbiotic origin (Gray and Spencer 1996). The exact timing of the first plastid-generating endosymbiosis, and the ecological and physiological conditions that facilitated such an event is not known, but it is commonly thought that plastids evolved from once free-living cyanobacteria that were originally ingested as food by a heterotrophic eukaryote. Under this scenario, rather than being digested, these prokaryotic cells escaped the confines of their phagocytic vacuole and gradually became fully integrated components of their eukaryotic hosts. As an obvious consequence of the cyanobacterial ancestry of their plastids, eukaryotic phototrophs perform oxygenic photosynthesis and have contributed greatly to the burial of organic carbon and oxygenation of Earth's atmosphere (Katz et al. 2004).

While the notion that plastids are derived from endosymbiotic cyanobacteria is now widely accepted, many important questions about the origin and diversification of plastids remain. The challenges associated with inferring the evolutionary history of plastids are in large part due to the exceptional structural, biochemical and molecular diversity seen in modern-day photosynthetic organisms. In this chapter, we provide an overview of the distribution of plastids across the known spectrum of eukaryotic life, summarize the diversity of photosynthetic pigments and storage carbon biochemistry seen in plants and algae, and present recent advances in our understanding of the tempo and mode of plastid diversification. Finally, we discuss the evolution of the plastid genome and proteome, providing recent insight into the significant role of lateral (or horizontal) gene transfer (LGT). As we shall see, the evolutionary history of plastids is exceedingly complex and while the use of molecular phylogenetics has improved our understanding of plastid evolution significantly, it has also raised as many questions as it has answered.

2 Distribution of Plastids

From an evolutionary perspective, the most fundamental distinction between different plastid types is between those whose ancestry can be traced directly to the original cyanobacterial endosymbiont (i.e., "primary" plastids) and those that were acquired indirectly as a result of an endosymbiosis between a plastid-bearing eukaryote and an unrelated eukaryotic host (i.e., "secondary" or "tertiary" plastids). The plastids of glaucophytes, rhodophytes (red algae) and Viridiplantae (green algae and land plants) are bound by two envelope membranes, which are thought to be derived from the inner and outer membranes of the original cyanobacterial endosymbiont (Jarvis and Soll 2001) (Fig. 1a–c). The lack of additional plastid membranes, a feature of the organelle in many other organisms, led to the notion that these plastids arose through a primary endosymbiotic event involving a cyanobacterial endosymbiont (Gibbs 1981). The evidence for and against a single origin for all primary plastids will be discussed in Sect. 4.1.

In contrast to the plastids of glaucophytes, rhodophytes and Viridiplantae, the euglenids and chlorarachniophytes are believed to have acquired their plastids from green

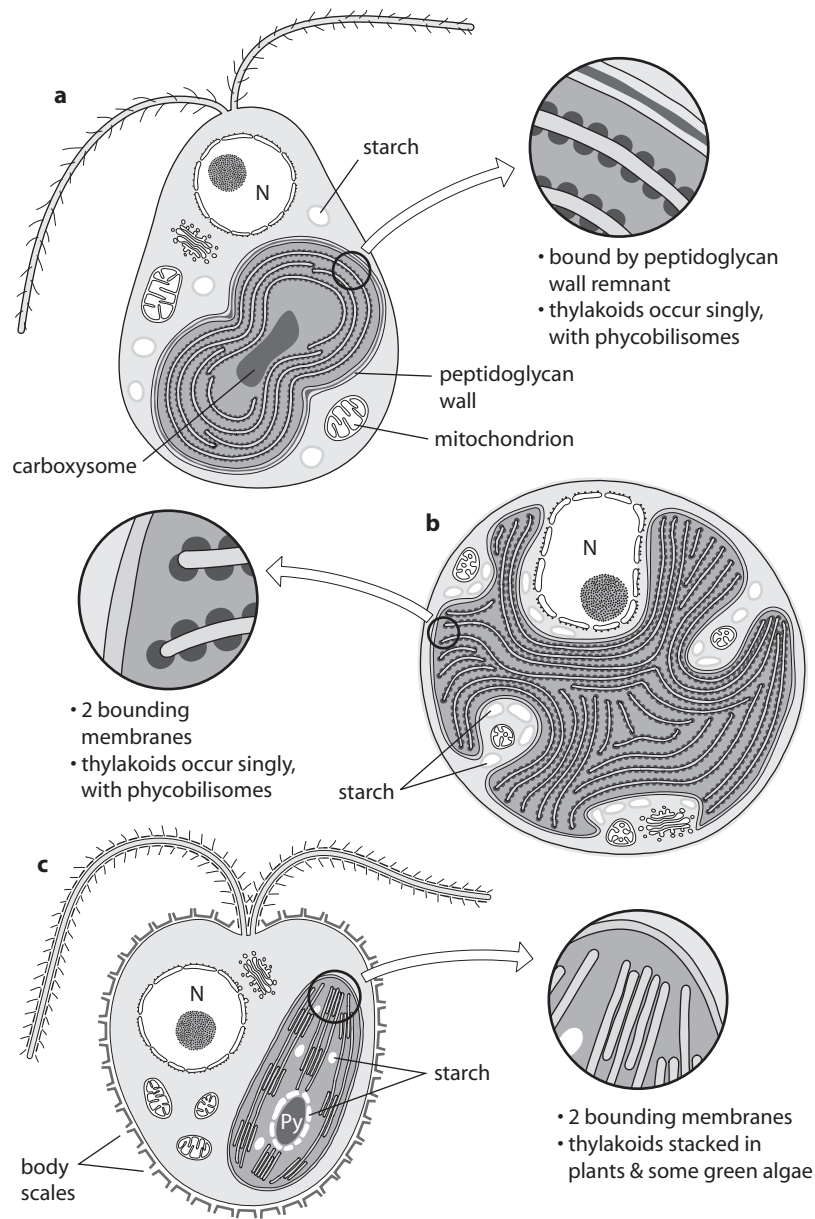


Fig. 1 Diversity of photosynthetic eukaryotes and their plastids. The plastids of glaucophytes (**a**), rhodophytes (**b**) and Viridiplantae (**c**) are bound by two membranes. Note the presence of phycobilisomes attached to the lumen side of the thylakoid membrane in **a** and **b**. The euglenids (**d**) and chlorarachniophytes (**e**) both possess plastids of green algal ancestry, which are surrounded by three and four membranes, respectively. The plastids of haptophytes (**f**), cryptophytes (**g**) and stramenopiles (**h**) are of red algal origin and are each surrounded by four membranes. Note the continuity of the nuclear envelope and the outermost plastid membrane, and the presence of ribosomes on the outer plastid membrane. Cells shown in **i** and **j** correspond to peridinin-containing dinoflagellates and apicomplexans, respectively. *N* nucleus, *Py* pyrenoid. (Art by L. Wilcox)

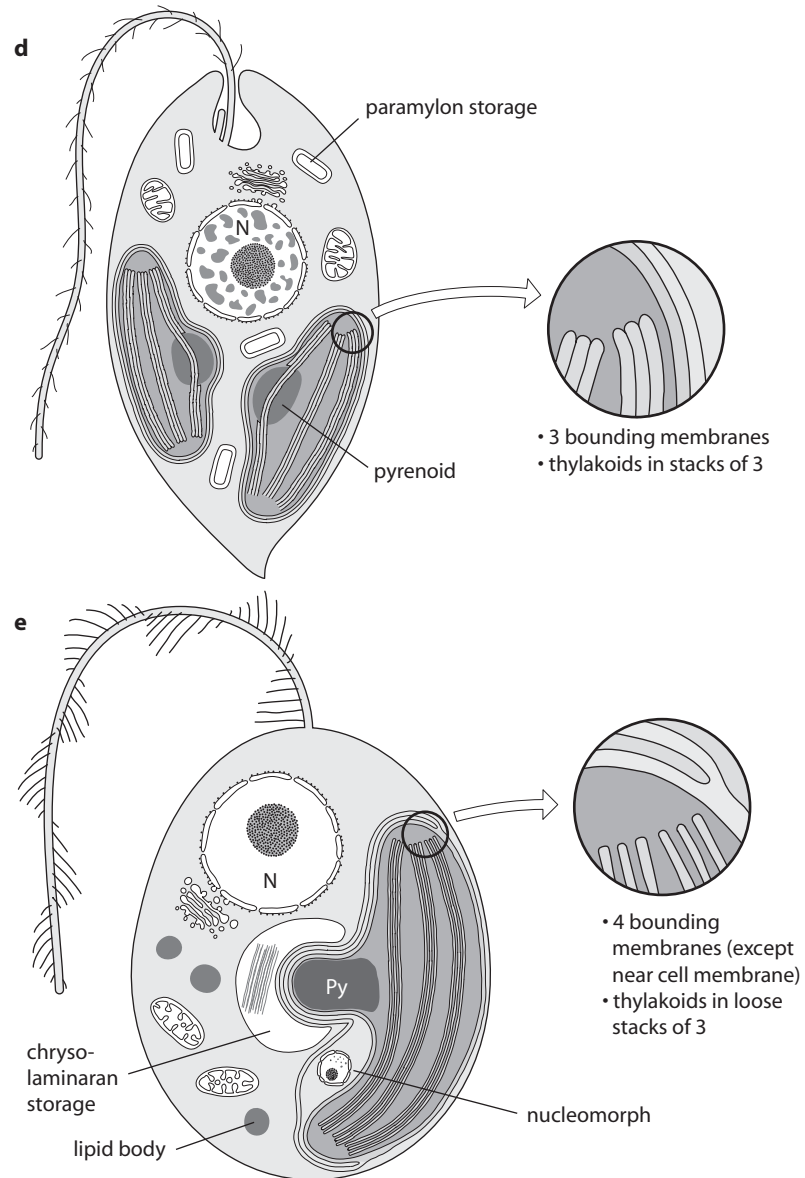


Fig. 1 (continued)

algae via secondary endosymbiosis (Table 1, Fig. 1d, e). Secondary or tertiary origins are proposed for the red-algae-derived plastids of cryptophytes, haptophytes, stramenopiles, most photosynthetic dinoflagellates, and apicomplexans (Table 1, Fig. 1f–j), although the origin of the apicomplexan plastid remains controversial (see below). With

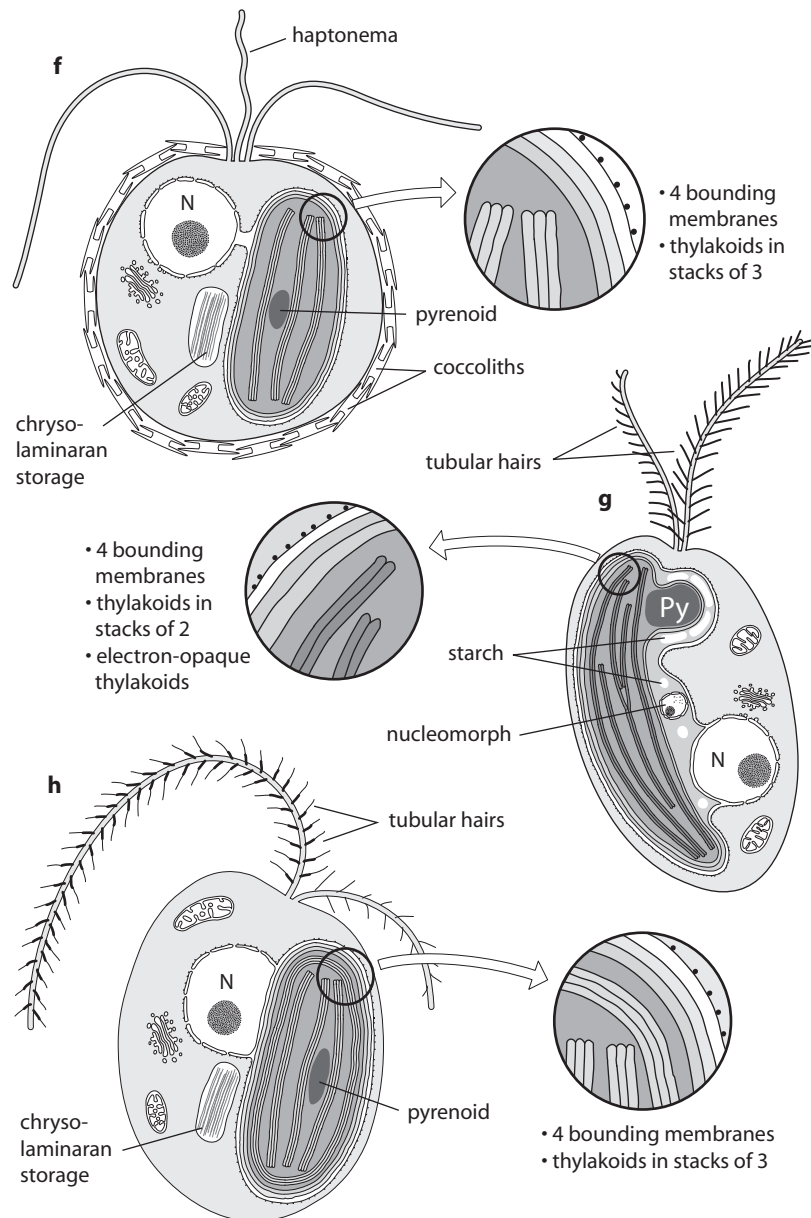


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respect to the abundance of plastid-containing species in each of these groups, all known members of the glaucophytes, rhodophytes, Viridiplantae and haptophytes possess photosynthetic or nonphotosynthetic plastids, indicating that plastid acquisition

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