

Review

The origin and early evolution of plants

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Plant (archaeplastid) evolution has transformed the biosphere, but we are only now beginning to learn how this took place through comparative genomics, phylogenetics, and the fossil record. This has illuminated the phylogeny of Archaeplastida, Viridiplantae, and Streptophyta, and has resolved the evolution of key characters, genes, and genomes – revealing that many key innovations evolved long before the clades with which they have been casually associated. Molecular clock analyses estimate that Streptophyta and Viridiplantae emerged in the late Mesoproterozoic to late Neoproterozoic, whereas Archaeplastida emerged in the late-mid Palaeoproterozoic. Together, these insights inform on the coevolution of plants and the Earth system that transformed ecology and global biogeochemical cycles, increased weathering, and precipitated snowball Earth events, during which they would have been key to oxygen production and net primary productivity (NPP).

Highlights

The origin of the first photosynthetic eukaryotes through to the first land plants transformed the Earth's biosphere.

There is no single unified view of the processes and timing of early plant evolution despite myriad fossil and geochemical evidence.

Phylogenetically targeted genomic, morphological, and Earth system data will be necessary to make significant advances in our understanding of early plant evolution given the deep timescales.

Early plant evolution

Plants (**Archaeplastida**; see [Glossary](#)) have transformed our planet, increasing energy input to the biosphere, altering the atmosphere, and forever changed global biogeochemical cycles [1–4]. Precisely when and how this occurred has been unclear, for lack of a coherent fossil record, a refined phylogenetic framework within which to interpret it, and genomic resources from which to elucidate the molecular innovations that have made such an evolutionary success of plants. Although a broad framework of archaeplastid evolution has been established for some time [5,6], subsequent refinements have begun to provide a more coherent understanding of plant evolution. All living plants belong to Archaeplastida ([Figure 1](#) and [Box 1](#)), named for the primary endosymbiotic union between a eukaryote and a cyanobacterium, from which the major group of photosynthetic eukaryotes arose ([Box 2](#)) [7]. Many photosynthetic eukaryotes acquired their chloroplasts through direct descent from the archaeplastid ancestor, from which the groups Rhodophyta (red algae), Glaucophyta, and Viridiplantae (green plants) are all derived [8]. Others acquired their plastids through secondary **endosymbiosis** either directly from these primary photosynthetic eukaryotes or indirectly via tertiary or quaternary endosymbiosis (e.g., dinoflagellates, ciliates, brown algae, cryptophytes, and haptophytes) [9]. Evolution of the primary archaeplastids reshaped the hydrosphere, cryosphere, and lithosphere [10], and the subsequent evolution of land plants transformed the continents and created new habitats, thus promoting diversity across the tree of life including animals [11], fungi [12], bacteria [2], and archaea. This led to development of more complex food webs owing to an increased efficiency of energy and nutrient transfer [13]. Here, we examine how new genomes, fossils, **phylogenomic**, and timescale analyses have revolutionised our understanding of early plant evolution and highlight the challenges that remain. This review focuses on the origin of Archaeplastida and the diversification of rhodophytes, glaucophytes, chlorophytes, and streptophytes; we do not address the evolution of land plants which has been thoroughly reviewed elsewhere [14–19].

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Interrelationships of Archaeplastida

There is no dispute that the early evolution of Archaeplastida led to the origin of rhodophytes, glaucophytes, and Viridiplantae [20]. However, their interrelationships have recently received much needed revision, with insights from phylotranscriptomics and genomics leading to, for example, a revision of the placement of glaucophytes and rhodophytes relative to green plants (Figure 2) [3,21,22]. Analysis of the first glaucophyte genome, *Cyanophora paradoxa*, provided strong evidence that glaucophytes and green plants are most closely related, with rhodophytes sister to this group [8,23]. Phylogenomic analyses of under-sampled algal lineages continue to reveal additional complexities during the origin of Archaeplastida (Figure 2). A new phylum, Rhodelphidia, has been identified as the sister group to rhodophytes [24], which is then most closely related to Picozoa [25].

Recent analyses have also changed our understanding of the origin of green plants (Viridiplantae [22]) that were traditionally considered to be composed of two groups, Chlorophyta and Streptophyta. Genome analysis of *Prasinoderma coloniale* identified Prasinodermatophyta as a possible third subclade of Viridiplantae that emerged before the divergence of Chlorophyta and Streptophyta [22]. Within the chlorophytes, prasinophytes (e.g., Chlorodendrophyceae, Nephroselmidiophyceae, Mamiellophyceae) have usually been considered to comprise a clade, but their relationships are disputed. Phylogenomic analyses suggest that prasinophytes are **paraphyletic** and comprise successive sister lineages to the core chlorophytes (Figure 2) [11,22,27]. The ancestor of Chlorophyta likely diversified in marine environments, leading to the evolution of the core chlorophytes that subsequently radiated into marine, freshwater, and terrestrial environments [11,28].

The interrelationships of charophytes and embryophytes have been highly contested. Morphologically, Charophyceae are the most complex and land plant-like of the streptophytes, and have therefore long been considered to be the sister group to land plants. However, a diversity of phylogenomic methods and datasets place the simple Zygnematophyceae as a sister group to land plants [3,29,30]. Mesostigmatophyceae and Chlorokybophyceae [31] form one group of streptophytes, with Klebsormidiophyceae, Charophyceae, Coleochaetophyceae, Zygnematophyceae, and Embryophyta (the land plants) subsequently diverging in succession (Figure 2). The charophyte grouping, traditionally composed of Klebsormidiophyceae, Charophyceae, Coleochaetophyceae, and Zygnematophyceae, is clearly paraphyletic and should be abandoned. The more useful and biologically coherent clade composed of Charophyceae, Coleochaetophyceae, and Zygnematophyceae and Embryophyta is often recognised as Phragmoplastophyta [32,33].

Insights from genomics and transcriptomics

Technical revolutions decreasing the cost of sequencing and the development of long-read sequencing (e.g., PacBio, Nanopore) have increased the quantity and quality of plant genomes available for study [34,35]. This has not only transformed our understanding of the early plant phylogeny but also provided novel insights into the origin of the first photosynthetic algae through to the first land plants. These comparative analyses have demonstrated how genes linked to the development and functioning of vital morphological traits appear during the evolution of Archaeplastida. A selection of these works are discussed here, although many more genome [36–42] and **comparative genomic** studies [43–48] have been published.

Although most extant Archaeplastida are **photoautotrophs**, engulfment of an ancient cyanobacterium would have required **phagotrophy** [49–51]. Analysis of genomes of the red algal sister group, Rhodelphidia, suggests a **mixotrophic** lifestyle (i.e., predation and phototrophy) for the

Glossary

Archaeplastida: a clade comprising the rhodophytes, glaucophytes, and Viridiplantae, all of which have as a synapomorphy the chloroplast that reflects the primary endosymbiosis with an ancestral cyanobacterium in their common ancestor.

Comparative genomics: comparative analysis of genome sequences to identify similarities and differences between species.

Cytoskeleton: the network of filaments and microtubules that organise, shape, and structure the cytoplasm of plant cells.

Endosymbiosis: a symbiotic relationship where one organism lives within the cells or body of another organism.

Mixotrophic: an organism that utilises a mixture of different energy and carbon sources (e.g., phagotrophic and photoautotrophic).

Molecular dating: analysis of molecular data to infer the date of divergence of different species calibrated using evidence from the fossil record.

Monophyletic: a group of organisms descended from a common ancestor, that includes all descendants.

Net primary productivity (NPP): a measure of the difference between the energy fixed by autotrophic organisms and their respiration.

Paraphyletic: a group of organisms descended from a common ancestor, that does not include all descendants.

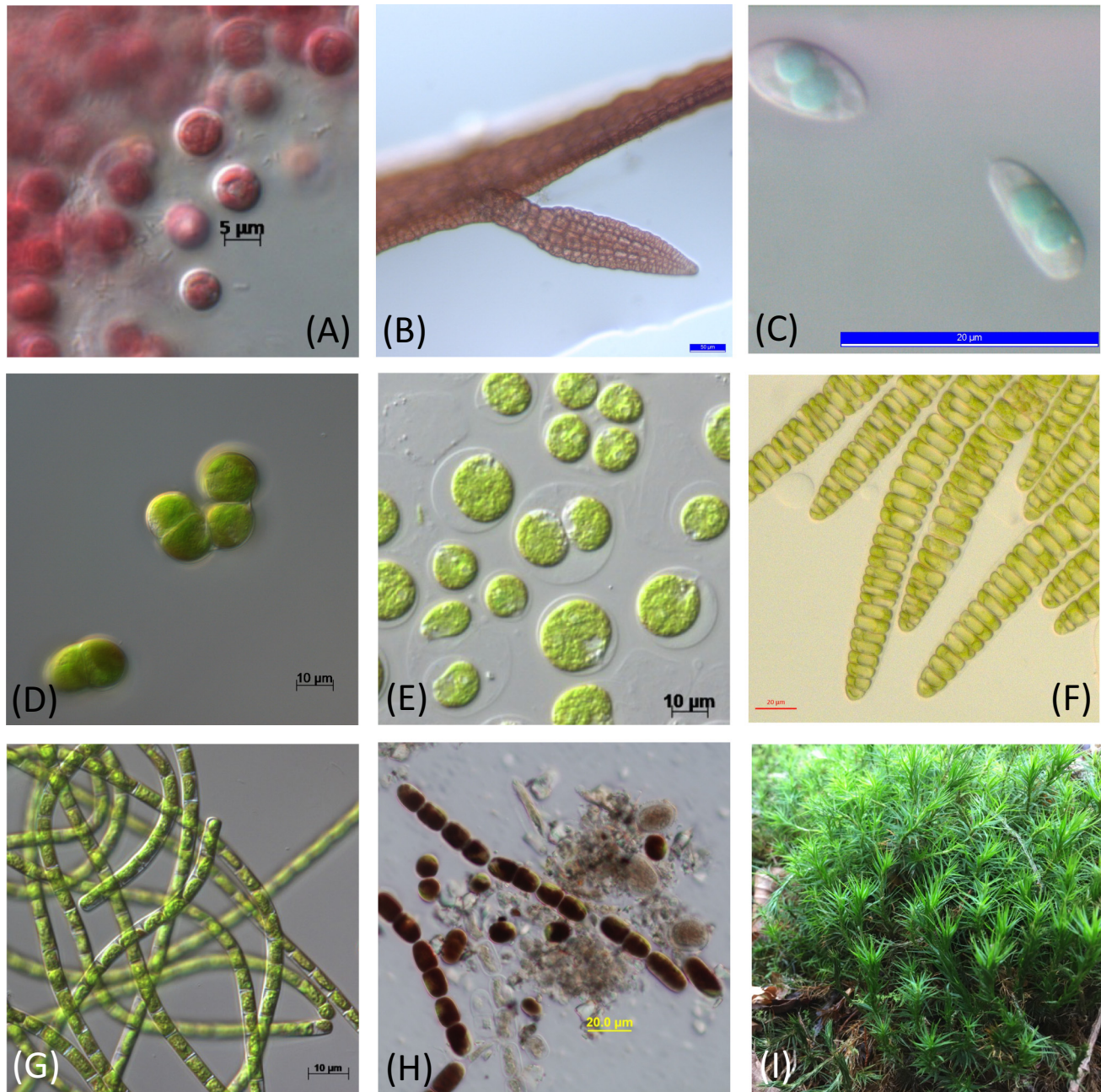
Phagotrophic: an organism capable of the engulfment of cells or particles.

Photoautotroph: photosynthetic organism that uses light energy to synthesise organic molecules from inorganic components through photosynthesis.

Phragmoplast: a cytoplasmic structure that forms at the centre of the spindle during the later stages of plant mitosis.

Phylogenomics: analysis of the evolutionary relationships between organisms using large-scale data from sequenced genomes and transcriptomes.

Plasmodesmata: microscopic channels between plant cell walls that enable direct cytoplasmic cell-to-cell communication and nutrient transport.



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Figure 1. The diversity of living plants. Examples of rhodophytes: (A) *Erythrolobus madagascarensis* (Porphyridiophyceae) and (B) *Hypoglossum sabahense* (Florideophyceae). Glaucophytes: (C) *Cyanophora paradoxa*. Chlorophytes: (D) *Leptosira obovata* (Trebouxiophyceae), (E) *Gonium pectorale* (Chlorophyceae), and (F) *Capsosiphon* sp. (Ulvophyceae). Streptophytes: (G) *Klebsormidium fluitans* (Klebsormidiophyceae), (H) *Mesotaenium berggrenii* and *Ancydonema nordenskiöldii* (Zygnematophyceae), and (I) *Polytrichum formosum* (Embryophyta). Images A–G courtesy of the Culture Collection of Algae and Protozoa (CCAP).

ancestor of rhodophytes and Archaeplastida [24]. This challenges traditional views on the nature of the plant ancestor, and provides a mechanistic hypothesis for the endosymbiotic origin of Archaeplastida. In this scenario, a partially phagotrophic lifestyle is a prerequisite for the

Box 1. Major groups of Archaeplastida

Archaeplastida is a highly diverse group that comprises an estimated 450 000–500 000 species (see [Figure 1](#) in main text) [151–154]. There are six distinct groups of Archaeplastida: the rhodophytes, glaucophytes, prasinodermatophytes, chlorophytes, paraphyletic charophytes, and the embryophytes (land plants) [3,22]. The rhodophytes comprise a **monophyletic** group consisting of ~6500 predominantly photoautotrophic species [58] which inhabit a diverse range of habitats [57]. The glaucophytes are a small group of freshwater unicellular algae that comprises 14 known species [155]. Viridiplantae (green plants) is a subgroup of the Archaeplastida and consists of three clades: Prasinodermatophyta, Chlorophyta, and Streptophyta [26]. Chlorophytes are monophyletic, and include ~8000 described species that display a diversity of adaptations, morphologies, and life histories [156]. Within the chlorophytes are the core chlorophytes (Trebouxiophyceae, Ulvophyceae, and Chlorophyceae) [11]. Streptophyta consist of the paraphyletic charophytes and embryophytes (see [Figure 2](#) in main text). Over 6000 charophyte species have been described, with Zygnematophyceae recognised as the most species-rich group [156]. The charophyte algae consist of six divergent lineages: the Mesostigmato-, Chlorokybo-, Klebsormidio-, Charo-, Coleochaeto-, and Zygnematophyceae (see [Figure 2](#) in main text). The embryophytes encompass the remaining plants that live on land: an estimated 450 000 species [151,157].

There are several phylogenetically nested definitions of plants in the scientific community [158]. Some consider that Embryophyta represent the plant kingdom, and that streptophytes and chlorophytes are algal outgroups. Others consider Streptophyta to be the most informative grouping of the plant kingdom. A third classification of plants is Viridiplantae, a grouping that includes all chlorophytes and streptophytes. The broadest definition of the plant kingdom is Archaeplastida that incorporates the rhodophytes, glaucophytes, and Viridiplantae [3,158]. Here, we use this broad definition of plants (Archaeplastida) and consider their early evolution.

endosymbiotic engulfment of a cyanobacterium and, when photoautotrophy became advantageous for acquiring nutrients and energy, phagotrophy was later lost. As mentioned, this endosymbiotic origin of the primary plastid is the main shared innovation of Archaeplastida.

The nuclear and plastid genomes of the ancestral archaeplastid were large and gene-rich [52] compared to the small genomes of rhodophytes, suggesting large-scale genome reduction with the early origin of red algae [24,53,54]. Subsequently, two cycles of genome reduction

Box 2. Endosymbiosis during early plant evolution

The internalisation of a prokaryote into a eukaryote is a rare phenomenon in evolution [159]. Indeed, only a few instances of very long-lived integrations have been identified, including the origin of the rhizarian amoeba, *Paulinella chromatophora*, and the origin of Archaeplastida that is characterised by primary endosymbiosis of an ancestral eukaryote engulfing an ancestral cyanobacterium [160,161]. The cyanobacterial symbiont evolved to become the lineage of plastids in extant plants (e.g., chloroplasts), thus enabling the evolution of the first photosynthetic eukaryotes. Based on phylogenomic evidence, archaeplastid plastids emerged from deep branching cyanobacteria, with the closest living relative identified as *Gloeomargarita lithophora* [7,162].

Subsequent symbiotic events involving descendants of this archaeplastid ancestor led to the spread of organelles throughout the tree of life. Secondary endosymbiosis of a red algal ancestor led to the donation of plastids to various eukaryotic groups, including haptophytes, cryophytes, dinoflagellates, and stramenopiles, which are dominant primary producers [60,108,163]. Secondary endosymbiosis has also taken place with a chlorophyte ancestor, leading to the origin of the Euglenophyta and Chlorarachniophyta [164]. In turn, tertiary, and even quaternary, endosymbioses have occurred from secondary red algae-derived endosymbionts (e.g., stramenopiles) [161].

During the early stages of endosymbiosis, the ancestral cyanobacterium and the eukaryotic host cell became physically and genomically integrated [165]. The early evolution of Archaeplastida is characterised by plastid gene loss, leading to greater metabolic unification between host and symbiont: for example, glycogen synthase genes present in free-living cyanobacteria are absent in plastids [160]. The eukaryote host also gained control of the expression of plastid genes with functions in photosynthesis and redox signalling [166]. Curiously, the genome of Picozoa, a heterotrophic eukaryote identified as the sister group to red algae that lack a plastid, shows no remnants of plastid-encoding genes [25]. This would suggest either the first instance of complete loss of a plastid or that the plastids of red algae have an origin different from that of other Archaeplastida. Further comparative genomics will be necessary to resolve the details of the endosymbiotic origin and evolution of Archaeplastida.

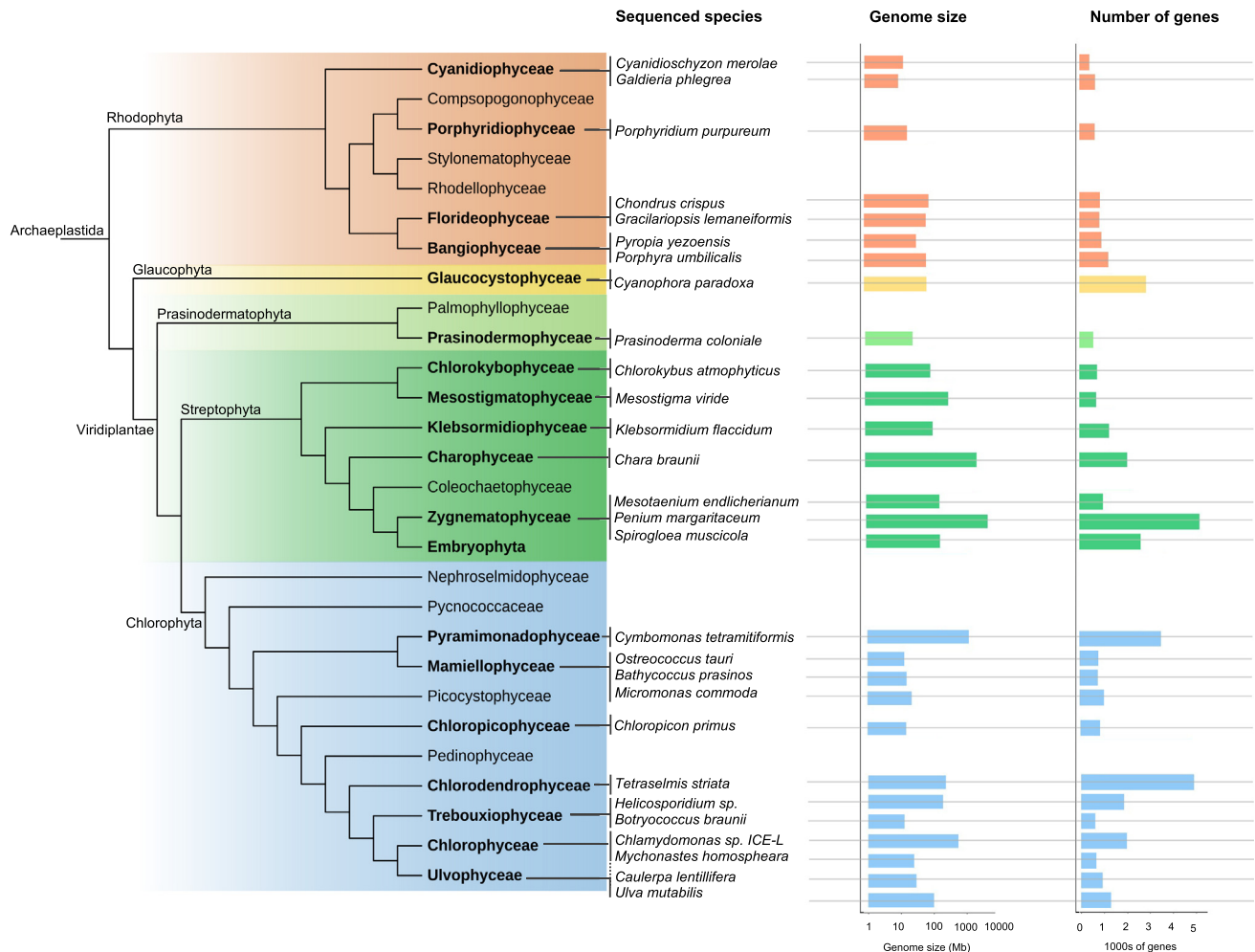


Figure 2. Phylogeny of early plant evolution with a selection of available genomic resources. The phylogeny is based on the latest literature [3,22,182]. Lineages are specified to class where appropriate. Lineages are in bold if genomic resources are publicly available. Genomes were selected to demonstrate the diversity of genome size within each class. Genome sizes and the number of protein-coding genes were sourced from [8,22,26,31,38,40,42,53,57,59,60,62,67,69,70,75,76,78,79,83,87,183–185].

have been identified leading to high gene loss [53,55] that has been linked to adaptation to extreme environments. Within red algae, larger genomes are linked to multicellularity, accompanied by an expansion of zinc-finger transcription factor families [56] and transposable elements [55]. Genome sizes, however, remain small compared to the genomes of Viridiplantae [55,56] (Figure 2). Furthermore, comparative genomics has revealed that rhodophytes lack **cytoskeleton** development genes present in other multicellular lineages [57], suggesting independent origins of multicellularity. Within the red algae, horizontal gene transfer has been identified as a common mechanism for obtaining novel genetic material [58–60], based on comparative genomic and phylogenetic analyses. These genes are part of key pathways (e.g., autophagy regulation and maltose biosynthesis), suggesting that prokaryote genes shaped the evolution of rhodophytes following widespread genome reduction [58].

Supporting inferences from morphology [61], genome analysis of red algae finds evidence for a lack of both flagella and centrioles which are found in many other eukaryotic cells [53].

Genetic analysis of red algae revealed genes involved in synthesising floridean starch (cytosol) [62,63], in contrast to the starch found in green plants [64]. Other shared characters of most red algae include pit connections, pit plugs, and unstacked thylakoid membranes to capture light energy [61]. Transcriptome analysis identified genes involved in lutein biosynthesis, which plays a role in protecting the photosynthetic machinery in the thylakoid membranes [65].

Within the revised phylogenetic framework, Prasinodermatophyta becomes critical to understanding the origin of green plants. Genomic evidence from *P. coloniale* suggests that the genome of the green plant ancestor was intermediate in size – between the small compact genomes of chlorophytes and the larger, complex genomes of streptophytes [22]. As this species is highly derived, its extant genome size does not necessarily represent an ancestral state. Bearing in mind this caveat, chlorophytes may be characterised by genome size reduction, similar to rhodophytes. The gene content of green plants also exhibits varied patterns. The origin of Viridiplantae is marked by the development of complex cell walls, which were the product of novel genes functioning in cellulose and starch biosynthesis [3,22,66]. These innovations allowed early green plants to colonise new environments through enhanced cellular protection. These broad patterns of genome evolution were echoed in the One Thousand Plant Transcriptome initiative which found high gene birth with the origin of Viridiplantae and elevated gene family expansion with the origin of streptophytes and embryophytes [3].

The early radiation of the chlorophytes led to a group of organisms rich in both genomic and morphological diversity. Analysis of prasinophyte genomes revealed that early diverging chlorophyte genomes remained small in size [38,67–70], whereas the genomes of core chlorophytes expanded greatly [71–74] (Figure 2). Genome analysis has begun to reveal the mechanisms behind the independent origins of multicellularity [75–78]. This transition, accompanied by an increase in organismal size, was made through the co-option of the retinoblastoma cell cycle pathway in the case of *Gonium pectorale* [71] by lineage-specific protein modification in *Volvox carteri* [72] and gene family expansions in *Ulva mutabilis* [76]. Originating in marine environments as planktonic unicellular algae, chlorophytes have evolved diverse adaptations, accompanied by their genomic underpinnings, including adaptations to extreme cold [73,79], as pathogens [80], and as lichen-forming [81] and coral symbionts [82].

The transition to terrestrial environments was a pivotal event in plant evolutionary history but how this was achieved was uncertain until recently [78]. Analyses of streptophyte genomes are revealing that terrestrialisation was preceded by innovations thought to be land plant-specific, suggesting that streptophyte algal ancestors were co-opted for life on land [31,66,78,83–85]. Genome analysis of streptophyte algae shows gene family expansions linked to plant–pathogen interactions and stress tolerance (e.g., desiccation) [31,83]. Innovations identified in the ancestor of Phragmoplastophyta include a **phragmoplast** and branching. However, other key land plant innovations evolved later, including a multicellular sporophyte, cuticle, fungal symbioses, and embryogenesis [78]. The proximity of fungal and bacterial symbionts to ancestral streptophytes led to widespread horizontal gene transfer, as identified by recent comparative analysis [86]. Functionally, these genes related to biotic stresses in the form of pathogen and fungal resistance, abiotic stresses in the form of dehydration and salinity tolerance, and specialised metabolism of UV-protective pigmentation, as well as biosynthesis of the phytohormones, auxin, cytokinin, and abscisic acid. Similar to rhodophytes, this analysis demonstrates the importance of fungi and bacteria during early plant evolution. Zygnematophyceae genomes are characterised by the gain and expansion of gene families linked to phytohormone signalling, cell-wall biosynthesis, and flavonoid compounds for UV protection [26,78,87,88]. Since the

divergence of Zygnematophyceae, gene and trait loss has occurred, highlighted by their simple body plans [78].

Vestiges of archaeplastid evolution from the fossil record

Interpreting the fossil record of early archaeplastids is challenging because the fossil remains of unicellular archaeplastid algae are not diagnostic and even multicellular archaeplastid algae can be difficult to discriminate from filamentous cyanobacteria. Furthermore, multicellularity has evolved multiple times independently (Box 3), making it difficult to distinguish convergence. Nevertheless, renewed interest in early eukaryote evolution has led to a flurry of new reports of ancient archaeplastid fossils, as well as reanalyses of old records.

Among the earliest possible claims of archaeplastid affinity is sausage-shaped *Grypania* (Figure 3A) that reached several tens of millimetres in length [89]. The oldest occurrences are from the Palaeoproterozoic (1874 Ma \pm 9 Myr) of Michigan, USA [89], based principally on their large size, although a cyanobacterial affinity is difficult to reject [90]. Cysts from the late Palaeoproterozoic–early Mesoproterozoic (1766–1381 Ma) of Shanxi Province, North China [91], have been interpreted as unicellular chlorophytes but, although many of these have a credible claim to eukaryote affinity, it is difficult to determine whether they belong to the eukaryote crown or stem. The putative rhodophytes *Rafatazmia chitrakootensis* (Figure 3B,C) and *Ramathallus lobatus* (Figure 3D,E) from the earliest Mesoproterozoic of India [92] are both multicellular, but *R. chitrakootia* has the strongest claim, based largely on the presence of pit plugs – although taphonomy experiments suggest that these may be diagenetic artefacts [93]. *Tawuia* has been interpreted as a coenocytic macroalga, known from records as old as 1.6 Ga [94], although even its eukaryote affinity is uncertain. Decimetre scale carbonaceous impressions from the (probably) earliest Mesoproterozoic (1.631–1.555 Ga) of Hebei Province, North China [95], have been attributed to Archaeplastida, based principally on their large size; this logic is sound but these fossils do not exhibit any diagnostic archaeplastid characteristics. *Arctacellularia tetragonala* (Figure 3F) from the latest Mesoproterozoic–earliest Neoproterozoic (1030–950 Ma) of the Congo Basin [96] preserves molecular residues of chlorophyll and has been attributed to Archaeplastida, although it is difficult

Box 3. Convergent evolution of multicellularity in plants

The early evolution of plant groups is characterised by multiple independent transitions to macroscopic and multicellular organisation [167]. Red algal morphology ranges from the unicellular class, Cyanidiophyceae [60], to branched multicellular species, while chlorophyte morphology spans unicellular organisms (e.g., *Ostreococcus tauri* [67]) to colonial (e.g., *V. carteri*, [72]) and multicellular algae (e.g., *U. mutabilis*, [76]). Streptophytes form six morphologically distinct groups: single-celled Mesostigmatales [122], sarcinoid Chlorokybales [31], filamentous Klebsormidiales [83], multicellular 3D Charales [78], multicellular 2D Coleochaetales, and filamentous Zygnematales [26]. The origins of multicellularity were advantageous because they allowed ancestral plants to occupy new adaptive niches, form new relationships with their environment, and avoid predation from microscopic predators (e.g., rotifers) [168].

Although multicellularity has emerged multiple times, distinct multicellular lifestyles differ in their developmental traits and mechanisms [118,169]. For example, macroscopic chlorophytes are characterised by cytomorphological traits including siphonous, siphonocladous, and multicellular forms [11]. The molecular mechanisms underpinning these traits are only beginning to be understood. Experimental analysis demonstrated that the *de novo* origin of multicellularity in *C. reinhardtii* was engineered through changes in the expression of genes linked to cell cycle and reproductive processes [168]. This adaptation was the product of lineage-specific gene expression, suggesting an independent origin as opposed to a mechanism shared with land plants. Recent analysis found that multicellular streptophytes may be associated with the origin of four groups of small RNAs that are involved in post-transcriptional regulation of genes linked to multicellularity and stress responses [170]. Within land plants, the activation of ROP GTPases in mosses enabled the development of 2D and 3D multicellularity [171]. With additional genomic resources and expression atlases from across the early plant tree of life, further patterns of gene family expansion and lineage-specific gene expression can be illuminated. Indeed, understanding the molecular basis for the independent origins of multicellularity is a major question in early plant evolution and may shed light on the origin of embryophytes as the dominant flora of terrestrial environments.



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Figure 3. Fossils of possible and probable early archaeplastids. (A) *Grypania spiralis* from the ~1.6 Ga Rohtas Formation, Semri Group, Vindhyan Supergroup, central India. (B,C) *Rafatazmia chitrakootensis*, described as a rhodophyte from the ~1.6 Ga Tiohan Dolomite, also from the Semri Group. (D,E) *Ramathallus lobatus*, described as a rhodophyte also from the Tiohan Dolomite. (F) *Arctacellularia tetragonala*, described as a phototrophic eukaryote preserving chemical remnants of chlorophyll, from the ~1 Ga BII Group, Mbuji-Mayi Supergroup of the Congo Basin, Democratic Republic of Congo. (G,H) *Bangiomorpha pubescens*, a rhodophyte from the 1.047 Ga Hunting, Angmaat, and Nanisivik formations of the Uluksan Group, Somerset and Baffin islands, northeastern Canada. (I) *Proterocladus antiquus*, a chlorophyte from the ~1 Ga Nanfen Formation of North China. (J) *Cooksonia pertoni*, an early vascular plant from the late Silurian of Wales. Image (A) courtesy of Bruce Runnegar (Los Angeles); (B–E) courtesy of Stefan Bengtson (Stockholm); (F) courtesy of Marie Catherine Sforna (Liege); (G,H) courtesy of Nick Butterfield (Cambridge); (I) courtesy of Shuhai Xiao (Virginia); and (J) courtesy of Dianne Edwards (Cardiff).

to reject a cyanobacterial affinity. There are also reports of so far unnamed multicellular (possible) chlorophytes from the earliest Neoproterozoic (950–830 Ma) of northwestern Canada [97]. None of these can be interpreted unequivocally as early records of Archaeplastida but, conversely, neither can many of them be rejected unequivocally as early members of this clade. The abundance of claims from around the Mesoproterozoic–Neoproterozoic transition may therefore be informative.

The oldest convincing records of Archaeplastida, *Bangiomorpha pubescens* (Figure 3G,H) and *Proterocladus antiquus* (Figure 3I), are of this age. *P. antiquus* from the (probably) earliest Neoproterozoic (1078–940 Ma) of Liaoning, North China [98], is known from branching multicellular thalli with a differentiated holdfast. It exhibits a strong similarity to siphonocladalean green algae [98], but it is difficult to exclude the possibility that such simple anatomy is convergent. As such, it is more securely interpreted as a total-group chlorophyte. *B. pubescens* from the latest Mesoproterozoic of Arctic Canada is similarly well characterised anatomically, known from a multicellular holdfast, filaments comprised of radially arranged cells, intercalary cell division growth (Figure 3G), and sexual dimorphism (evidenced by reproductive spores; Figure 3H) [99]. *B. pubescens* compares favourably to extant *Bangia*, but its characteristics are shared primitive features of rhodophytes and, as such, it is most securely interpreted as a total-group rhodophyte [100]. Nevertheless, with a minimum age of 1030 Ma [101], this makes *B. pubescens* the oldest unequivocal record of crown-Archaeplastida.

Setting aside *A. tetragonala*, algal biomarkers (molecular fossils of membrane lipids) do not commonly occur in the geologic record until the late Cryogenian, and this has been interpreted as evidence that photosynthetic eukaryotes did not rise to dominance over bacterial primary producers until 659–645 Ma [13]. However, this may be an artefact of preservation [94], given a record of macroscopic archaeplastid algae that extends throughout the Neoproterozoic [102]. Otherwise, the Ediacaran Weng'an biota of South China has been interpreted to record a diversity of rhodophytes preserved to a cellular level of resolution, all attributed to stem-Corallinales and, therefore, to crown-Florideophyta and -Rhodophyta [103]. However, none preserve key diagnostic features such as carpogonia, and so they are best assigned to total-group rhodophytes. Unequivocal records of land plants do not occur until the Silurian (Figure 3J). Thus, while the fossil record demonstrates origination of Archaeplastida, Rhodophyta, and (perhaps crown-) Viridiplantae before the Neoproterozoic, we must combine fossil and molecular evidence to obtain a better estimate of the timescale of early plant evolution.

Timescale of early plant evolution

Inferring the timescale of early plant evolution is crucial for understanding the environmental context of plant evolution, the coevolution of fungi, bacteria, and animals [12,13,104], and transformations in biogeochemical and atmospheric cycles [4,105]. Surprisingly few attempts have been made to date the deep divergences in plant evolution [12,100,106–110], and these differ as much in their estimated timescales as in the methodological approaches they employ (Figure 4). In large part, this occurs because of the challenge of interpreting the fossil record to provide calibrations for molecular clock analyses. For example, many studies have followed the optimistic interpretations of the fossil record, employing *Bangiomorpha* to calibrate Bangiophyta and *Proterocladus* to calibrate stem- or crown-Ulvophyceae [111]. Inevitably, molecular clock analyses calibrated in this way will result in evolutionary timescales that are older overall than if *Bangiomorpha* and *Proterocladus* are instead employed to calibrate the total-group Rhodophyta and Chlorophyta, respectively. Conversely, some recent analyses have eschewed robust evidence constraining the age of embryophytes [107,109,112], resulting in an estimated Proterozoic origin of crown-embryophytes and concomitantly older ages for Streptophyta, Viridiplantae, and Archaeplastida. This is because they reject geologic evidence for maximum constraints on the age of clades. However, the evidence for a Phanerozoic origin of crown-embryophytes is overwhelming [106,107,113–115]. Systematic biostratigraphic sampling for marine archaeplastid algal cysts in Cambrian and Ediacaran rocks has shown that land plant-like spores do not co-occur before the mid-Cambrian. This is informative because algal cysts and land plant spores have a similar composition and fossil preservation; before the middle Cambrian, these commonly

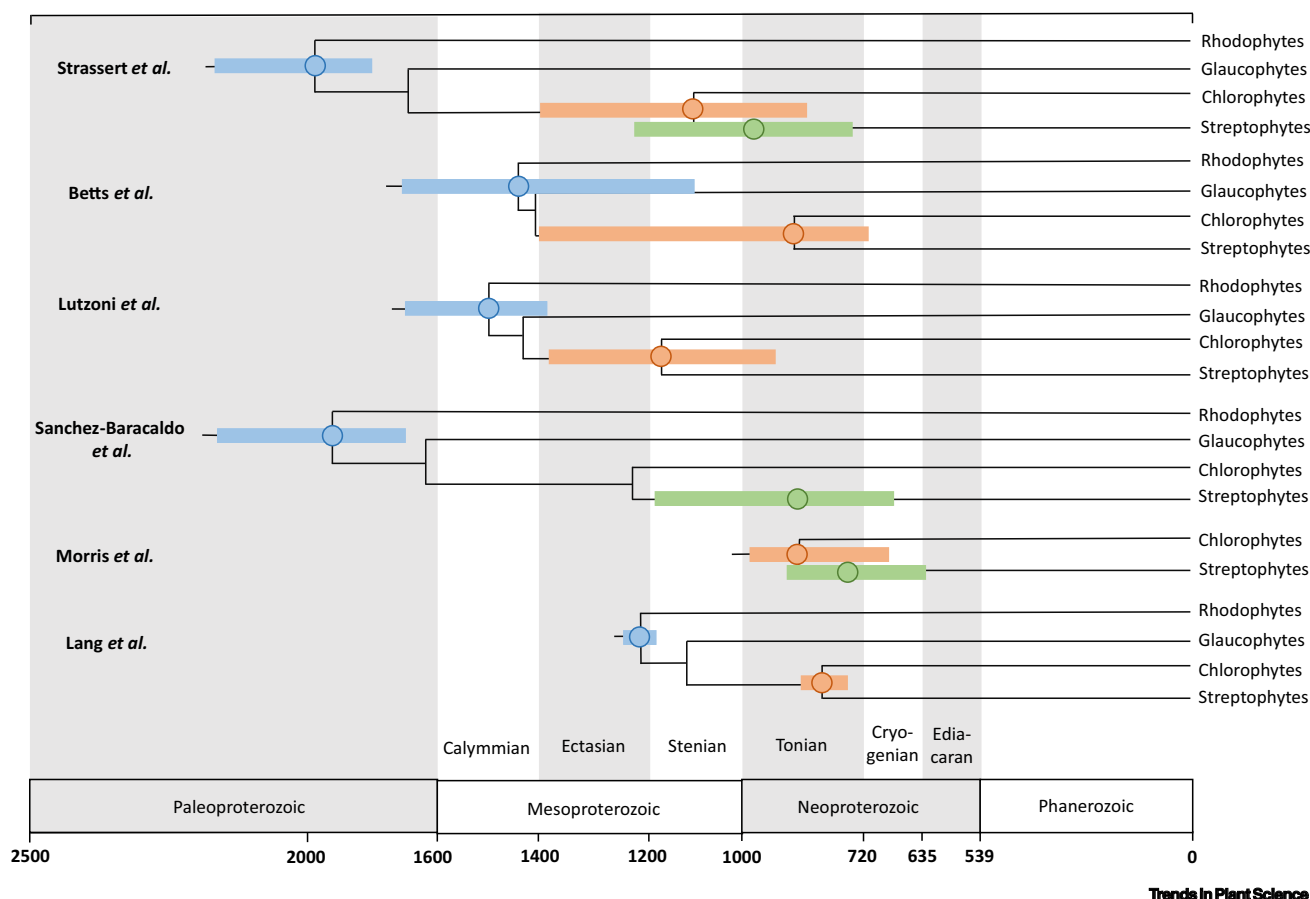


Figure 4. Summary of molecular estimates for the timescale of archaeplastid evolution. Dates at the bottom of the figure refer to millions of years ago. Blue bars highlight divergence time estimates for the ancestor of Archaeplastida. Orange bars highlight divergence time estimates for the ancestor of Viridiplantae. Green bars highlight divergence time estimates for the ancestor of Streptophyta. Data from Betts *et al.* [100], Lang *et al.* [110], Lutzoni *et al.* [12], Morris *et al.* [106], Sánchez-Baracaldo *et al.* [116], and Strassert *et al.* [108].

co-occur in marine sedimentary sequences after river transport of land plant spores to sea basins. The presence of archaeplastid algal cysts demonstrates the right preservational conditions for land plant spores; they do not occur because they had not yet evolved [106].

Molecular dating has navigated these challenges, as well as others, including modelling variation in the rate of molecular evolution between evolutionary lineages, to estimate Archaeplastida to have originated in a middle Palaeoproterozoic to early Mesoproterozoic interval (2137–1807 Ma [108], 1667–1118 Ma [100], 1650–1390 Ma [12], 2117–1694 Ma [116], and 1231–1198 Ma [110]; Figure 4). Viridiplantae are estimated to have emerged between the middle Mesoproterozoic to middle Neoproterozoic era (972.4–669.9 Ma [106], 1400–850 Ma [108], 1200–700 Ma [100], 822–775 Ma [110]). The first streptophytes originated during the middle Mesoproterozoic to late Neoproterozoic era (890.9–629.1 Ma [106], 1340–910 Ma [12], 1250–750 Ma [108], 1180–663 Ma [116]), with crown-embryophytes emerging during a middle Cambrian to earliest Ordovician interval [14,106]. Although these analyses represent the most comprehensive attempts to date the early plant phylogeny, additional molecular data and new fossil calibrations will further constrain their divergence times.

Physiology and evolutionary development

The morphology and physiology of ancestral plants has been difficult to discern because of the paucity of fossil evidence and the general difficulty in interpreting it. Through experimental studies and ancestral state reconstruction based on extant taxa, the evolutionary adaptations of early plants are being illuminated.

The morphological diversity of rhodophytes spans unicellular (e.g., Cyanidiophyceae [60]) to large, complex species (e.g., Bangiales [117]), but the ancestral nature has been unclear. Ancestral state reconstruction infers that the ancestor of red algae and Archaeplastida was unicellular [11,118,119]. Comparative genomics has revealed that key adaptations were shared among all red algae, including pigmentation by phycobiliproteins, chlorophyll *a* used to capture light energy, and a lack of cytoskeletal structures linked to motility [58,120]. Glaucophytes also have plastids containing phycobiliproteins and chlorophyll *a*, as well as flagellae that enable motility [8].

Transcriptome analysis has revealed that the origin of Viridiplantae was marked by the loss of phycobiliproteins and the gain of the photosynthetic pigment chlorophyll *b*, thus enabling a greater absorption of light compared to older ancestors [3]. Ancestral state reconstruction has revealed that the ancestor of Viridiplantae was likely unicellular and emerged in a freshwater planktonic habitat [11,28]. Physiological and gene expression analysis revealed that high-light stress responses appeared in the ancestor of Viridiplantae through changes to plastid protein import, thus potentially aiding a planktonic lifestyle [121].

Morphological studies demonstrate a diverse array of cellular organisations in the streptophytes [26,31,78,83,122] where the ancestor was most likely multicellular [11]. This diversity is reflected in their adaptations to water availability, with streptophytes found in brackish, freshwater, terrestrial, icy, and subaerial habitats [123,124]. The cell walls of Streptophyta consist of novel polymers (e.g., xylans) that provide structural and functional integrity (Box 4) [125,126]. Filamentous growth

Box 4. Cell walls

The development of different cell-wall types and structures would have enabled early plants to adapt to different environmental pressures, including protection against UV radiation, reduction of water loss, and protection against predation and pathogens [172]. Plant cell walls are composed of a complex network of polysaccharide polymers such as cellulose and hemicellulose [173]. Four distinct structural groups of hemicelluloses have been identified: β -glucans, mannans, xylans, and xyloglucans [173]. Additional cell-wall polymers such as pectin and lignin are found in land plants [174]. Lignin has also been found in the red alga, *Calliarthron cheilosporioides* [175], although this has most likely evolved convergently [176]. Each of these polymers emerged at different points during early plant evolution, and influenced the composition and function of ancestral plant groups.

The biosynthesis of these different polymers requires distinct genetic pathways. By understanding the evolution of these biosynthetic pathways, we can begin to infer the evolution of plant cell walls. Cellulose is present in all Archaeplastida [177], although the genetic mechanisms by which it is synthesised have changed over the course of early plant evolution. *KORRIGAN*, *STELLO*, *KOBITO*, and *CTL1* genes are present in the ancestor of Viridiplantae, whereas additions to the cellulose synthesis pathway appear in the ancestor of Klebsormidiaceae and Phragmoplastophyta, as well as in the ancestor of Zygnematophyceae and land plants [178]. In this analysis, a single species was used to represent the Mesostigmataceae and red algae, so the complete evolution of the cellulose synthesis genetic toolkit remains unclear. Analysis of the *Porphyra umbilicalis* genome identified two glycosyltransferase genes similar to the cellulose synthase-like genes of Viridiplantae [57]. These are involved in mannan biosynthesis, suggesting a common origin of mannans in the ancestor of Archaeplastida. Moreover, Bangiophyceae have cellulose-based cell walls in their filamentous sporophytes, and the cell walls of Florideophyceae are composed of cellulose, which further supports an origin in the ancestor of Archaeplastida.

The biosynthesis of xyloglucan, a streptophyte innovation [125,179], is governed by xyloglucan endotransglucosylate/hydrolase (XTH). Recent phylogenomic analysis demonstrated that genes encoding XTH were transferred horizontally from fungi into ancestral streptophytes [180]. This event occurred during the glaciation events of the Cryogenian, and it is therefore hypothesised that they aided adaptations to icy environments. These and other modifications were important for the evolution of the cell wall of ancestral charophytes, and further changes occurred in the land plant ancestor [181].

emerged in the ancestor of Klebsormidiophyceae and Phragmoplastophyta [78]. Innovations of the ancestor of Phragmoplastophyta include **plasmodesmata** and apical cell growth, both at the tips and rhizoids [78]. With an anchoring system, streptophyte algal ancestors began to form symbiotic associations with fungi [127] and bacteria [26], thus aiding the transition to land. In the ancestor of Zygnematophyceae and land plants, the expansion of the genetic toolkit led to adaptations to terrestrial stressors including UV light irradiation, desiccation, and heat tolerance [26,87,88,128–131].

Implications for Earth system evolution

This new understanding of early plant evolution has important implications for how photosynthetic eukaryotes have coevolved with the Earth system (both affecting and being affected by it) (Figure 5).

Before Archaeplastida, cyanobacteria dominated **NPP**, including in microbial mats on land [132]. Terrestrial NPP may have approached ~25% of modern levels, but little would have escaped oxidation and contributed to organic carbon burial (the long-term oxygen source) [133]. Marine NPP supported an organic carbon burial flux of at least a quarter of today's value, and maintained an oxidising atmosphere with $pO_2 \geq 0.01$ PAL (present atmospheric level) [134] and oxygenated surface waters, but a largely anoxic deep ocean [135]. The biological carbon pump was likely less efficient (i.e., a smaller fraction of marine NPP burial), resulting in comparable ocean nutrient (phosphorus) levels to today [135–137], although others assume a much more efficient pump and much lower nutrient levels [138].

Entering this world, phagotrophic eukaryotes would have transformed ecology. By consuming cyanobacterial cells, they created a niche for larger photosynthetic cells (which are less efficient at diffusive nutrient uptake per unit volume) [139]. The mixotrophic ancestor of Archaeplastida could have competed with cyanobacteria even in low-nutrient surface waters (in the same way as mixotrophic algae do in the ocean gyres today) [136]. Marine NPP may not have changed much because early archaeplastid algae and cyanobacteria can achieve similar productivity (after all, the former contain the latter). However, the biological pump may have become more efficient, thus lowering ocean phosphorus levels – although the (sparse) biomarker record remains dominated by prokaryotes until the mid-Neoproterozoic [13].

From a freshwater origin, Viridiplantae could have adapted in two directions – to the saline ocean and to terrestrial mats. They had probably already originated by the Tonian Period in which archaeplastid algal biomarkers suggest that they surpassed red algae in terms of NPP, but prokaryotes remained dominant [13], and protistan predators created a further size-structured ecology [140]. A resulting increase in the efficiency of the biological pump could explain a change in phosphorus cycling and a possible rise in atmospheric pO_2 in the Tonian [136]. Early green plants entering microbial mats on land could explain the evidence for increased terrestrial NPP and weathering enhancement in the Tonian, especially if rhizoids had already evolved, and via streptophyte symbioses with fungi and bacteria. Enhanced weathering in turn potentially contributed to global cooling into the Cryogenian Period [135,141].

Viridiplantae were well adapted to the cryoconite meltwater ponds that would have formed on snowball Earth [142]. In addition, based on divergence time estimates and adaptations of extant glacier algae (i.e., to desiccation, high irradiance, and extreme temperatures), it has been proposed that streptophyte algae dominated surface ice environments of Cryogenian Snowball Earth [143]. Extant glacier algae produce dark pigmentation, which protects them

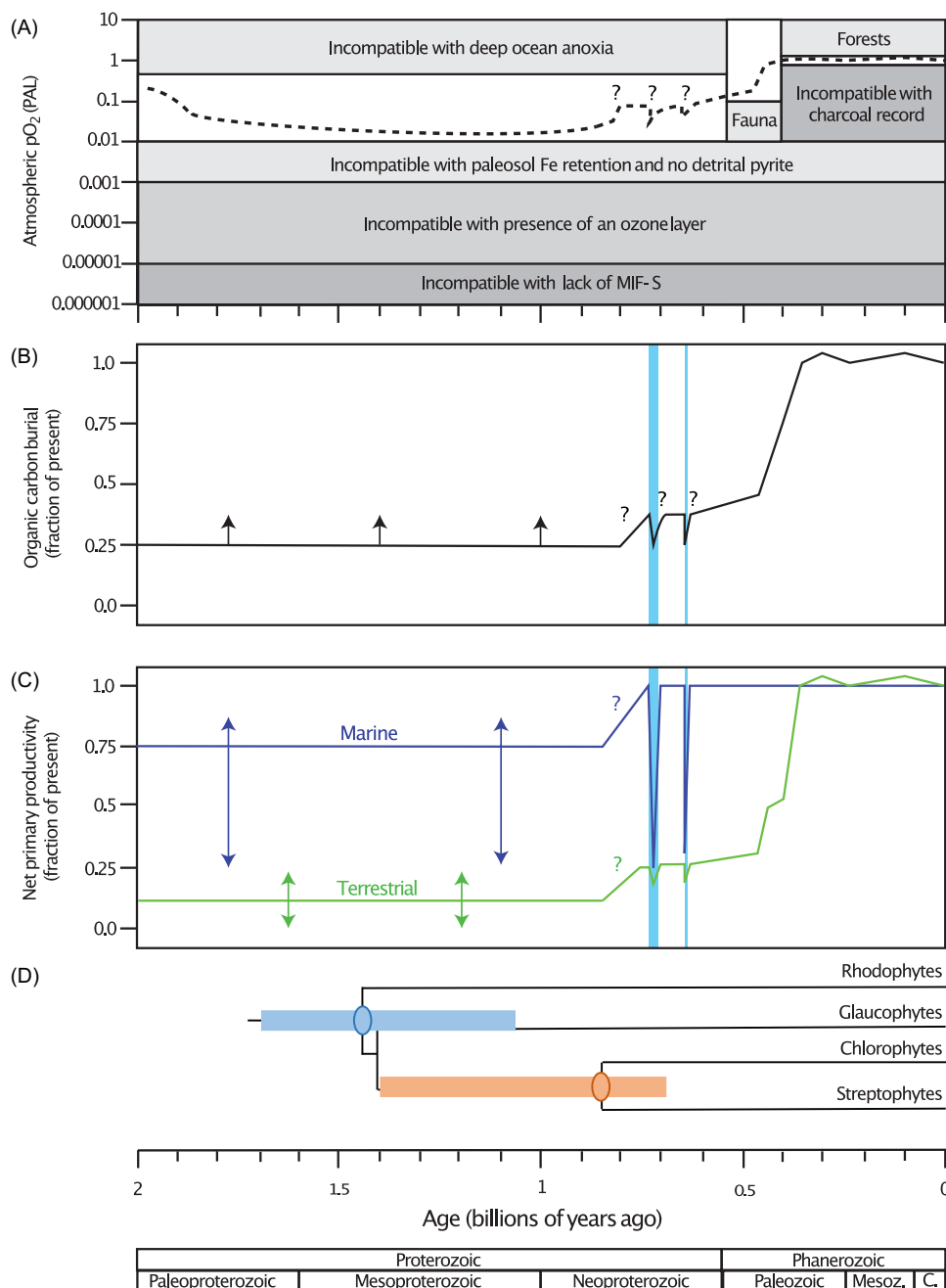


Figure 5. Coevolution of plants and the Earth system. A schematic, semi-quantitative reconstruction informed by data and modelling [4,105,134–137,186]; question marks denote particularly uncertain hypothesised changes. (A) Constraints on atmospheric oxygen (pO_2 ; PAL, present atmospheric level) together with a tentative reconstruction (broken line). (B) Total organic carbon burial flux (the long-term net source of pO_2) relative to the present. Upward arrows denote a lower limit (to maintain an oxidising atmosphere). Pale blue vertical bars denote snowball Earth intervals. (C) Net primary production (NPP) on land and in the ocean (each relative to present). Arrows pointing in both directions highlight considerable uncertainty in Proterozoic NPP. (D) Simplified phylogeny and timescale of archaeplastid evolution (based on Figure 4). Abbreviations: C., Cenozoic; Mesoz., Mesozoic; MIF-S, mass-independent fractionation of sulfur isotopes.

from exposure to high irradiance [123]. This adaptation may potentially have increased the melt rate of snowball Earth, thus facilitating the diversification of streptophyte algal lineages, particularly that of the ancestor of Zygnematophyceae and embryophytes. Exaptations of ancestral streptophytes to environmental stressors could therefore have been crucial for the transition to terrestrial habitats. Early archaeplastids may also have been key to oxygen production through the snowball Earth glaciations, as well as to transient ocean oxygenation events in their aftermaths. The subsequent Ediacaran Period was a time of repeated redox and carbon cycle oscillations – potentially an inherent property of an Earth system transitioning from low to high atmospheric pO_2 [144]. The contribution of early plants to organic carbon burial could have helped to maintain this transition.

Concluding remarks and future perspectives

Several barriers remain to a more complete understanding of early plant (Archaeplastida) evolution. These include genomic resources for phylogenetically informative but hitherto under-sampled lineages, including (but not limited to) glaucophytes, early diverging chlorophytes, and rhodophytes. These will elucidate the nature of ancestral Archaeplastida, Viridiplantae, and Streptophyta, and will highlight variation within early plant lineages. Model organisms will also be vital to establish the function of genes across early plant evolution and within younger plant ancestors. Existing model organisms have furnished many advances in our understanding of the genetic, physiological, and developmental diversity of early plants including *Penium margaritaceum* (Zygnematophyceae), *Chara braunii* (Charophyceae) [145], and *Chlamydomonas reinhardtii* (Chlorophyceae) [146]. The development of additional model systems, particularly those derived from within the chlorophytes and rhodophytes, promises to broaden our understanding of early plant evolution. With a well-resolved phylogeny, a refined timescale will contextualise inferences about the coevolution of early Archaeplastida and the Earth system. Analysis of genome data has provided many advances in our understanding of the evolution of Archaeplastida [23,53,57], Viridiplantae [22,67,69,70,72,74,76], and Streptophyta [26,31,78,83,87], but these analyses need to be considered in the context of fossil, physiology, and evolutionary developmental studies. Therefore, to capitalise on this abundance of data, a total evidence approach could provide powerful insights into early plant evolution by considering data sources from multiple disciplines (see Outstanding questions), as is becoming more widespread [31,76,79,128,147–150].

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Declaration of interests

No interests are declared.

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Outstanding questions

The precise nature of the endosymbiotic origin of the Archaeplastida remains enigmatic.

How commonplace is the transition to multicellular morphology in early plant lineages?

Are genes that share sequence homology functionally homologous across deep evolutionary timescales?

The timing of early plant diversification requires refinement.

Is lineage-specific reductive evolution masking the complexities of ancestral plants?

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