

Review

The origin and early evolution of plants

Alexander M.C. Bowles,^{1,2,*} Christopher J. Williamson,¹ Tom A. Williams,² Timothy M. Lenton,³ and Philip C.J. Donoghue^{2,*}

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].

¹School of Geographical Sciences, University of Bristol, University Road, Bristol BS8 1SS, UK

²Bristol Palaeobiology Group, School of Biological Sciences and School of Earth Sciences, Life Sciences Building, University of Bristol, Bristol BS8 1TQ, UK

³Global Systems Institute, University of Exeter, Laver Building, North Park Road, Exeter EX4 4QE, UK

*Correspondence: zl20161@bristol.ac.uk (A.M.C. Bowles) and phil.donoghue@bristol.ac.uk (P.C.J. Donoghue).



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.

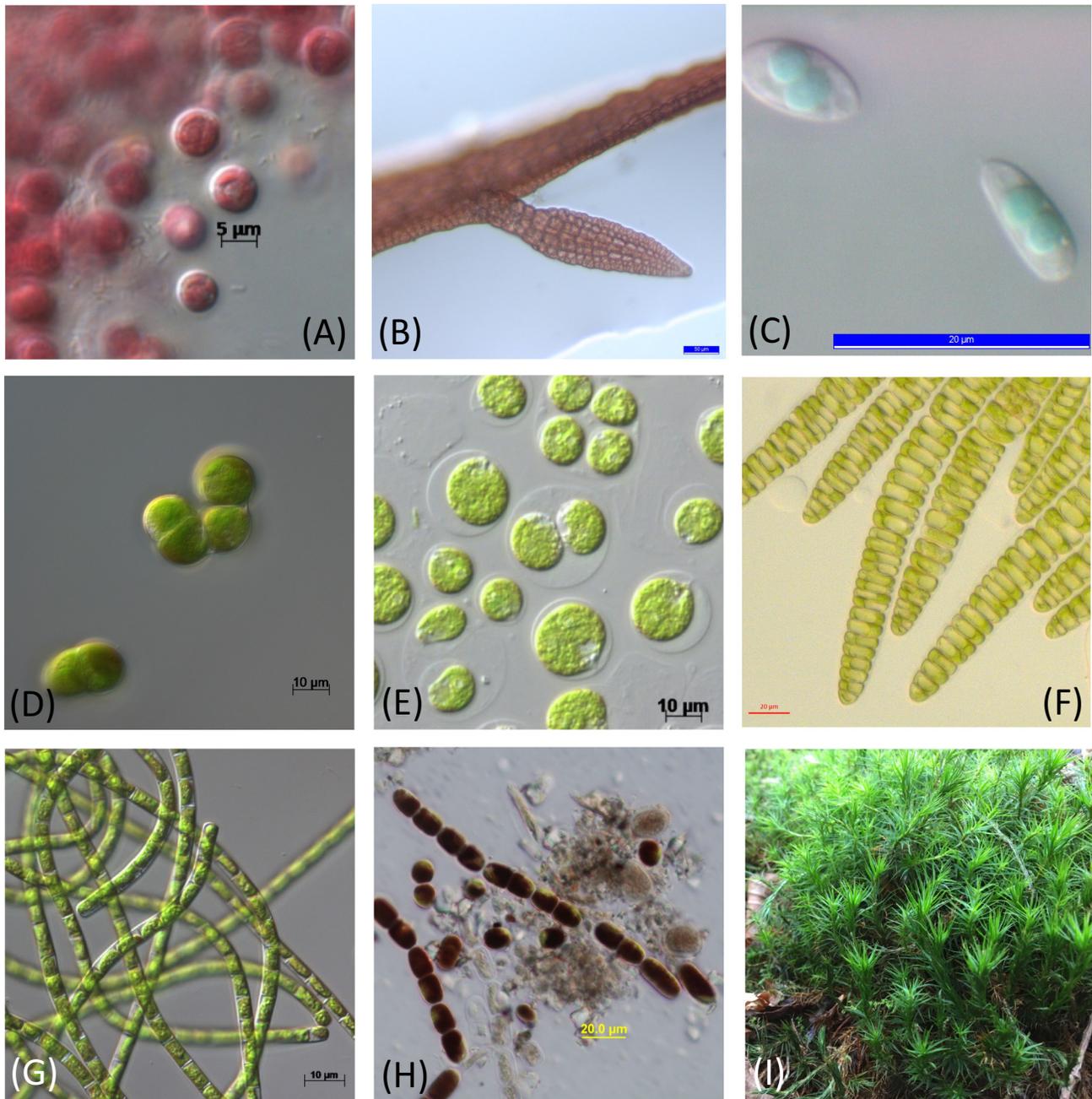
Phagotrophic: an organism capable of the engulfment of cells or particles.

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.



Trends in Plant Science

Figure 1. The diversity of living plants. Examples of rhodophytes: (A) *Erythrolobus madagascarens* (Porphyridiophyceae) and (B) *Hypoglossum sabahense* (Florideophyceae). Glaucophytes: (C) *Cyanophora paradoxa*. Chlorophytes: (D) *Leptosira obovata* (Trebouxiophyceae), (E) *Gonium pectorale* (Chlorophyceae), and (F) *Capsosiphon* sp. (Ulvoephyceae). Streptophytes: (G) *Klebsormidium fluitans* (Klebsormidiophyceae), (H) *Mesotaenium berggrenii* and *Ancylonema 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.

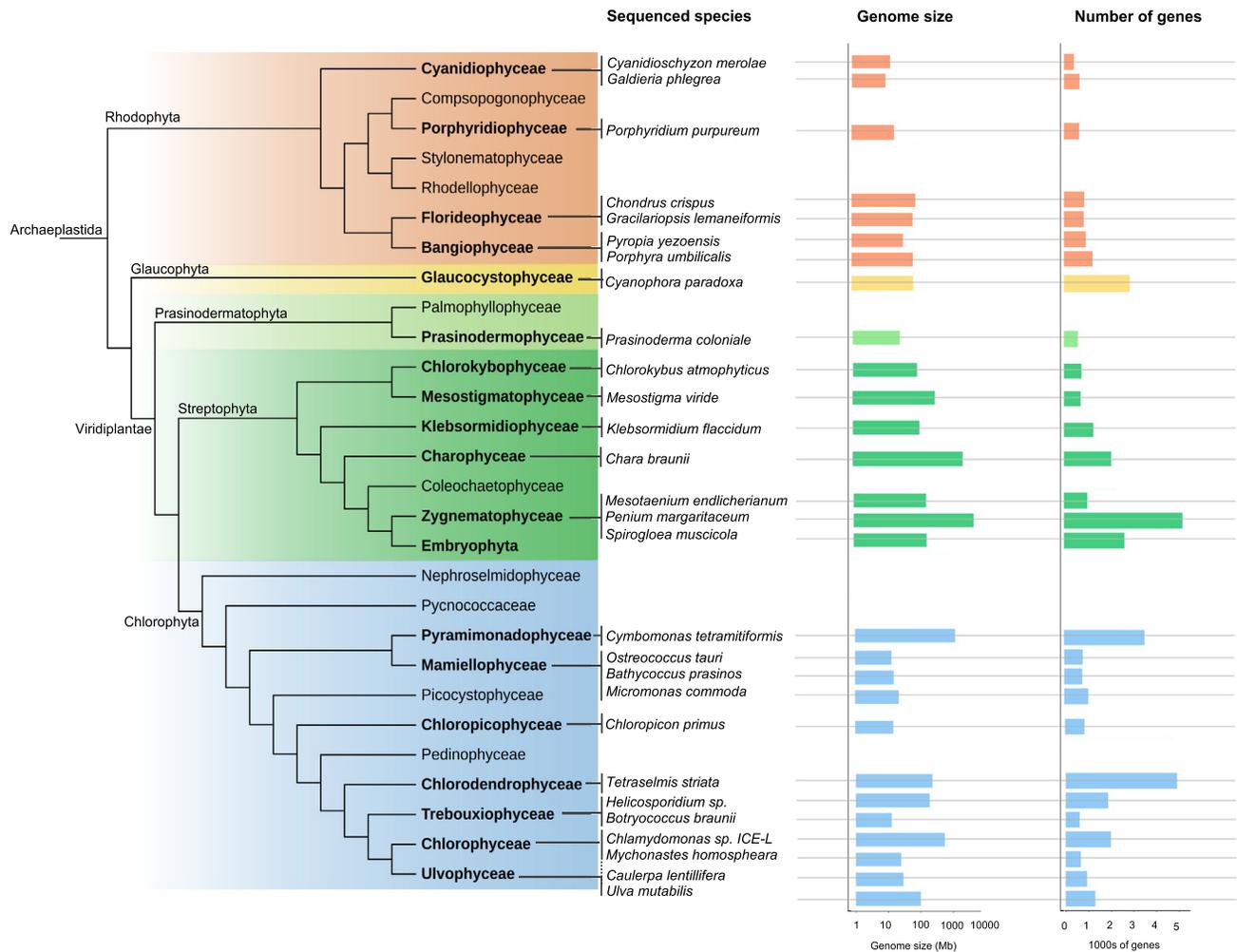
The nuclear and plastid genomes of the ancestral archaeplastid were large and gene-rich [52] compared to the small genomes of rhodophytes, suggesting large-scale genome reduction with the early origin of red algae [24,53,54]. Subsequently, two cycles of genome reduction

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.



Trends in Plant Science

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

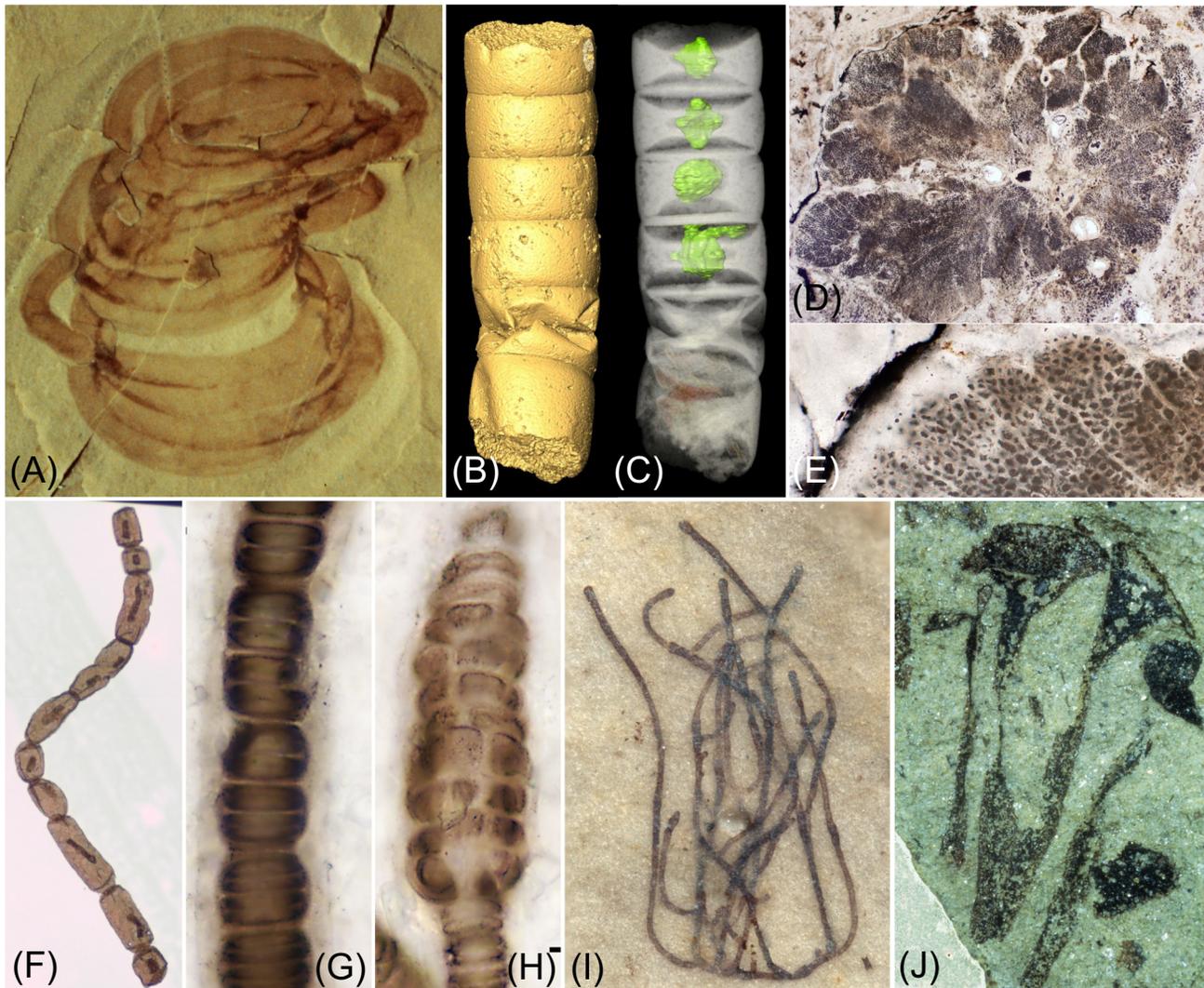
Interpreting the fossil record of early archaeplastids is challenging because the fossil remains of unicellular archaeplastid algae are not diagnostic and even multicellular archaeplastid algae can be difficult to discriminate from filamentous cyanobacteria. Furthermore, multicellularity has evolved 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 ± 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 Mesostigmales [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.



Trends in Plant Science

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) *Rafatzmia 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 Ulukhan 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

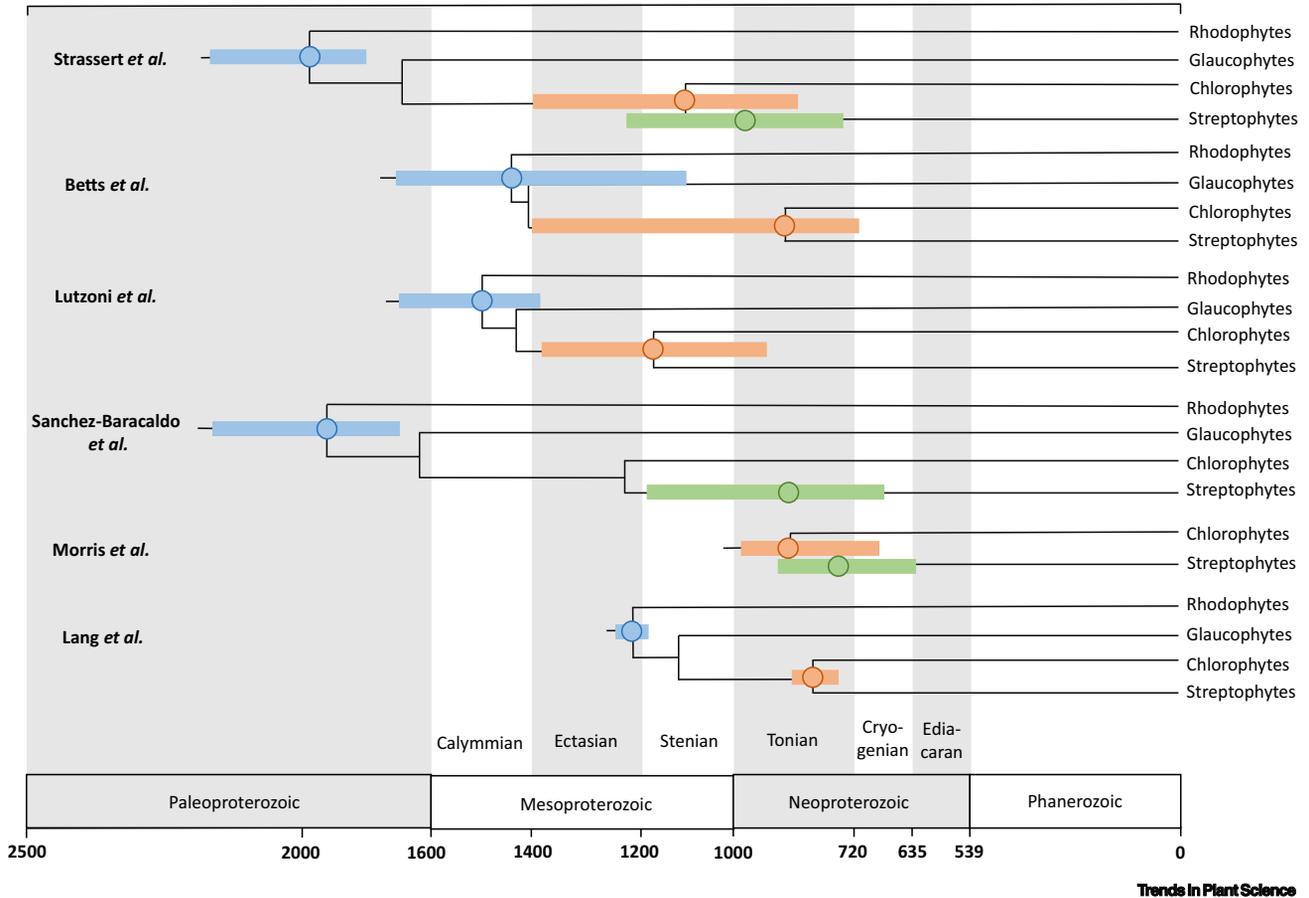


Figure 4. Summary of molecular estimates for the timescale of archaeplastid evolution. Dates at the bottom of the figure refer to millions of years ago. Blue bars highlight divergence time estimates for the ancestor of Archaeplastida. Orange bars highlight divergence time estimates for the ancestor of 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

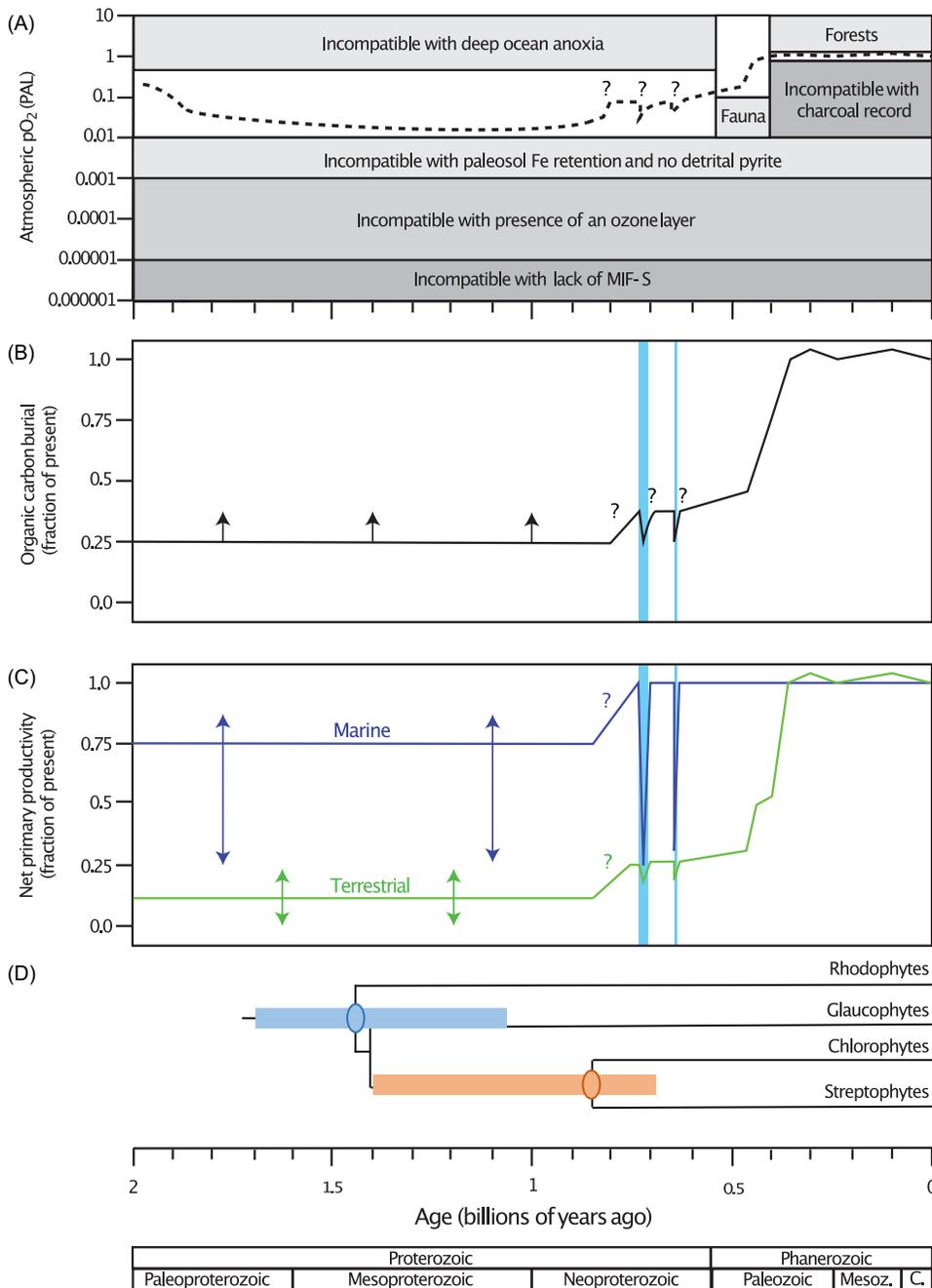
This new understanding of early plant evolution has important implications for how photosynthetic eukaryotes have coevolved with the Earth system (both affecting and being affected by it) (Figure 5).

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



Trends in Plant Science

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 pO₂ [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].

Acknowledgments

We wish to acknowledge funding from the Leverhulme Trust ('iDAPT' RPG-2020-199 to C.J.W. and P.C.J.D., and RF-2022-167 to P.C.J.D.); the Natural Environment Research Council (NE/P013678/1 to P.C.J.D., and NE/P013651/1 to T.M.L.) part of the Biosphere Evolution, Transitions, and Resilience (BETR) programme cofunded by the Natural Science Foundation of China (NSFC); the John Templeton Foundation (62220 to P.C.J.D., T.A.W., and T.M.L.); and the Gordon and Betty Moore Foundation (GBMF9741 to P.C.J.D. and T.A.W.). We thank Stefan Bengtson, Nick Butterfield, Dianne Edwards, Emmanuelle Javaux, Bruce Runnegar, Marie Catherine Sforna, and Shuhai Xiao for providing images of fossils, and the Culture Collection of Algae and Protozoa (CCAP) for images of extant algae used in this article.

Declaration of interests

No interests are declared.

References

- Lenton, T. and Watson, A. (2013) *Revolutions That Made the Earth*. Oxford University Press
- Delaux, P.M. and Schornack, S. (2021) Plant evolution driven by interactions with symbiotic and pathogenic microbes. *Science* 371, eaba6605
- Leebens-Mack, J.H. et al. (2019) One thousand plant transcriptomes and the phylogenomics of green plants. *Nature* 574, 679–685
- Lenton, T.M. et al. (2016) Earliest land plants created modern levels of atmospheric oxygen. *Proc. Natl. Acad. Sci. U. S. A.* 113, 9704–9709
- Keeling, P.J. (2004) Diversity and evolutionary history of plastids and their hosts. *Am. J. Bot.* 91, 1481–1493
- Palmer, J.D. et al. (2004) The plant tree of life: an overview and some points of view. *Am. J. Bot.* 91, 1437–1445
- Ponce-Toledo, R.I. et al. (2017) An early-branching freshwater cyanobacterium at the origin of plastids. *Curr. Biol.* 27, 386–391

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?

8. Price, D.C. *et al.* (2019) Analysis of an improved *Cyanophora paradoxa* genome assembly. *DNA Res.* 26, 287–299
9. Zimorski, V. *et al.* (2014) Endosymbiotic theory for organelle origins. *Curr. Opin. Microbiol.* 22, 38–48
10. Kashiwara, Y. *et al.* (2019) Taming chlorophylls by early eukaryotes underpinned algal interactions and the diversification of the eukaryotes on the oxygenated Earth. *ISME J.* 13, 1899–1910
11. Del Cortona, A. *et al.* (2020) Neoproterozoic origin and multiple transitions to macroscopic growth in green seaweeds. *Proc. Natl. Acad. Sci. U. S. A.* 117, 2551–2559
12. Lutzoni, F. *et al.* (2018) Contemporaneous radiations of fungi and plants linked to symbiosis. *Nat. Commun.* 9, 5451
13. Brocks, J.J. *et al.* (2017) The rise of algae in Cryogenian oceans and the emergence of animals. *Nature* 548, 578–581
14. Donoghue, P.C.J. *et al.* (2021) The evolutionary emergence of land plants. *Curr. Biol.* 31, 1281–1298
15. Harrison, C.J. (2017) Development and genetics in the evolution of land plant body plans. *Philos. Trans. R. Soc. B Biol. Sci.* 372, e2015.0490
16. de Vries, J. and Archibald, J.M. (2018) Plant evolution: landmarks on the path to terrestrial life. *New Phytol.* 217, 1428–1434
17. Rensing, S.A. (2018) Great moments in evolution: the conquest of land by plants. *Curr. Opin. Plant Biol.* 42, 49–54
18. Kenrick, P. and Crane, P.R. (1997) The origin and early evolution of plants on land. *Nature* 389, 33–39
19. Pires, N. and Dolan, L. (2012) Morphological evolution in land plants: new designs with old genes. *Philos. Trans. R. Soc. B Biol. Sci.* 367, 508–518
20. Gitzendanner, M.A. *et al.* (2018) Plastid phylogenomic analysis of green plants: a billion years of evolutionary history. *Am. J. Bot.* 105, 291–301
21. Harris, B.J. *et al.* (2020) Phylogenomic evidence for the monophyly of bryophytes and the reductive evolution of stomata. *Curr. Biol.* 30, 2001–2012
22. Li, L. *et al.* (2020) The genome of *Prasinoderma coloniale* unveils the existence of a third phylum within green plants. *Nat. Ecol. Evol.* 4, 1220–1231
23. Price, D.C. *et al.* (2012) *Cyanophora paradoxa* genome elucidates origin of photosynthesis in algae and plants. *Science* 335, 843–847
24. Gawryluk, R.M.R. *et al.* (2019) Non-photosynthetic predators are sister to red algae. *Nature* 572, 240–243
25. Schön, M.E. *et al.* (2021) Single cell genomics reveals plastid-lacking Picozoa are close relatives of red algae. *Nat. Commun.* 12, 6651
26. Cheng, S. *et al.* (2019) Genomes of subaerial Zygnematophyceae provide insights into land plant evolution. *Cell* 179, 1057–1067
27. Repetti, S.I. *et al.* (2021) Nuclear genome of a pedinophyte pinpoints genomic innovation and streamlining in the green algae. *New Phytol.* 233, 2144–2154
28. Li, X. *et al.* (2021) Large phylogenomic datasets reveal deep relationships and trait evolution in chlorophyte green algae. *Genome Biol. Evol.* 13, evab101
29. Puttick, M.N. *et al.* (2018) The interrelationships of land plants and the nature of the ancestral embryophyte. *Curr. Biol.* 28, 733–745
30. Wickett, N.J. *et al.* (2014) Phylotranscriptomic analysis of the origin and early diversification of land plants. *Proc. Natl. Acad. Sci. U. S. A.* 111, 4859–4868
31. Wang, S. *et al.* (2019) Genomes of early-diverging streptophyte algae shed light on plant terrestrialization. *Nat. Plants* 6, 95–106
32. Lecointre, G. and Le Guyader, H. (2007) *The Tree of Life: A Phylogenetic Classification*. Harvard University Press
33. Wodniok, S. *et al.* (2011) Origin of land plants: do conjugating green algae hold the key? *BMC Evol. Biol.* 11, 104
34. Usadel, L. (2022) Published plant genomes: phylogenetic relationships for red algae, glaucophytes, green algae and non-flowering land plants with genomes sequenced and published. Published online. https://www.plabipd.de/plant_genomes_pn.ep
35. Li, F. (2018) Surfing the genomic new wave. *Nat. Plants* 4, 393
36. Schönknecht, G. *et al.* (2013) Gene transfer from bacteria and archaea facilitated evolution of an extremophilic eukaryote. *Science* 339, 1207–1210
37. Bogen, C. *et al.* (2013) Reconstruction of the lipid metabolism for the microalga *Monoraphidium neglectum* from its genome sequence reveals characteristics suitable for biofuel production. *BMC Genomics* 14, 926
38. Burns, J.A. *et al.* (2015) Comparative genomics of a bacterivorous green alga reveals evolutionary causalities and consequences of phago-mixotrophic mode of nutrition. *Genome Biol. Evol.* 7, 3047–3061
39. Xu, Y. *et al.* (2022) Chromosome-level genome of *Pedinomonas minor* (Chlorophyta) unveils adaptations to abiotic stress in a rapidly fluctuating environment. *New Phytol.* 235, 1409–1425
40. Matsuzaki, M. *et al.* (2004) Genome sequence of the ultrasmall unicellular red alga *Cyanidioschyzon merolae* 10D. *Nature* 428, 653–657
41. Craig, R.J. *et al.* (2021) Comparative genomics of *Chlamydomonas*. *Plant Cell* 33, 1016–1041
42. Pombert, J.F. *et al.* (2014) A lack of parasitic reduction in the obligate parasitic green alga *Helicosporidium*. *PLoS Genet.* 10, e1004355
43. Fang, J. *et al.* (2021) Chloroplast genome traits correlate with organismal complexity and ecological traits in Chlorophyta. *Front. Ecol. Evol.* 9, 791166
44. Liang, H. *et al.* (2019) Phylogenomics provides new insights into gains and losses of selenoproteins among Archaeplastida. *Int. J. Mol. Sci.* 20, 3020
45. Xu, Y. *et al.* (2019) Molecular evidence for origin, diversification and ancient gene duplication of plant subtilases (SBTs). *Sci. Rep.* 9, 12485
46. Goh, F. *et al.* (2019) Gains and losses of metabolic function inferred from a phylotranscriptomic analysis of algae. *Sci. Rep.* 9, 10482
47. Hess, S. *et al.* (2022) A phylogenomically informed five-order system for the closest relatives of land plants. *Curr. Biol.* 32, 4473–4482.e7
48. Irisarri, I. *et al.* (2021) Unexpected cryptic species among streptophyte algae most distant to land plants. *Proc. R. Soc. B Biol. Sci.* 288, 20212168
49. Nowack, E.C.M. and Weber, A.P.M. (2018) Genomics-informed insights into endosymbiotic organelle evolution in photosynthetic eukaryotes. *Annu. Rev. Plant Biol.* 69, 51–84
50. Ponce-Toledo, R.I. *et al.* (2019) Horizontal and endosymbiotic gene transfer in early plastid evolution. *New Phytol.* 224, 618–624
51. Rockwell, N.C. *et al.* (2014) Primary endosymbiosis and the evolution of light and oxygen sensing in photosynthetic eukaryotes. *Front. Ecol. Evol.* 2, 66
52. Muñoz-Gómez, S.A. *et al.* (2017) The new red algal subphylum Proteorhodophytina comprises the largest and most divergent plastid genomes known. *Curr. Biol.* 27, 1677–1684
53. Collén, J. *et al.* (2013) Genome structure and metabolic features in the red seaweed *Chondrus crispus* shed light on evolution of the Archaeplastida. *Proc. Natl. Acad. Sci. U. S. A.* 110, 5247–5252
54. Lee, J.M. *et al.* (2016) Parallel evolution of highly conserved plastid genome architecture in red seaweeds and seed plants. *BMC Biol.* 14, 75
55. Lee, J.M. *et al.* (2018) Analysis of the draft genome of the red seaweed *Gracilaria chorda* provides insights into genome size evolution in rhodophyta. *Mol. Biol. Evol.* 35, 1869–1886
56. Petroll, R. *et al.* (2021) Signatures of transcription factor evolution and the secondary gain of red algae complexity. *Genes (Base)* 12, 1055
57. Brawley, S.H. *et al.* (2017) Insights into the red algae and eukaryotic evolution from the genome of *Porphyra umbilicalis* (Bangioophyceae, Rhodophyta). *Proc. Natl. Acad. Sci. U. S. A.* 114, 6361–6370
58. Bhattacharya, D. *et al.* (2013) Genome of the red alga *Porphyridium purpureum*. *Nat. Commun.* 4, 1941
59. Qiu, H. *et al.* (2015) Evidence of ancient genome reduction in red algae (Rhodophyta). *J. Phycol.* 51, 624–636
60. Qiu, H. *et al.* (2013) Adaptation through horizontal gene transfer in the cryptoendolithic red alga *Galdieria phlegrea*. *Curr. Biol.* 23, 865–866

61. Yoon, H.S. *et al.* (2010) Evolutionary history and taxonomy of red algae. In *Red Algae in the Genomic Age* (Seckbach, J. and Chapman, D.J., eds), pp. 25–42, Springer
62. Sun, X. *et al.* (2018) Genomic analyses of unique carbohydrate and phytohormone metabolism in the macroalga *Gracilariopsis lemaneiformis* (Rhodophyta). *BMC Plant Biol.* 18, 94
63. Yu, Y. *et al.* (2021) Floridean starch and floridoside metabolic pathways of *Neoporphyra haitanensis* and their regulatory mechanism under continuous darkness. *Mar. Drugs* 19, 664
64. Miyagishima, S.-Y. and Tanaka, K. (2021) The unicellular red alga *Cyanidioschyzon merolae* – the simplest model of a photosynthetic eukaryote. *Plant Cell Physiol.* 62, 926–941
65. Chan, C.X. *et al.* (2012) *Porphyra* (Bangiophyceae) transcriptomes provide insights into red algal development and metabolism. *J. Phycol.* 48, 1328–1342
66. Bowles, A.M.C. *et al.* (2020) The origin of land plants is rooted in two bursts of genomic novelty. *Curr. Biol.* 30, 530–536
67. Derelle, E. *et al.* (2006) Genome analysis of the smallest free-living eukaryote *Ostreococcus tauri* unveils many unique features. *Proc. Natl. Acad. Sci. U. S. A.* 103, 11647–11652
68. Palenik, B. *et al.* (2007) The tiny eukaryote *Ostreococcus* provides genomic insights into the paradox of plankton speciation. *Proc. Natl. Acad. Sci. U. S. A.* 104, 7705–7710
69. Moreau, H. *et al.* (2012) Gene functionalities and genome structure in *Bathycoccus prasinos* reflect cellular specializations at the base of the green lineage. *Genome Biol.* 13, R74
70. Worden, A.Z. *et al.* (2009) Green evolution and dynamic adaptations revealed by genomes of the marine picoeukaryotes *Micromonas*. *Science* 324, 268–272
71. Hanschen, E.R. *et al.* (2016) The *Gonium pectorale* genome demonstrates co-option of cell cycle regulation during the evolution of multicellularity. *Nat. Commun.* 7, 11370
72. Prochnik, S.E. *et al.* (2010) Genomic analysis of organismal complexity in the multicellular green alga *Volvox carteri*. *Science* 329, 223–226
73. Blanc, G. *et al.* (2012) The genome of the polar eukaryotic microalga *Coccomyxa subellipsoidea* reveals traits of cold adaptation. *Genome Biol.* 13, R39
74. Merchant, S.S. *et al.* (2007) The *Chlamydomonas* genome reveals the evolution of key animal and plant functions. *Science* 318, 245–251
75. Arimoto, A. *et al.* (2019) A siphonous macroalgal genome suggests convergent functions of homeobox genes in algae and land plants. *DNA Res.* 26, 183–192
76. De Clerck, O. *et al.* (2018) Insights into the evolution of multicellularity from the sea lettuce genome. *Curr. Biol.* 28, 2921–2933
77. Featherston, J. *et al.* (2018) The 4-celled *Tetrabaena socialis* nuclear genome reveals the essential components for genetic control of cell number at the origin of multicellularity in the volvocine lineage. *Mol. Biol. Evol.* 35, 855–870
78. Nishiyama, T. *et al.* (2018) The *Chara* genome: secondary complexity and implications for plant terrestrialization. *Cell* 174, 448–464
79. Zhang, Z. *et al.* (2020) Adaptation to extreme Antarctic environments revealed by the genome of a sea ice green alga. *Curr. Biol.* 30, 3330–3341
80. Bakula, Z. *et al.* (2021) A first insight into the genome of *Prototheca wickerhamii*, a major causative agent of human protothecosis. *BMC Genomics* 22, 168
81. Armaleo, D. *et al.* (2019) The lichen symbiosis re-viewed through the genomes of *Cladonia grayi* and its algal partner *Asterochlois glomerata*. *BMC Genomics* 20, 605
82. Iha, C. *et al.* (2021) Genomic adaptations to an endolithic lifestyle in the coral-associated alga *Ostreobium*. *Curr. Biol.* 31, 1393–1402
83. Hori, K. *et al.* (2014) *Klebsormidium flaccidum* genome reveals primary factors for plant terrestrial adaptation. *Nat. Commun.* 5, 3978
84. Skokan, R. *et al.* (2019) PIN-driven auxin transport emerged early in streptophyte evolution. *Nat. Plants* 5, 1114–1119
85. Maugamy-Calès, A. *et al.* (2016) Apparition of the NAC transcription factors predates the emergence of land plants. *Mol. Plant* 9, 1345–1348
86. Ma, J. *et al.* (2022) Major episodes of horizontal gene transfer drove the evolution of land plants. *Mol. Plant* 15, 857–871
87. Jiao, C. *et al.* (2020) The *Penium margaritaceum* genome: hallmarks of the origins of land plants. *Cell* 181, 1097–1111
88. de Vries, J. *et al.* (2018) Embryophyte stress signaling evolved in the algal progenitors of land plants. *Proc. Natl. Acad. Sci. U. S. A.* 115, 3471–3480
89. Han, T.M. and Runnegar, B. (1992) Megascopic eukaryotic algae from the 2.1-billion-year-old Negaunee iron-formation, Michigan. *Science* 257, 232–235
90. Sharma, M. and Shukla, Y. (2009) Taxonomy and affinity of early Mesoproterozoic megascopic helically coiled and related fossils from the Rohtas Formation, the Vindhyan Supergroup, India. *Precambrian Res.* 173, 105–122
91. Agić, H. *et al.* (2017) Diversity of organic-walled microfossils from the early Mesoproterozoic Ruyang Group, North China Craton – a window into the early eukaryote evolution. *Precambrian Res.* 297, 101–130
92. Bengtson, S. *et al.* (2017) Three-dimensional preservation of cellular and subcellular structures suggests 1.6 billion-year-old crown-group red algae. *PLoS Biol.* 15, e2000735
93. Carlisle, E.M. *et al.* (2021) Experimental taphonomy of organelles and the fossil record of early eukaryote evolution. *Sci. Adv.* 7, eabe9487
94. Tang, Q. *et al.* (2021) The Proterozoic macrofossil *Tawuia* as a coenocytic eukaryote and a possible macroalga. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 576, 110485
95. Zhu, S. *et al.* (2016) Decimetre-scale multicellular eukaryotes from the 1.56-billion-year-old Gaoyuzhuang Formation in North China. *Nat. Commun.* 7, 11500
96. Sioma, M.C. *et al.* (2022) Intracellular bound chlorophyll residues identify 1 Gyr-old fossils as eukaryotic algae. *Nat. Commun.* 13, 146
97. Maloney, K.M. *et al.* (2021) New multicellular marine macroalgae from the early Tonian of northwestern Canada. *Geology* 49, 743–747
98. Tang, Q. *et al.* (2020) A one-billion-year-old multicellular chlorophyte. *Nat. Ecol. Evol.* 4, 543–549
99. Butterfield, N.J. (2000) *Bangiomorpha pubescens* n. gen., n. sp.: implications for the evolution of sex, multicellularity, and the Mesoproterozoic/Neoproterozoic radiation of eukaryotes. *Paleobiology* 26, 386–404
100. Betts, H.C. *et al.* (2018) Integrated genomic and fossil evidence illuminates life's early evolution and eukaryote origin. *Nat. Ecol. Evol.* 2, 1556–1562
101. Gibson, T.M. *et al.* (2018) Precise age of *Bangiomorpha pubescens* dates the origin of eukaryotic photosynthesis. *Geology* 46, 135–138
102. Bykova, N. *et al.* (2020) Seaweeds through time: morphological and ecological analysis of Proterozoic and early Paleozoic benthic macroalgae. *Precambrian Res.* 350, 105875
103. Xiao, S. *et al.* (2004) Phosphatized multicellular algae in the Neoproterozoic Doushantuo Formation, China, and the early evolution of florideophyte red algae. *Am. J. Bot.* 91, 214–227
104. Selosse, M.-A. *et al.* (2015) Plants, fungi and oomycetes: a 400-million year affair that shapes the biosphere. *New Phytol.* 206, 501–506
105. Lenton, T.M. *et al.* (2012) First plants cooled the Ordovician. *Nat. Geosci.* 5, 86–89
106. Morris, J.L. *et al.* (2018) The timescale of early land plant evolution. *Proc. Natl. Acad. Sci. U. S. A.* 115, 2274–2283
107. Nie, Y. *et al.* (2020) Accounting for uncertainty in the evolutionary timescale of green plants through clock-partitioning and fossil calibration strategies. *Syst. Biol.* 69, 1–16
108. Strasser, J.F.H. *et al.* (2021) A molecular timescale for eukaryote evolution with implications for the origin of red algal-derived plastids. *Nat. Commun.* 12, 1879
109. Su, D. *et al.* (2021) Large-scale phylogenomic analyses reveal the monophyly of bryophytes and Neoproterozoic origin of land plants. *Mol. Biol. Evol.* 38, 3332–3344
110. Lang, D. *et al.* (2010) Genome-wide phylogenetic comparative analysis of plant transcriptional regulation: a timeline of loss, gain, expansion and correlation with complexity. *Genome Biol. Evol.* 2, 488–503
111. Hou, Z. *et al.* (2022) Phylotranscriptomic insights into a Mesoproterozoic–Neoproterozoic origin and early radiation of green seaweeds (Ulvoophyceae). *Nat. Commun.* 13, 1610

112. Hedges, S.B. *et al.* (2018) Accurate timetrees require accurate calibrations. *Proc. Natl. Acad. Sci. U. S. A.* 115, 9510–9511
113. Clarke, J.T. *et al.* (2011) Establishing a time-scale for plant evolution. *New Phytol.* 192, 266–301
114. Smith, S.A. *et al.* (2010) An uncorrelated relaxed-clock analysis suggests an earlier origin for flowering plants. *Proc. Natl. Acad. Sci. U. S. A.* 107, 5897–5902
115. Magallón, S. *et al.* (2013) Land plant evolutionary timeline: gene effects are secondary to fossil constraints in relaxed clock estimation of age and substitution rates. *Am. J. Bot.* 100, 556–573
116. Sánchez-Baracaldo, P. *et al.* (2017) Early photosynthetic eukaryotes inhabited low-salinity habitats. *Proc. Natl. Acad. Sci. U. S. A.* 114, 7737–7745
117. Sutherland, J.E. *et al.* (2011) A new look at an ancient order: generic revision of the bangiales (Rhodophyta). *J. Phycol.* 47, 1131–1151
118. Benítez, M. *et al.* (2018) Dynamical patterning modules, biogeneric materials, and the evolution of multicellular plants. *Front. Plant Sci.* 9, 871
119. Cock, J.M. and Collén, J. (2015) Independent emergence of complex multicellularity in the brown and red algae. In *Evolutionary Transitions to Multicellular Life* (Ruiz-Trullo, I. and Nedelcu, A.M., eds), pp. 335–361, Springer
120. Sfriso, A.A. *et al.* (2018) Phycoerythrin productivity and diversity from five red macroalgae. *J. Appl. Phycol.* 30, 2523–2531
121. Knopp, M. *et al.* (2020) Major changes in plastid protein import and the origin of the Chloroplastida. *iScience* 23, 100896
122. Liang, Z. *et al.* (2019) *Mesostigma viride* genome and transcriptome provide insights into the origin and evolution of Streptophyta. *Adv. Sci.* 7, 1901850
123. Williamson, C.J. *et al.* (2019) Glacier algae: a dark past and a darker future. *Front. Microbiol.* 10, 524
124. Fürst-Jansen, J.M.R. *et al.* (2020) Evo-physio: on stress responses and the earliest land plants. *J. Exp. Bot.* 71, 3254–3269
125. Kim, S.J. *et al.* (2020) The synthesis of xyloglucan, an abundant plant cell wall polysaccharide, requires CSLC function. *Proc. Natl. Acad. Sci. U. S. A.* 117, 20316–20324
126. Jensen, J. *et al.* (2018) Identification of an algal xylan synthase indicates that there is functional orthology between algal and plant cell wall biosynthesis. *New Phytol.* 218, 1049–1060
127. Delaux, P.M. *et al.* (2015) Algal ancestor of land plants was pre-adapted for symbiosis. *Proc. Natl. Acad. Sci. U. S. A.* 112, 13390–13395
128. Bowman, J.L. *et al.* (2017) Insights into land plant evolution garnered from the *Marchantia polymorpha* genome. *Cell* 171, 287–304
129. de Vries, J. *et al.* (2020) Heat stress response in the closest algal relatives of land plants reveals conserved stress signaling circuits. *Plant J.* 103, 1025–1048
130. Han, X. *et al.* (2019) Origin and evolution of core components responsible for monitoring light environment changes during plant terrestrialization. *Mol. Plant* 12, 847–862
131. Zhao, C. *et al.* (2019) Evolution of chloroplast retrograde signaling facilitates green plant adaptation to land. *Proc. Natl. Acad. Sci. U. S. A.* 116, 5015–5020
132. Lenton, T.M. and Daines, S.J. (2017) Matworld – the biogeochemical effects of early life on land. *New Phytol.* 215, 531–537
133. Planavsky, N.J. *et al.* (2021) Evolution of the structure and impact of Earth's biosphere. *Nat. Rev. Earth Env.* 2, 123–139
134. Daines, S.J. *et al.* (2017) Atmospheric oxygen regulation at low Proterozoic levels by incomplete oxidative weathering of sedimentary organic carbon. *Nat. Commun.* 8, 14379
135. Lenton, T.M. and Daines, S.J. (2017) Biogeochemical transformations in the history of the ocean. *Annu. Rev. Mar. Sci.* 9, 31–58
136. Lenton, T.M. and Daines, S.J. (2018) The effects of marine eukaryote evolution on phosphorus, carbon and oxygen cycling across the Proterozoic–Phanerozoic transition. *Emerg. Topics Life Sci.* 2, 267–278
137. Lenton, T.M. (2020) On the role of models in understanding the rise of complex life. *R. Soc. Interface Focus* 10, 20200018
138. Reinhard, C.T. *et al.* (2017) Evolution of the global phosphorus cycle. *Nature* 541, 386–389
139. Armstrong, R.A. (1994) Grazing limitation and nutrient limitation in marine ecosystems: steady state solutions of an ecosystem model with multiple food chains. *Limnol. Oceanogr.* 39, 597–608
140. Porter, S.M. and Knoll, A.H. (2000) Testate amoebae in the Neoproterozoic Era: evidence from vase-shaped microfossils in the Chuar Group, Grand Canyon. *Paleobiology* 26, 360–385
141. Lenton, T.M. and Watson, A.J. (2004) Biotic enhancement of weathering, atmospheric oxygen and carbon dioxide in the Neoproterozoic. *Geophys. Res. Lett.* 31, L05202
142. Hoffman, P.F. *et al.* (2017) Snowball Earth climate dynamics and Cryogenian geology-geobiology. *Sci. Adv.* 3, e1600983
143. Žárský, J. *et al.* (2022) Cryogenian glacial habitats as a plant terrestrialisation cradle – the origin of the Anydrophytes and Zygnematoxycyceae split. *Front. Plant Sci.* 12, 735020
144. Alcott, L.J. *et al.* (2019) Stepwise Earth oxygenation is an inherent property of global biogeochemical cycling. *Science* 366, 1333–1337
145. Domozych, D.S. *et al.* (2016) Charophytes: evolutionary giants and emerging model organisms. *Front. Plant Sci.* 7, 1470
146. Sasso, S. *et al.* (2018) The natural history of model organisms: from molecular manipulation of domesticated *Chlamydomonas reinhardtii* to survival in nature. *eLife* 7, e39233
147. Stull, G.W. *et al.* (2021) Gene duplications and genomic conflict underlie major pulses of phenotypic evolution in gymnosperms. *Nat. Plants* 7, 1015–1025
148. Guo, X. *et al.* (2021) *Chloranthus* genome provides insights into the early diversification of angiosperms. *Nat. Commun.* 12, 6930
149. Liu, Y. *et al.* (2022) The cycad genome and the early evolution of seed plants. *Nat. Plants* 8, 389–401
150. Chen, H. *et al.* (2022) Insights into the ancient adaptation to intertidal environments by red algae based on a genomic and multiomics investigation of *Neoporphyra haitanensis*. *Mol. Biol. Evol.* 39, msab315
151. Christenhusz, M.J.M. and Byng, J.W. (2016) The number of known plant species in the world and its annual increase. *Phytotaxa* 261, 201–217
152. Corlett, R.T. (2016) Plant diversity in a changing world: status, trends, and conservation needs. *Plant Divers.* 38, 10–16
153. Guiry, M.D. *et al.* (2014) AlgaeBase: an on-line resource for algae. *Cryptogam. Algol.* 35, 105–115
154. Lughadha, E.N. *et al.* (2016) Counting counts: revised estimates of numbers of accepted species of flowering plants, seed plants, vascular plants and land plants with a review of other recent estimates. *Phytotaxa* 272, 82–88
155. Figueroa-Martinez, F. *et al.* (2019) Plastid genomes from diverse glaucophyte genera reveal a largely conserved gene content and limited architectural diversity. *Genome Biol. Evol.* 11, 174–188
156. Guiry, M.D. (2012) How many species of algae are there? *J. Phycol.* 48, 1057–1063
157. Pimm, S.L. *et al.* (2014) The biodiversity of species and their rates of extinction, distribution, and protection. *Science*. 344, e1246752
158. Delwiche, C.F. and Timme, R.E. (2011) Plants. *Curr. Biol.* 21, 417–422
159. Stephens, T.G. *et al.* (2021) Why is primary endosymbiosis so rare? *New Phytol.* 231, 1693–1699
160. Gavelis, G.S. and Gile, G.H. (2018) How did cyanobacteria first embark on the path to becoming plastids? Lessons from protist symbioses. *FEMS Microbiol. Lett.* 365, fny209
161. Lhee, D. *et al.* (2021) Amoeba genome reveals dominant host contribution to plastid endosymbiosis. *Mol. Biol. Evol.* 38, 344–357
162. Moore, K.R. *et al.* (2019) An expanded ribosomal phylogeny of cyanobacteria supports a deep placement of plastids. *Front. Microbiol.* 10, 1612
163. Stiller, J.W. *et al.* (2014) The evolution of photosynthesis in chromist algae through serial endosymbioses. *Nat. Commun.* 5, 5764
164. Ponce-Toledo, R.I. *et al.* (2018) Secondary plastids of euglenids and chlorarachniophytes function with a mix of genes of red and green algal ancestry. *Mol. Biol. Evol.* 35, 2198–2204

165. Archibald, J.M. (2015) Genomic perspectives on the birth and spread of plastids. *Proc. Natl. Acad. Sci. U. S. A.* 112, 10147–10153
166. Woehle, C. *et al.* (2017) Expansion of the redox-sensitive proteome coincides with the plastid endosymbiosis. *Nat. Plants* 3, 17066
167. Parfrey, L.W. and Lahr, D.J.G. (2013) Multicellularity arose several times in the evolution of eukaryotes. *BioEssays* 35, 339–347
168. Herron, M.D. *et al.* (2019) De novo origins of multicellularity in response to predation. *Sci. Rep.* 9, 2328
169. Niklas, K.J. and Newman, S.A. (2020) The many roads to and from multicellularity. *J. Exp. Bot.* 71, 3247–3253
170. Wang, S. *et al.* (2021) Genome-wide analyses across Viridiplantae reveal the origin and diversification of small RNA pathway-related genes. *Commun. Biol.* 4, 412
171. Bao, L. *et al.* (2022) The cellular function of ROP GTPase prenylation is important for multicellularity in the moss *Physcomitrium patens*. *Development* 149, dev200279
172. Niklas, K.J. *et al.* (2017) The evolution of hydrophobic cell wall biopolymers: from algae to angiosperms. *J. Exp. Bot.* 68, 5261–5269
173. Zhang, B. *et al.* (2021) The plant cell wall: biosynthesis, construction, and functions. *J. Integr. Plant Biol.* 63, 251–272
174. Renault, H. *et al.* (2017) A phenol-enriched cuticle is ancestral to lignin evolution in land plants. *Nat. Commun.* 8, 14713
175. Martone, P.T. *et al.* (2009) Discovery of lignin in seaweed reveals convergent evolution of cell-wall architecture. *Curr. Biol.* 19, 169–175
176. Labeeuw, L. *et al.* (2015) Ancient origin of the biosynthesis of lignin precursors. *Biol. Direct* 10, 23
177. Popper, Z.A. *et al.* (2011) Evolution and diversity of plant cell walls: from algae to flowering plants. *Annu. Rev. Plant Biol.* 62, 567–590
178. Lampugnani, E.R. *et al.* (2019) Cellulose synthesis – central components and their evolutionary relationships. *Trends Plant Sci.* 24, 402–412
179. Del Bem, L.E.V. and Vincentz, M.G.A. (2010) Evolution of xyloglucan-related genes in green plants. *BMC Evol. Biol.* 10, 341
180. Shinohara, N. and Nishitani, K. (2021) Cryogenian origin and subsequent diversification of the plant cell-wall enzyme XTH family. *Plant Cell Physiol.* 62, 1874–1889
181. Herburger, K. *et al.* (2018) Localisation and substrate specificities of transglycanases in charophyte algae relate to development and morphology. *J. Cell Sci.* 131, jcs203208
182. Federhen, S. (2012) The NCBI Taxonomy database. *Nucleic Acids Res.* 40, D136–D143
183. Steadman Tyler, C.R. *et al.* (2019) High-quality draft genome sequence of the green alga *Tetraselmis striata* (Chlorophyta) generated from PacBio sequencing. *Microbiol. Resour. Announc.* 8, e00780
184. Browne, D.R. *et al.* (2017) Draft nuclear genome sequence of the liquid hydrocarbon-accumulating green microalga *Botryococcus braunii* race B (Showa). *Genome Announc.* 5, e00215
185. Liu, C. *et al.* (2020) Genome analyses provide insights into the evolution and adaptation of the eukaryotic picophytoplankton *Mychonastes homosphaera*. *BMC Genomics* 21, 477
186. Lenton, T. *et al.* (2018) COPSE reloaded: an improved model of biogeochemical cycling over Phanerozoic time. *Earth Sci. Rev.* 178, 1–28