Cryogenian glacial habitats as a plant terrestrialization cradle – the origin of Anydrophyta and Zygnematophyceae split

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Abstract

For tens of millions of years (Ma) the terrestrial habitats of Snowball Earth during the Cryogenian period (between 720 to 635 Ma before present - Neoproterozoic Era) were possibly dominated by global snow and ice cover up to the equatorial sublimative desert. The most recent time-calibrated phylogenies calibrated not only on plants, but on a comprehensive set of eukaryotes, indicate within the Streptophyta, multicellular Charophyceae evolved in Mesoproterozoic to early Neoproterozoic, while Cryogenian is the time of likely Anydrophyta origin (common ancestor of Zygnematophyceae and Embryophyta) and also of Zygnematophyceae – Embryophyta split. Based on the combination of published phylogenomic studies and estimated diversification time comparisons we found strong support for the possibility Anydrophyta likely evolved in response to Cryogenian cooling, and that later in Cryogenian secondary simplification of multicellular Anydrophytes resulted in Zygnematophyceae diversification. We propose Marinoan geochemically documented expansion of first terrestrial flora has been represented not only by Chlorophyta, but also by Streptophyta – including the Anydrophyta – and later by Zygnematophyceae, thriving on glacial surfaces until today. It is possible multicellular early Embryophytes survived in less abundant, possibly relatively warmer refugia, relying more on mineral substrates allowing retention of flagella-based sexuality. Loss of flagella and sexual reproduction by conjugation evolved in Zygnematophyceae during Cryogenian in a remarkable convergent way as in Cryogenian-appearing zygomycetous fungi. We thus support the concept the important basal cellular exaptations to terrestrial environments evolved in streptophyte algae and propose this was stimulated by the adaptation to glacial habitats dominating the Cryogenian Snowball Earth. Including the glacial lifestyle in the picture of the rise of land plants increases the parsimony of connecting different ecological, phylogenetic and physiological puzzles of the journey from aquatic algae to the terrestrial floras.

Introduction - timing the rise of terrestrial flora

The timing of the evolution of terrestrial flora, the branching of Streptophyta lineages leading finally to Embryophyta and their further diversification has been a subject of interest since the 19th century. Intense debate in recent years is fuelled by the emergence of large genomic and transcriptomic datasets. The investigation of these ancient events is based on a combination of data sources and there are challenges linked with their interpretations. The first is an almost complete lack of fossil record of transition stages of the terrestrialization and the extinction of close relatives of the early land plants. This was highlighted recently by the support of monophyly of the bryophytes as sister clade to tracheophytes (Civáň et al., 2014, Cox et al., 2014, Puttick et al., 2018), leaving the gap between the first land plants and the closest living lineages even larger. Second is the uncertainty of the timing estimates (contrasting predictions and large confidence intervals) based on the molecular clock reaching further back in time. The third source of independent information about primary production on land is the geological/geochemistry record, though with only very limited taxonomic/systematic resolution.

1.1 Fossil evidence of terrestrialisation

Due to well-acknowledged poor fossilisation of plant remnants, spores are considered the best early markers of the land plants' occurrence. Currently the oldest known trilete spores assignable to Embryophytes are from the Upper Ordovician (Steemans et al., 2009, Edwards et al., 2014, Rubinstein and Vajda, 2019) along with poorly preserved seemingly polysporangiate mesofossils (Salamon et al., 2018). Widespread occurrence of non-trilete Cryptospores (Edwards et al., 2014) in Ordovician, starting in middle Ordovician (Dapingian), may be a sign for a great Ordovician diversification of land plants (Servais et al., 2019). Interpretations in Servais et al. (2019), however, are compromised by the misunderstanding – based on the current phylogenetic consensus – that bryophytes and tracheophytes are monophyletic clades, and therefore tracheophytes did not evolve from bryophytes (Civáň et al., 2014, Cox et al., 2014, Puttick et al., 2018). Current data supports the hypothesis that during Ordovician there were already diversified tiny, possibly polysporangiate, cryptophyta type floras (cryptophyta sensu Edwards et al., 2014 are extinct plants producing cryptospores; do not mix with Cryptophyceae algae) and therefore the very first land plant adaptations of Streptophytes occurred much earlier – starting most probably in Precambrian. Lycopods affiliated flora of extinct tracheophyte Baragwanathias, well documented in the Silurian with Cooksonias (Wenlock-Pridoli) and Rhyniophytes, similarly indicates a long undocumented evolution and diversification of land plants preceding earliest known fossils. We will discuss the potential importance of Cryogenian acritarchs for understanding the evolution of land plants later.

1.2 Time-calibrated phylogeny

From the phylogenetic perspective the plants have their origin in a highly diversified branch of an otherwise relatively small group of green algae called Streptophyta, which together with the large group Chlorophyta and a small group Prasinodermatophyta (Li et al., 2020) comprise the green plants (Viridiplantae). The deepest basal lineage of Streptophyta is formed by the unicellular biflagellate monotypic genera Mesostigma, described as a rarely but regularly occurring inhabitant of freshwater phytobenthos in wintertime (Lauterborn, 1894), and an aerophytic colonial monotypic genera Chlorokybus (Lemieux et al., 2007). The algal representatives of Streptophyta, the paraphyletic group charophytes, further include the filamentous Klebsormidiophyceae (Stewart and Mattox, 1975) with biflagellate zoospores combining features of the early Streptophyta as small square-shaped scales cover their spores and of terrestrial plants due to stress tolerance of vegetative cells (Holzinger et al., 2014). These three lineages are also referred to as “lower-branching KCM grade” of Streptophyta (de Vries and Archibald, 2018). Further distinct streptophyte lineage is Charophyceae (Rabenhorst, 1870) characteristic by their complex multicellular body architecture, which since the 19th century intuitively led to their traditional placement as the sister group to plants until the early molecular studies (Karol, 2001). Together with the lineages Coleochaetophyceae (Delwiche et al., 2002) and Zygnematophyceae (= Conjugatophyceae, Guiry, 2013; Cheng et al., 2019) it is referred to as higher “branching ZCC-grade” of Streptophyta by de Vries and Archibald (2018). The recently generally accepted topology of the streptophyte phylogenetic tree recognises Zygnematophyceae as the closest living lineage to land plants (Clarke et al., 2011, Wickett et al., 2014, Morris et al., 2018a, Leebens-Mack et al. 2019 and Su et al. 2021). Rensing (2020) proposed to call the common ancestor of Zygnematophyceae and Embryophyta “Anydrophyta” - pointing out their key ability to resist drought. New molecular phylostratigraphic analyses (Su et al. 2021; Strassert et al. 2021) date the main splits of the Streptophycean lineages, and especially split between Zygnematophyceae and Embryophyta much earlier than estimates based on the appearance of the first spores in the fossil material (Fig. 1A) or even relatively recent influential time-calibrated phylogeny by Morris et al. (2018). The new time-calibrated phylogenies based on the Viridiplantae (Su et al., 2021) and eukaryotes (Strassert et al., 2021) suggest likely Cryogenian origin of Anydrophytes as well as split of Zygnematophyceae. This dating is explicitly acknowledged (as a less probable scenario) by Lutzoni et al. (2018) and Jiao et al. (2020).

1.3 Isotopic and chemical evidence of early land plants in the geological record – green Cryogenian

There is an independent line of evidence with very limited taxonomic resolution, but integrating the signal of terrestrial productivity over large temporal and spatial scales, namely the isotopic composition of marine sediments with interstitial precipitates with a characteristic isotopic fingerprint (Fayek et al., 2001). There is evidence for significant terrestrial primary production from isotopic analyses of the Neoproterozoic marine interstitial carbonates based on combined oxygen and carbon isotope data compilation. The study suggests the terrestrial expansion of photosynthesising communities preceded the significant climate perturbations of the Neoproterozoic glaciations (Knauth and Kennedy, 2009). It needs to be noted that the term "terrestrialization" is often understood differently among biologists – who usually give it a more specific meaning of organisms inhabiting soils, surfaces of rocks and sediments – and geologists who usually mean inhabited surface of the continents including lakes, rivers and other freshwater habitats (e.g. glaciers). The conclusions of (Knauth and Kennedy, 2009) are formulated in the latter sense; they compare the signal of exploding photosynthesizing communities with phanerozoic terrestrial primary production where there is no doubt about its origin in terrestrial habitats *sensu stricto*. Moreover, the study of Hoshino et al. (2017) finds C_{29} 24-ethylsteranes are systematically absent from sediments deposited before the onset of the Snowball Earth events, but are present in rocks deposited during and directly after the Marinoan deglaciation, implying an origin of stigmasteroid biosynthesis during the glaciation. The authors concluded this extended glaciation period was an evolutionary stimulant, not only a bottleneck (Hoshino et al.; 2017). We can thus draw a simplified framework where fossil records show solid evidence for already complex multicellular land plants (Embryophytes) in Ordovician/Silurian. Molecular data models extend the possible timing for the origin of Anydrophytes and phylogenetic split between Zygnematophyceae and Embryophytes to either Neoproterozoic (Su et al., 2021), Cryogenian (Strassert et al., 2021) or Ediacaran/Cambrian (Morris et al., 2018). The rise in terrestrial primary productivity documented in sedimentary geologic isotopic records dates to the Tonian and Cryogenian (Knauth and Kennedy, 2009) or, based on sterol biosynthesis evolution, to final Marinoan glaciation (Hoshino et al., 2017). Since the fossil material of already well-developed floras with reinforced bodies is relatively scarce it is likely missing fossil evidence of earlier evolutionary stages indicates not only their poor fossilisation ability rather than their absence, but also the Rodinia continent break up and erosion in Cryogenian. This allows to infer that Cryogenian origin of the first land floras is a highly parsimonious scenario, and needs to be further critically considered and developed because of its important implications for physiology and ecology of not only the early terrestrial floras, but also extant land plants.

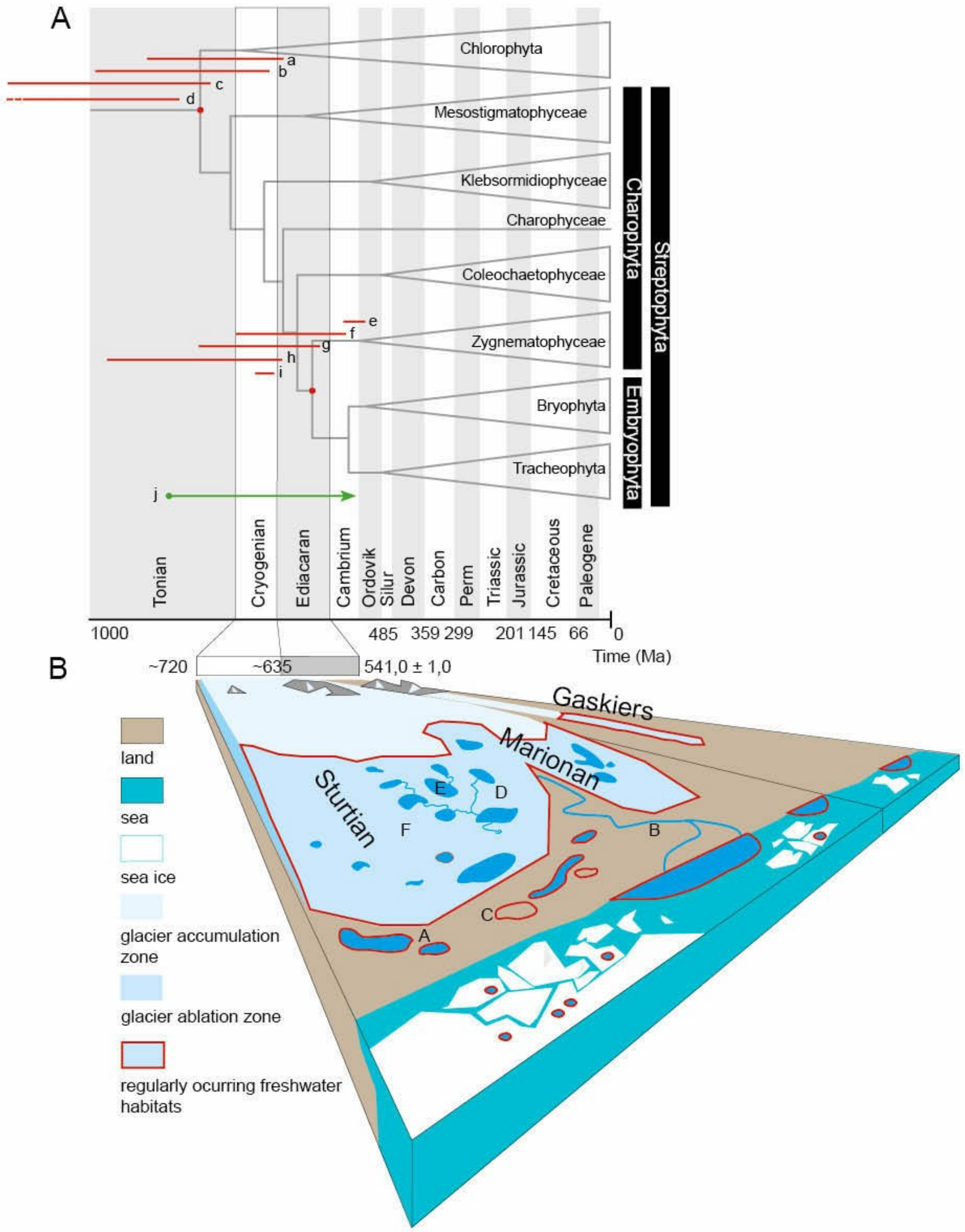

Figure 1 A: The phylogenetic tree with time estimates for the splits of Chlorophyta - Streptophyta and Charophyta - Embryophyta.

Tree adopted from Morris et al. 2018 and Donoghue & Paps 2020, projected over timescale based on international geostratigraphic chart (2020). The red lines at the respective node represent 95% highest posterior densities of estimates presented by Morris et al. 2018 and Hedges et al. 2018, Su et. al. 2021 and Strassert et al. 2021: **a** - Streptophyta, Morris et al., all calibrations, **b** - Streptophyta, Hedges et al., mesozoic calibrations, **c** - Streptophyta, Hedges et al., Spermatophyta calibration, **d** - Streptophyta, Strassert et al., **e** - Embryophyta, Morris et al., all calibrations, **f** - Embryophyta, Hedges et al., mesozoic calibrations, **g** - Embryophyta, Hedges et al., Spermatophyta calibration, **h** - Su et al. 2021, **i** - Embryophyta, Strassert et al. 2021. **j** - Influx of terrestrial carbon is apparent in carbonates younger than 850 Ma according to study of Knauth and Kennedy 2009, who infer an explosion of photosynthesizing communities on late Precambrian land surfaces.

Figure 1 B: Schematic presentation of the potential freshwater habitats in a low latitude Cryogenian catchment.

The picture represents habitats inhabited by members of Streptophyceae in current biosphere A) Lentic habitats, (*Mesostigma, Chara*). , B) fluvial habitats (*Klebsormidium*, various *Zygnematophyceae* in the phytobenthos), C) subaeric habitats, moist or periodically submerged surfaces (e. g. *Chlorokybus*, *Coleochaete*). Supraglacial habitats represent to some extent functional analogs to all three previous types of habitats by D) supraglacial lakes and cryoconite melt ponds, E) supraglacial streams and by F) the melting surface of bare ice, which is typically inhabited by zygnematophycean genera *Mesotaenium*, *Ancylonema* and *Cylindrocystis* where the first two develop regularly large-scale blooms e.g. on the Greenland ice sheet but are reported in the ablation zones of glaciers world-wide).

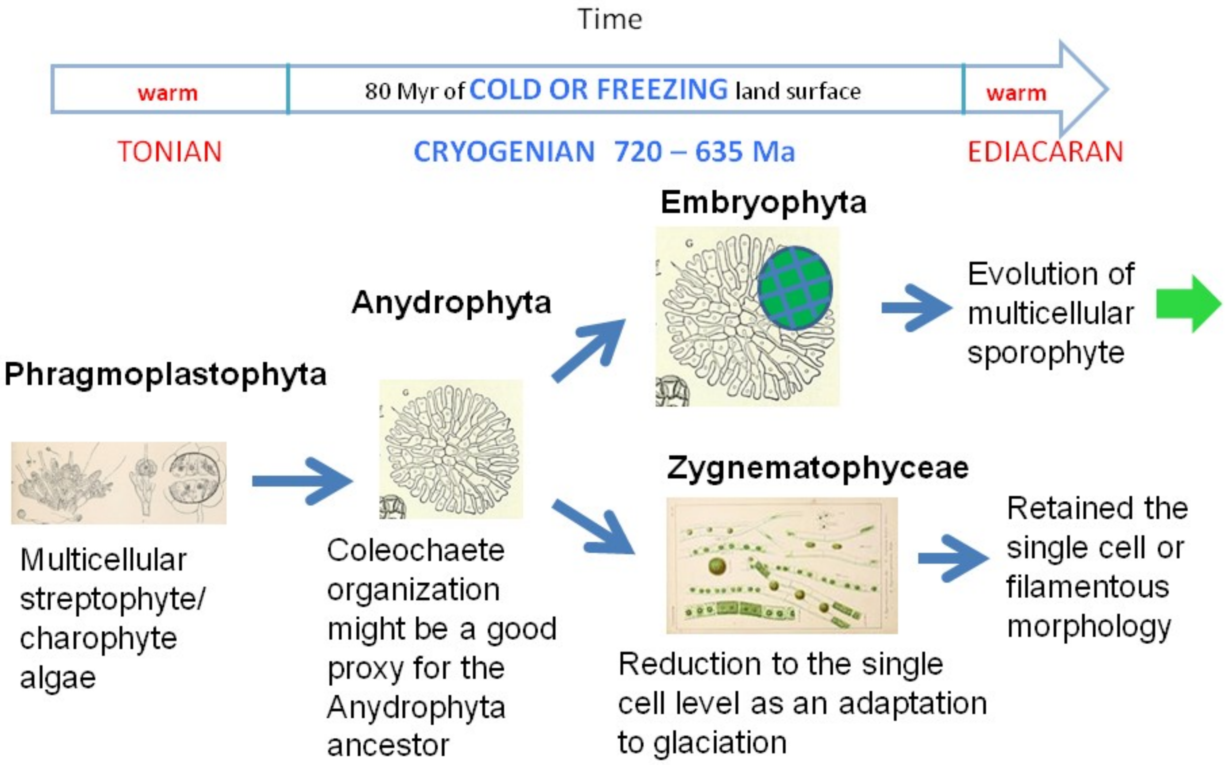

Figure 2: Hypothetical scenario of Anydrophyta establishment and Zygnematophyceae split off by the evolutionary reduction under the extended Cryogenian glaciations. Extant Charophyta are used as mere signs for unknown ancestral types of Phragmoplastophyta, Anydrophyta or Embryophyta.

2. Palaeogeography of the Cryogenian

When searching for key aspects of the environment inhabited by ancestors of the recent continents inhabiting chlorophyte and streptophyte algae and Embryophyta we inevitably enter the ground of speculations except for one generally accepted feature: their freshwater origin (Sánchez-Baracaldo et al., 2017). Thus we focus on the presence, character and spatio-temporal extent of freshwater habitats in the mid to late Neoproterozoic world – especially in Cryogenian.

The Cryogenian marks the period when the supercontinent Rodinia broke up. At the beginning of Cryogenian (720 Ma) the first rift basins developed in the continental crust of Rodinia, and 635 Ma at the end of Cryogenian continued rifting resulted in the breakup of the supercontinent into several blocks (Li et al., 2013). Early advanced chemical weathering of the Rodinia continent resulted in sequestration of the atmospheric CO2 in a quantity sufficient for global cooling resulting in the Snowball Earth glaciations conditions (Hoffman and Schrag, 2002). Under these conditions the oceans were covered with sea ice and the glaciers covered most of the Rodinia land surface between 0 - 70° latitude (Li et al., 2013). There are two major glaciations recognised in the course of Cryogenian, the Sturtian and Marionan. The Snowball Earth hypothesis assumes complete glaciation of the Earth's surface (Hoffman and Schrag, 2002), which would intuitively make the biotic colonisation of the continents impossible. However, as summarised and discussed by Eyles, (2008) the Snowball Earth glaciations possibly took place as a series of consecutive geo-tectonically predisposed regional glaciations. In the Marinoan glacial epoch, the sedimentological and geochemical records support a deglaciation interval with the onset of glaciolacustrine and non-glacial lacustrine and ice-free marine conditions (Williams et al., 2008; Wang et al., 2008; Hoffman et al., 2012; Hoffman et al., 2017). The continents were possibly not completely glaciated even in the maxima of actual glaciation epochs. Exposed alluvial plains and tidal flats allowed the development of subaeric periglacial zones with permafrost (Retallack, 2015; Bai et al., 2020). The phytane, pristane and sterane in marine sediments provide evidence there was no break in the activity of photosynthetic eukaryotes during the Cryogenian glacial epochs (Wang et al., 2008, Hoshino et al. 2017).The Neoproterozoic land system differed from the phanerozoic starting from Devonian until today mainly by the absence of a continuous vegetation cover with a root system (Bose et al., 2012). The Neoproterozoic landsystem was thus similar to recent arid regions, or during the global glacial epochs to the continental polar regions. The dominant terrestrial environment was alluvial plains with unstable river beds even though the meandering rivers also occurred (Barkat et al., 2020). Along the coast there were river deltas and tidal flats where the aeolic sedimentation of loess and wadded sands also took place (Williams et al., 2008, Retallack, 2011).The list of potential freshwater habitats wouldn't be complete if we didn't include the surface of melting glaciers themselves. Any glacial system in or close to balance with a climate, which allows the hydrological cycle to develop, must have an ablation zone where melting periodically occurs on an annual (polar areas) or daily (tropics) basis (Benn and Evans, 2010). For organisms that can cope with the supraglacial conditions this environment can provide a habitat for long-term survival (Hodson et al., 2008, Stibal et al., 2012, Anesio and Laybourn-Parry. 2012). This especially includes different kinds of cyanobacteria and algae (Lutz et al., 2018; Williamson et al., 2019; Yallop et al., 2012), but also sometimes moss balls ("glacier mice") which are able to sustain cold-adapted invertebrates (Zawierucha et al. 2015, 2021). However, in the case of polar glacier conditions the adapted mosses lifecycle is disrupted and reduced to vegetative phase missing sexual reproduction (recently e.g. Hotaling et al., 2020) in contrast to glacial Zygnematophyceae.

3. Adaptations to cold, snow, ice, drought and high irradiance exposed conditions of Cryogenian, and the evolution of streptophytic Anydrophytes and their cellular exaptations facilitating further terrestrialization

As proposed by Stebbins and Hill (1980) and later developed further – such as by Becker (2013) or Harholt et al. (2016) – plant terrestrialization or land plant evolution started at the single-cell stage of Streptophyte evolution (i.e. before the complex multicellularity evolved. Chlorophyte clade aerophytic algae likely adapted on the cellular level to dry land conditions much earlier in Proterozoic. This hypothesis was recently further supported strongly by studies of plant cell wall and stress responses evolution (Harholt et al., 2016; Jensen et al., 2018 de Vries et al., 2018). The charophycean green algae were already living on land and had been doing so for some time before the emergence of land plants (Harholt et al., 2016). Similarly, de Vries et al. (2018) show Embryophyte stress signalling evolved in the algal progenitors of land plants. But in most published cases environments similar to our extant freshwater to land transitions (lake shores, periodic water bodies, wet aerophytic algae environments) are considered as possible terrestrialization biotopes (e.g. Rensing 2020; Fürst-Jansen et al., 2020). Based on our adopted timing scenario above, Streptophycean dry land adaptations started on the single-cell level in late Mesoproterozoic/Tonian before Cryogenian glaciations and led in Mesoproterozoic or Tonian to the establishment of multicellular Streptophyta - Charophyceae and Coleochaetophyceae. Here we propose the idea tens of millions of years of prevalently cold or freezing environments of Cryogenian period are the environmental factors that crucially shaped future land plant cellular adaptations to land plant exposition and these adaptations worked as exaptations (preadaptations) for the future Embryophyte transition to the dry land.

While Rensing (2020) pointed out the ability to survive desiccation as a key factor in the already terrestrial ancestors of Zygnematophyta and Embryophyta, we point out a well-known fact: on the physical, physiological and molecular levels the stress imposed by desiccation has related and similar impacts on the plant organisms as the stress imposed by freezing. The surfaces of recent glaciers with bare ice inhabited by simple Zygnematophyceae (Williamson et al. 2019) and cryoconite occasionally colonised by long-term populations of vegetatively propagating mosses (Heusser 1972, Belkina and Vilnet 2016) are a living example of survival and growth strategies on glacial surfaces with possible implications for their common ancestor. The life on melting glacial surfaces has one important advantage over life in the proglacial area in terms of the predictability of water availability driven by seasonal or diurnal changes in insolation. The production of liquid water can be facilitated by the attachment of organisms to darker particles with lower albedo than the surrounding ice as observed in globular mosses (glacier mice) attaching to and accumulating cryoconite sediment (Porter et al. 2008; Belkina and Vilnet 2016). Alternatively the same effect can be achieved by lowering the albedo of the cells by production and accumulation of pigments as purpurogallin in the case of glacial Zygnematophyceae (Remias et al. 2012). If we accept the supraglacial habitats - as cryoconite panes, ponds, lakes or melting bare ice - as a freshwater aquatic habitat (Fig. 1 B and Fig. 2) inhabited by some cryogenian Chlorophyta and Streptophyta it has important implications for understanding early land plant adaptations and the term refugia in the Cryogenian context. We especially emphasise this aspect when generating hypothetical, yet realistic, scenarios for the survival of multicellular (though small and simple) Anydrophyta.

Recent genomic analyses of the basal Streptohytes representatives (*Mesostigma* and *Chlorokybus*) and inference for their common ancestor clearly indicate terrestrial adaptations of the photosynthetic apparatus - especially to high irradiance (photo-oxidative damage and photorespiration) - and transcription factors regulating dry land stress responses are also appearing there (Wang et al., 2020). Many studies of Embryophyta as well as algal Streptophyta indicate a tight coupling between the adaptation to high irradiation, as well as cold stress and drought stress (e.g. De Vries et al. 2017; De Vries et al., 2018; Chen et al., 2021a). These three stresses result in the major energetic cellular imbalance and ROS production, and are best studied in model plants, especially *Arabidopsis* (e.g. Kilian et al., 2007; Rasmussen et al. 2013). De Vries et al. (2018) systematically compared KCM (basal) vs. ZCC (Zygnematophyceae – see above) Charophyta and concluded "...ZCC-grade streptophyte algae have a more fine-tuned stress response, especially toward cold." Intimate connection between drought and cold/freeze stresses is well documented in CBF/DREB transcription factors (C-repeat binding factor/ dehydration responsive element binding factor) in both stresses, and it is clear their evolution was boosted in Streptohytes and especially in lineage going to Embryophytes (Jiao et al., 2020; Rensing 2020). Activation of DREB TFs is positively regulated by ICE1 (Inducer of CBF expression 1) transcriptional regulator which is a direct target of OST1 kinase (Zhu 2016; Chen et al., 2021a). SNF1-related protein kinases2 (SnRK2) protein kinase family member Open Stomata1 (OST1), which was originally identified for its role in stomatal closure (Mustilli et al., 2002), is the central regulator of cold-signalling pathway – and not only in the *Arabidopsis* via activation of DREB TFs (Lamers et al., 2020; Chen et al. 2021a). Already the CKIN2 (A) family of chlorophytic *Chlamydomonas reinhardtii* is closely related to the land plant SnRK2, and contains a conserved SnRK2 box and ABA box (but without relation to ABA-dependent signalling which evolved later in Streptohytes - Embryophytes) after the kinase domains (Komatsu et al., 2020). ABA box of *C. reinhardtii* CKIN2 (A) is smaller and contains fewer acidic residues than in *Arabidopsis*. Obvious SnRK2s with an ABA box similar to that of land plants have been identified in *Klebsormidium* (Komatsu et al., 2020). The overall conservation of sequence structure and gene expression profile strongly suggests a link between CKIN2 and abiotic stress response regulation. Indeed, many CKIN2s are expressed in response to abiotic stresses, such as hyperosmolarity, ultraviolet (UV) radiation exposure and low temperatures (Colina et al. 2019; Komatsu et al., 2020). In response to cold, SNRK2/OST1 phosphorylates the transcription factors ICE1, but also Basic Transcription Factor3 (BTF3) (Ding et al., 2015, 2018). Low-temperature-induced OST1 phosphorylation activity is up-regulated independently of the plant hormone abscisic acid (ABA), a known inducer of OST1 activity in response to osmotic stress (Ding et al., 2015). OST1/SNRK2 kinase of land plants type evolved early in Streptophyte clade and SNRK2 from *Klebsormidium nitens* does complement quadruple LOF mutant in moss (Shinozawa et al., 2019), and it would be interesting to also test its functions in cold adaptation.

Late embryogenesis abundant (LEA) proteins protect other cytoplasmic proteins from aggregation during desiccation, osmotic and low-temperature stress conditions (Shinde et al., 2012). Among several sub-clades of LEA proteins LEA2 proteins are not found in chlorophyte algae, so it seems they evolved after the split of chlorophytes from streptophytes (Becker et al., 2020). Newly evolved class of LEA proteins might provided an essential protection to cellular proteins during not only desiccation, but also cold/freeze stress. The Anydrophyta evolved two additional subfamilies for better protection (Becker et al., 2020) and we propose this happened under the Cryogenian glaciations environmental pressure.

Origin of Anydrophyta was linked to several crucial horizontal gene transfers – facilitated by the co-existence of Charophyta with different kind of microbes and fungi on the surfaces of land (Lutzoni et al., 2018; Chen et al., 2021b). Three transcription factor families (GRAS, HDKNOX2 and BBR/BPC), a homolog of the PYR/PYL/RCAR-like abscisic acid (ABA) receptor and genes involved in 1,4 b-xylan formation (GUX1-5, PARVUS) and galactan/RG I pectin synthesis (GALS1-3) were likely gained in the common Anydrophyta ancestor of Zygnematophyceae and Embryophyta (Cheng et al., 2019). Interestingly, Jiao et al. (2020) found desiccation regulating transcription factors of the GRAS and DREB families expanded in desmid *Penium* (Rensing 2020).

Evolution of land plants chloroplast – embryoplast, with all important innovations (see de Vries et al., 2016) - could be also understood as being promoted during the Cryogenian glaciations in Streptohytes and explain at least part of exaptations, which are pointed out and discussed in de Vries et al. (2016). We hypothesise that important phase of the evolution of embryoplast could be located into the Cryogenian and its glaciations – as e.g. transfer of specific genes from plastid to nuclear genome and evolution of nuclear encoded plastid RNA polymerase/NEP (De Vries et al., 2016; Cheng et al., 2019).

Exposure of early algal Streptophytes to high irradiance (including UV light) under the prevalent cold glaciation conditions of Cryogenian land surfaces might be potentially linked to the well-documented large regulatory overlap in stress gene expression reaction to high irradiance, drought and cold stresses (de Vries et al., 2017; Chen et al., 2021a). Moreover, light signal is necessary to full development of cold (not heat) acclimation (Catalá et al., 2011). It is best studied in model *Arabidopsis* where it was shown this signalling input into the cold adaptation is mediated by HY5 bZIP TF and also COP1 photomorphogenesis regulator is possibly involved (Catalá et al., 2011). While COP1 was already present in eukaryote plant ancestor, this HY5 TF evolved only in the common Chlorophyte and Streptophyte ancestor. Low-temperature pathways stimulated by HY5 includes genes encoding CHI, CHS, and FLS – three key enzymes in the anthocyanin biosynthetic pathway important not only in cold response, but especially in high irradiation protection due to their antioxidative/anti-ROS properties (e.g. recently Saigo et al., 2020). The key enzyme in the phenylpropanoid pathway PAL was acquired by horizontal gene transfer in Streptophyta (Emiliani et al. 2009, Cheng et al., 2019), and precursors of lignin biosynthetic pathway were possibly involved in stress responses and biotic interactions in basal Streptophyta (de Vries et al., 2017). Blue-light receptor phototropin (already evolved in a common ancestor of Viridiplantae; Li et al., 2015) was found to function as a cold sensor in liverwort *Marchantia polymorpha*, suggesting low-temperature and light cues are integrated immediately at the sensor level (Fujii et al., 2017). Phytochromes which are crucial not only for red-light signalling, but also for temperature-stress signalling, evolved in a common ancestor of Streptohpyta (Han et al. 2019; Wang et al., 2020) and data from Angiosperms indicate they are able to co-regulate e.g. isoprenoid metabolism in response to the temperature shift (Bianchetti et al., 2020)

Detailed experimental analysis of high light combined with cold stress in three lower branching [Mesostigmatophyceae, Chlorokybophyceae, and Klebsormidiophyceae (KCM)] and three higher branching streptophyte algae [Charophyceae, Coleochaetophyceae, and Zygnematophyeae (ZCC)] by De Vries et al. (2017 – see also above) clearly show co-regulation of high light and cold stress responses originally described in Angiosperms (esp. *Arabidopsis*) is already present in basal Streptophyta. This led De Vries et al. (2017) to conclude Embryophyte/land plant stress signalling already evolved in algal Streptophyta. Data from other studies (de Vries et al., 2020b; Wang et al., 2020 and Jiao et al., 2020) clearly support the interpretation proposed by de Vries et al. (2017) and Fürst-Jansen et al. (2020). Here we argue these basal cellular adaptations to dry land in Streptophyte lineage evolved in a long cold and freezing period of Cryogenian. So adaptations to cold oligotrophic freshwater and periodic ice/dry high-light land conditions are in fact exaptations which allowed in multicellular early Embryophytes (diverging from Anydrophytes upon the Zygnematophyceae split) continuation of final transition to the dry land in the warm Ediacaran period.

4. Zygnematophyceae diverged from multicellular Anydrophyta later in Cryogenian adapting to ice-dominated surfaces

Current dating (e.g. Jiao et al. 2020; also summarised in other timing reports) excludes the original hypothesis of Becker (2013) the Streptophytes and Chlorophytes split occurred during Cryogenian, as Streptophytes lineage started most probably already before or during the Tonian (e.g. Cheng et al., 2019; Jiao et al. 2020; Strassert et al. 2021). As we propose above - an interesting and appealing possibility opened by these recent timings – is multicellular Charophyta evolved at or even before the

Tonian and Anydrophyte clade of Streptophytes evolved at the beginning or during the first part of the Cryogenian (Jiao et al. 2020; Strassert et al. 2021). Crucial to further elaboration of our hypothesis is the dating of the diversification of Zygnematophyceae from Anydrophyta, as well as to the Cryogenian (Strassert et al., 2021). We propose Cryogenian is the scene of both. First came Anydrophyta evolution from the common multicellular Charophyta ancestor (closest relatives are Coleochaetophyceae). Then later in Cryogenian the diversification into extremely cold-adapted cryophilic early Zygnematophyceae (Conjugatophyceae) and early Embryophyta which were not reduced to single cell/filamentous level (see further); and also kept flagellated cells - sexual process based on motile gametes. It is certainly possible to speculate most less cold-adapted early Embryophyta survived Cryogenian glaciations as a minority flora in the relatively warmer edaphic refuges. And that late Cryogenian continental greening (see above Knauth and Kennedy 2009; Hoshino et al., 2017) was dominated not only by first terrestrial chlorophytes (Lutzoni et al., 2018) but also, and maybe especially, by Anydrophytes and later also extremely well cold-adapted early Zygnematophyceae. So in contrast to Knauth and Kennedy (2009) who speculate about expansion of a primitive land biota possibly composed of protists, mosses, fungi and liverworts starting at least by 1 Ga year ago we propose this biota originally formed mostly by different groups of green algae included after the beginning of Cryogenian, and streptophytic Anydrophytes – which split later during the Cryogenian – into extremely cold-adapted and reduced (from multicellular to unicellular status – see following chapter) early Zygnematophyceae and early Embryopyta lineages.

Already Stebbins and Hill (1980) argued the same evolutionary constraint of dry land drove the convergent evolution of Zygnematophyceae and zygomycetous fungi (including Mucoromycota; former Zygomycota - Naranjo– Ortiz and Gabaldon 2019b; Chang et al., 2021) - loss of flagella and sexuality by conjugation. "'Zygomycetous' refers to a paraphyletic phylum (Zygomycota), and this in turn to a sexual structure, the zygospore, that is common to most lineages ascribed to it" (Naranjo–Ortiz and Gabaldon 2019b). These authors put forward a hypothesis to explain fungal terrestrialzation which involves icy environments as facilitators of the transition from water to terrestrial environments. They elaborate following scenario: "following course of events for fungal terrestrialization: (i) Snowball Earth scenarios created a diversification of microbial niches. This is not a necessity, since ice environments are not exclusive to ice ages, but the timing of the diversification suggests that it might have played an important role. (ii) Fungi arrived in ice environments as zoosporic predators of algae. (iii) Highly osmotic microniches and accumulation of algal necromass favoured the development of hyphal growth and true osmotrophy to exploit these nutrient sources effectively even in limited time windows. (iv) Intermittent conditions favoured the development of resistant resting spores" (Naranjo– Ortiz and Gabaldon 2019b). Here we further elaborate their hypothesis and indicate that as loss of flagella and sex by conjugation of zygomycetous fungi coincides with the Cryogenian glaciations (Taylor and Berbee, 2006; Lutzoni et al., 2018; Naranjo – Ortiz and Gabaldon 2019a; Chang et al., 2021) so the split of Zygnematophyceae from Anydrophytes happened under the same selective pressure of Cryogenian glaciations. Sexuality based on mere conjugation without flagellated gametes possibly facilitated in zygomycetous fungi and Zygnematophycea in a more effective and therefore evolutionarily more adaptive lifecycle as compared to flagellated gametes mediated sexuality of other Cryogenian land-inhabiting organisms. It is generally accepted that in contrast to microbes or single-cell organisms the lower limit for completion of the lifecycle in multicellular organisms (with the exception of endothermal animals) appears to be between 0 - 2 °C (Clarke 2013). In glacial conditions especially basal bodies and flagella are so functionally constrained even snow-adapted Chlorophyte flagellates *Chlamydomonas nivalis* and *Haematococcus pluvialis* become cysts in response to cold stress (de Carpentier et al., 2019), and after a temperature downshift Chlamydomonas cells resorb their flagella (Valledor et al., 2013). Microtubular cytoskeleton is also sensitive to cold conditions in plants (Nick 2013) and it is generally accepted cold stable MT networks are much less dynamic while dynamic MTs are overly sensitive to cold (Wallin and Stromberg 1995).

Overall preference of basal extant Zygnematophyta to bare ice or extremely oligotrophic acidic fresh water might still bear witness to this original early zygnematophytes Cryogenian adaptation. So not only chlorophytes (Lutzoni et al., 2018), but also anydrophytes and early zygnematophytes and early embryophytes co-evolved and radiated contemporaneously with land fungi already in Cryogenian explaining early evolution of symbiosis regulating genes in Streptophytes (deVries and Archibald 2018; de Vries et al., 2020a). As shown by streptophyte algal genus Spirotaenia, which has been shown to be a member of the Mesostigmatophyceae (Gontcharov and Melkonian 2004; Wickett et al., 2014) conjugation in streptophyte green algae is a homoplasious feature; the result of independent convergent evolution (Cheng et al., 2019) – in both cases potentially linked to glaciation conditions.

Stress-resistant zygospores of Zygnematophyceae are covered by surface cell wall sporopolenin-like material (Permann et al., 2021) so we looked into known Cryogenian acritarchs and, despite an overall reduction in acritarchs diversity during the Cryogenian (Huntley et al., 2006), few new types of acritarchs appeared which seem possible to be potentially interpreted as Zygnematophyceae zygospores (Moczydlowska 2008) even on the ultrastructural level (Moczydlowska et al., 2010). This possibility will certainly require the attention of specialists in the future (see also Discussion – Moczydlowska and Liu 2020).

5. Evolutionary reduction from multicellularity of Anydrophytes to single-cell or filamentous status in Zygnematophyceae

Despite the lack of a systematic analysis it is generally assumed Zygnematophyceae evolved by reduction or loss of morphological complexity – based on the loss of not only flagella, but also of plasmodesmata and apical tip growth (Moody 2020). This assumption is also well supported by the topology of the phylogenetic tree, as both the sister clade of Anydrophyta (*Coleochaet*e) and the sister clade of Zygnematophyceae (Embryophyta) are multicellular. It was proposed the different mechanisms of cell division between land plants and Zygnematophyceae results partially from simplification of the phragmoplast of the putative common ancestor (Anydrophyte) in the Zygnematophyceae; in more derived desmids phragmoplast is lost totally (Buschmann and Zachgo, 2016). To support the idea of secondary Zygnematophyceae simplification we propose using recently published analyses of early evolution of land plant receptor kinases (Gong and Han 2021) and several reports on transcription factors evolution. Comparison of independently evolved multicellular organisms indicates evolutionary multiplication of receptor kinases and transcription factors – both crucial mediators of intercellular communication and tissue differentiation – are a convergent feature of multicellular animals, land plants, Chlorophytes and brown algae (Cock et al., 2010; de Clerk et al. 2018). Comparing data from Cheng et al. (2019), Gong and Han (2021) and Jiao et al. (2020) we conclude that not only Lys-M symbiosis-related and SD receptor kinases are lost in Zygnematophyceae (Cheng et al., 2019; Gong and Han 2021), but overall kinase-associated domains types are significantly reduced in Zygnematophyceae as compared to Chara or Embryophytes (Gong and Han 2021). But the exceptionally high number of different types of transcription factors still retained in single-cell Zygnematophyceae might be understood considering secondary reductions in structural complexity into the unicellular status are not necessarily accompanied by reductions in total transcription factors complements as proposed by Jiao et al. (2020). Using the ratio between evolutionary losses and gains of genes orthologous groups as a proxy of evolutionary reduction it is obvious in Zygnematophycea losses significantly prevail – even in contrast to quite a big proportion of losses in Chara (0.8 in *Chara brownii* against 1.2 in *Spirogloea muscicola* and 1.0 for *Mesotaenium endlicherianum* – based on Cheng et al., 2019). All these features of

Zygnematophyceae compared to sister clades support the idea of secondary reduction of multicellularity of parental Anydrophyte clade in Zygnematophyceae lineage. This secondary simplification of Zygnematophyceae also fits well to above discussed differences between lower temperature limits for unicellular (- 20°C) vs. multicellular (around 0°C) organisms in respect to lifecycle completion (Clarke 2013).

Discussion and summary

Only relatively recently (2015) the beginning of Cryogenian was shifted from 850 Ma to 720 Ma, and the very nature of Cryogenian period is subject of vivid and ongoing discussions. Therefore data published on Cryogenian until 2015 (e.g. acritarchs) should be carefully reconsidered in this new context. For our point here, however, the general consensus Cryogenian was millions of years of extremely cold climate dominated by continental glaciations is sufficient. Based on different authors, scenarios for the climate extremity ranges from severe “Snowball Earth” to mild “Slushball Earth” (Hofmann et al., 2017; Bai et al. 2020 – Marinoan red beds). With the interruption of more than 10 millions of years of warmer interlude, it lasted about 80 million years/Myr.

The crucial contentious point for our hypothesis is the dating/timing of major evolutionary splits in the Streptophyte lineage. Late dating of Streptophytes establishment to late Tonian/early Cryogenian and Anydrophyte split to Zygnematophyceae-Embryophytes to late Ediacaran or Cambrian, as proposed by Morris et al. (2018a), is challenged directly first by Hedges et al. (2018) and very recently by several reports – but especially relevant are Nie et al. (2020), Jiao et al. (2020), Su et al. (2021), Strassert et al. (2021) and Moczydlowska and Liu (2020). These authors use different approaches for dating calibrations. Su et al. (2021) based solely on Archeplastida data, comparing three dating strategies, propose Streptophyte lineage establishment in Paleoproteozoic/Mesoproterozoic and Anydrophyta establishment, and also diversification into Zygnematophyceae and Embryophyceae in late Tonian or Cryogenian. Strassert et al. (2021) are using a robust approach for their calculations involving the context of whole Eukaryota and common ancestor of Coleochaete and Embyophyta - i.e. immediate ancestor of Anydrophytes – is placed essentially within the Cryogenian era. As stressed by Su et al. (2021): “We found that studies favoring a Neoproterozoic origin of land plants (980–682 Ma) are informed more by molecular data whereas those favoring a Phanerozoic origin (518–500 Ma) are informed more by fossil constraints. Our divergence time analyses highlighted the important contribution of the molecular data (time-dependent molecular change) when faced with contentious fossil evidence.” Critically important evaluation of how clock-partitioning and fossil calibration strategies affect uncertainty of evolutionary timescales of green plant evolution allows, and indicates again possible establishment and diversification of Anydrophytes in the Cryogenian (Nie et al. 2020). Timescale ranges of dry-land fungi plant co-evolution also allows there is a small probability the terrestrial colonization by Embryophyta could have occurred as early as 727 Ma (i.e. around the beginning of Cryogenian; Lutzoni et al. 2018). Timescales by Jiao et al. (2020) also permit Cryogenian as possible time of Anydrophytes origin and late Cryogenian as Zygnematophytes differentiation (Suppl. Tab. S1E in Jiao et al. 2020). We can therefore conclude Cryogenian period as possible time of Anydrophyte origin and diversification of Zygnematophyceae is well permitted by the current available time-calibrated phylogeny timing data. This is in agreement with "early" pre-Cryogenian and possibly pre-Tonian timing of the establishment of multicellular Charophytes (Su et al., 2021) and is well fitting with a clear evidence Chlorophyte and Red algae were already well established 1400 Ma (recently based on fossils analyses Zhang et al. 2021; Archeplastida origins 1900 Ma – e.g. Strassert et al., 2021), while acritarchs with clear Desmids affinity are present in early Ediacaran (Moczydlowska and Li, 2020; see also further).

Current plant terrestrialization timing debate (see above, Fig. 1) – including the emergence of Anydrophytes and Zygnematophyceae streptophytic clades - permits to consider seriously Cryogenian Snowball Earth with continents covered by snow, ice and (periodic) cold water masses as a period relevant to shape plant cellular and developmental adaptations to continental dry land. Importantly – regardless in fact of exact dating of Chlorophyte and Streptophyte clades divergences – it is clear all green algae inhabiting Cryogeninan continents had to adapt to specific chronic glaciations conditions. See, for instance. an interesting comparative case study for *Draparnaldia* chlorophyte aerophytic alga from order Chaetophorales (Caisová 2020). Recent advancements in deep-plant phylogenetics unequivocally resolves *Mesostigma* and *Chlorokybus* as most basal clade of Streptohyta (Wang et al.; 2020). It might not therefore possibly be in this context and accidental these extant basal Charophyta are oligotrophic, cold adapted and in case of e.g. *Chlorokybus atmophyticus* also aerophytic species. Considering the hypothesis of tens of millions of years of adaptation to cold Cryogenian we should accept all early Streptophyta lineages living under such conditions were fully adapted to different versions of such glacial environment – i.e. they were to different degree psychrophilic or cryophilic - and our current ambient temperature conditions would be a heat stress conditions for them - with an important exception of polar mountains and alpine regions. Evolution of Cryogenian psychrophilic land flora of Chlorophyta, Anydrophyta, and later in Cryogenian and also Zygnematophyceae, might not only explain at least part of the geochemical greening of Neoproterozoic (Knauth and Kennedy, 2009; Hoshino et al., 2017), but have contributed to the possible rise in oxygen level before the end of the Cryogenian along with oceanic algal plankton (several models in Cole et al., 2020).

Based on the diversification estimates of Chlorophyte vs. Streptophyte algae in early 21st century and appreciation of Cryogenian as an important evolutionary driver for photosynthesis mechanisms evolution Becker (2013) proposed an interesting hypothesis that Snowball Earth conditions of long Cryogenian era of Neoproterozoic was the time of evolutionary split leading to the divergence between the Streptophyta and Chlorophyta lineages. Based on improved current time-calibrated phylogeny calculations we are suggesting Cryogenian cold and dry continents were the arena for the evolutionary origin of common Embryophyte-Zygnematophyceae ancestor Anydrophyta, and due to extended duration of global glaciations Zygnematophyceae split off by simplification from Anydrophyta as a cryophilic flora still happened in later stages of Cryogenian. Well-established regulatory interconnection between cold/freeze, high light and drought stress physiological responses is possibly best illustrated by the DREB/CBF transcription factor family regulating drought and cold stress responses (Lamers et al., 2020; Chen et al. 2021a - see above). Light input into the cold adaptation analysed in extant model plants (e.g. *Arabidopsis* or *Marchantia polymorpha*; it also includes regulation of anthocyanins ROS inhibitors biosynthesis in cold; see above) mediated via both red light and blue light receptors affecting DREB/CBF transcriptional regulation (Fujii et al., 2017; Shi et al., 2018; Bianchetti et al., 2020) also indicates this feature for Anydrophyta as strongly supported by comparative cold and light stress experiments with basal Charophyta vs. Zygnematophyceae (deVries et al., 2018). It is inevitable both green algae lineages - Chlorophyta and Streptophytes - inhabiting surfaces of continents during the Cryogenian era had to pass the same extended environmental bottleneck and constraint. That resulted in the evolution of important cellular and physiological adaptations which functioned as exaptations/preadaptations in early Embryophyta for further terrestrialization continuing in warmer Ediacaran and early Paleozoic. This is in agreement with the original hypothesis of Stebbins and Hill (1980) updated by Harholt et al. (2016) and nicely experimentally supported by de Vries et al. (2018) that terrestrialization already started on the single-cell level in algae. This interpretation was, however, not adopted by Bowles et al. (2020) who proposed a separation of the genomic origins of first multicellularity and only then the terrestrialization stress adaptations in plants. In fact our hypothesis that already multicellular Charophytes evolved into Anydrophytes (and reduced into Zygnematophycea) during Cryogenian and made during this epoch crucial dry-land adaptations (also at the cellular level) is also in agreement with this Bowles et al. (2020) two-step scenario. We consider, however, based on our adopted timing scenario, that Charophytes dry land adaptations really started in Streptophytes on single-cell level in late Mesoptoterozoic - early Neoproterozoic/Tonian (i.e. before Cryogenian glaciations) and led in Mesoproterozoic or Tonian to the establishment of multicellular Charophytes (see timings above). So Streptophytes entered Cryogenian not only as land-adapted single-cell/colonial or filamentous algae (*Chlorokybus*, *Klebsormidium*), but also in multicellular Charales/Coleochateophyceae status and Anydrophyta evolved as an adaptation of already multicellular Charophyta to the Cryogenian harsh glacial conditions. Due to an extended selective pressure of 80 Ma years of Cryogenian glacial conditions Zygnematophycea evolved by secondary simplification from Anydrophytes still in Cryogenian as cryophlic algae with a lifecycle (i.e. sexual process) optimised for cold and dry conditions. It is accepted in the same period zygomycetous fungi (originally Zygomycota) also lost the flagella and evolved conjugation as a mechanism of sexual reproduction (Liu et al., 2006; Taylor and Berbee, 2006; Lutzoni et al., 2018; Naranjo - Ortiz and Gabaldon 2019; Chang et al., 2021). The hypothesis the same selective pressure of dry land stress conditions resulted in an independent evolution of conjugation in algae and fungi was originally proposed by Stebbins and Hill (1980). We believe an independent convergent (homoplasy) evolution of conjugation in zygomycetous fungi and Zygnematophyceae supports our whole concept, that Zygnematophyceae evolved under the same Cryogenian selective environmental conditions as zygomycetous fungi.

Emergence of Zygnematophyceae is expected to contribute to the acritarchs diversity (Moczydlowska et al., 2010; see above) and, while several morpho-types of acritarchs allow zygospore interpretation, during the Tonian and Cryogenian virtually new types of acritarchs appeared. “It shows the antiquity of certain morphologies and it suggests that the primary diversification of eukaryotes was well underway earlier than previously assumed, but it has been slow, until the Tonian-Cryogenian periods when new taxa emerged” (Agic et al., 2017). Very important support to our hypothesis is a recent report by Moczydlowska and Liu (2020) explicitly showing existence of advanced desmids-like zygospores with the Zygnematophycea affinity acritarchs at the very beginning of Ediacaran. This also makes timings of splits of Anydrophyta and Zygnematophyceae vs. Embryophyta as proposed by Morris et al. (2018a,b) very improbable.

We further support the idea of the reduction of organismal complexity from Anydrophyte multicellularity to unicellularity or filamentous growth in Zygnematophycea as the result of superadaptation to glacial conditions. As mentioned above, lower temperature limits for unicellular (-20°C) vs. multicellular (around 0°C) organisms in respect to lifecycle completion possibly played a crucial role in Zygnematophyceae evolution (Clarke 2013). In this context it might not be a pure accident basal aerophytic Zygnematophyceae are cold tolerant or directly psychro- or cryophilic (e.g. *Mesotaenium* or *Ancylonema* – Procházková et al., 2021). Loss of dependence on microtubuli-based motility of gametes during the sexual process could be explained as an adaptation for the persistent cold or freezing conditions, or lack of stable mineral substrate in both land zygomycetous fungi as well as Zygnematophyceae (see above).

We propose Anydrophytes emergence in Cryogenian was a crucial initial event in the terrestrialization and land plant evolution, and following Zygnematophyceae split off was a result of glacial habitats reductive evolutionary adaptation during extended Cryogenian period.

Conflict of Interest

The authors declare the research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

Author Contributions

Jakub Ž. and Viktor Ž. coined the initial idea of this hypothesis, and were joined from the beginning by Vojtěch Ž. with expertise in phylogenetic analyses and Martin H. with expertise in polar geology. Jakub Ž., Viktor Ž., Martin H. and Vojtěch Ž. wrote the paper. All authors read and approved the submitted manuscript.

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