Transitions between marine and freshwater environments provide new clues about the origins of multicellular plants and algae

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TRANSITIONS BETWEEN MARINE AND FRESHWATER ENVIRONMENTS PROVIDE NEW CLUES ABOUT THE ORIGINS OF MULTICELLULAR PLANTS AND ALGAE

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List of abbreviations:

APG - Angiosperm Phylogeny Group

Ca - calcium

$CaCO_3$- calcium carbonate

Cl^- - chloride

Gya - billion years ago

K - potassium

Mya - million years ago

Na – sodium

Si - silicon

Abstract

Marine-freshwater and freshwater-marine transitions have been key events in the evolution of life, and most major groups of organisms have independently undergone such events at least once in their history. Here we first compile an inventory of bidirectional freshwater and marine transitions in multicellular photosynthetic eukaryotes. While green and red algae have mastered multiple transitions in both directions, brown algae have colonized fresh water on maximally six known occasions, and angiosperms have made the transition to marine environments only two or three times. Next we review the early evolutionary events leading to the colonization of current habitats. It is commonly assumed that the conquest of land proceeded in a sequence from marine to freshwater habitats. However, recent evidence suggests that early photosynthetic eukaryotes may have arisen in subaerial or freshwater environments and only later colonized marine environments as hypersaline oceans were diluted to the contemporary level. Although this hypothesis remains speculative, it is important to keep these alternative scenarios in mind when interpreting the current habitat distribution of plants and algae. Finally we discuss the roles of structural and functional adaptations of the cell wall, reactive oxygen species scavengers, osmoregulation, and reproduction. These are central for acclimatization to freshwater or to marine environments. We observe that successful transitions appear to have occurred more frequently in morphologically simple forms and conclude that, in addition to physiological studies of euryhaline species, comparative studies of closely related species fully adapted to one or the other environment are necessary to better understand the adaptive processes.

Keywords: Macroalgae, aquatic plants, marine-freshwater and freshwater-marine transitions, adaptation, evolution

1. FRESHWATER AND MARINE HABITATS

Water bodies cover 71% of the Earth’s surface, either as oceans, lakes, rivers or as ice (Ott 1988). Approximately 97.6% of all water on Earth is saline and only 2.4% is fresh water (although estimates vary depending on the author). Most of this fresh water is found as groundwater or as ice, and only 0.009% occurs within lakes and rivers (Wetzel 2001). Fresh water is defined as water with a salinity ≤ 0.5 g dissolved salts$\cdot L^{-1}$ (International Symposium for the Classification of Brackish Waters 1958), and the global average for lakes and rivers is 0.12 $g\cdot L^{-1}$ of salt (Wetzel 2001). The reason for differences in salinity among water bodies is the water cycle: surface water (both salty and fresh) evaporates and precipitates as fresh water. A part of this fresh water precipitates on land and gradually flows back to the sea, dissolving and transporting salts on its way. In parallel, the evaporation of large basins in combination with the rise of land masses generates new terrestrial salt reserves. Ocean salinity has been modeled to have varied over the last 600 My between 30 to 60 $g\cdot L^{-1}$ with a current mean of 35 $g\cdot L^{-1}$ (Hay et al. 2006). Mainly the sodium(Na)/potassium(K) balance in seawater is thought to have shifted in favor of Na over time due to the higher potential of K to bind to clay and thus to be removed from seawater (MacIntyre 1970).

Seawater is not just a concentrated version of fresh water, as a number of processes impact ion distribution in each environment. For one, salts (including nutrients) are washed into the ocean at different rates. Thus, the availability of macro- and micronutrients differs significantly between freshwater and marine environments. Primary production in the majority of freshwater ecosystems is most often limited by the availability of phosphorus (Schindler 1977), whereas marine environments are primarily limited by nitrogen (Hecky and Kilham 1988; Zehr and Ward 2002) or trace elements such as iron (Martin et al. 1990). Also, once eluted from the soil, calcium ions (Ca^{2+}) readily precipitate as calcium carbonate ($CaCO_3$), whereas Na^+ remains in solution and is efficiently transported to the ocean.

Freshwater environments are therefore mainly Ca^{2+}-dominated whereas seawater is Na^{+}-dominated. Nevertheless, there is usually more total carbonate in marine environments, compared to fresh water (Table 1).

Fresh water composition depends more on the surrounding terrestrial environment and is highly variable compared to seawater. Factors that influence fresh water composition include chemical interactions with the soil, the geological context, weathering, precipitation (quantity and quality), temperature, stream discharge, nutrient uptake, and physical and biological transformations (Feller 2009). Geologists distinguish between rock-dominated and precipitation-dominated fresh water (Gibbs 1970). Rock-dominated fresh water is usually found at higher altitudes and salt concentrations are highly dependent on the material of the basin; it is usually rich in silicate (Si) and K. Precipitation-dominated fresh water occurs primarily in leached areas with high rainfall. Its ion composition reflects that of the rain, with ions occurring in similar proportions as in seawater, even in water bodies that are far inland. Finally, evaporation has a strong impact on the ion composition of fresh water, increasing salinity and removing $CaCO_3$ due to precipitation from solution.

Life on Earth is generally thought to have originated ~4 billion years ago in primordial, hypersaline oceans (Martin et al. 2008) with salinities $> 80\ g \cdot L^{-1}$ (Pinti 2005). From there, bacteria and eukaryotes gradually colonized freshwater and then terrestrial environments. Recently, an alternative scenario has been proposed in which life first arose in non-marine settings (*i.e*. subaerial or freshwater) (Wellman and Strother 2015) and only later colonized marine habitats. It is possible that early eukaryotes including the ancestors of the major macro-algal lineages also originated and diversified in this non-marine setting 2-1.1 Gya, and that the colonization of marine environments may have been stimulated during times of lethal land surface conditions. In either scenario, habitat transitions were key events in the early evolution of photosynthetic, multicellular eukaryotes.

However, most extant lineages - from archaeans to metazoans - are found in both fresh water and seawater, indicating that each of them also independently made a transition between these environments at least once in their recent evolutionary history. When, how often, and under what conditions these transitions have occurred (and can occur) are questions fundamental to our understanding of habitat diversification in the broadest sense and to explain the distribution of marine, freshwater, and terrestrial biodiversity.

In this review, we first compile an inventory of extant marine-freshwater and freshwater-marine transitions in multicellular, photosynthetic eukaryotes (Figure 1) and then discuss our findings in the context of current hypotheses about their evolutionary and geological history. We define multicellular photosynthetic protists/algae as a physically connected set of genetically identical cells with the ability to produce distinctive reproductive structures, although we also included some siphonous algae in our review. We consider an alga as marine if it naturally occurs and reproduces in seawater (see above), and as freshwater, if it naturally occurs and reproduces in fresh water (salinity $\leq 0.5\ g \cdot L^{-1}$). Species found in brackish water are, in almost all cases, also able to tolerate marine conditions and were thus considered marine. Terrestrial species are those found outside of waterbodies, although some species also occur in fresh water, and some might require regular exposure to fresh water (e.g. abundant rain for reproduction). Please note that, across the different lineages examined in this review, particular taxonomic ranks (families, genera, species) are not always equivalent.

2. CENSUS OF MARINE-FRESHWATER AND FRESHWATER-MARINE TRANSITIONS

Unicellular and non-photosynthetic multicellular organisms

Unicellular protists and bacteria occur in extremely large populations with generally short generation times and fast evolutionary rates (Baer et al. 2007). These properties facilitate large-scale dispersal into different environments. Nevertheless, in a recent study Logares et al. (2009) demonstrated that among these organisms, separate clades have adapted to either marine or freshwater environments, a separation probably due in part to the energetic costs associated with osmoregulation and ion homeostasis.

Multicellular organisms (with exceptions) are generally characterized by comparatively smaller population sizes, longer generation times and a slower rate of evolution (Baer et al. 2007). Nevertheless, many of these lineages too, are found in both marine and freshwater environments. In animals, marine to freshwater transitions (and vice versa) have been particularly well-studied in fish (Vega and Wiens 2012). In addition, several species of fish are also able to migrate between fresh water and seawater in the course of their lives. These diadromous fish rely on specialized membrane transporters and compatible osmolytes to adjust intracellular osmolarity and ion concentrations. Active osmoregulation, however, depends on a sufficient supply of energy. Plants and macroalgal species that live permanently submerged have to deal with reduced light quality and quantity and thus reduced energy supply. Adaptations in photosynthetic pigments (Dawes 1998) and/or specific structural and physiological adaptations related to osmotolerance for marine vs. freshwater conditions are therefore required (see section 4).

Archaeplastida

The supergroup Archaeplastida or Plantae (includes: Glaucophyta, the Viridiplantae, and the Rhodophyta) arose from a primary endosymbiosis event with a cyanobacterium and a heterotrophic eukaryote (McFadden 2001). It is the most diverse group of multicellular photosynthetic eukaryotes, reaching substantial abundances in marine, freshwater, and terrestrial habitats. The Glaucophytes are rare, unicellular organisms at the root of the Archaeplastida that occur predominantly in fresh water, although recent 18S metabarcoding data from the Tara Oceans Project revealed glaucophyte sequences in oceanic environments (see Supplementary dataset W5 in de Vargas et al. 2015). The Viridiplantae (the green lineage) split into two monophyletic groups, the Streptophyta, and the Chlorophyta, approximately 1,200-750 million years ago (Becker and Marin 2009) and includes green algae, charophytes, and terrestrial plants. Rhodophytes (red algae) are mainly multicellular marine algae but also comprise freshwater and a very few, partially terrestrial species (Sheath and Vis 2015).

Streptophyta

The most basal multicellular streptophytes are the Klebsormidiophyceae (Figure 1A). They are small, filamentous freshwater and terrestrial algae; only 41 different species of this class are currently registered in AlgaeBase (Guiry and Guiry 2015). Some members of the Klebsormidiophyceae can survive and grow in saline waters up to 60 $g \cdot L^{-1}$ (Karsten and Rindi 2010), and *Klebsormidium marinum* (Deason) P.C.Silva, K.M.Mattox & W.H.Blackwell has been found close to the sea (Deason 1969). However, we are unaware of any confirmed findings in marine environments. The Zygnematophyceae (= Conjugatophyceae) is a group of small unicellular or filamentous algae with over 3000 species (Guiry and Guiry 2015). Among them, the Zygnematales are generally considered a freshwater order (Lee 2008), although a few findings of *Spirogyra* spp. have also been recorded from saline lakes (Hammer 1986) and estuaries (Attrill 1998). The second order within this class, the Desmidiales, comprises thousands of microscopic freshwater species (Brook 1981; Hall and Mccourt 2015). The multicellular representatives (*Spondylosium, Desmidium, Onychonema, Hyalotheca*, *Cosmocladium*, *Groenbladia*, *Sphaerozosma*) (McCourt et al. 2000), are almost exclusively freshwater organisms. To our knowledge, the only (possible) exception is an unconfirmed report of *Sphaerozosma vertebratum* Brébisson ex Ralfs from Indian coastal waters (Thayalan et al. 2013). The Coleochaetophyceae, with ~35 species, are also predominantly found in fresh water (Cook and Graham 2016).

Higher morphological complexity, including tissue differentiation and more elaborate body plans, is found in the Charophyceae, comprising only a single order, the Charales (Lee 2008). Charales, also called stoneworts due to the fact that some species in the group can become heavily calcified, are closely related to terrestrial plants. Their thalli can be up to 1 m long, and they form underwater meadows in freshwater ponds and streams. Although the vast majority of the ~700 known species of Charales (Guiry and Guiry 2015) grow in fresh water (John and Rindi 2015), there are also examples from brackish water, notably in the upper Baltic Sea (Schubert and Blindow 2004) and salt-contaminated lakes in Australia (Burne et al. 1980). *Lamprothamnium* spp. generally inhabit estuaries and coastal pools where the salinity can vary rapidly between fresh and full strength seawater. *Tolypella salina* R.Corillion is found in salt marshes along the French Atlantic coast (Lambert et al. 2013), while the majority of *Tolypella* species occur in fresh water. It may be assumed that within the Charales at least two independent transitions from freshwater to marine environments have taken place.

The largest group of streptophytes are the Embryophyta (land plants). They separated from the charophytes and the Zygnematophyceae (Wodniok et al. 2011), and colonized a terrestrial habitat approximately 470 million years ago (Sanderson et al. 2004). Embryophytes are currently estimated to comprise 200,000 to 450,000 species (Scotland and Wortley 2003). About 4,500 of them live in aquatic[1] environments. However, Les et al. (1997) estimated that only 130 species of land plants have entirely returned to fully submerged aquatic environments. This is presumed to have happened during several independent transitions, which have occurred in the Alismatidae, the Ceratophyllaceae (Ceratophyllales), and Callitrichaceae (Asterids). While in the cases of Ceratophyllaceae and Callitrichaceae the entire families are restricted to fresh water (possibly due to their lack of roots and rhizomes) (Arber 1920), five families within the lower monocot order Alismatales made the transition to

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[1] Please note that our use of aquatic includes both fresh water and seawater

marine environments on at least two occasions (Figure 1B). As the sister-group of each of the marine groups of seagrasses is found in fresh water, and as freshwater forms are clearly more common than marine forms, a transition from fresh water to seawater is more parsimonious than a direct transition from terrestrial environments as noted by Les et al. (1997). In addition, there may have been a secondary re-colonization of freshwater environments by a marine ancestor within the Potamogetonaceae (suggested in Figure 1).

Chlorophyta

Approximately 80% of the >6,000 green algal species (Guiry and Guiry 2015) are freshwater and about 20% are marine or brackish species (John and Rindi 2015). Microscopic species are usually found in fresh water and macrophytic taxa in marine waters (John and Rindi 2015). Multicellular chlorophytes have developed in four lineages, the Palmophyllales (Mamiellophyceae), the Trebouxiophyceae, the Chlorophyceae, and the Ulvophyceae (Leliaert et al. 2012). Here, we attempt to give an overview of marine-freshwater or freshwater-marine transitions in these classes, keeping in mind that for many of the species, molecular phylogenies are lacking and highly convergent morphology severely limits the utility of morphological classification.

The Palmophyllales constitute a small group of early-branching chlorophytes with only three genera (*Palmophyllum*, *Verdigellas*, and *Palmoclathrus*) restricted to deep-water or low light marine environments (Zechman et al. 2010; Leliaert et al. 2011).

The Trebouxiophyceae comprise ~700 species (Guiry and Guiry 2015), of which some members enter symbiotic relationships with fungi to form lichens, while others are common in freshwater plankton. Although this group consists mainly of unicellular or simple colony-forming representatives, the Microthamniales, Phyllosiphonales, and Prasiolales also form filaments and simple thalli. Freshwater forms comprise the majority of the Trebouxiophyceae, and multicellular representatives include only freshwater (Microthamniales) and terrestrial forms (Phyllosiphonales). To our knowledge, there are no known multicellular marine forms within the Trebouxiophyceae (Leliaert et al. 2012). At least one clade of the Prasiolales, however, frequently occurs in the supralittoral of cold-temperate and polar oceans, and a few species can be cultivated in vitro in full-strength seawater medium (Rindi et al. 2007; Heesch et al. 2016).

The Chlorophyceae comprise ~3,500 species (Guiry and Guiry 2015), many of which are unicellular or colonial (notably the Chlamydomonadales). These groups are not included in this review. Among the filamentous forms, most occur primarily in fresh water (John and Rindi 2015), although several freshwater to marine transitions have occurred. One freshwater to seawater transition probably arose in the Chaetopeltidales, a freshwater/terrestrial order that also comprises marine species in the genus *Pseudulvella* (Sanchez-Puerta et al. 2006). While mostly from fresh water, the Chaetophorales (Caisová et al. 2011 and references therein), comprise eleven marine or partially marine genera (*Arthrochaete*, *Didymosporangium*, *Elaterodiscus*, *Endophyton*, *Entodictyon*, *Gongrosira*, *Kymatotrichon*, *Protoderma,* *Sporocladopsis*, *Uronema, Thamniochloris*; see e.g. Lee 1980; Nielsen 1988; Stuercke and McDermid 2004).

The Ulvophyceae are a very diverse group of multicellular green algae with ~1,700 species (Guiry and Guiry 2015), including unicellular, multicellular, siphonous/coenocytic (single cell with multiple nuclei), and siphonocladous (several cells each with multiple nuclei) forms. Different groups are thought to have independently evolved multicellularity (Cocquyt et al. 2010a). The Ulvophyceae are mainly marine, but some species are also found in freshwater (Ichihara et al. 2009a) or terrestrial habitats. A few orders of Ulvophyceae such as the Scotinosphaerales and the Oltmannsiellopsidales are not included here as they comprise only simple or unicellular algae (e.g. Škaloud et al. 2013 and references therein).

Within the multicellular Ulvophyceae, only the Trentepohliaceae (~100 species; Guiry and Guiry 2015) are thought to contain exclusively terrestrial/freshwater species (Lopez-Bautista 2006). Its sister clade, comprising the Cladophorales, Bryopsidales, and Dasycladales (Cocquyt et al. 2010b), together accounting for >1,000 species (Guiry and Guiry 2015), is predominantly marine. The Bryopsidales include siphonous and siphonocladous algae that can form dense seabed meadows. All known members are marine. This order also comprises the invasive species *Caulerpa taxifolia* (M.Vahl) C.Agardh. The Cladophorales are generally considered a marine order, but freshwater taxa are known from both of its principal clades (Hanyuda et al. 2002), thus corresponding to at least two independent adaptations. One clade comprises the genera *Aegagropila* (freshwater, including the so-called lake balls or Marimo balls), *Pithophora* (freshwater), *Arnodiella* (freshwater), *Wittrockiella* (marine), and some *Cladophora* (marine and freshwater). Of the species examined by Hanyuda et al. (2002), the second clade comprises only two species (*Rhizoclonium hieroglyphicum* (C.Agardh) Kützing and *Cladophora glomerata* (L.) Kützing) that occur in seawater and fresh water, and the remaining 29 are marine. The Dasycladales are mainly unicellular or siphonous and are dominantly marine (Lee 2008), although e.g. *Batophora oerstedii* J.Agardh was also found in freshwater environments (Valet 1979).

The Ulotrichales are a heterogeneous group of primarily uniseriate, filamentous green algae comprising ~170 species (Guiry and Guiry 2015). They are found in marine, brackish, freshwater, and terrestrial environments (e.g. Friedl and O'Kelly 2002; Lee 2008 and references therein). As the morphology of these species is highly variable and few molecular phylogenies are available, the number of transitions between freshwater and marine environments cannot be estimated. In some cases species thought to belong to the same genus have different habitat preferences (e.g. *Codiolum kuckuckii* Skottsberg & Levring (freshwater; Silva and Chacana 2005) vs. *Codiolum brevipes* Foslie (marine; Lokhorst and Trask 1981);

Ulothrix zonata (F.Weber & Mohr) Kützing (freshwater; Graham et al. 2004) vs. *Ulothrix implexa* (Kützing) Kützing (marine; Bartsch and Kuhlenkamp 2000)).

The Ulvales, represented by >300 species (Guiry and Guiry 2015), are characterized by a cylindrical or sheet-like morphology (Lee 2008). The Bolbocoleaceae and the Phaeophilaceae are considered marine (e.g. Hauck 1876; Wynne 2011), while the Cloniophoraceae are found only in freshwater or brackish environments. Members of the genus *Dilabifilum* are found mainly in freshwater or terrestrial habitats (John and Rindi 2015) but also hypersaline environments (Vinogradova and Darienko 2008). The largest families within the Ulvales, *i.e.* the Kornmanniaceae, Ulvaceae, and Ulvellaceae, are represented by both freshwater and marine taxa, though they are mainly marine (Wehr and Sheath 2003). In each of these families, it is likely that multiple independent colonizations of fresh water have occurred. For example, most members of the genus *Blidingia* are marine, but some populations of the otherwise marine *Blidingia marginata* (J.Agardh) P.J.L.Dangeard ex Bliding have been encountered in fresh water (as *Blidingia minima* var. *ramifera* Bliding, nom. inval.) (Iima et al. 2004). Four species in the genus *Pseudendoclonium* (*P. akinetum* Tupa, *P. basiliense* Vischer, *P. laxum* D.M.John & L.R.Johnson, and *P. prostratum* Tupa) have been described from fresh water (Tupa 1974; Whitton and John 2014). This may well constitute another transition, although the monophyly of the genus remains questionable (Mullins 2007). Most species within the Ulvaceae are marine or brackish water species, but several independent transitions to fresh water have occurred in the genus *Ulva*. *U. flexuosa* Wulfen (comprising *U. intestinalis* L.; Mareš et al. 2011) and its sister species *U. meridionalis* R.Horimoto & S.Shimada (Horimoto et al. 2011) constitute the most common freshwater clade, frequently forming blooms in eutrophicated or salt-contaminated waters. A second clade consists of *U. limnetica* K. Ichihara & S. Shimada (Ichihara et al. 2009a). It is only known from freshwater bodies in Japan. Finally, *U. maeotica* (Proshkina-Lavrenko) P.Tsarenko and *U. simplex*

(K.L.Vinogradova) H.S.Hayden, Blomster, Maggs, P.C.Silva, M.J.Stanhope & J.R.Waaland have been described in marine and freshwater habitats in the Ukraine (Burova et al. 2011), but their phylogenetic relationship has not been investigated.

Within the Ulvellaceae, only two genera have freshwater representatives: *Entocladia* and *Ulvella*. *Entocladia gracilis* Hansgirg is the only freshwater species in the genus (John and Rindi 2015), whereas at least three species of *Ulvella* have colonized fresh water, *i.e.*, *U. bullata* (C.-C.Jao) H.Zhu & G.Liu, *U. tongshanensis* H.Zhu & G.Liu, and *U. prasina* (C.-C.Jao) H.Zhu & G.Liu (Zhu et al. 2015).

Rhodophyta

Red algae occur in both freshwater and marine environments (Hirano 1965; Vis and Sheath 1996). Approximately 97% of the ~7,000 described species (Guiry and Guiry 2015) are marine, occurring in both intertidal and subtidal zones. Compared with green algae, there are only very few unicellular representatives.

Freshwater species exist in almost all red algal orders (Sheath and Vis 2015): only one higher taxon of red algae, the subclass Ahnfeltiophycidae with its 11 described species, lacks freshwater representatives (Figure 1A). Most freshwater red algae live in rivers and streams rather than in lakes (Wehr and Sheath 2003). They are usually filamentous (Figure 2) and smaller than marine species, with a narrower size range from 1-10 cm vs. <1-30 cm for marine species (Sheath and Hambrook 1990).

There are also red algal species that occur in both fresh water and seawater, e.g. *Bangia atropurpurea* (Mertens ex Roth) C.Agardh and *Bostrychia moritziana* (Sonder ex Kützing) J.Agardh (Youngs et al. 1998). The related species, *Bostrychia scorpioides* (Hudson) Montagne, is common in saltmarshes worldwide. Members of the genus *Hildenbrandia* (but different species) are likewise present in both environments. Based on a molecular phylogeny of North American taxa there are several independent marine and freshwater clades (Sherwood and Sheath 1999). In European *Hildenbrandia* spp., the freshwater species form a monophyletic group, suggesting that only one transition to fresh water took place in Europe (Sherwood et al. 2002) and that the ancestral state was marine.

The Porphyridiophyceae, the Stylonematophyceae, the Compsopogonophyceae, and the Rhodellophyceae (together comprising ~130 species; Guiry and Guiry 2015) contain species whose unicellular or simple filamentous morphologies occur in both marine and freshwater environments; as do members of the subclass Nemaliophycidae (~ 900 species; Guiry and Guiry 2015). Of the eight orders three are exclusively freshwater, one is mixed and four are marine (Lam et al. 2016). Only very few microscopic species of red algae have been reported as terrestrial, notably *Porphyridium purpureum* (Bory) K.M.Drew & R.Ross (Hoffmann 1989), *P. sordium* Geitler, and *Rufusia pilicola* Wujek & Timpano (Sheath and Vis 2015).

Exclusively marine groups have mainly been confined to the Corallinophycidae (>700 species; Guiry and Guiry 2015) since members of this group have calcified cell walls (Lee 2008) (but see Charales). It was only in 2013 that the first freshwater species of Corallinophycidae, *Pneophyllum cetinaensis* Kaleb, Zuljevic & Peña, was discovered in a Croatian river characterized by extremely high pH and concentrations of calcium carbonate (Žuljević et al. 2016). Among most freshwater habitats, there is a general over-representation of red algae in softer water, however, it has been suggested that recent invaders of fresh water are restricted to ion-rich environments (Sheath and Hambrook 1990).

Stramenopila

Phaeophyceae

The largest class among multicellular stramenopiles is the Phaeophyceae, which comprises forms from tiny filaments to giant kelps. Brown algae are very rare in fresh water. Of ~2,000 currently accepted brown algal species (Guiry and Guiry 2015), only seven (0.35%) have been found in fresh water, and all are small, filamentous or crust-forming (Figure 2; see below). They have been classified within three families (although one genus, *Porterinema*, is currently incertae sedis): the Ectocarpaceae, the Lithodermataceae, and the Sphacelariaceae, the latter two families both members of the order Sphacelariales (Silberfeld et al. 2014).

The Ectocarpaceae are small and filamentous. Two species have independently colonized fresh water. One transition was made by *Pleurocladia lacustris* A. Braun, which has been found in both marine and in freshwater environments, but more frequently in freshwater (Wehr et al. 2013). Its sister species, *P. lucifuga* (Kuckuck) Wilce, is exclusively marine. The second transition may have occurred in *Ectocarpus*. A strain of *E. subulatus* Kützing (Peters et al. 2015) isolated from a freshwater environment in Australia (West and Kraft 1996) is still able to grow in full marine medium (Dittami et al. 2012). It is currently the only freshwater report of *Ectocarpus*, with the exception of one report from a highly salt-contaminated river in Germany (Geissler 1983). Given the phylogenetic position of the freshwater strains of Ectocarpaceae, the most parsimonious explanation for these results would be two independent colonizations of fresh water within the family.

Two additional and probably independent transitions to fresh water have occurred within the Sphacelariales. At least one occurred in the Lithodermaceae, which comprises four genera of small crust- or tuft- forming algae; two of which (*Lithoderma* and *Pseudolithoderma*) are exclusively marine, and two others (*Bodanella* and *Heribaudiella*), with one species each, are restricted to fresh water. *Heribaudiella fluviatilis* (Areschoug) Svedelius can, at times, be one of the dominant species of benthic algae in smaller rivers (Wehr and Sheath 2003). Within the Sphacelariaceae, *Sphacelaria* has two freshwater species: *Sphacelaria lacustris* Schloesser & Blum reported from Lake Michigan, USA (Schloesser and Blum 1980); and *S. fluviatilis* C.-C. Jao recorded from China and the United States (McCauley and Wehr 2007; Necchi 2016).

A fifth marine-freshwater transition in brown algae probably occurred within the species *Porterinema fluviatile* (H.C.Porter) Waern, an alga which branches very early in the brown algal tree (McCauley and Wehr 2007) and is currently not attributed to a specific order. This species has a global distribution with populations occurring both in freshwater and in marine environments in North America and in Europe. A possible sixth example is a strain of *Ectocarpus*-like brown algae tentatively named *Ectocarpoides piscinalis* nom. nud. isolated from a domestic freshwater aquarium in Northampton, UK. Preliminary molecular analyses indicate that this isolate constitutes a yet undescribed brown algal species, possibly in a new order (Belcher et al. 2009).

Among the larger brown algae, especially among species belonging to the Fucales, temporary tolerance for low salinity is commonly observed. For example, *Fucus ceranoides* var. *limnicola* S.M.Baker & M.H.Bohling is frequently found in upper estuaries with high freshwater influence (Khfaji and Norton 1979) and *F. radicans* L.Bergström & L.Kautsky is permanently submerged in waters of low salinity (3–5 $g \cdot L^{-1}$) in the northern Baltic (Bergstrom et al. 2005). Also, populations of *F. vesiculosus* L. have been observed at low salinities in the Baltic, but have lost sexual reproduction (Tatarenkov et al. 2005). Several ecophenes of *Fucus* are also known from salt marshes and have previously been referred to as *F. cottonii* M.J.Wynne & Magne (Neiva et al. 2012). There is no documented occurrence of wracks/rockweeds in freshwater or terrestrial habitats. Likewise, the largest brown algae, belonging to the Laminariales (or kelps), are exclusively marine.

In summary, we know of maximally six marine-freshwater transitions in brown algae. None have led to diversification or wide-spread dominance in freshwater systems. Given the overwhelming dominance of marine representatives it is likely that the common ancestor of brown algae was indeed marine; however, this does not extend to all stramenopiles.

Schizocladiophyceae, Phaeothamniophyceae, and Tribophyceae

The Schizocladiophyceae comprise only one member, *Schizocladia ischiensis* E.C.Henry, K.Okuda & H.Kawai, which is marine and was collected at the Island of Ischia, Gulf of Naples, in the Mediterranean (Kawai et al. 2003).

The Phaeothamniales have previously been considered part of the Chrysophyceae, but based on molecular phylogenetic data have been erected as a new class, the Phaeothamniophyceae (Bailey et al. 1998). The three principal genera are *Phaeoschizochlamys, Phaeothamnion,* and *Stichogloea*, all of which have been described from fresh water. Other genera tentatively associated with this class are not available in culture, and their placement in this group remains uncertain (Bailey 2010). The only known marine species of Phaeothamniales is *Chrysophaeum lewisii* W.R.Taylor, but its position within this order would need to be confirmed by molecular data.

Among the Tribophyceae, which comprise mostly freshwater algae, three orders are known to form filaments or to be siphonous, the Botrydiales (multinucleate cells), the Tribonematales, and the Vaucheriales. All three of these orders mainly occur in fresh water, and several have also colonized terrestrial habitats. Within the Vaucheriales ~20 species have been found in marine or brackish environments (South and Whittick 2009). Based on a phylogenetic tree of 32 *Vaucheria* strains (21 species; Andersen and Bailey 2002), the marine representatives form two groups: one comprising only *Pseudodichotomosiphon* sp., a genus closely related to *Vaucheria* (exact phylogenetic position uncertain; Fukushi-Fujikura et al. 1991), and the other comprising all other marine species in this group. The most parsimonious explanation for this distribution would be two separate transitions from freshwater to marine habitats, one in *Pseudodichotomosiphon* and one in *Vaucheria.*

3. MARINE AND FRESHWATER ORIGINS OF PHOTOSYNTHETIC EUKARYOTES

In order to understand the directionality of transitions between fresh water and seawater in photosynthetic eukaryotes, we have to understand the evolution of these organisms in their deep time, ancestral environments. It is generally assumed that photosynthesis was first acquired by a common eukaryotic ancestor of the red, green and glaucophyte lineages; and then subsequently transmitted to the haptophyte, cryptophyte, and stramenopile lineages via secondary or tertiary endosymbiosis events (Archibald 2009). The timing of the primary endosymbiosis event is still a matter of debate but estimated at between 2.1 Gya and 900 mya, depending on the methods used and the interpretation of fossils (Han and Runnegar 1992; Cavalier-Smith 2009; Parfrey et al. 2011; McFadden 2014). The physical environment of the primary endosymbiosis event remains uncertain, but some indications can be derived from the cyanobacterium that became the plastid and from the host.

On the plastid side, phylogenetic analyses based on 30 different cyanobacterial taxa have show that the cyanobacterial group closest to plastids contains both freshwater/terrestrial (e.g. *Synechocystis*) and marine genera (e.g. *Trichodesmium*) (Ochoa de Alda et al. 2014). However, a more recent and comprehensive study by Ponce-Toledo et al. (2017) has identified the freshwater cyanobacterium *Gloeomargarita lithophora* as the closest known relative of plastids. Moreover, based on ancestral state reconstructions of early plastids and cyanobacteria, a freshwater origin seems to be more consistent (Blank 2013b). A recent comparison of cyanobacterial genomes (Dagan et al. 2013) concluded that a freshwater origin was probably necessary for water-splitting photosynthesis. It has also been suggested that early cyanobacteria (prior to the primary endosymbiosis event) likely lacked important genes involved in the synthesis of the compatible solutes trehalose, glucosylglycerol, glucosylglycerate and glycine betaine (Blank 2013a), implying that they may not have been able to colonize seawater at that time. This view is supported by estimates of the chemical composition of the early oceans at the time of primary endosymbiosis in which ancient seawater was probably two to three times more saline than today (Huston et al. 2010) and much richer in Ca^{2+} and iodine (Pinti 2005). Moreover, in the period from 2500 - 580 mya, the oceans were likely anoxic or only moderately oxic (Anbar et al. 2002; Johnston et al. 2009).

On the host side, the earliest branching within the Archaeplastida is still not resolved with certainty (Jackson and Reyes-Prieto 2014) but is thought to have been between the ancestor of the green and red lineages, and the glaucophytes (Rodríguez-Ezpeleta et al. 2005). The fact that extant members of the glaucophytes occur almost exclusively in fresh water (Kies and Kremer 1986) suggests that ancestral glaucophytes may also have been freshwater organisms. However, even if this is true, it is still unclear whether this also applies to the ancestor of all Archaeplastida. In the case of red algae, the earliest branching group of the red algae, the Cyanidales, occurs in hot springs with varying salinity and chemical composition (Reeb and Bhattacharya 2010). Therefore, and based on their reduced genomes (Collén et al. 2013; Qiu et al. 2015), it has been suggested that the ancestor of red algae may have also emerged in a hot spring, *i.e*. non-marine environment (Qiu et al. 2015). Though it will always remain speculative, modern marine representatives of ancient Archaeplastida may well be descendants of non-marine organisms.

A traditional argument against an early freshwater origin of Archaeplastida is based on the supposition that lakes and rivers were ephemeral along with the probable absence of biological vectors able to transport algae or spores between freshwater systems at the time. The oldest known lakes and rivers, such as Lake Baikal (Russia, 25 My) or the Finke River (Australia, 350 My) are still “young” (Haines et al. 2001; Colman et al. 2003). Using geochemical proxies Wellman and Strother (2015) suggest that primary production in terrestrial settings was probably established between 3.0 and 2.7 Ga. These aeroterresterial forms may have created a link between freshwater habitats. Thus, non-marine aquatic and aeroterresterial forms may have played the pivotal role in primordial times, with only later a link to the marine environment. Such early aeroterrestrial organisms would have needed protection against UV radiation (Mulkidjanian et al. 2006), which today comes from the ozone layer, *i.e.*, the interaction of photosynthetic oxygen with water. Even though oxygen was not yet plentiful, protection against UV could have been augmented by other UV absorbing gases, such as methane (Hessen 2008). Accordingly, the aeroterrestrial ‘flora’ would have been able to take advantage of an increasingly protective habitat and greater access to newly forming freshwater environments.

The main challenge to resolving the original ancestral habitats is that the earliest divergences are not known and the deep evolutionary radiations were rapid. The best we can do with class and ordinal level phylogenies of the three lineages is to examine the transitions that have occurred in extant taxa (which we do) and estimate directionality based on available taxon sampling and sister-group observations. Though coarse, it provides some additional indications for the aeroterrestrial/freshwater - marine sequence.

But what about the stramenopiles? Here the timing of the secondary or tertiary endosymbiosis events (at the origin of the stramenopiles) is important. We speculate that, if this event (or events) occurred in seawater, the genes required for fresh water tolerance were not transferred to the nucleus of the host (or hosts) and therefore lost. If so, this would provide one possible explanation for why so few brown algae have colonized fresh water. On the other hand, unicellular stramenopiles such as diatoms are found in both environments with many transitions, possibly in both directions. Most xanthophytes also occur in fresh water, so that no clear conclusions about the ancestral state of stramenopiles can be drawn.

Across all lineages, morphological complexity is clearly a factor that impacts the ease of environmental transitions. Microscopic (unicellular) representatives of all photosynthetic lineages have undergone numerous recent back-and-forth transitions between seawater and freshwater environments. Green algae have many unicellular representatives, and most of their multicellular morphologies remain simple; they have also frequently transitioned to marine environments and back (see section 2). In contrast, the red algae have relatively few unicellular representatives, and the multicellular forms are morphologically complex and dominant in marine environments; there have been few transitions to fresh water. The brown algae comprise the most morphologically complex algae and are almost exclusively marine. Finally, the streptophytes comprise the morphologically most complex plant species dominating terrestrial and freshwater habitats. Within this group, only the seagrasses (~60 species) have made a permanent transition to the marine environment (Les et al. 1997; Olsen et al. 2016).

4. PHYSIOLOGICAL AND GENOMIC ADAPTATIONS TO SEAWATER AND FRESH WATER

It is clear that marine-freshwater or freshwater-marine transitions have been common in photosynthetic eukaryotes (Figure 1). Still, we have only rudimentary understanding of the genomic changes underlying the physiological adaptations. Canonical understanding is usually derived from comparative acclimation experiments with euryhaline species that are capable of growing in both environments. For example, a recent study in the freshwater green alga *Ulva limnetica* used suppression subtractive hybridization in combination with quantitative real-time-PCR to compare gene expression profiles of freshwater vs. seawater-grown cultures of the same strain (Ichihara et al. 2011). An up-regulation was observed in enzymes involved in the degradation of sorbitol, probably as a means of reducing intracellular osmotic pressure, as well as the activation of reactive oxygen species scavengers. Also, an earlier study of the same strain under the same conditions detected the accumulation of lectin-like proteins in fresh water-grown cultures (Ichihara et al. 2009b), but the molecular role of these proteins for fresh water tolerance remains unknown.

Salt tolerant *Chara longifolia* C.B. Robinson and *Lamprothamnium* sp. were shown to respond to salinity changes by increasing vacuolar concentrations of K^+, Cl^- and sometimes sucrose, but not Na^+ (Beilby 2015). In both taxa, membrane potential is maintained by an increased activity of proton pumps. In an older study, *Lamprothamnium papulosum* (K.Wallroth) J.Groves was also shown to modify levels of cell wall sulfated polysaccharides with varying salinity (Davis and Lipkin 1986; Shepherd and Beilby 1999).

In red algae, the discovery of the coralline freshwater red alga, *Pneophyllum cetinaensis,* constitutes an interesting case study of a recent (probably within the last 120,000 years) but irreversible transition to fresh water (Žuljević et al. 2016), but so far the necessary genomic and physiological adaptations have not been studied. Another example is *Bangia atropurpurea,* which is able to grow in fresh water (Reed 1980). In acclimation experiments to full marine salinity, this species was shown to rapidly synthesize large quantities of floridoside, thought to serve as an osmoprotectant for the cells (Reed 1985). *B. atropurpurea* from the Great Lakes (USA) has been shown to exhibit reduced growth in seawater at a salinity of 26 $g \cdot L^{-1}$, but this effect was reversed (*i.e.* reduced growth in fresh water compared to seawater) after three generations of acclimation to seawater (Sheath and Cole 1980).

By analogy to the Baltic *Fucus vesiculosus* described in section 2 (Tatarenkov et al. 2005), the *Bangia* populations also lack sexual reproduction in fresh water, despite the fact that they have maintained their presence in the Great Lakes since the 1960s and probably originated from fresh water-adapted European populations (Shea et al. 2014). Indeed, sexual reproduction may merit particular attention when studying the adaptation to fresh water, as has previously been argued by Raven (1999). Specifically, the fusion of gametes is highly sensitive to the surrounding osmotic conditions, and mechanisms to block polyspermy in marine algae frequently rely on the influx of Na^+, while freshwater algae generally rely on the efflux of Cl^-.

Within the brown algae, the aforementioned freshwater strain of *Ectocarpus subulatus* provides a model for the transition between both environments. Here a combination of metabolite and transcriptome profiling revealed that over half of all examined genes and most metabolites were differentially expressed between the two conditions (Dittami et al. 2012). In this case, changes included the upregulation of genes involved in cell wall sulphation in seawater, which was confirmed using stained antibodies (Torode et al. 2015). This freshwater strain of *E. subulatus* has never been observed to reproduce sexually in the laboratory (A. Peters, personal communication as well as eight years of observation in our laboratory).

Differential gene expression analyses and physiological characterization of euryhaline organisms can shed light on the physiological acclimations needed to cope with osmoregulation and ion homeostasis in fresh water vs. seawater. However, they provide little information on the adaptations to either environment and their evolution after the initial transition. It is these adaptations that, once completed, may prevent a move back to the former environment. Comparisons of sister taxa that are strictly freshwater or strictly marine would provide valuable information to answer these questions, but are still rare.

An important example for such adaptations to life in marine vs. freshwater environments is cell wall sulphation. This process is present in all marine algae (red, green, and brown) and seagrasses (Kloareg and Quatrano 1988), but has not been found in freshwater plants or freshwater algae. Both aforementioned euryhaline red and brown algal species, *L. papulosum* and *E. subulatus*, have been shown to regulate cell wall sulphation depending on their environment (Shepherd and Beilby 1999; Torode et al. 2015). Interestingly, in a recent genome analysis of the marine angiosperm, the seagrass *Zostera marina*, Olsen et al. (2016) showed that the enzymes responsible for cell wall sulphation in *Z. marina* re-evolved from carbohydrate sulfatases, which may be active on a wider range of substrates. Such comparisons illustrate the value of comparative genomics in deciphering the adaptations related to freshwater-marine habitat preferences and may shed light on the evolutionary events that have led to or prevented marine-freshwater transitions more recently.

5. CONCLUSIONS

Bidirectional marine-freshwater transitions have occurred in multicellular photosynthetic eukaryotes all across the eukaryotic tree, but branches that are specialized to one or the other habitat have clearly emerged. At one extreme, streptophytes dominate freshwater and terrestrial habitats, with only a few species (the seagrasses) having colonized the sea from freshwater ancestors. At the other extreme, brown algae, with the exception of a few morphologically simple species, are found only in seawater. Green and red algae hold an intermediate position and have successfully made the transition between seawater and fresh water many times. As a general trend, successful transitions appear to occur more frequently in morphologically simple organisms, as illustrated in the case of brown algae, but also to a certain extent in green algae and plants. Unicellular organisms have not been treated in this review but follow in parallel with this observation, frequently found in both types of habitats.

It is commonly assumed that the colonization of fresh water was the intermediate step that allowed a gradual colonization of land by a marine, green algal lineage (Becker and Marin 2009). While there is little doubt that plants have colonized terrestrial environments from fresh water, we cannot rule out the possibility of an original freshwater/terrestrial origin of photosynthetic eukaryotes followed by secondary colonization of marine habitats. To learn more about these early and later evolutionary transitions and the underlying mechanisms responsible for habitat constraint, the availability of omics resources, in combination with comparative and experimental approaches, will allow us to unravel the determinants of these fundamentally different evolutionary trajectories.

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TABLE LEGENDS

Table 1: Overview of the typical composition of seawater and fresh water in selected streams. An asterisk (*) indicates global averages of major ions in river waters according to Wetzel (2001), followed by ranges found in the literature for different water bodies (Goldberg 1965; Ott 1988; Wetzel 2001; Wehr and Sheath 2003; Salminen et al. 2005). The term brackish water refers to a mixture of seawater and fresh water with salinities ranging from 0.5 to 30 g·L^{-1}.

	Seawater	Fresh water
Overall salinity	**30-40 g·L^{-1}**	**<0.5 g·L^{-1}**
Chloride (Cl^-)	540 nM	0.22 mM* (< 8.6 mM)
Sodium (Na^+)	500 mM	0.27 mM* (< 10 mM)
Sulfate (SO_4^{2-})	28 mM	0.12 mM* (< 5 mM)
Magnesium (Mg^{2+})	54 mM	0.17 mM* (0.002-2 mM)
Calcium (Ca^{2+})	10 mM	0.37 mM* (0.005-10 mM)
Potassium (K^+)	9.7 mM	0.06 mM* (< 1.3 mM)
Bicarbonate (HCO_3^-)	2.3 mM	< 16 mM
Bromide (Br^-)	800 µM	< 12 µM
Boric acid (H_3BO_3)	400 µM	< 90µM
Strontium (Sr^{2+})	90 µM	< 50µM
Nitrate (NO_3^-)	0.01-50 µM	< 1 mM
Nitrite (NO_2^-)	0.01-5 µM	< 100 µM

Ammonium (NH_4^+)	0.1-5 µM	< 20µM
Phosphate(PO_4^{3-})	2.5 µM	<10 µM
Silicate (SiO_4^{4-})	0-180 µM	1-500 µM
Iodine (I^-)	0.5 µM	0.1-40 nM

FIGURES

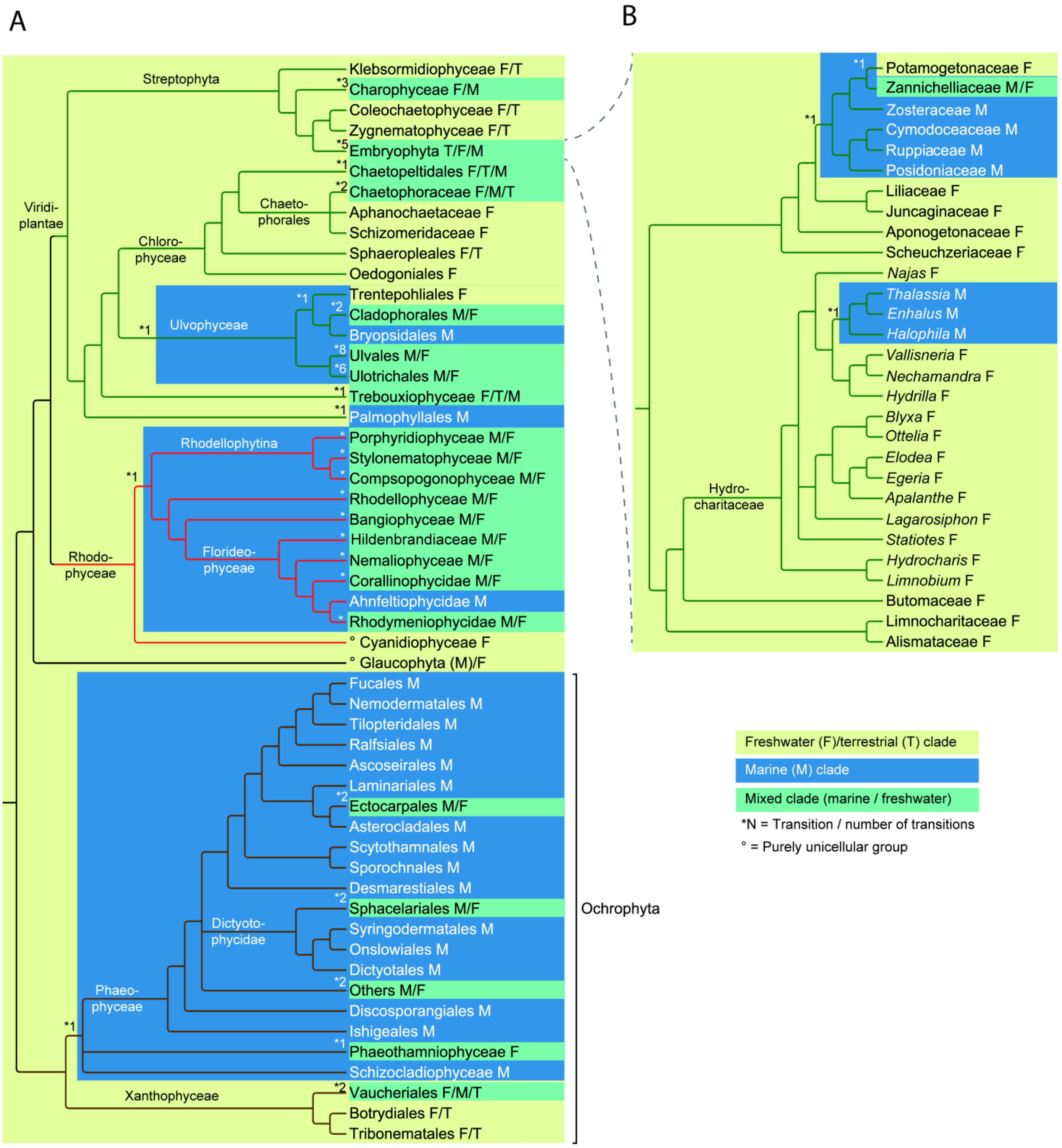

Figure 1: A) Backbone taxonomic relationships at the class and order levels according to Kawai et al. (2007), Brown and Sorhannus (2010), Silberfeld et al. (2010, 2011) for stramenopiles; Friedl and O'Kelly (2002), Cocquyt et al. (2010b), Leliaert et al. (2012) for the green lineage; and Le Gall and Saunders (2007), Scott et al. (2011) for red algae. The tree shows only the branching order; branch length has no significance and taxon sampling within

branches varies widely. Yellow background indicates a probable freshwater/terrestrial habitat, blue background a marine/brackish water habitat, and green the intermediate branches with both marine and freshwater representatives. Presumed marine-freshwater and freshwater-marine transitions are marked by * and the minimum number of putative transitions is indicated where possible. ° denotes branches with no multicellular representatives; F, freshwater; M, marine; T, terrestrial. For example F/M means that both freshwater and marine representatives are found in a branch. B) Zoom on *Alismatales* after Les et al. (1997) with modifications according to (APG 2009). Note: There is no absolute proof for the ancestral habitats of the different lineages.

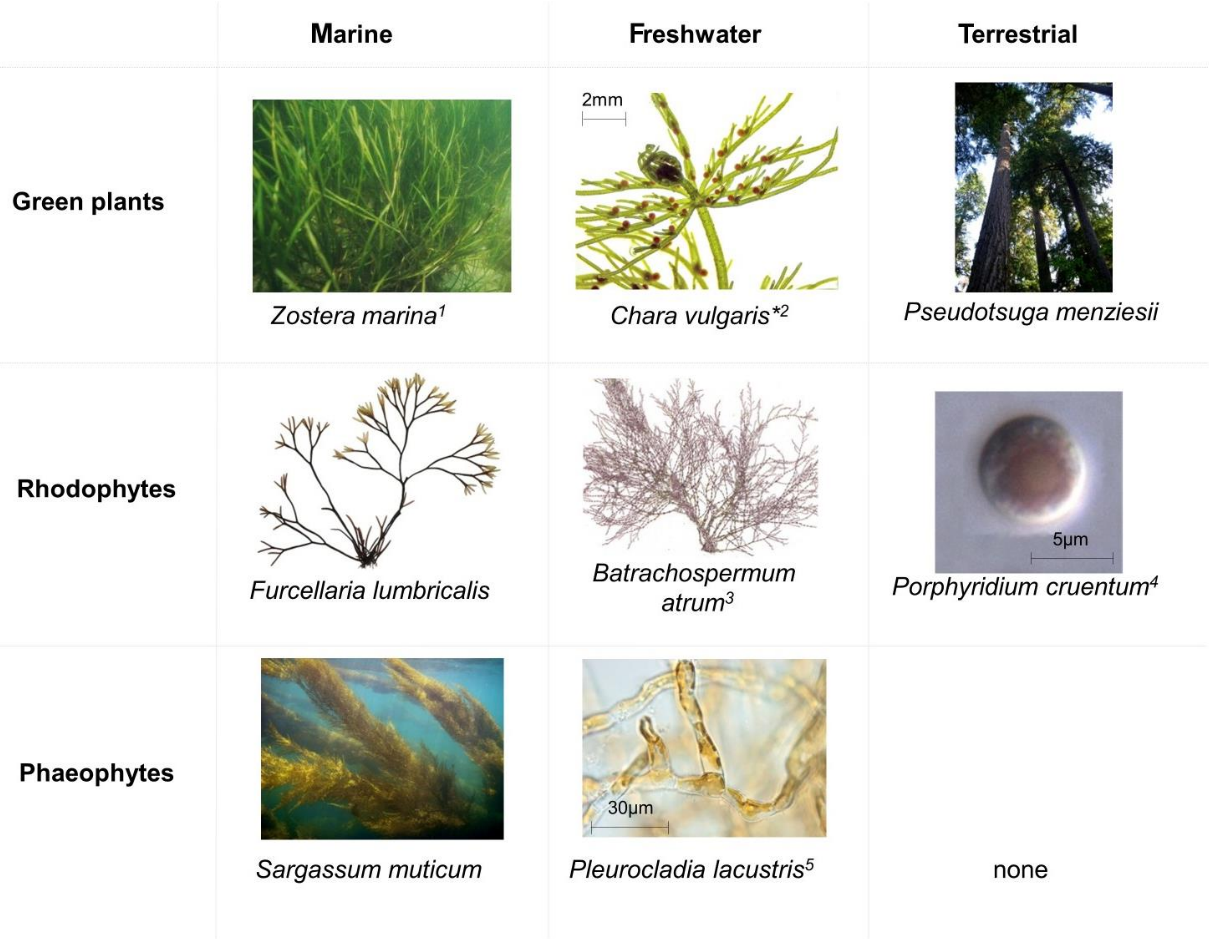

Figure 2: Examples of the morphological complexity reached by representatives of the green, red, and brown lineages in marine, freshwater, and terrestrial habitats, respectively. [1] Photo courtesy of Thorsten Reusch; [2] photo courtesy of Chris Carter; [3] photo courtesy of Marina Aboal Sanjurjo; [4] photo courtesy of the Roscoff Culture Collection (strain RCC 653); [5] strain SAG 25.93