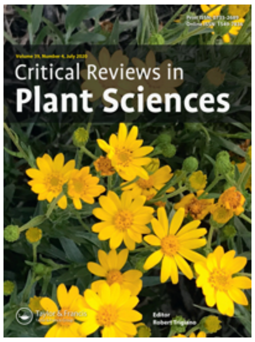

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Phylogeny and Evolution of the Brown Algae

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ABSTRACT
The brown algae (Phaeophyceae) are a group of multicellular heterokonts that are ubiquitous in today's oceans. Large brown algae from multiple orders are the foundation to temperate coastal ecosystems globally, a role that extends into arctic and tropical regions, providing services indirectly through increased coastal productivity and habitat provisioning, and directly as a source of food and commercially important extracts. Recent multi-locus and genome-scale analyses have revolutionized our understanding of the brown algal phylogeny, providing a robust framework to test evolutionary hypotheses and interpret genomic variation across diverse brown algal lineages. Here, we review recent developments in our understanding of brown algal evolution based on modern advances in phylogenetics and functional genomics. We begin by summarizing modern phylogenetic hypotheses, illuminating the timescales over which the various brown algal orders diversified. We then discuss key insights on our understanding of brown algal life cycle variation and sexual reproduction systems derived from modern genomic techniques. We also review brown algal speciation mechanisms and the associated biogeographic patterns that have emerged globally. We conclude our review by discussing promising avenues for future research opened by genomic datasets, directions that are expected to reveal critical insights into brown algal evolution in past, present, and future oceans.

KEYWORDS
Biogeography; complex life cycles; diversity; genomics; seaweed; speciation

I. The nature and origin of brown algae

The brown algae (Phaeophyceae) comprise approximately 2000 described species, and are one of few eukaryotic lineages to have evolved complex multicellularity (Charrier *et al.*, 2008; Knoll, 2011; Cock *et al.*, 2014). Along with other multicellular groups such as metazoans, fungi and green plants, brown algae possess several key characteristics that have enabled them to thrive as macroscopic organisms (Charrier *et al.*, 2008), including cell-to-cell adhesion and communication (Charrier *et al.*, 2008; Cock *et al.*, 2010; 2014; Deniaud-Bouët *et al.*, 2014), tissue differentiation (Fritsch, 1935; Kloareg and Quatrano, 1988), internal transport of sugars (Fritsch, 1935; Schmitz and Srivastava, 1976) and the capacity for three dimensional growth (Fritsch, 1935; Starko and Martone, 2016a). These features have contributed to the emergence and diversification of the world's largest marine autotrophs (e.g. Laminariales, Fucales) besides clonal plants (e.g. Arnaud-Haond *et al.*, 2012), and have restructured the dynamics of coastal marine ecosystems around the world (Steinberg *et al.*, 1995; Steneck *et al.*, 2002; Pyenson and Vermeij, 2016; Starko *et al.*, 2019; Vermeij *et al.*, 2019). Brown algae also exhibit striking morphological variation across species, differing substantially in their level of complexity at the levels of cells, tissues and organs (Fritsch, 1935). A thorough understanding of brown algal evolution and systematics is essential for disentangling the processes underlying the evolution of

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complexity in this group and its implications for coastal ecosystems globally.

Brown algae play fundamental roles in the functioning of coastal marine ecosystems. Large brown algae, particularly those in the orders Laminariales, Tilopteridales, Fucales, and Desmarestiales, act as ecosystem engineers (Bruno and Bertness, 2001; Schiel and Foster, 2006; Mineur *et al.*, 2015, Teagle *et al.*, 2017) and are dominant members of intertidal and shallow subtidal ecosystems worldwide (Steneck *et al.*, 2002; Schiel and Foster, 2006; Teagle *et al.*, 2017). Large brown algae form complex underwater forests that dramatically increase the structural complexity of marine ecosystems (Steneck *et al.*, 2002; Teagle *et al.*, 2017) and alter environmental factors such as light (Gerard, 1984; Connell, 2003a; Gattuso *et al.*, 2006), fluid dynamics (Hurd and Stevens, 1997; Stephens and Hepburn, 2014), sedimentation (Connell, 2003b; Filbee-Dexter *et al.*, 2016) and food availability (Duggins *et al.*, 1989; Estes *et al.*, 2016). Large brown algae also provide habitat for a wide range of other taxa (Steneck *et al.*, 2002; Graham, 2004; Teagle *et al.*, 2017; Hind *et al.*, 2019), including many commercially important animals (Bologna and Steneck, 1993; Smale *et al.*, 2013; Markel *et al.*, 2017), and serve as essential nursery grounds for many species (Holbrook *et al.*, 1990; Kitada *et al.*, 2019). Besides habitat provision, brown algae are a key source of productivity along the coast (Mann, 1973; Pfister *et al.*, 2019) and can significantly increase secondary productivity in nearshore ecosystems through direct herbivory and increased detrital production (Duggins *et al.*, 1989; Krumhansl and Scheibling, 2012). This energy input plays an important role in maintaining food security for many large mammals (Estes *et al.*, 2016; Pyenson and Vermeij, 2016; Vermeij *et al.*, 2019), including humans, and is believed to have facilitated the spread of human populations from Asia to North America prior to the Holocene, the so-called "kelp highway" hypothesis (Erlandson *et al.*, 2015; Braje *et al.*, 2017). As humanity further ventures into the Anthropocene, brown algae are becoming key players in ocean-based strategies for combating climate change given their role in sequestering carbon (Krause-Jensen and Duarte 2016; Krause-Jensen *et al.*, 2018; Hoegh-Guldberg *et al.*, 2019). A new frontier of "charismatic carbon" in the form of seaweed farming could regionally offset carbon emissions from agriculture and provide additional benefits by restoring coastal habitats and alleviating ocean acidity (Froehlich *et al.*, 2019). Altogether, the ecosystem services provided by brown algal forests are conservatively estimated to value USD $500,000–1,000,000 per year per km of coastline (Filbee-Dexter and Wernberg, 2018). Given that forests of large brown algae dominate approximately 25% of the world's coastlines (Wernberg *et al.*, 2019), the global value of ecosystem services provided by brown algae is likely to be in the hundreds of billions of USD per year.

In addition to the indirect benefits that they provide to humans by maintaining ecosystem functioning in nearshore marine environments, brown algae hold direct economic value through food harvests and commercial extracts (Mautner, 1954; Vásquez *et al.*, 2014; Bennett *et al.*, 2016; Milledge *et al.*, 2016). Brown algae have long been used as a food source by human communities with coastal access (Tseng, 1981; Druehl, 1988; McHugh, 2003). Today, brown algae are harvested from the wild and through aquaculture operations around the world (Fleurence *et al.*, 2012; Charrier *et al.*, 2017; Bennion *et al.*, 2019). The global harvest of brown macroalgae from wild stocks is estimated at more than half a million tonnes per year and has been increasing in recent decades (Mac Monagail *et al.*, 2017). The polysaccharide metabolism of brown algae is unique among photoautotrophs (including red and green algae) and many of these polysaccharides are desirable for their bioactive properties. For example, fucose-containing sulfated polysaccharides (FCSPs), found in the cell wall and extracellular matrices of brown algae (Deniaud-Bouet *et al.*, 2014; Kloareg and Quatrano, 1988), can have anti-inflammatory, anti-viral, anti-biotic, anti-oxidant, anti-coagulant, and anti-adhesive properties (Li *et al.*, 2008; Morya *et al.*, 2012), and are widely used in medicine and cosmetics (Li *et al.*, 2008; Fitton, 2011). Alginates, carbohydrate polymers made up of mannuronic and guluronic acids (Kloareg and Quatrano, 1988) act as gelling agents in food products, have medical and commercial applications as absorbents (Skaugrud *et al.*, 1999; Lee and Mooney, 2012), and serve as the basis of macroalgal bio-fuel development (Wargacki *et al.*, 2012). Brown algae also concentrate halogens, such as iodine, as a means of coping with various forms of stress (e.g. heat stress, ultraviolet radiation, herbivory, and oxidative stress; La Barre *et al.*, 2010). As a result of micronutrient sequestration, brown algae are harvested and sold commercially as dietary supplements, both for human consumption (Fitton, 2003; Leblanc *et al.*, 2006), and for animal feed (Øverland *et al.*, 2019; Pereira *et al.*, 2019).

In the broader context of eukaryotic evolution, brown algae originated within the heterokonts (i.e. stramenopiles), one of four major groups in the

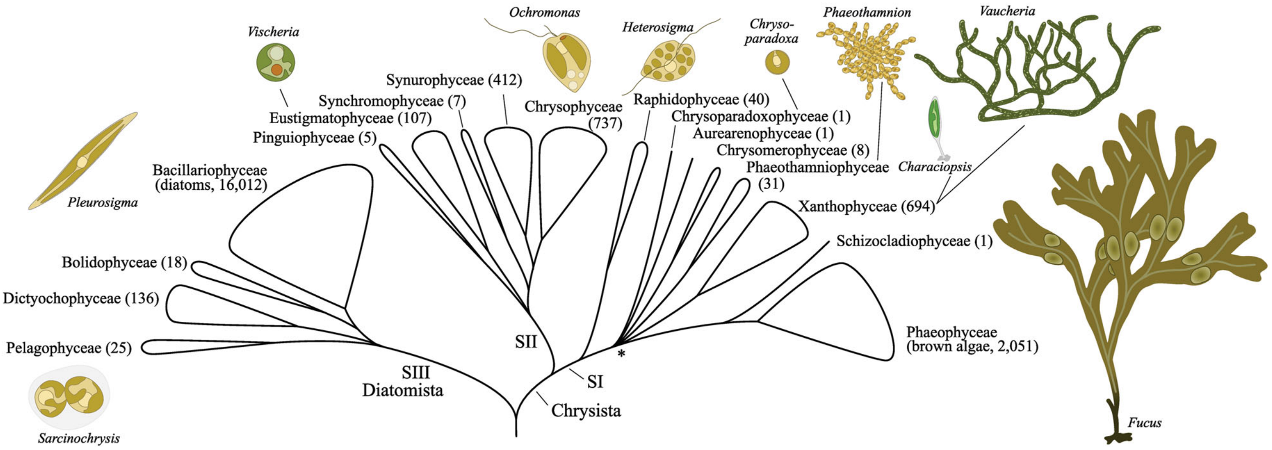


Figure 1. Summary diagram of phylogenetic relationships among the classes of photosynthetic heterokonts, derived from results presented in Kawai *et al.* (2003), Yang *et al.* (2012), Derelle *et al.* (2016), Han *et al.* (2019), Kim *et al.* (2019), Thakur *et al.* (2019) and Wetherbee *et al.* (2019). The asterisk represents the ancestral node of the majority of the SI clade, dated to the late Paleozoic (∼310 Ma; Brown and Sorhannus, 2010). The species counts given in parentheses after each class are from AlgaeBase (Guiry and Guiry, 2020).

eukaryotic lineage containing Telonemea, Stramenopiles, Alveolata, and Rhizaria (TSAR lineage; Burki *et al.*, 2019). The photosynthetic heterokonts share an ancestral endosymbiotic event of phagocytosis of a red alga, giving rise to their plastids (Keeling, 2013), and are part of the Ochrophyta, a lineage of mainly unicellular and mostly photosynthetic lineages including diatoms, chrysophytes, synurophytes, xanthophytes and many less well-known groups (Figure 1). While the relationships among many classes of Ochrophyta remain unresolved, three main groups (SI, SII, SIII) are supported in most phylogenies (Figure 1). The brown algae are situated within lineage SI, as part of a radiation of classes during the late Paleozoic (∼310 Ma; asterisk in Figure 1). However, phylogenetic analyses have struggled to resolve the SI lineage further due to insufficient power of the selected genetic markers (e.g. Yang *et al.*, 2012, Wetherbee *et al.*, 2019). Moreover, genome-scale studies have not included many of the lesser-known classes (e.g. Derelle *et al.*, 2016; Kim *et al.*, 2019; Thakur *et al.*, 2019). Multicellularity in the Ochrophyta is not exclusive to the brown algae, with several classes in the clade SI-radiation having at least some simple multicellular representatives (e.g. Phaeothamniophyceae) or macroscopic siphonous species (e.g. *Vaucheria* and *Botrydium* in the Xanthophyceae). There is still considerable debate about the evolutionary processes that underlie transitions to multicellularity but several possible advantages have been proposed, including reduced predation due to increased size, increased production of reproductive cells for dispersal, and efficient allocation of distinct biological functions to different specialized cell types. The class Schizocladiophyceae includes only one species, *Schizocladia ischiensis*, which forms small filaments. Schizocladiophyceae is the sister lineage to brown algae, suggesting that simple multicellularity was already present in the Paleozoic ancestor of the brown algae (Brown and Sorhannus, 2010; CAP in Figure 2).

Brown algal classification schemes have traditionally relied on a combination of thallus morphology, life history traits, types of spores and gametes, and cytoskeletal characteristics (reviewed by de Reviers *et al.*, 2007). DNA sequencing dramatically altered our view of brown algal relationships and the evolution of traits. The earliest phylogenetic studies were limited by the coarse resolution of chosen markers (i.e. 18S; Tan and Druehl, 1993), but further work has dramatically enhanced our knowledge of brown algal systematics by including multiple markers, time calibrated phylogenies (Silberfeld *et al.*, 2010; Martin and Zuccarello, 2012; Starko *et al.*, 2019; Yip *et al.*, 2020), and, more recently, genome-scale datasets for some brown algal groups (Jackson *et al.*, 2017; Starko *et al.*, 2019).

Given the socio-ecological importance of brown algae, their relevance to key evolutionary transitions and processes, and the considerable new insight being shed on brown algae today, we aim to review contemporary knowledge of brown algal evolution. In this review paper, we provide the latest interpretation of the phylogenetic relationships of brown algal lineages derived from molecular data, summarize new insights on the evolution of life history traits, and provide an up-to-date overview of biogeography and mechanisms promoting reproductive isolation. We conclude our

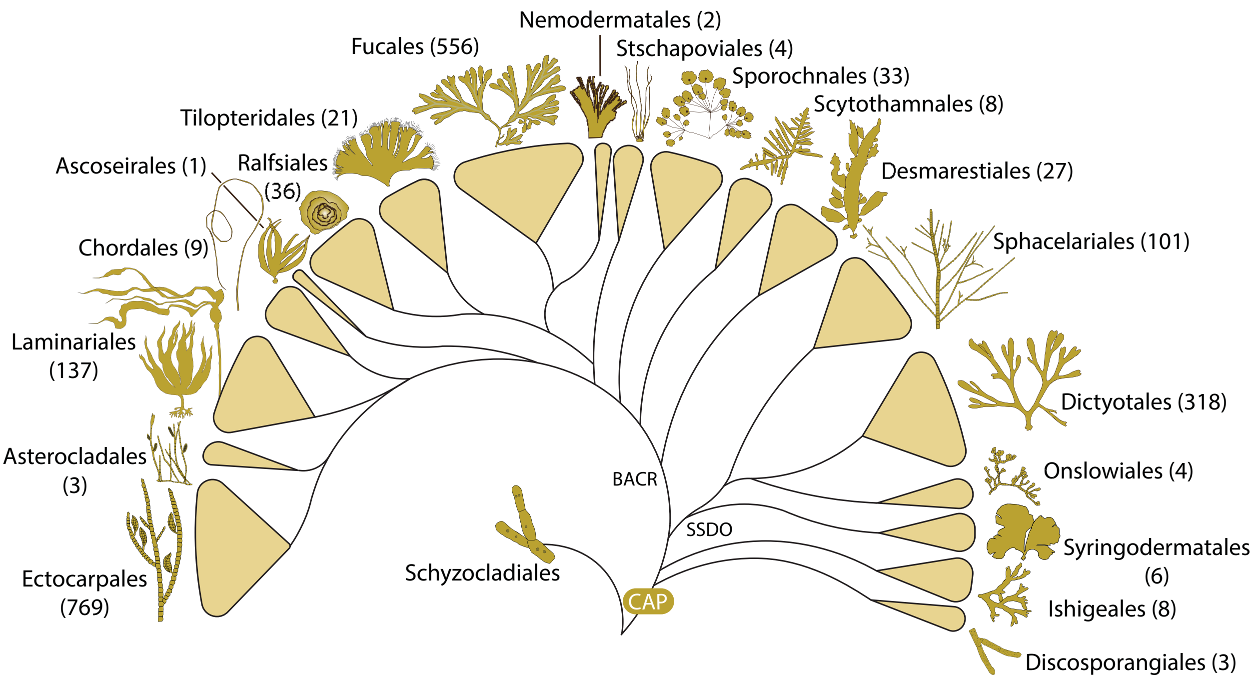


Figure 2. Phylogeny of the brown algal orders based on 12 markers (18S, 5.8S, 28S, *atp*B, *psb*A, *psa*B, *psa*A, *rbc*L, *psb*C, *cox*1, *cox*3, *nad*1). In brackets are the numbers of species within each order according to AlgaeBase (Guiry and Guiry, 2020). CAP: common ancestor of Phaeophyceae; SSDO: Sphacelariales, Syringodermatales, Dictyotales, Onslowiales clade; BACR: brown algal crown radiation.

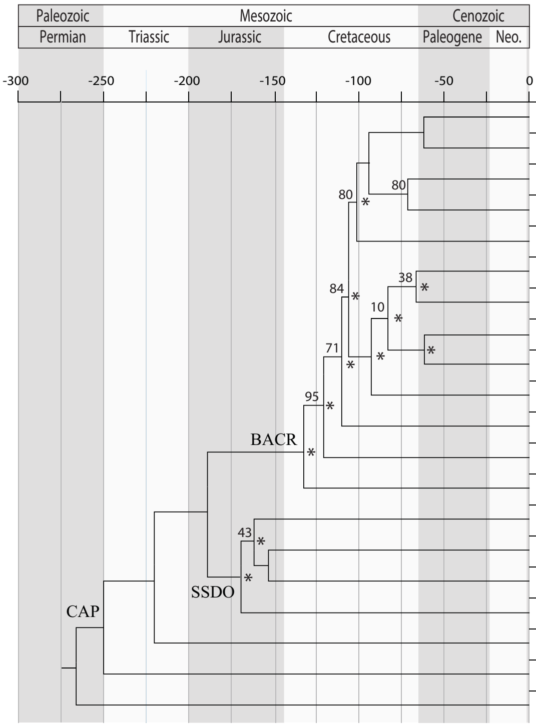
review by offering perspectives on promising avenues for further understanding brown algal evolution.

II. Phylogenetic history of the brown algae

Molecular phylogenies overturned the traditional, 20th century view of brown algal classification, which had been based on a combination of life cycle structure, thallus architecture and gametic traits. For example, the widely held hypothesis that the morphologically more complex orders had diverged from filamentous Ectocarpales early in the diversification of the brown algae was confidently rejected by phylogenetic evidence. Instead, the Ectocarpales were close relatives of one the most morphologically complex groups of brown algae, the Laminariales. Ancestral state reconstructions based on molecular phylogenies indicate that parenchymatous growth has probably reverted to filamentous growth multiple times (Silberfeld *et al.*, 2010). Likewise, life history traits and gametic differentiation display complex evolutionary patterns with transitions from isogamy through anisogamy to oogamy having occurred several times independently (Silberfeld *et al.*, 2010), the genetic underpinnings of which have only recently been described (see life history traits, section III.B). Such pliability means molecular data has been instrumental in confidently defining brown algal relationships. In this section, we review the brown algal orders, characteristic features within the groups, and provide information on evolutionary events based on molecular evidence, where available.

Molecular data have clearly shown that the overall phylogenetic structure of the brown algae includes two orders that resulted from early divergence events (Figure 2), a large clade composed of four orders (Sphacelariales, Syringodermatales, Dictyotales, Onslowiales, coined the SSDO clade), and a large and initially poorly resolved radiation comprising all remaining brown algal orders and referred to as the brown algal crown radiation (BACR). Increased gene-sampling has significantly improved the resolution of the BACR and has created a robust phylogenetic framework to interpret brown algal evolution, though the precise affinities among a small number of lineages remain unresolved.

Calibrated phylogenies, although admittedly based on limited fossil evidence, have also provided insight into the timescales of brown algal evolution. Fossilization of brown algae is rare, especially given hard bodied lineages are known in only two extant genera (*Newhousia* and *Padina*, the latter of which deposits a thin layer of aragonite on the surface of the thallus only: Miyata *et al.*, 1977; Kraft *et al.*, 2004). Red and green macroalgal lineages were also present alongside the brown algae, leading to confusion and



	Genome availability	Gametes	Life-cycle	Structure: Gametophyte	Structure: Sporophyte	Pyrenoids	Plastid shape	Growth: Gametophyte	Growth: Sporophyte	Pheromone
Ectocarpales	W	Is, An, O	Het	Fi	Fi	Py	R	D	D	Cy
Asterocladales		An	Iso?	Fi	Fi	PyI	E	A	A	
Laminariales	W	O	Het	Fi	Pa	-	Di	D	I	Cy, E
Chordales		An, O	Het	Fi	Pa	-	Di	D	D, I	
Ascoseirales		Is	Het	R	Pa	-	Di	-	I	Cy
Ralfsiales		An	Iso, Het	Dc	Dc	-	Cs, Di	D?	D?	
Tilopteridales		O	Iso, Het	Pa	Pa	-	Di	T	T	Cy
Fucales	Mt, Ch	O	Het	R	Pa	-	Di	-	A	Cy, Ac, *
Nemodermatales		An	Iso	Dc	Dc	-	Di	D?	D?	
Stschapoviales		O	Het	R	Pa	-	Di	-	D	Cy
Sporochnales		O	Het	Ps	Ps	-	Di	T	T	Cy, E
Scytothamnales		An	Het	Pa	Fi	Py	S, Ax	I	A	Cy
Desmarestiales	Mt	O	Het	Fmc, Fi	Ps	-	Di	T	T	Cy
Sphacelariales		Is, An, O	Iso	Fi	Fi	-	Di	A	A	Cy
Onslowiales			Iso	Fi	Fi	-	Di	A	A	
Dictyotales	Mt, Ch	An, O	Iso	Pa	Pa	-	Di	A, M	A, M	Cy
Syringodermatales		Is	Het	R	Pa	-	Di	D	A	Cy
Ishigeales	Mt	Is	Iso	Ps	Ps	-	Di	D?	D?	
Discosporangiales		Is?	Iso	Fi	Fi	-	Di	A	A	

Figure 3. Time calibrated maximum likelihood phylogeny of the brown algae, using the following fossil evidence: *Paleocystophora* (Fucales) and *Julescraneia grandicornis* (Laminariales) from the Monterey Formation Miocene deposits (13–17 Ma; Parker and Dawson, 1965), and *Padina*-like species (Dictyotales) from the Gangapur formation, Early Cretaceous (145.5–99.6 Ma; Rajanikanth, 1989). Nodes lacking bootstrap values are fully supported for both maximum likelihood and bayesian phylogenetic trees. Topological conflicts with bayesian trees are indicated by an *. W: Whole; Mt: Mitochondrion; Ch: Chloroplast; Nu: Nuclear; Is: Isogamous; An: Anisogamous; O: Oogamous; Het: Heteromorphic; Iso: Isomorphic; Fmc: Few microscopic cells; Fi: Filamentous; Ps: Pseudoparenchymatous (haplostichous); Pa: Parenchymatous (polystichous); R: reduced; Dc: Pseudoparenchymatous discoid; Py: Pyrenoids without invaginations; PyI: Pyrenoids with invaginations; A: Apical; D: Diffuse; I: Intercalary; M: Marginal; T: Trichothallic; R: Ribbon-shaped; E: Elongated; Di: Discoid; S: Stellate; Ax: Axial; Cs: Cap-shaped; Cy: Cyclic hydrocarbons; Ac: Acyclic hydrocarbons; Ep: Epoxyde; *C11 and C8-olefins. Empty cells: no data available; ?: doubtful identification, –: absence of trait; CAP: common ancestor of Phaeophyceae; SSDO: Sphacelariales, Syringodermatales, Dictyotales, Onslowiales clade; BACR: brown algal crown radiation.

debate as to how to classify fossil specimens with simple and convergent features. For example, Upper Devonian species *Drydenia foliata*, *Hungerfordia dichotoma*, and *Enfieldia mutilata* (380–360 Ma; Fry and Banks, 1955), and the Late Pennsylvanian-Early Permian genus *Perissothallus* (300 Ma; Krings *et al.*, 2007) are fossil specimens variously linked to extant brown, green, and red algal species. Only a few fossils have been assigned to brown algal lineages with enough confidence to time-calibrate phylogenetic trees (Figure 3; Silberfeld *et al.*, 2010). The oldest is a species preserved in Early Cretaceous (145–100 Ma) clay shales of the Gangapur Formation in India. The specimen displays a fan-shaped thallus and a zonation pattern consistent with the extant genus *Padina* (Rajanikanth, 1989). Miocene deposits (dated to 13–17 Ma) from the Monterey Formation in California offer three more fossilized brown algae: *Julescraneia grandicornis*, an extinct species intermediate in morphology between the extant laminarialean genera, *Pelagophycus* and *Nereocystis*, and the extinct genera *Paleocystophora* and *Paleohalidrys*, the root names of which are derived from extant genera of the Sargassaceae that display a characteristic sympodial branching pattern (Parker and Dawson, 1965). Though earlier brown algal fossils have been proposed (citations above), the fossil evidence used to calibrate phylogenetic trees suggests the brown algal orders diversified almost entirely within the Mesozoic Era (252–66 Ma), surviving the cataclysm that claimed the Dinosaurs.

A. Early divergence events

The orders Discosporangiales and Ishigeales branched from the other brown algal lineages early in the evolutionary history of the brown algae sometime at the beginning of the Mesozoic Era (~250 Ma; Figure 2). These two orders only contain a total of 11 recorded species (Guiry and Guiry, 2020) but differ markedly from other brown algae. **Discosporangiales** exhibit uniseriate, branched filaments with apical meristematic cells, but lack the heterotrichous growth pattern (prostrate and upright thalli projections) common in many other brown algal orders. *Discosporangium mesarthrocarpum* also features unique disc-shaped reproductive organs. Traditionally, *Discosporangium* and *Choristocarpus* were treated as members of the Sphacelariales on the basis of their apical growth, but molecular phylogenies have indicated that these genera are from a distinct order (Draisma *et al.*, 2001; Burrowes *et al.*, 2003; Kawai *et al.*, 2007), leading to the reinstatement of Discosporangiales as originally proposed by Schmidt (1937) and the inclusion of Choristocarpaceae in the order (Kawai *et al.*, 2007).

The **Ishigeales** include branched, upright or flattened parenchymatous thalli up to 10–20 cm high. The genus *Ishige* was traditionally classified in the defunct order Chordariales (now Chordariaceae within Ectocarpales), however, its higher rank taxonomy was controversial given the lack of important features such as pyrenoids in the chloroplast (Hori, 1971) and a heteromorphic life history (Hori, 1993). Phylogenetic analyses revealed its distinct position apart from most of the brown algae (Tan and Druehl, 1994; Peters and Ramírez, 2001), leading to creation of a new order Ishigeales (Cho *et al.*, 2004).

B. Mid-Mesozoic diversification

Sometime during the Mid-Mesozoic (approximate timeframe for the Jurassic period, 200–145 Ma; Figure 3), the SSDO clade split from the lineage that gave rise to the remaining extant brown algal orders and diversified into what are now four orders: Sphacelariales, Syringodermatales, Dictyotales, and Onslowiales. Of these lineages, the most prominent is the **Dictyotales**, which currently encompasses a great deal of brown algal species diversity (318; Figure 2). The success of Dictyotales can be partially attributed to their affinity for tropical climates, a biome largely uninhabited by the other brown algal orders (except for the tropical fucoids, see tropical biogeography, subsection IV.B.3). Molecular work has revealed remarkable diversity concentrated in a few genera, including *Dictyota* (Bittner *et al.*, 2008; Tronholm *et al.*, 2010), *Lobophora* (Sun *et al.*, 2012; Vieira *et al.*, 2016; Camacho *et al.*, 2019), and *Padina* (Ni-Ni-Win *et al.*, 2008; 2010; 2012; 2018; Ni-Ni-Win, Arai, *et al.*, 2011; Ni-Ni-Win, Draisma, *et al.*, 2011). All Dictyotales are characterized by an isomorphic alternation of generations, with parenchymatous sporophyte and gametophyte thalli. Two tribes are recognized based on either having a single apical cell (Dictyoteae; De Clerck *et al.*, 2006; Bittner *et al.*, 2008) or having many localized or marginal apical cells forming dichotomously branched or fan-shaped thalli (Zonarieae). Dictyotales are also unique among brown algae in that they include calcified taxa (i.e. *Padina* and *Newhousia*; Kraft *et al.*, 2004), a feature that may have facilitated their presence in the fossil record (Rajanikanth, 1989). Meiosis typically produces four nonmotile spores that produce the isomorphic gametophyte. Sexual reproduction is oogamous and the sperm have only an anterior flagellum, possessing, however, a second flagellar basal body (Manton, 1959), with the exception of several species of *Zonaria* which are reported to have two flagella (Phillips and Clayton, 1991; 1993; Phillips 1997).

Sphacelariales has been characterized by a thallus structure in which branched filaments grow from a conspicuous parenchymatous, terete thallus (Prud'homme van Reine, 1982; 1993). They display isomorphic life histories with various types of sexual reproduction including isogamy, anisogamy and oogamy (Figure 3). The taxonomy of Sphacelariales was revised considerably by Draisma, Prud'homme van Reine, *et al.*, (2010), broadening the description of the order to include foliose and crustose taxa (Kawai *et al.*, 2005; Kawai, Hanyuda, Draisma, *et al.*, 2015; Silberfeld *et al.*, 2014). Likely owing to the diminutive character of the Sphacelariales, considerable genetic diversity discordant with recorded morphospecies has been revealed in some locations (e.g. Northeast Pacific; Chan, 2018). **Onslowiales** is a small order comprising two genera which were traditionally classified in Sphacelariales. Members of the **Syringodermatales** have fan-shaped thalli that develop by lateral cohesion of filaments arising from a marginal meristem. The life history patterns are remarkably divergent within the order's single genus *Microzonia* (Camacho *et al.*, 2018), with gametophytes being either filamentous or reduced to only 4 or 2 cells (Henry and Müller, 1983; Henry, 1984; Kawai and Yamada, 1990).

C. The brown algal crown radiation

The remaining brown algal orders form a conspicuous clade that radiated throughout the Cretaceous period (145–66 Ma), the BACR (Figure 3). The BACR contains the most ecologically and economically important orders, including the Fucales and Laminariales. Silberfeld *et al.*, (2010) suggested that the BACR resulted from recovery following an extinction event, potentially linked with volcanic activity and subsequent oxygen depletion in earth's oceans 129–134 Ma (though dysoxia has not been confirmed during this event; Peate, 1997). Hypotheses explaining diversification of the BACR at the ordinal level are otherwise scant. Ancestral state reconstructions provided by Silberfeld *et al.*, (2010) suggest that the ancestor to the BACR had a heteromorphic life history, oogamous fertilization, intercalary growth of pseudoparenchymatous tissue, and chloroplasts containing several pyrenoids. Orders have variously reverted back to isomorphic life histories and terminal growth, and adoption of anisogamous or isogamous fertilization. Parenchymatous tissue and reductions to single plastids have also evolved independently multiple times. Such pliability in key features remains a mystery within the brown algae, and the genetic underpinnings of such dynamic evolutionary events are only beginning to be worked out (see life history traits, section III.B).

Desmarestiales and Scytothamnales represent the earliest branching orders within the BACR (approximately 125 Ma), and together account for only 35 described species (primarily within the genus *Desmarestia*). Members of **Desmarestiales** are globally distributed but are hypothesized to have evolved in the Southern Hemisphere, where they are a prominent member of Antarctic assemblages (Peters *et al.*, 1997). Members of **Scytothamnales** are predominantly known from temperate to cold water regions of the Southern Hemisphere, with two globally distributed tropical species. Desmarestiales develop a pseudoparenchymatous thallus through apical meristems and are notable for the ability of some members to accumulate sulfuric acid within cells, which is interpreted as an anti-herbivory defense mechanism (Pelletreau and Muller-Parker, 2002). Scytothamnales features branched, filamentous or terete, parenchymatous species (Tanaka *et al.*, 2007).

The remaining taxa of the BACR are classified into 12 orders, which vary dramatically in external morphology, cytology, and life history traits. **Ascoseirales** is a monotypic order featuring the Antarctic species *Ascoseira mirabilis*, which forms a large parenchymatous thallus with intercalary growth, holdfast and stipe, and is characterized by a diplontic life cycle, a feature that appears in only one other brown algal order, the Fucales. Reproductive structures in *Ascoseira* are borne in conceptacles that produce chains of large cells containing eight isogamous, flagellate gametes (Moe and Henry, 1982; Clayton, 1987), while unfused gametes may also develop into sporophytes (i.e. parthenogenesis/antherogenesis).

Fucales is a large order of more than 500 species and 9 families, members of which are major components of coastal ecosystems globally, including cold water regions of the Northern (*Fucus, Ascophyllum, Pelvetiopsis*, *Silvetia*, etc.) and Southern Hemisphere (*Durvillaea, Cystophora,* etc.), as well as in warm temperate to tropical coastal ecosystems (*Cystoseira s.l.*, *Sargassum, Turbinaria*, etc.). Diversity is highly skewed toward Sargassaceae, which comprises ca. 30 genera and over 90% of described species. Fucaceae and Seirococcaceae comprise 5 genera each and ca. 28 species, whereas the remaining 6 families are monospecific or monogeneric and together comprise no more than 15 species. Erect thalli are parenchymatous, often with differentiation between holdfast, stipe and branches (terete or leafy), and pneumatocysts (air bladders) that provide buoyancy (Figure 1). Growth results from the division of apical cells and cell division in associated meristematic regions except for *Durvillaea* and *Notheia*. The life cycles of Fucales are oogamous with oogonia and spermatangia borne on specialized branches known as receptacles. Gametophytic stages are highly reduced and retained in the conceptacles in the sporophytic thallus, so that plants superficially regenerate only from sporophytic thalli. Unfertilized eggs are incapable of developing parthenogenetically. The phylogeny and diversification of Fucales has been the subject of several studies (e.g. Serrão *et al.*, 1999; Coyer *et al.*, 2006; Fraser *et al.*, 2010; Draisma, Ballesteros, *et al.*, 2010; Cánovas *et al.*, 2011; Bruno de Sousa *et al.*, 2019; Yip *et al.*, 2020).

The sister orders Ectocarpales and Asterocladales emerged late within the BACR, close to the end of the Cretaceous period (66 Ma), with markedly different outcomes in species diversity. **Asterocladales** comprise a single genus *Asterocladon,* which is distributed from tropical to temperate coasts. **Ectocarpales**, on the other hand, is the most speciose brown algal order, with more than 750 species in more than 100 genera and 5 to 6 families, though the taxonomy at the genus and family rank is far from resolved. Traditionally, four orders were recognized based on a combination of two characters: thallus construction and chloroplast morphology (i.e. Ectocarpales *s.s.*, Chordariales, Dictyosiphonales and Scytosiphonales). However, the presence of intermediate forms and subsequent phylogenetic work led to the collapse of these orders into Ectocarpales *s.l.* New families were also established, such as Adenocystaceae (Rousseau *et al.*, 2000) and Petrospongiaceae (Racault *et al.*, 2009), or reinstated (e.g. Acinetosporaceae, Peters and Ramírez, 2001). The phylogenetic resolution of the genetic markers used for these revisions was limited, however, and phenotypic characters for defining these families remain scarce. *Ectocarpus* was the first brown alga to have a fully annotated genome, and insights into brown algal evolution continue to develop from this model organism (Cock *et al.*, 2010; detailed in life history traits, section III). Among the key discoveries were genes potentially associated with multicellular development, a high proportion of introns (40.4% of the genome), an integrated viral genome, red algal genes derived from the secondary endosymbiosis event that initiated the divergence of the Ochrophyta, and insights into various metabolic functions as compared to other photosynthetic lineages (Cock *et al.*, 2012).

Laminariales was also late to emerge in the BACR, branching from its sister Chordales in the early Cenozoic. Members of the **Laminariales** are often referred to as "kelps," although debate remains about whether this is a taxonomic or functional term, as some large brown algae from other orders are also commonly referred to as kelp (see Fraser, 2012, for a review of the debate). Today, the Laminariales includes the largest marine macroalgae, and often form large 'kelp forests,' which provide habitats for a wide range of other taxa. The largest among them, *Macrocystis*, can achieve lengths exceeding 50 m and is one of the fastest growing organisms on the planet. Although the Laminariales are most common in cold and temperate waters (Krumhansl *et al.*, 2016), they also grow in tropical waters where they are confined to deeper (colder) habitats (Graham *et al.*, 2007). Laminariales are the most structurally complex macroalgae and possess significant cellular and tissue differentiation, including phloem-like structures that transport sugar throughout their large thalli and distinctive differentiation between stipe, blade and holdfast that may facilitate their ability to achieve large sizes in biomechanically challenging environments (Johnson and Koehl, 1994; Drobnitch *et al.*, 2015; Starko and Martone, 2016a; Liggan and Martone, 2018). Kelp growth is mediated by an intercalary meristem that is in the transition between stipe and lamina, allowing the development of perennial sporophytes. The unique position of this intercalary meristem has been hypothesized to facilitate long term coexistence between laminarialean algae and surface-feeding herbivores (i.e. Vermeij *et al.*, 2019).

Laminariales possess two distinctive generations: a large parenchymatous sporophyte that alternates with a microscopic, filamentous gametophyte stage. Evolutionary and ecological knowledge of gametophytes remains poor relative to the sporophyte stage, though sequence data have been used to detect gametophytes in situ (Fox and Swanson, 2007; Robuchon *et al.*, 2014; Bringloe *et al.*, 2018). These studies indicate gametophyte distributions are, at times, disjunct with the accompanying sporophytes, suggesting gametophytes could persist in locations where environmental conditions do not favor growth and survival of the sporophyte. During reproduction events, female gametophytes are known to produce lamoxirene, a gamete-attracting pheromone that also functions to stimulate the synchronized release of sperm from antheridia (Maier, 1995).

A number of phylogenetic studies based on increasingly large datasets have gradually resolved relationships among species of the previously broader Laminariales, and revealed knowledge about their evolution (Lane *et al.*, 2006; Kawai *et al.*, 2008; 2013; Jackson *et al.*, 2017; Starko *et al.*, 2019). Phylogenomic analyses recently distinguished the Chordales (Starko *et al.*, 2019), which were historically viewed as "simple" kelps with traits that were thought to be ancestral compared with the remaining ("complex") kelp families. Ancestral state reconstruction subsequently revealed several characters unique to the Chordales (simple kelps), rather than ancestral to the Laminariales (complex kelps) as originally supposed. For instance, a hapteral (root-like), rather than a discoid, holdfast was likely the ancestral state to the Laminariales, and annual life histories have evolved multiple times throughout the order with a perennial life history featured in the ancestor. Complex traits such as a stiff stipe, tissue cavitation, and various forms of branching have also evolved independently across multiple lineages. Phylogenomic analyses have revealed that the crown age of the Laminariales (31.5 Ma) corresponded with the Eocene-Oligocene boundary. Laminariales are hypothesized to have expanded into niches that were opened by global cooling and mass extinction of marine life at this time (Ivany *et al.*, 2000), leading to the accelerated diversification of this group. Their diversification predated the appearance of sea otters and various benthic feeding fauna, suggesting Laminariales provided an important food and habitat resource driving the evolution of marine faunal lineages in the North Pacific.

Chordales is a small order, sister to the Laminariales, with nine known species in three genera and three families distributed in temperate to cold-water regions of the Northern Hemisphere. Morphology and life history patterns are diverse among families, although all members show heteromorphic life histories with annual, large parenchymatous sporophytes and minute filamentous gametophytes. *Akkesiphycus* (Akkesiphycaceae) has fragile lanceolate sporophytes with diffuse growth, and sexually monomorphic dioecious gametophytes producing anisogamous gametes (Kawai, 1986; Kawai and Sasaki, 2000). *Pseudochorda* (Pseudochordaceae) has terete sporophytes without localized meristems and sexually monomorphic or dimorphic, filamentous, oogamous gametophytes (Kawai and Kurogi, 1985; Kawai and Nabata, 1990). *Chorda* (Chordaceae) has terete sporophytes with localized meristems and trumpet-shaped hyphae, and sexually dimorphic filamentous oogamous gametophytes (Kylin, 1933). Although traditionally only one species *C. filum* was recognized, molecular phylogenetic studies have revealed considerable species diversity, including four new species recently described from the Pacific and the Arctic regions (Kawai *et al.*, 2019). In contrast to Laminariales, sex attractants have not been identified in Chordales.

The remaining BACR orders are Tilopteridales, Stschapoviales, Sporochnales, Ralfsiales, and Nemodermatales, and each further showcases the plasticity in morphology and life history traits of brown algae below the ordinal level. The thallus structures observed in the **Tilopteridales** are highly diverse across families. The family Tilopteridaceae includes three filamentous genera (South, 1975; Hooper *et al.*, 1988) with nearly isomorphic life histories, whereas members of Cutleriaceae have heteromorphic life histories with terete or membranous gametophytes and crustose sporophytes (Fritsch, 1945); finally, Phyllariaceae is composed of genera forming large sporophytes that also form forests and microscopic gametophytes, both resembling Laminariales in external morphology. The order **Stschapoviales** is known only from cold water regions in the Northern Hemisphere, with the three monotypic genera *Halosiphon* (Halosiphonaceae), *Platysiphon* (Platysiphonaceae) and *Stschapovia* (Stschapoviaceae; Kawai and Sasaki, 2004; Kawai, Hanyuda, Draisma, *et al.*, 2015; Kawai, Hanyuda, Yamagishi, *et al.*, 2015). The thalli are terete with assimilatory filaments in whorls. *Halosiphon* shows a typical heteromorphic life history with large sporophytes and monoecious filamentous gametophytes. In contrast, *Stschapovia* and *Platysiphon* appear to show a modified life history without alternation between two different generations, as in Ascoseirales and Fucales. The order **Sporochnales** contains 33 species in 11 genera that are distributed in temperate to sub-tropical regions. Pseudoparenchymatous thalli are filamentous to terete, and macroscopic sporophytes alternate with minute, filamentous gametophytes producing eggs and sperm. **Ralfsiales** is composed of 36 species from 7 genera distributed from tropical to cold water regions. The order is primarily composed of species with crustose thalli, but some have terete erect thalli (Kawai, 1989), characterized by discoidal early development of the thallus, intercalary plurilocular gametangia with terminal cells, terminal unilocular zoidangia, and a crustose phase in the life history. Neoralfsiaceae (Lim *et al.*, 2007) and Hapalospongidiaceae (León-Alvarez *et al.*, 2017) are recent additions to the order. The order **Nemodermatales** consists of two crustose monotypic genera from temperate coasts, *Nemoderma* (Nemodermataceae) and *Zeacarpa* (Zeacarpaceae) (Phillips *et al.*, 2008; Kawai *et al.*, 2016).

III. Evolution of life history traits and sexual reproduction

The life cycle is a fundamental biological feature that influences the evolution of various traits including reproduction systems and modes of dispersion and must be taken into account to fully understand the biology of a species. Brown macroalgae exhibit a wide variety of life cycles, sexual systems, and reproductive modes (for a recent review see Liu *et al.*, 2017). Their life cycles range from isomorphic haplodiplontic life cycles, in which both the gametophyte and sporophyte exhibit similar levels of multicellular development (e.g., *Dictyota dichotoma*), to diplontic life cycles, where only the diploid generation is multicellular (e.g., *Fucus* spp.). When gametophytes and sporophytes are morphologically different, the cycle is considered heteromorphic. In the brown algae, the diploid sporophyte is generally dominant (i.e., larger) compared to the haploid gametophyte, except in a few genera, such as *Scytosiphon*, where the haploid phase is a large, upright thallus and the diploid phase a prostrate crust (Heesch *et al.*, 2019).

Phylogenies based on morphological and molecular characters suggest that the ancestral condition of brown algal sexual reproduction was haplodiplontic, with similar haploid and diploid phases (i.e., isomorphic; Fritsch, 1949; Henry, 1984; Clayton, 1988; Cho *et al.*, 2004; Silberfeld *et al.*, 2010; Heesch *et al.*, 2019). Modifications of this isomorphic life cycle have occurred in several lineages, which involved either a reduction in size of the gametophyte generation (transition to a heteromorphic cycle, e.g., Syringodermatales, prior to the ancestor of the BACR) or loss of this haploid generation (transition to a diplontic life cycle, e.g., Ascoseirales, Fucales, genus *Tilopteris* in Tilopteridales; Silberfeld *et al.*, 2010; Heesch *et al.*, 2019). Transitions to diplontic cycles appear to have been irreversible, as there have been no transitions back to a haplodiplontic life cycle. In contrast, multiple transitions have occurred from heteromorphic to isomorphic life cycles (Silberfeld *et al.*, 2010; Heesch *et al.*, 2019). Analysis of the evolutionary processes driving these transitions remains a productive area of research for the brown algae. The annotated genome of *Ectocarpus* has also provided invaluable insights into the genes that regulate life history traits. In this section, we review emerging knowledge relating to life history traits in the brown algae, including the mechanisms underlying the maintenance of life cycle types, and the genes involved in alternating life history stages and sexual differentiation.

A. Evolutionary drivers of brown algal life cycles

Bell (1982) remarked that "the casualness of the few attempts to provide a functional account of haploidy and diploidy constitutes a major scandal." Since Bell's comment, however, new theoretical models and experimental studies have emerged (Valero *et al.*, 1992; Mable and Otto, 1998; Coelho *et al.*, 2007). Masking of deleterious mutations and short-term benefits of diploidy compared with haploidy were the first explanations of dominance of the diploid phase in most plants and animals (Crow and Kimura, 1965). As most deleterious mutations are recessive (Manna *et al.*, 2012), diploids (but not haploids) benefit from the short-term advantage of masking but they suffer from the long-term disadvantage of accumulating deleterious mutations in populations that ultimately reach the species genome (i.e., genetic load; Crow and Kimura, 1965). Later it was shown that the low level of genetic load in haploids, due to purging, can overcome this short-term advantage of diploids if there is strong linkage between the locus that determines life cycle structure (i.e., either a haplontic or diplontic life cycle) and the locus subject to deleterious mutations (Perrot *et al.*, 1991; Otto and Marks, 1996).

In this context, transitions between haplontic and diplontic life cycles over evolutionary time have been interpreted as tradeoffs between short-term individual-level benefits due to masking (diploidy) and longer-term advantages of more efficient selection against deleterious mutations (haploidy). Specifically, haploidy could be favored if there is little mixing (i.e., crossing) with diploids (Otto and Marks, 1996). Recently, Heesch *et al.*, (2019) tested the prediction of Otto and Marks (1996) that inbreeding or asexual reproduction favors haploid life cycles, extensively examining the correlation between the sexual system of a species (monoecious/dioecious) and the relative dominance (i.e., size) of the haploid and diploid phases of the life cycle for over 70 species of brown algae. This analysis supported the prediction that transitions toward dominance of the haploid phase would be more frequent when the sexual system was monoecious. Nevertheless, as having separate sexes is not always a good proxy for the mating system (Krueger-Hadfield *et al.*, 2015), estimates of inbreeding coefficients within natural populations should be carried out to shed further light on the link between mating system and ploidy level (Heesch *et al.*, 2019).

To further investigate the relationship between reproductive system and life cycle type in brown algae, we surveyed 177 peer-reviewed papers published between 1984 and 2019, 72 of which provided information about reproductive systems in 37 species of brown algae, of which 20 had a diplontic life cycle (e.g., Fucales), 13 were heteromorphic with a dominant diploid phase (12 Laminariales and 1 Tilopteridales) and only 4 exhibited an isomorphic life cycle (i.e., Dictyotales and Ectocarpales, but see Couceiro *et al.*, 2015; see Supplemental Material for methods; Figure 4). This new literature survey indicated marked intraspecific reproductive system variability at the population level. Mating system variation within species has been widely reported in land plants, where it is due to environmental and genetic factors (Goodwillie *et al.*, 2005). In particular, selfing (and asexual reproduction) may be favored in newly colonized sites or at range margins by providing reproductive assurance (Baker, 1955; Peck *et al.*, 1998; Hargreaves *et al.*, 2014). A textbook example of this phenomenon in the brown algae is *Fucus vesiculosus*, which shows contrasting reproductive systems in the Atlantic Ocean compared to the Baltic Sea, in that asexual reproduction becomes common at its ecological (Baltic Sea) margin (Tatarenkov *et al.*, 2005) where sexual reproduction is impaired by salinity (Serrão *et al.*, 1996). Other examples include the laminarialean kelp *Laminaria digitata* and the isomorphic *Dictyota dichotoma,* which both show increased asexual reproduction at the southern limit of their range distributions (Oppliger *et al.*, 2014; Steen *et al.*, 2019). The number of publications describing reproductive systems in brown algae has increased 20-fold since the Bell (1997) and the Mable and Otto (1998) studies (Figure 4A). The new literature survey only partially supported Otto and Marks' model (1996). As expected, increased recombination (mixed mating

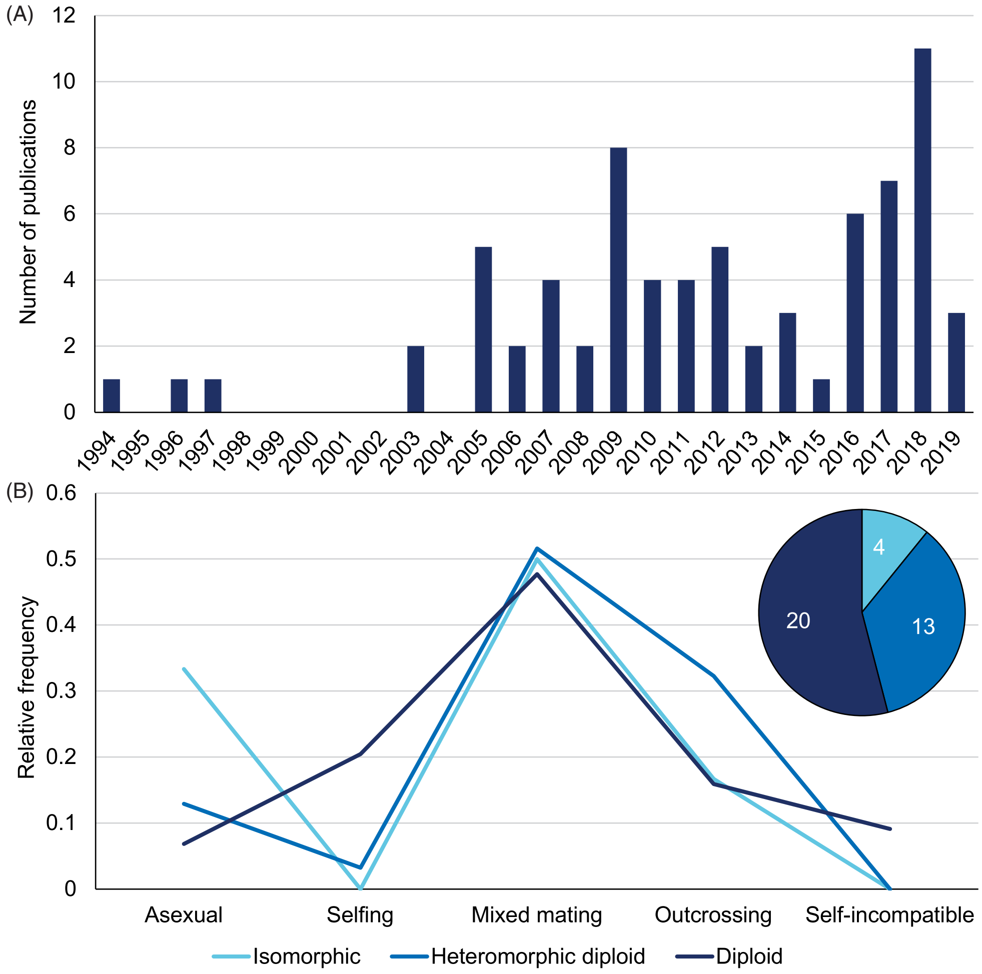


Figure 4. Literature survey of studies conducted prior to January 2020 that have addressed the relationship between mating system and life cycle type (dominant ploidy phase). (A) Number of publications concerning different reproductive systems over the last 25 years. (B) Relative frequencies of species showing different reproductive systems according to their life cycle. The pie chart represents the total number of studied species for each type of life cycle. Heteromorphic diploid refers to a diploid-dominant haplodiplontic life cycle. No heteromorphic haploid-dominant life cycle studies were found. Additional information can be found in the Supplemental Material.

systems and outcrossing) appeared to be linked to the dominant diploid phase (diplontic or species with a heteromorphic life cycle with diploid dominance); however, an increased degree of asexuality with haploid dominance was not consistently detected, as both asexual reproduction and mixed mating appeared to be prevalent in species with isomorphic life cycles (Figure 4B). These results may be attributed to the relatively low number of population genetics studies published in species characterized by a haploid dominant life cycle (see Supplemental Material). Moreover, no information for haplontic life cycles was available in the literature, likely owing to the rarity of these cycles among brown algae.

Different models predict that differences in ecological niches, or differences in survival/fertility between haploid and diploid individuals, can play an important role in the evolution of life cycles, favoring the stable coexistence of haploid and diploid stages (Hughes and Otto, 1999; Rescan *et al.*, 2016; Scott and Rescan, 2017). Differences in ecological niches between life cycle generations have been observed in many seaweed species, including brown algae with heteromorphic life cycles (Valero *et al.*, 1992; Mable and Otto, 1998; Thornber and Gaines, 2004; Coelho *et al.*, 2007). Few studies, however, have attempted to estimate differences in ecological niche or fitness between haploid and diploid phases in isomorphic haplodiplontic seaweeds (mainly in the red algae, Rhodophyta; Destombe *et al.*, 1993; Pacheco-Ruiz *et al.*, 2011). Demographic studies carried out on laminarialean kelp populations (heteromorphic haplodiplontic) have taken into account the fitness of individuals during the dominant diploid phase (sporophyte) in the field (Pereira *et al.*, 2017), or during the haploid phase (gametophyte) under laboratory conditions (Pereira *et al.*, 2011; Oppliger *et al.*, 2012), but the fitness of haploids and diploids have not been compared directly, largely due to the challenges of studying the gametophyte in situ (Schiel and Foster, 2006) and cultivating large sporophytes in the lab.

Compounding the challenge of understanding fitness tradeoffs in brown algal life cycles, work on *Ectocarpus* spp. life cycles indicates there is potential for intraspecific variability of stage dominancy. Earlier work by Müller (1964) produced *Ectocarpus siliculosus* gametophytes and sporophytes of similar size in culture, with sporophytes absent in field observations. However, the life cycle of this species can be rather heteromorphic in the field, as microscopic epilithic diploid sporophytes and macroscopic epiphytic gametophytes were reported growing on *Scytosiphon* in Naples (Couceiro *et al.,* 2015). In contrast, the same species studied at another location, near Roscoff, had only diploid individuals, either epilithic or epiphytic, and reproducing clonally on various seaweeds (Couceiro *et al.,* 2015). Thus, within-species variation for brown algal life cycles occurs in nature, as in red seaweeds (Destombe *et al.,* 1989).

B. The genetic basis of life cycle alternation

With the recent emergence of the filamentous brown alga *Ectocarpus* as a model system for genetic and genomic analyses (Cock *et al.*, 2011; Coelho *et al.*, 2012; Brodie *et al.*, 2017), it has become possible to investigate the genetic mechanisms underlying diverse aspects of brown algal biology, including the regulation of life cycle transitions. The recent advent of tools such as high-quality genome assembly (Cormier *et al.*, 2017), high-density genetic maps (Heesch *et al.*, 2010; Avia *et al.*, 2017), extensive transcriptomic data, and cloning-by-sequencing methodologies (Godfroy *et al.*, 2017) now make it possible to use the *Ectocarpus* model to identify genetic loci underlying phenotypic variation.

This forward genetic approach has been applied to the analysis of two *Ectocarpus* life cycle mutants, *ouroboros* (*oro*) and *samsara* (*sam*; Coelho *et al.*, 2011; Arun *et al.*, 2019). *Ectocarpus* has an isomorphic haplodiplontic life cycle, which involves alternation between two types of filamentous thallus corresponding to the sporophyte and gametophyte generations. Individuals that lack functional copies of either the *ORO* or the *SAM* gene are unable to deploy the sporophyte developmental program and, instead, develop as gametophytes. Genetic characterization of the *ORO* and *SAM* genes showed that they encode two different three amino acid loop extension homeodomain transcription factors (TALE HD TFs) (Arun *et al.*, 2019). TALE HD TFs have been also implicated in life cycle regulation in the green lineage (Viridiplantae) in both green algal models and land plants. This similarity between life cycle regulators in the brown and green lineages suggests that they probably have common ancestry and are therefore derived from a regulatory system that already existed at the crown radiation of the eukaryotic supergroups (Arun *et al.*, 2019). Given that mating type factors are thought to function primarily as detectors of syngamy, to initiate the diploid phase of the life cycle (Perrin, 2012), the hypothesis of a deep evolutionary origin of life cycle regulators is further supported by reports that distantly-related homeodomain or homeodomain-like proteins act as mating type factors in both fungi and social amebae (Nasmyth and Shore, 1987; Van Heeckeren *et al.*, 1998; Hull *et al.*, 2005; Hedgethorne *et al.*, 2017). Consistent with the deep evolutionary history of this life cycle regulatory system, *ORO* and *SAM* orthologues were found in a broad range of brown algae (Arun *et al.*, 2019). Other Ochrophyta lineages also possess TALE HD TFs but they are too divergent from the brown algal proteins to confidently identify them as *ORO* or *SAM* orthologues. Functional analysis of TALE HD TFs from other lineages will therefore be needed to further trace the detailed evolutionary history of the *ORO* and *SAM* genes within Ochrophyta.

Several hundred genes are differentially expressed between the sporophyte and gametophyte generations of the *Ectocarpus* life cycle (Coelho *et al.*, 2011; Arun *et al.*, 2019; Lipinska *et al.*, 2019), indicating that *ORO* and *SAM* regulate a complex program of gene expression. These generation-biased genes are predicted to carry out diverse functions but, interestingly, there appears to be a correlation between enriched gene functions (gene ontology terms) and phenology. Analysis of the *Ectocarpus* life cycle in the field indicates that the sporophyte is probably the overwintering stage as it is present, often in microscopic form, for most of the year, whereas the gametophyte only appears in the spring for a limited period (Couceiro *et al.*, 2015). These respective features of each generation are correlated with a general preponderance of metabolic genes upregulated in the sporophyte (i.e., survival and maintenance) compared to genes with roles in growth and cell division upregulated in the gametophyte (i.e., rapid seasonal growth; Coelho *et al.*, 2011).

The developmental complexity of brown algae varies enormously. Moreover, because of the broad range of haplodiplontic life cycles in brown algae, the sporophyte and gametophyte generations can vary in terms of size, morphological complexity and ecological function. A recent analysis of generation-biased gene expression in

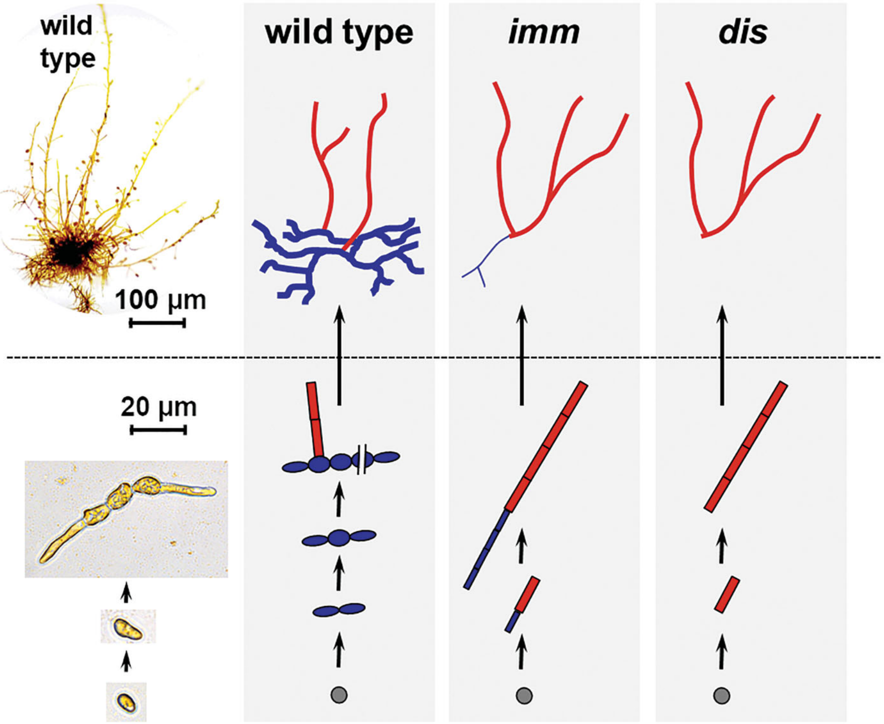


Figure 5. Phenotypes of the *Ectocarpus immediate upright* (*imm*) and *distag* (*dis*) mutants during the sporophyte generation. Schematic representations of development from a single initial cell with apical and basal tissues in red and blue, respectively. Wild type individuals produce an extensive network of basal filaments before producing upright (apical) filaments, whereas the *imm* mutant only produces a small rhizoid and the *dis* mutant completely lacks basal tissues.

four different brown algae with different life cycles and different levels of developmental complexity indicated that generation-biased gene sets turn over rapidly during evolution (Lipinska *et al.*, 2019). Therefore, a picture is emerging of strongly conserved master regulators, such as ORO and SAM combined with highly variable sets of downstream differentially expressed genes. This conservation of master regulators is a theme that has also been observed in other developmental contexts, for example in animals, where conserved orthologues of the *eyeless* gene direct the construction of very different types of eye in organisms as diverse as mammals and fruit flies (Quiring *et al.*, 1994).

Recently, forward genetics has also been used to identify genes playing key roles during the development of the sporophyte and/or gametophyte generations. One of the questions that these experiments aimed to address concerns the evolutionary origins of the sporophyte and gametophyte developmental programs, in particular the extent to which these programs have emerged independently for the two generations. The recent identification of two genes that play key roles in the development of the basal systems that attach *Ectocarpus* individuals to substrata has begun to address this question. The first of these genes, *DISTAG (DIS),* is required for the deployment of basal systems during both the sporophyte and gametophyte generations (Godfroy *et al.*, 2017). This was a surprising observation because the basal systems of the two generations are very different (Peters *et al.*, 2008). In the gametophyte, asymmetric division of the initial cell, a meiospore, leads to the production of a small rhizoid and an upright filament that will develop into the apical thallus. In the sporophyte, on the other hand, the initial cell divides symmetrically, and an extensive network of basal filaments is established before the upright filaments of the apical system are produced (Figure 5). The basal systems of the two generations therefore differ in terms of their developmental programs, their size and the cell types involved (i.e., rhizoid cells in the gametophyte, round and elongated filament cells in the sporophyte) but nonetheless depend on a common genetic component for their development. The *DIS* gene encodes tubulin binding cofactor Cd1 (TBCCd1), which is thought to have a role associated with the cytoskeleton (Godfroy *et al.*, 2017). TBCCd1 is an ancient protein that has been conserved across diverse eukaryotic supergroups and *DIS* orthologues have been found in all brown algae analyzed to date. However, the functions of these genes in the other brown algae remain to be investigated.

Mutation of the second gene, *IMMEDIATE UPRIGHT (IMM)*, leads to the extensive basal system of the sporophyte being replaced by a small rhizoid, which resembles the rhizoid of the gametophyte (Figure 5; Peters *et al.*, 2008). There is no visible phenotype during the gametophyte generation. The sporophyte phenotype has been interpreted to indicate that the extensive basal system of this generation evolved from a simpler rhizoid-like system, an evolutionary event that specifically affected the sporophyte generation (Macaisne *et al.*, 2017). Taken together, therefore, analysis of the *dis* and *imm* mutants has indicated that evolution of the sporophyte and gametophyte developmental programs has involved both sharing of genetic components (*DIS*) and the evolution of generation-specific programs (*IMM*). *IMM* encodes a protein of unknown function with a conserved, repeated cysteine-rich domain (Macaisne *et al.*, 2017). *IMM* orthologues have been identified in several brown algal orders but the function of these proteins is unclear as these species do not exhibit delayed deployment of apical organs during the sporophyte generation. The conserved cysteine-rich domain of the IMM protein has been called the EsV-1-7 domain because it was first observed in a gene from the *Ectocarpus* virus EsV-1. Other Ochrophyta lineages possess no more than one EsV-1-7 domain gene but there appears to have been a spectacular expansion of this gene family in the brown algae, for example, with 91 gene family members being detected in *Ectocarpus* (Macaisne *et al.*, 2017). Given the key developmental role of the *IMM* gene, it has been suggested that the expansion of this gene family may have played a role in the evolution of complex multicellularity in the brown algae. Interestingly, EsV-1-7 domain genes are patchily distributed across the eukaryotic tree and have been found in three diverse viral genomes, leading to the suggestion that viruses may have mediated horizontal transfer of these genes during eukaryotic evolution (Macaisne *et al.*, 2017).

C. Evolution of brown algal sex chromosomes and sexual differentiation systems

Brown algae are characterized by a striking diversity of sexual systems, levels of sexual dimorphism and reproductive modes, and these traits are labile across the different groups (see above). The most prevalent system has separate sexes during the haploid stage of the life cycle (dioicy) but several transitions to co-sexuality (monoicy) have occurred during brown algal evolution (Luthringer *et al.*, 2014; Heesch *et al.*, 2019). Only one group, the Fucales, has evolved sex determination (dioecy) in the diploid stage of the life cycle, and, again, shifts have occurred between separate sexes and co-sexuality (monoecy) multiple times within this lineage (Cánovas *et al.*, 2011). This broad diversity of sex-related traits makes the brown algae exceptional models to investigate the forces driving the evolution of sex determination. In particular, the range of analytical tools available for *Ectocarpus* sp. has allowed significant progress to be made in our understanding of the mechanisms underlying sex determination and differentiation in this model species. *Ectocarpus* sp. has a haploid, dioicous sexual system in which male and female sexes are determined after meiosis in the sporophyte, depending on whether the meio-spores inherit a U (female) or a V (male) chromosome (Coelho *et al.*, 2018). The sex chromosomes of *Ectocarpus* sp. were the first eukaryotic UV system to be described in detail (Ahmed *et al.*, 2014). The nonrecombining sex-determining regions (SDR) of the U and V chromosomes are ∼1 Mbp in length, occupying about a 10th of the sex chromosome (Cormier *et al.*, 2017). The male haplotype of the SDR contains 17 protein-coding genes and three pseudogenes, whereas the female haplotype contains 15 protein-coding genes and seven pseudogenes. Genes at the male and female SDRs in *Ectocarpus* sp. are highly divergent at the sequence level, suggesting that these regions have been evolving independently for a long period of evolutionary time. Because of the lack of recombination, both SDRs are enriched in transposable elements and gene poor compared with autosomes, a characteristic that is shared with Y and W nonrecombining regions (Bachtrog *et al.*, 2014).

The availability of classical genetic tools for *Ectocarpus* has been an asset to understand sex determination and sex chromosomal dominance in UV systems. Genetic crosses using the *oro* life cycle mutant (producing a functional diploid gametophyte; Coelho *et al.*, 2011; Arun *et al.*, 2019; see above) have shown that the male SDR on the V chromosome is dominant over the female SDR, implying the existence of a male master sex-determining gene(s) within the male SDR. One male-specific SDR gene, which is strongly upregulated during fertility and is predicted to encode a high mobility group (HMG) domain transcription factor, is a good candidate for this master regulator (Ahmed *et al.*, 2014). HMG domain genes are involved in sex determination in animals and mating type determination in fungi (Idnurm *et al.*, 2008; Graves and Peichel, 2010). Interestingly, orthologues of the *Ectocarpus* HMG domain gene are consistently male-linked in all brown algal species that have been investigated so far (Lipinska *et al.*, 2017).

Comparative genomic analyses across nine brown algal species has identified a core set of genes that has been stably maintained within their SDRs, suggesting that these genes play a role in sex determination, and/or that these genes were present on the ancestral chromosome and have been trapped in this chromosomal region since the recombination suppression event that gave rise to the SDR. This set of genes includes the HMG domain gene. In addition to this conserved set of genes, substantial modifications occurred in each of the brown algal SDRs, involving gene loss, gene gain and relocation of genes from the SDR to autosomes (Lipinska *et al.*, 2017). Gene loss and gene gain events have also played a role in the evolution of sex-determination systems in several metazoan lineages (Emerson *et al.*, 2004; Potrzebowski *et al.*, 2008), highlighting common features between haploid and diploid sexual systems. Gene gain in brown algal U and V sex chromosomes has occurred via transposition from other chromosomes and engulfment of neighboring genes located in the pseudo-autosomal region (PAR, Lipinska *et al.*, 2017). The genes that have been acquired by the nonrecombining regions are expressed mainly during the haploid, gametophyte generation. This observation agrees with models predicting that haploid sex chromosomes should evolve by gaining genes favorable for the haploid phase of the life cycle (Bull, 1983).

The PAR of the *Ectocarpus* sex chromosome recombines at a similar rate to the autosomes (Luthringer *et al.*, 2015). Therefore, the expectation was that the structural and evolutionary characteristics of this region would be similar to those of the autosomes (Otto *et al.*, 2011). Surprisingly, however, this is not the case (Luthringer *et al.*, 2015). Moreover, the PAR is enriched in genes that are preferentially or exclusively expressed during the sporophyte (diploid) generation of the life cycle, and many of these genes do not have homologs in other brown algal clades (Luthringer *et al.*, 2015). A modelling-based approach evaluating the enrichment in sporophyte-biased gene expression for the PAR suggested differential pressures in males and females acting on alleles that are advantageous during the sporophyte generation of the life cycle. Recent data indicates that the PAR exhibits more neutral evolution compared with autosomal regions, and that genes in this region may be under balancing selection (Avia *et al.*, 2018), in agreement with theoretical expectations that linked neutral diversity increases exponentially with the number of selected loci (Navarro and Barton, 2002). It is currently unknown if the PAR of *Ectocarpus* is representative of PARs in other UV systems, and investigations of sex chromosomes in other brown algae will be crucial to address this question.

Sex chromosomes play a major role in sex determination, but most of the phenotypic differences between males and females are caused by differential expression of genes that are present in both sexes, a phenomenon known as sex-biased gene expression (Parsch and Ellegren, 2013). Only about 10% of the transcriptome is sex-biased in *Ectocarpus* (Lipinska *et al.*, 2015), which is not surprising given the phenotypic similarities between sexes in this species (Ahmed *et al.*, 2014). Interestingly, other brown algae with more marked morphological differences between sexes had only a small fraction of sex-biased genes, ca. 7-12% in the kelp *Saccharina latissima* (Monteiro *et al.*, 2019), and 9-14% in *Fucus vesiculosus* (Martins *et al.*, 2013). It appears that overall, brown algae exhibit less conspicuous sex-biased transcriptomes compared with animal systems, where a large proportion of the genome may be differentially regulated in males and females. This is probably because phenotypic sexual dimorphism is less pronounced in the brown algae (Luthringer *et al.*, 2014; Lipinska *et al.*, 2015). Interaction between the sexes in most brown algae is indirect, through broadcast spawning of gametes that meet and fuse in the seawater, without any further intervention of the gametophyte. The success of reproduction is therefore ensured by strategies such as releasing gametes at the optimal phase of the tide or by providing gametes with efficient phototactic and pheromone systems (Maier, 1995; Pearson and Serrão, 2006) and not by developing a high level of sexual dimorphism at the gametophyte level.

It is a common observation that male-biased genes in XY sexual systems tend to evolve more rapidly than unbiased genes at the level of their protein-coding sequence (Ellegren and Parsch, 2007). Analysis of the evolutionary rates of sex-biased compared with unbiased genes in *Ectocarpus* indicated that both male- and female-biased genes had faster evolutionary rates than unbiased genes (Lipinska *et al.*, 2015). These genes also showed evidence of stronger positive selection compared to autosomal genes, suggesting that their faster evolutionary rates are at least partly driven by adaptive evolution.

IV. Reproductive isolation and speciation

A. Speciation mechanisms

The "species problem" has been with us since before Darwin. While defining the meaning of "species" is a thorny and complex problem beyond the scope of this review, recent advances in our understanding of brown algae have shed light on the mechanisms by which lineages diverge. Brown algae vary widely in traits that influence their potential for speciation and diversification, such as life history strategies, dispersal mechanisms and potential, as well as apparent scope for ecological diversification. For instance, the potential for dispersal in brown algae can vary from a few centimeters (Hays, 2007; Barner *et al.*, 2011) to hundreds of kilometers (Smith, 2002; Fraser *et al.*, 2020). In the sister species *Postelsia palmaeformis* and *Nereocystis luetkeana*, the difference in potential for long distance dispersal is dramatic, in that *P. palmaeformis* is characterized by drooping, deeply grooved blades, promoting highly localized dispersal and selfing (Barner *et al.*, 2011), while *N. luetkeana* produces dehiscent sori on blades near the surface- up to tens of meters from the substratum, presumably promoting greater dispersal distances (Dayton, 1985). This type of variation in dispersal potential is widely represented throughout the brown algae, with some species capable of forming enormous rafts that can cross oceans (Smith, 2002) while others generally disperse only locally or through a series of "stepping stones" (Billot *et al.*, 2003). The substantial differences in traits among lineages are expected to manifest as variation in diversification rates, which is supported by diversification analyses (Cánovas *et al.*, 2011; Starko *et al.*, 2019) and the heterogeneity in the species richness of lineages across the brown algal phylogeny (Figure 2; Silberfeld *et al.*, 2010). In this subsection, we summarize the main mechanisms known to drive speciation and lineage diversification across the brown algae and critically evaluate the state of knowledge of these various mechanisms.

1. Barriers to reproduction

Natural populations of brown algae reproduce sexually by external fertilization (broadcast spawning; e.g., many Fucoids, Ectocarpales and Dictyotales) or functional brooding (i.e., retention of fertilized eggs, e.g., Sargassaceae). The frequent aggregation of closely related species in natural habitats suggests that barriers to hybridization should be very important. Nevertheless, pheromonal systems for sperm attraction are simple; often the same active molecule is shared across a large group of species (Müller *et al.*, 1971; 1979; 1981; Müller and Jaenicke, 1973; Jaenicke *et al.*, 1974; Müller and Gassmann, 1980). Moreover, the high cross-specific fertility in experimental crosses within and even between genera (Bolton *et al.*, 1983; Kraan and Guiry, 2000; Coyer *et al.*, 2002; Müller *et al.*, 2019) have led these authors to assume that specificity in gamete recognition or gamete incompatibility might not be the key factors in producing or maintaining species boundaries. This provides an apparent paradox, where substantial species diversity appears to have arisen, and maintained in sympatry, with few intrinsic barriers to reproduction. There are, however, examples where barriers to crossing are observed between closely related species pairs (Tom Dieck, 1992; reviewed by Bartsch *et al.*, 2008). Interestingly, hybrid inviability between sympatric sister species may contrast with viability at greater evolutionary distances and/or geographic isolation (Tom Dieck, 1992; Martins *et al.*, 2019). For example, sister species *Laminaria hyperborea* and *L. digitata* are incompatible (Tom Dieck, 1992), while *Laminaria digitata* and *L. pallida*, which are more distantly related but differ in geographic range (Rothman *et al.*, 2017; Martins *et al.*, 2019) are partially compatible, suggesting that reproductive barriers may only be reinforced when species are sympatric. Reinforcement can even be population specific within species ranges, as exemplified by *Fucus vesiculosus* and *F. spiralis*. These species co-occur along most of their range with limited introgression, but are extensively introgressed where allopatric populations (separated by habitat) contact, suggesting lower reinforcement of the allopatric versus sympatric populations (Moalic *et al.*, 2011). Similarly, hybrids appear to be more common in recent versus old contact zones in Atlantic *F. distichus* and *F. serratus* (Hoarau *et al.*, 2015).

Ecological factors and life history traits can also affect gene flow between diverging populations and reinforce species or lineage boundaries. Alone or in concert, variations in reproductive phenology, niche occupancy, and mating system can be strong segregating factors. For example, both the sex ratio and the length of the vegetative growth stage during the gametophyte generation can be influenced by temperature (Oppliger *et al.*, 2011; 2012). Such variation in contact zones could contribute to reduced cross fertility between species. Gamete or meio-spore dispersal distances are generally limited in brown algae, minimizing potential adverse effects of dilution on fertilization efficiency (Reed *et al.*, 2004; Pearson and Serrão, 2006). High densities of individuals are also likely important because pheromone gradients for sperm attraction are effective only at mm scales (Lüning and Müller, 1978). Additionally, the prevalence of negative phototaxis and/or negative buoyancy of gametes, or a microscopic gametophyte phase suggests that fertilization has evolved to take place at or near the (2-dimensional) benthos rather than in the water column. There is good evidence from fucoids that the sophisticated sensing mechanisms used to synchronize gamete release to narrow temporal windows (reviewed by Pearson and Serrão, 2006) vary at hourly scales between sympatric congenerics (Monteiro *et al.*, 2012, 2016). Such small variations in reproductive timing may provide strong reproductive isolation (e.g. in sympatric interfertile corals; Levitan *et al.*, 2004). Controls over gamete release and dispersal may therefore largely restrict opportunities for natural hybridization, in addition to post-zygotic effects on fitness.

A major shift in speciation research has come with the recognition that reproductive barriers often remain semipermeable and gene flow may occur even while species differentiate (see Hausdorf, 2011, and refs therein). Although most interspecific hybrids are sterile or less fit than their parents, some may survive and reproduce, enabling the transfer of neutral and adaptive variants across species boundaries (introgressive hybridization), or even the formation of novel evolutionary lineages (homo- and allopolyploid speciation, and hybrid clones). Brown algae have been pivotal in linking hybridization and introgression with historical biogeography. Periodic range dissections and expansions associated with climatic oscillations (e.g., glacial-interglacial cycles) often result in secondary contact between vicariant lineages and sister species, where heterosis (Martins *et al.*, 2019) and/or lack of reinforcement (Hoarau *et al.*, 2015) can potentially result in increased genetic transfer. These contact zones are predicted to be more frequent at (but not restricted to) higher latitudes, for instance along trans-Arctic routes and the Aleutian Arch (where western and eastern expanding Pacific populations meet), but have seldom been objectively examined beyond a few case studies showing very limited intraspecific gene-flow in sibling species (Tellier, Tapia, *et al.*, 2011; Neiva *et al.*, 2018). Fine-scale studies of these contact zones are likely to clarify isolation mechanisms underlying brown algal speciation. Signatures of past and ongoing hybridization and introgression, typically genetic admixture (e.g. hybrid microsatellite genotypes), conflicts among organellar genomes (Tellier, Faugeron, *et al.*, 2011), and conflicts between organellar and nuclear genomes, have been detected in natural populations for a wide range of brown algal taxa (Hodge *et al.*, 2010; Neiva *et al.*, 2010; Moalic *et al.*, 2011; Zardi *et al.*, 2011; Geoffroy *et al.*, 2015; Kogame *et al.*, 2015; Montecinos *et al.*, 2017a), pinpointing their taxonomic ubiquity and importance in brown algal evolution.

Macromutations (e.g., polyploidy) can also cause barriers to reproduction and result in "instant speciation," often with accompanying evolutionary opportunity (see Sousa *et al.*, 2019). By comparison with other groups, like embryophytes, the incidence of polyploidy is poorly understood in brown algae. The recent confirmation of two late-Pleistocene allopolyploid lineages in the fucoid genus *Pelvetiopsis* are unique thus far, remarkably involving the same extant paternal ancestor (Neiva *et al.*, 2017; Sousa *et al.*, 2019). In *Pelvetiopsis*, the allopolyploid *P. limitata* is currently the most widespread and abundant species of the genus, whereas its paternal and maternal diploid ancestors are a narrow-endemic climatic relict (*P. arborescens*) and a presumably extinct species (Sousa *et al.*, 2019). Climatic shifts, perhaps associated with hybrid vigor, have been invoked to explain its successful establishment beyond the contracting ancestors' ranges. Perenniality, self-compatible hermaphroditism, and other correlates of polyploidy in land plants are also found in some species-rich genera of brown algae, suggesting that it might be more widespread. Furthermore, across some of the most species-rich orders of brown algae (e.g., Laminariales, Ectocarpales, Fucales, Dictyotales) genomes sizes can vary several-fold (Phillips *et al.*, 2011), leaving open the possibility that polyploid speciation has occurred deeper in the past. However, current genome data do not support hypotheses of ancient polyploidy, at least for Laminariales and Ectocarpales (Cock *et al.*, 2010; Ye *et al.*, 2015; Nishitsuji *et al.*, 2016; 2019; Dittami *et al.*, 2020; Shan *et al.*, 2020). Thus, further analyses are required to understand the processes that have led to observed variation in genome size.

2. Allopatric speciation

There is substantial evidence that geographical isolation has played a major role in patterns of speciation and diversification across various brown algal clades. Vicariance events are common when tectonic or climatic shifts cause two or more populations to be isolated from each other. Long distance dispersal events may also allow populations to invade new parts of the globe, potentially leading to isolation from the parent population. This is presumably the dominant process in lineages such as *Lessonia* or *Durvillaea*, where species rarely overlap in range and patterns of speciation tend to represent lineage dispersal pathways (Fraser *et al.*, 2010; Zuccarello and Martin, 2016). Similarly, recent phylogeographic analyses of both the

Laminariales (Starko *et al.*, 2019) and the genus *Sargassum* (Yip *et al.*, 2020) indicate that region-specific diversification is likely a common process. The high number of regionally endemic large brown algae in each of the Southern Hemisphere temperate regions (S. America, S. Africa and Australia/New Zealand) suggests that trans-oceanic distances remain effective barriers to dispersal (Peters *et al.*, 1997; Phillips, 2001; Bolton, 2010), contrasting with the comparatively contiguous landmasses in the Northern Hemisphere.

A history of repeated cycles of environmental or ecological change resulting in population subdivision is theoretically conducive to speciation (Gavrilets *et al.*, 1998; Gavrilets, 2003). While glaciations periodically erase and re-distribute genetic lineages, they also promote evolutionary novelty, and have played an important role in promoting allopatric lineage divergence in the brown macroalgae during the Pleistocene (2.6 Ma–12 ka). Widespread amphiboreal taxa provide a paradigmatic example. Exchanges between Pacific and Atlantic basins (and to a lesser degree across the Atlantic) are only possible during brief interglacial periods when seasonally ice-free marine routes allow dispersal and colonization past the Bering Strait and across the Arctic. The subdivision of *Saccharina latissima* and *Fucus distichus* – two of the most widespread, polymorphic and ecologically plastic brown algae of the Northern Hemisphere – into vicariant Atlantic and Pacific phylogroups support this general background of episodic dispersal versus chronic isolation (Coyer *et al.*, 2011; Neiva *et al.*, 2018). In *Saccharina latissima*, NW Atlantic and Pacific lineages reveal remarkable genetic integrity in a large zone of high-Arctic secondary contact, suggestive of reproductive isolation and incipient speciation (Neiva *et al.*, 2018). Similar patterns of vicariance between trans-Arctic populations are evident in many other brown algae but remain to be rigorously assessed using large population level datasets (exemplar genera include *Chordaria*, *Desmarestia*, *Dictyosiphon*, *Petalonia*, and *Pylaiella*; Saunders and McDevit, 2013; Bringloe and Saunders, 2019). The full extent to which glacial cycles act as a trans-Arctic "speciation pump" to amplify brown algae diversification also remains unassessed.

3. Sympatric, parapatric and peripatric speciation

Although allopatric speciation arising from geological and climatic processes is likely to have been an important process in establishing the modern diversity and distribution of brown algal species across modern oceans, there are many examples of brown algal speciation that did not depend on strict geographical isolation. Geographical clines may be associated with gradients in environmental conditions, and segregation of populations along these gradients can lead to lineage divergence or speciation, presumably through parapatric or peripatric speciation (sensu Funk and Omland, 2003). In the *Lessonia nigrescens* species complex (Laminariales), two cryptic species are recognized along the coast of Chile, with only a narrow overlap in ranges (Tellier *et al.*, 2009) but complete reproductive isolation (Tellier, Tapia, *et al.*, 2011). The heat tolerance of these cryptic species differs and matches their corresponding latitudinal distributions, suggesting that genetic and ecological divergence are linked (Oppliger *et al.*, 2012; López-Cristoffanini *et al.*, 2013). In this case, the phylogeny recovered a monophyletic clade for the northern species, nested within the southern species (Tellier *et al.*, 2009), suggesting that speciation occurred at the northern range margin of the southern species following a combination of adaptation and founder effects (i.e., parapatric speciation; Funk and Omland, 2003). Similarly, the widespread species *Fucus vesiculosus* shows intraspecific lineage divergence both near the southern range edge (Cánovas *et al.*, 2011) and in the marginal brackish Baltic Sea (Tatarenkov *et al.*, 2007). In both cases, divergence is associated with habitat shifts and physiological changes consistent with local adaptation (Serrão *et al.*, 1996; Pearson *et al.*, 2000; Saada *et al.*, 2016).

Ecological speciation is a mechanism of sympatric speciation linking ecology and evolution, whereby divergent selection within a species leads to speciation. The best studied examples of this process in brown algae are in the order Laminariales, where ecological explanations have been invoked to understand the diversity of species with overlapping ranges. Kelps (Laminariales) of the Northeast Pacific coast began diversifying recently (∼30 Ma, Starko *et al.*, 2019) and predominantly in one oceanic basin (the North Pacific), suggesting ecological speciation played an important role early in their evolution. Between Mexico and Alaska, upwards of two dozen species of Laminariales are currently recognized (Guiry and Guiry, 2020), many of which have extensive and overlapping latitudinal ranges but play different ecological roles. Estes and Steinberg (1988) proposed that ecological differences such as susceptibility to grazing may have been essential in driving species divergence and lineage diversification. Interestingly, ecological differences between species often lead to some degree of spatial segregation between species. For example, where the ranges of *Laminaria digitata* and *Laminaria hyperborea* overlap in the North Atlantic, these species tend to occupy differing tidal heights. Moreover, intraspecific lineage

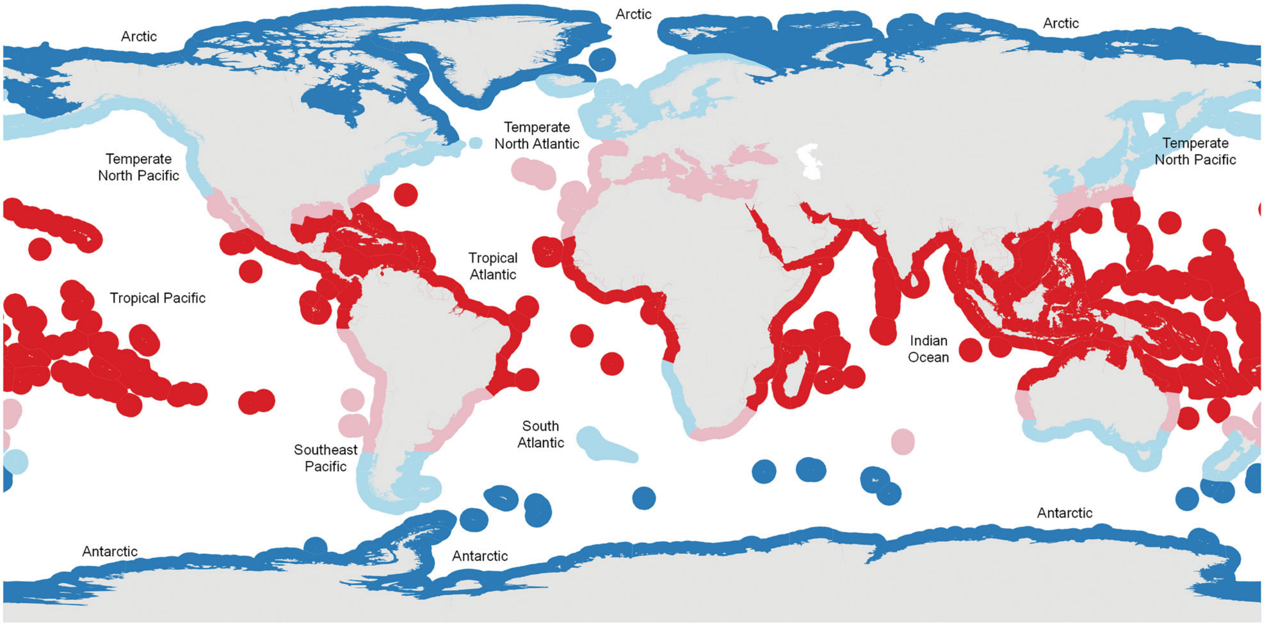


Figure 6. Biogeographic subdivisions of marine biodiversity, modified from those described by Spalding *et al.* (2007). Dark blue = Arctic; light blue = cold-temperate; pink = warm-temperate; red = tropical.

differentiation and, in some cases, true speciation events have been known to occur over local environmental gradients such as tidal height, depth, and wave exposure (e.g. Blanchette *et al.*, 2002; Miller *et al.*, 2000; Roberson and Coyer, 2004; Fraser, Hay, *et al.*, 2009; Augyte *et al.*, 2018). This pattern further holds true across the laminarialean phylogeny where niche partitioning across local gradients of wave exposure may have promoted diversification (Starko *et al.*, 2020). For example, it is common for large brown algal sister species to have largely overlapping geographical ranges but use entirely different habitats, such as in *Postelsia palmaeformis* (high intertidal) and *Nereocystis luetkeana* (subtidal) or *Saccharina latissima* (sheltered coasts) and *S. angustissima* (wave exposed coasts) (Augyte *et al.*, 2018; Starko *et al.*, 2020). Moreover, several ecologically relevant characteristics, such as buoyancy, branching and wave resistance strategies have evolved repeatedly across the kelps (Starko & Martone 2016b, Starko *et al.*, 2019), suggesting that species diversification was associated with ecological diversification in sympatry.

Further evidence of speciation in the absence of geographical isolation is evident in the Fucaceae. The multilocus phylogenetic approach of Cánovas *et al.*, (2011) showed that hermaphroditism is a derived trait and that the hermaphrodite lineage (*F. spiralis* and relatives) forms a paraphyletic sister clade with the ancestral extant southern populations of dioecious *Fucus vesiculosus*. Given the absolute habitat differentiation that prevails currently (saltmarsh versus open coast intertidal) in this southern range, dioecious and hermaphrodite divergence may have been parapatric/peripatric, with a switch in mating system from outcrossing to selfing-dominated (Perrin *et al.*, 2007) likely contributing to reproductive isolation between the nascent lineages. Such association between ecological speciation and shifts in mating systems and/or life cycles have been observed also in kelps (see above) and *Ectocarpus* spp. (Couceiro *et al.*, 2015). Even though these are still few examples, they highlight the possible role of the complex and variable life cycles of brown algae in promoting speciation without strong geographic isolation.

B. Historical biogeography

The underlying mechanisms for reproductive isolation are widely known in the brown algae, however, the trajectories leading to notable differences in assemblages across the globe follow in the wake of geological history and climate. Though the biogeography of brown algae could be subdivided into increasingly fine scale ecoregions (Lüning, 1990b, lists 23), here we review the evolution of assemblages with respect to three broad and historically recognized climate delineations: temperate (cold and warm), polar, and tropical assemblages (Figure 6). We also conclude our review with a brief overview of the rare occasions in which the brown algae have ventured into freshwater.

1. Temperate

Most brown algae live in temperate waters where some lineages act as the dominant foundation species in coastal ecosystems. As the oceans cooled following the Eocene optimum (∼32 Ma), several lineages of brown algae convergently evolved large thallus sizes and began to form upright, structurally complex habitats. The Laminariales, Fucales, Desmarestiales, and Tilopteridales all have members that form important marine habitats or ‘forests.’ The Laminariales diversified in the North Pacific as the oceans cooled in the late Cenozoic (Starko *et al.*, 2019) and now dominate the temperate coastlines in this basin (Bolton, 2010). Members of the Laminariales have only recently spread to other oceanic basins (within the past 10 Ma; i.e., Atlantic, Southern Hemisphere), and are consequently much less diverse in these areas (Bolton, 2010; Starko *et al.*, 2019). Rather, Fucales form important habitats in these areas. In the North Atlantic, the largely intertidal family Fucaceae dominate and reach their highest diversity, forming habitat along with *Saccorhiza,* one of two members of Tilopteridales (the other being related *Phyllariopsis*) to have achieved a large thallus. In the Southern Hemisphere, endemic fucoids such as *Durvillaea, Phyllospora,* and *Scytothalia* dominate temperate areas, coexisting with a small number of laminarialean species. Members of the Sargassaceae (Fucales), although largely tropical (see below), are also important constituents of temperate brown algal forests. While fucoids are among the dominant coastal habitat forming species throughout the globe, fucoid diversity in the Northern Hemisphere is largely restricted to the intertidal zone, potentially reflecting an effect of competition with (subtidal) laminarialean kelps.

Much of the cryptic brown algal diversity observed today has a strong geographical signal, to a large degree imprinted by repeated cycles of population extinctions/colonizations and vicariance/contact events during the last stages of the Pleistocene (2.5 Ma ago to 12 ka). During glacial periods, including the Last Glacial Maximum (LGM, 26-19 ka), ice-sheet expansion into temperate latitudes extirpated seaweeds from much of their modern distributions. Such local extinctions under the direct effect of the ice expansion occurred along all circumpolar regions but were especially extensive along shallower and enclosed seas and coastlines. Because of the equatorward shifts of isotherms, seaweed glacial ranges reached lower latitudes and are assumed to have been latitudinally compressed. The rise of trans-oceanic land barriers (e.g., Beringia, currently at −50 m) associated with global sea level regressions (down to −120 m), and the replacement of high-latitude stepping stones with ice barriers in the Northern Hemisphere, also contributed to lengthy isolation of many regional assemblages, which is reflected in the genetics of contemporary populations (Neiva *et al.*, 2018; Bringloe and Saunders, 2018; 2019; Bringloe *et al.*, 2020). In the current interglacial period (Holocene, 12 ka- present), warmer climates, marine transgressions and seasonally ice-free marine routes allowed macroalgal assemblages (or subsets of populations within species) to vastly expand their ranges polewards (e.g. Fraser, Nikula, *et al.*, 2009; Neiva, Pearson, *et al.*, 2012), often associated with range contraction at lower latitudes (Neiva *et al.*, 2014; Assis, Araújo, *et al.*, 2018). This led to novel, sometimes transient, trans-oceanic colonizations and secondary contact in several brown algal species (Neiva *et al.*, 2018; Bringloe *et al.*, 2020).

In the NE Atlantic, where isotherms are more splayed latitudinally, agreement between genetic hotspots (characterized by high levels of genetic diversity, and even unique endemic lineages), and climatic refugia (areas with suitable climatic conditions during both glacial and interglacial extremes) has been documented across many brown algal taxa (Hoarau *et al.*, 2007; Neiva, Pearson, *et al.,* 2012; Neiva, *et al.,* 2014; Assis *et al.*, 2016; Assis, Serrão, *et al.*, 2018), underscoring the importance of long-term regional persistence in driving regional diversity. These areas were identified beyond ice-sheet limits, along western Ireland, Brittany and northwest Iberia, in addition to the Canadian Maritimes in the NW Atlantic (Neiva *et al.*, 2016; Assis, Araújo, *et al.*, 2018). More recently, upwelling areas (Lourenço *et al.*, 2016), deep off-shore reefs (Assis *et al.*, 2016; Assis, Araújo, *et al.*, 2018) and other thermally buffered regions (e.g. Neiva *et al.*, 2017) have been recognized as important areas where relict populations (and gene-pools) persevere (Assis, Araújo, *et al.*, 2018). In contrast, areas colonized only post-glacially (e.g. Scandinavia) tend to have homogenous genetic compositions. This pattern is expected at high latitudes due to consecutive genetic bottlenecks and gene surfing experienced along expanding fronts (Excoffier and Ray, 2008).

Similar links between climatic shifts, range dynamics and intra- or inter-specific diversity are evident in other temperate assemblages as well (Fraser, Spencer, *et al.*, 2009; Hu *et al.*, 2017; Zhang *et al.*, 2019). In the SE Pacific (Chile), many seaweeds show complex genetic subdivisions at 42° S (Guillemin *et al.*, 2016), matching the limits of coastal ice during the last glacial maximum (LGM; McCulloch *et al.*, 2000) and around 30° S, possibly matching the northward limit of the Western Drift during the same period (Guillemin *et al.*, 2016). Moreover, many species are endemic to the most southern region (i.e. the Magellan region; Santelices and Meneses, 2000) indicating that glacial refuges retained regional diversity. Similarly, in the Northeast Pacific, refugial islands and archipelagos have been found to possess endemic species or genotypes (e.g., Aleutian archipelago: Starko *et al.*, 2018, St. George Island: Kawai *et al.*, 2013; Haida Gwaii: Saunders and McDevit, 2014) suggesting that these areas represent relic assemblages.

2. Polar

While species diversity of the brown algae predominantly resides in temperate climates, the Arctic region nonetheless played a major role in the evolution of Northern Hemisphere lineages. The Arctic basin began as an embayment of the Pacific Ocean until this connection was severed approximately 66 Ma (Lawver *et al.*, 1990; Marincovich *et al.*, 1990). Aside from intermittent connections with the world's oceans and seas, brown algae in the Arctic basin would have evolved in relative isolation until the North Atlantic opened 15 Ma ago (Lawver *et al.*, 1990). Global temperatures early in the evolution of the Arctic (66 Ma; Jenkyns *et al.*, 2004) were 30 °C warmer than today, and gradually cooled until the initiation of glacial cycles 2.6 Ma (Miller *et al.*, 2010). The Arctic was likely an important area for "biotic innovations" in response to colder, seasonal waters that trickled southwards and settled into contemporary temperate assemblages (Hickey *et al.*, 1983), particularly in the geologically younger Atlantic basin. As with temperate assemblages, recent cycles of glaciation had a major impact on contemporary distributions of brown algae in the Arctic.

Genetic surveys have nonetheless revealed surprising levels of diversity unique to the Arctic basin (Saunders and McDevit, 2013; Laughinghouse *et al.*, 2015; Küpper *et al.*, 2016; Bringloe *et al.*, 2020), a finding difficult to reconcile with the historical view of Arctic populations as extensions of temperate species (Lee, 1973), a simple depiction perhaps further justified by the dull character of Arctic seaweeds. Genetic surveys and hindcasting of macroalgal distributions during the LGM, however, have recently revealed potential refugial locations much further north than previously recognized (Assis, Araújo, *et al.*, 2018), including southern Greenland, which is proposed as the epicenter for the evolution of novel diversity in the East Canadian Arctic (Bringloe *et al.*, 2020). Notable cases of brown algae with distinct intraspecific Arctic lineages include *Alaria esculenta* (Bringloe and Saunders, 2018; Bringloe *et al.*, 2020), *Saccharina latissima* (a "cold temperate" lineage; Neiva *et al.*, 2018), and *Fucus distichus* (Laughinghouse *et al.*, 2015). Unknown species of Acinetosporaceae, Chordariaceae, Desmarestiaceae, and Scytosiphonaceae are reported from the Arctic (Küpper *et al.*, 2016), among others reviewed by Bringloe *et al.*, (2020). Resolving the extent of perennial ice cover, the importance of marine encroachment by continental ice-sheets, and ultimately reaching a consensus regarding the locations of refugial populations during the last glacial maximum are areas of research that continue to evolve in the brown algae.

The Antarctic experienced a markedly different geological history compared to its northern counterpart, a history reflected in its brown algae. Antarctica has evolved largely free from the other continents since the early Cenozoic (66 Ma), with the Antarctic Circumpolar Current (ACC) further promoting this isolation over the past 30 Ma (Lüning, 1990a). As such, endemism has been more favorably viewed as a prominent feature of the Antarctic brown algae, with more than a third of its species considered endemic (Wiencke and Amsler, 2012, estimate 44% across the heterokonts). While Laminariales dominate as canopy forming species in the Arctic, the Antarctic is devoid of laminarialean kelps and instead dominated by Desmarestiales, which likely originated in the Southern Hemisphere (Peters *et al.*, 1997). Antarctica also features the endemic habitat forming *Ascoseira mirabilis*, the only species of the order Ascoseirales. As with the Arctic, phylogenetic knowledge of Antarctic brown macroalgae is limited to a few studies (Hu *et al.*, 2016), with only a handful of articles presenting genetic data (Mystikou *et al.*, 2014; Küpper *et al.*, 2019), and only Peters *et al.*, (1997) presenting phylogenetic interpretations (see above, and Yang *et al.*, 2014 for an updated phylogeny of the Desmarestiales). Genetic structure in *Macrocystis pyrifera* is likely influenced by the ACC, which appears to carry haplotypes between distant subantarctic islands (Macaya and Zuccarello, 2010). However, this species does not occur anywhere on Antarctica and likely colonized the subantarctic region recently (Macaya and Zuccarello, 2010). The population structure of *Durvillaea antarctica* from Sub-Antarctic islands suggest sea ice was extensive during the LGM, pushing polar populations into refugia along the coastlines of New Zealand (Fraser, Hay, *et al.*, 2009; Fraser, Hay, Nikula, *et al.*, 2009 Fraser, Spencer, *et al.*, 2009; Fraser *et al.*, 2020).

Brown algae at higher latitudes face unique environmental challenges. Seasonal changes at high latitudes result in a condensed 24 h summer light regime followed by months of darkness, during which time ocean waters shift to freezing and ice conditions. Variances in nutrient availability and salinity are also important in the Arctic. Some brown macroalgae anticipate seasonal changes to time photosynthetic rate, growth, and reproduction, and in doing so maximize the efficiency of these processes (reviewed extensively by Wiencke *et al.*, 2007, and more recently by Wiencke and Amsler, 2012). Perhaps the clearest example of a brown alga adapted for polar conditions, the Arctic kelp *Laminaria solidungula* is known to complete all of its growth under ice during months of darkness, using the summer months exclusively for carbon storage (Dunton and Schell, 1986). As a result, this kelp and similarly adapted seaweeds are recorded from extraordinary latitudes, as far as 82°N in Jörgen Brönlunds-Fjord where coastal waters remain frozen almost year-round (Lund, 1951).

3. Tropical

Brown algae are less prevalent in the tropics, with most tropical diversity stemming from Dictyotales (particularly *Dictyota, Lobophora,* and *Padina*; Silberfeld *et al.*, 2014; Vieira *et al.*, 2017) and Fucales (primarily *Sargassum*). Although most lineages of large habitat forming algae (e.g., Fucaceae, Laminariales, Durvilliaceae) are generally absent from tropical regions, the genus *Sargassum* is a notable exception with more than 350 currently recognized species (Yip *et al.*, 2020). Despite the warm oligotrophic waters of the tropics, *Sargassum* manages to form analogous habitats to kelp forests in some areas (Coleman and Wernberg, 2017; Fulton *et al.*, 2019), indicating that large brown algae are capable of evolving tolerance to low nitrogen and high temperatures. *Sargassum* diversified ∼4.3 Ma in the Indo-Pacific, where its species richness is the greatest, and spread globally into sub-tropical and temperate regions (Yip *et al.*, 2020). *Sargassum* spp. compete with corals, and, although they can tolerate low levels of nitrogen, they tend to be more competitively successful against corals in areas of high nitrogen (Hughes *et al.*, 1999) or low herbivory (Bellwood *et al.*, 2006). Although other fucoids are present in the tropics (e.g., *Turbinaria ornata*), these tend to be smaller, lacking the scale of their large habitat forming counterparts.

The Dictyotales are species rich, widely distributed, and one of the few lineages common in the tropics. The Dictyotales arose through a divergence event relatively early in brown algal evolution (see brown algal phylogeny, subsection II.B) in the tropical southern Tethys of the Middle Jurassic, and today reaches peak species diversity in the tropical Indo-Pacific (Vieira *et al.*, 2017; Steen *et al.*, under revision). The high diversity of Dictyotales is mainly attributable to two diversification bursts, following the Cretaceous-Tertiary boundary, in *Lobophora* and *Dictyota*, respectively. Diversification rates in Dictyotales were markedly higher in the tropics. *Lobophora* radiated and remained in tropical to warm-temperate waters, while *Dictyota* expanded into colder temperate regions while preserving its presence in the tropics (Steen *et al.*, under revision). Today, *Dictyota*, *Lobophora* and *Padina* are ecologically important benthic components in tropical and sub-tropical reef ecosystems (e.g. Briones-Fourzán and Lozano-Álvarez, 2001, Kaullysing *et al.*, 2016; Vieira, 2020).

Aside from Dictyotales and Fucales, the paucity of brown algal representation across orders in the tropics suggests that there are important factors limiting their dispersal, persistence, and perhaps their diversification in warmer waters. Environmental conditions are likely not conducive to the success of many lineages of large brown algae. In particular, laminarialean kelps generally require cool temperatures and have high nitrogen demands, preventing them from establishing in tropical oligotrophic waters and mostly restricting them to temperate and arctic regions. Even the most heat tolerant genus *Ecklonia* barely occurs in the tropics, and is restricted to deep (i.e. cool) waters of tropical upwelling regions (Graham *et al.*, 2007). Biotic interactions have also been invoked to explain the limited diversity and dominance of tropical brown algae. Unlike temperate regions where mass extinctions and global cooling may have provided ecological opportunities for brown algae to dominate (Estes and Steinberg, 1998; Cánovas *et al.*, 2011; Vermeij *et al.*, 2019; Starko *et al.*, 2019), tropical climates have characterized much of earth's history since the appearance of brown algae (Figure 3). Corals and red algae have long dominated tropical regions, occupying niches and leading to less ecological opportunities for the brown algae. Recent work on tropicalization of temperate reefs has shown that large brown algae are quickly eliminated by the invasion of tropical herbivorous fishes (see Vergés *et al.*, 2014; 2016; 2019), suggesting a mechanism that may have prevented the success of brown algae in the tropics historically. These factors likely do not occur in isolation. For example, *Sargassum* spp. continue to compete with corals, and the balance of this interaction is often mediated by herbivorous fish (Bellwood *et al.*, 2006). This hypothesis is further supported by the fact that species of *Dictyota*, one of the few brown algal genera that is common in the tropics, are highly chemically defended and capable of maintaining high biomass even in the presence of heavy predation (Hay *et al.*, 1987; Wiesemeier *et al.*, 2007).

Substantial changes in the presence and abundance of certain tropical brown algal species have occurred in recent years owing to anthropogenic effects and climate-change-induced invasions. Notable examples of species introduced by transport vectors (e.g. boats, barges) include *Colpomenia* along Pacific shores of North America and both Atlantic and Pacific shores of South America (Lee *et al.*, 2013), *Dictyota flabellata* and *Sargassum muticum* in Hawaii (Abbott and Huisman, 2003), and the general widespread invasion of *S. muticum* (Louime *et al.*, 2017). Most concerning is the migration of *S. fluitans* and *S. natans* from the Sargasso Sea into various regions of the Atlantic, including Brazil (de Széchy *et al.*, 2012), the Dominican Republic (Mendez-Tejeda and Rosado Jiménez, 2019), Ghana (Addico and deGraft-Johnson, 2016), and many other island nations of the Caribbean (Louime *et al.*, 2017). Massive blooms have resulted in the "great Atlantic *Sargassum* belt," a phenomenon that began in 2005. In 2018, the *Sargassum* belt stretched over 8850 km from West Africa to the Caribbean Sea, and generated over 20 million metric tons of biomass that smothered tropical coastlines (Wang *et al.*, 2019). Climate change and increased micro- and macronutrients due to pollution are likely playing a role in the massive increase in biomass and movement of *Sargassum* around the Atlantic (Louime *et al.*, 2017). These immense golden blooms have severe ecological, economical, and human health impacts, but also have the potential to inspire innovations in climate change mitigation (via carbon sequestration; Gouvêa *et al.*, 2020), bio-fuel refinement, agriculture fertilizer, and eco-friendly charcoal alternatives (reviewed by Louime *et al.*, 2017).

4. Freshwater

Despite the ubiquity of brown algae in marine environments globally, very few lineages have colonized freshwater ecosystems (Wynne and Bold, 1985; McCauley and Wehr, 2007; Sheath and Wehr, 2015; Wehr, 2015; Dittami *et al.*, 2017). Although up to seven independent transitions from marine to freshwater habitats have occurred in brown algae (Dittami *et al.*, 2017), none have resulted in widespread diversification, and freshwater lineages have remained restricted to filamentous or crustose forms (Wynne and Bold, 1985; McCauley and Wehr, 2007; Dittami *et al.*, 2017).

Freshwater species are known from two orders: Ectocarpales and Sphacelariales. The first description of a freshwater brown alga was *Pleurocladia lacustris* (Braun, 1855), a widely distributed member of the Ectocarpales. *Ectocarpus* also invaded freshwater independently of *Pleurocladia* (West, 1996; McCauley and Wehr, 2007) with the freshwater species *Ectocarpus subulatus* found in Australia and Europe (Wehr *et al.*, 2015). These species are not obligate freshwater taxa and are capable of surviving in saltwater (McCauley and Wehr, 2007; Dittami *et al.*, 2012; Wehr *et al.*, 2013). Differences in the gene expression profiles of freshwater and marine populations indicate that genomic changes have occurred to stabilize the transition to freshwater (Dittami *et al.*, 2012; 2017; 2020; Meslet-Cladière *et al.*, 2013). Most other freshwater brown algae are from the Sphacelariales, all of which are obligate freshwater inhabitants (Sheath and Wehr, 2015). Two sister species, *Heribaudiella fluviatilis* and *Bodanella lauterborni* likely share a freshwater ancestor and possibly represent the most ancient invasion of freshwater, leading to strong anti-coastal distributions (Wehr and Stein, 1985; McCauley and Wehr, 2007; Sheath and Wehr, 2015; Wehr, 2015). While these species can be easily distinguished based on morphology and variability in the *rbc*L plastid locus, no nucleotide polymorphisms exist between these species in the LSU rRNA gene, suggesting that speciation of these two entities nonetheless occurred recently in evolutionary time (McCauley and Wehr, 2007). Members of the genus *Sphacelaria* have also invaded freshwater, yielding the two freshwater obligate species *Sphacelaria lacustris* and *S. fluviatilis* (Dittami *et al.*, 2017). Further work is needed to determine if this represents a single or multiple invasions of freshwater by the genus.

Porterinema fluviatile is another widespread freshwater brown alga whose phylogenetic placement remains unclear. While some authors have suggested that *P. fluviatile* may be a member of the Ralfsiales, the Sphacelariales, or the Scytosiphonaceae (Silberfeld *et al.*, 2014), limited molecular data suggest that *Porterinema* is a distinct and poorly explored lineage (McCauley and Wehr, 2007). Similarly, another filamentous freshwater species was recently isolated from a freshwater aquarium in the United Kingdom and potentially represents a new taxonomic order (Belcher *et al.*, 2009; Dittami *et al.*, 2012). Cumulatively, these studies indicate that unexplored diversity remains in freshwater brown algae with the potential to influence our understanding of evolution in the brown algal phylogeny.

Although freshwater species are rare, many brown algae exhibit some level of tolerance to low salinity (Gordillo *et al.*, 2002; Tatarenkov *et al.*, 2005; Dittami *et al.*, 2017), a feature most notable in the Fucales (Serrão *et al.*, 1996; Tatarenkov *et al.*, 2005). Populations of many species of *Fucus* can persist in salt marshes and estuaries (Kucera and Saunders, 2008; Neiva, Hansen, *et al.*, 2012). Interestingly, these populations all assume a reduced and spindly morphology, which was previously recognized as *Fucus cottonii* (Kucera and Saunders, 2008; Neiva, Hansen, *et al.*, 2012). Molecular evidence indicates that this distinct morphology and ability to inhabit low salinity environments has evolved multiple times in parallel across the genus, with members of *Fucus distichus, F. vesiculosus* and *F. spiralis* all possessing populations with this form (Kucera and Saunders, 2008; Neiva, Hansen, *et al.*, 2012).

V. Conclusions and perspectives

Our knowledge of brown algal evolution has improved dramatically in recent decades, a process that has undoubtedly been accelerated by advances in sequencing capabilities. The affordability of high throughput sequence data will continue to propel the field of brown algal evolution toward large-scale genomic datasets. Complete genome sequences have been reported so far for six brown algae, the Ectocarpales *Ectocarpus* sp. (Cock *et al.*, 2010), *E. subulatus* (Dittami *et al.*, 2020), *Cladosiphon okamuranus* (Nishitsuji *et al.*, 2016), *Nemacystus decipiens* (Nishitsuji *et al.*, 2019) and the kelps *Saccharina japonica* (Ye *et al.*, 2015) and *Undaria pinnatifida* (Shan *et al.*, 2020). An important initiative for the future is the Phaeoexplorer project (led by Roscoff Biological Station and Genoscope), which aims to provide 67 annotated genome assemblies of 47 brown algal species, plus four related unicellular and multicellular Ochrophyta. In addition, at the level of individual species a considerable amount of transcriptomic data is being generated (e.g. Monteiro *et al.*, 2012; Martins *et al.*, 2013; Monteiro *et al.*, 2019), together with genome-scale genotyping data based on RAD-seq or genome resequencing. Analysis of these new data is expected to provide further substantial advances in our understanding of brown algal evolution in several different contexts, including genome-wide investigations of spatial and temporal population structure (Guzinski *et al.*, 2018; Kobayashi *et al.*, 2018; Le Cam *et al.*, 2020), genetic maps and Quantitative Trait Locus analyses (Avia *et al.*, 2017), genome evolution (Avia *et al.*, 2018), and phylogenomics (Fraser *et al.*, 2016). We conclude our review by providing perspectives on promising avenues for studying brown algal evolution, opened up by the availability of genomic data.

A. Resolving the brown algal phylogeny

Phylogenetic placement of the brown algal orders is currently based on multiple genes, but relationships within some of the major clades are unresolved; for instance, the location of Sphacelariales within the SSDO clade (Figure 3). Alignments of additional orthologous genes from genomic data will continue to clarify these relationships. It should also be noted that time calibration of the brown algal phylogeny is based on limited fossil records. Alignment of homologous regions across brown algal genomes and with genomes of other members of the Ochrophyta will offer alternative molecular clocks for revising and dating the evolutionary timelines presented here. Many relationships at lower taxonomic levels (family, genus, species) are also unresolved, particularly in less well-studied or more species-rich orders (e.g. Tilopteridales and Ectocarpales, respectively). Extending genome data for these orders will be an important step toward developing a comprehensive phylogeny of the brown algae.

Species delineations within the brown algae today are largely validated through the genetic species concept and rely heavily on organellar DNA barcode markers. While DNA barcoding has been an immensely successful tool for understanding species diversity within the brown algae, this method reflects the evolutionary history of the organelles themselves and not necessarily that of the host species, especially given the relatively recent evolution of brown algae in comparison to green and red algae. Consequently, organellar capture and introgression can obscure the true relationships between populations and species (see reproductive barriers, subsection IV.A.1). Genome-wide nuclear data can also be used to evaluate species boundaries, and this approach promises to offer significant advancement toward a more accurate brown algal species concept, which will either validate or rewrite the work that has been carried out using organellar sequence data.

B. Evolution of brown algal morphological, life cycle and reproductive traits

A recurring theme within the brown algal phylogeny is the incongruence between relationships inferred from molecular data and the morphological and life history traits exhibited by the various lineages. The development of a robust phylogenetic framework will provide a context in which to investigate the evolutionary history of these traits and, in particular, to relate trait variations and transitions to ecological and geographical events over evolutionary time. The availability of complete genome sequences for individual lineages will provide powerful tools to investigate these questions, though it will nonetheless be a major challenge to link genomic features (genotype) to morphological or life history traits (phenotype) in an evolutionary context. Recently developed genetic tools provide the means to address this problem by identifying genes associated with specific biological processes. For example, the *ORO* and *SAM* genes are conserved across the brown algae (Arun *et al.*, 2019) and therefore represent a logical starting point when looking for genetic signatures associated with variations in the life cycle. Similarly, it will be important to identify the regulatory genes that underlie other brown algal traits and to analyze their function across the brown algae.

The evolution of life history traits also needs to be addressed using theoretical and empirical approaches based on population genetics in an evolutionary ecology framework. However, as mentioned above, the application of these approaches is currently heavily biased toward a small number of model brown algae, primarily from the Ectocarpales and Laminariales. The scope of these analytical approaches will therefore need to be broadened to include other model orders with markedly different ecological and life history strategies, such as Fucales and Dictyotales (e.g. tropical taxa), or orders that have converged on similar ecological roles (i.e. kelp in the broad sense, with members from Desmarestiales, Fucales, Laminariales, and Tilopteridales). Moreover, there is little to no information about species that have a dominant haploid phase (Figure 4). Currently important questions include: What is the frequency of life cycle variants within and among populations? What are the drivers of such variation? Is life cycle variation plastic or genetically determined?

C. Epigenetics

To date, brown algal evolution has been investigated almost exclusively in a genetic framework, but epigenetic processes (i.e. processes that do not involve modification of the underlying genomic blueprint) also play important roles and therefore need to be taken into consideration. By responding to changes in the environment, epigenetic processes mediate acclimatization and therefore act as a buffer, allowing longer-term adaptive (genetic) responses. Moreover, the ability of a species to implement epigenetic responses will affect its long-term capacity to respond to environmental changes, an important characteristic in the context of climate change. Transcriptomic studies are already providing information about epigenetic processes in terms of the control of gene expression levels (Monteiro *et al.*, 2012; Martins *et al.*, 2013; Monteiro *et al.*, 2019). A key challenge for the future will be to extend this type of analysis to a broader range of model species/orders and to additional environmental contexts and parameters (as mentioned above). It will also be important to better understand the processes underlying transcriptomic responses, in particular processes that occur at the chromatin level. Methods have been adapted to detect and quantify post-translational modifications of histones in brown algae (Bourdareau *et al.*, 2020) and a recent study has reported a low level of DNA methylation in *S. japonica* (Fan *et al.*, 2020). Note, however, that DNA methylation does not appear to be present in all brown algae, notably *Ectocarpus* (Cock *et al.*, 2010). These emerging tools are expected to provide new insights into brown algal biology and the mechanisms underlying evolutionary innovations in this group of organisms.

D. Evolution of complex multicellularity

Brown algae are also important from an evolutionary point of view because they independently acquired complex multicellularity and have emerged as the third most complex group of multicellular organisms on the planet. Another major objective will be to improve our understanding of brown algal developmental biology, as comparisons of developmental processes in brown algae with those of animals and land plants is expected to provide important, general insights into the molecular events that underlie this key evolutionary transition. Based on recent advances, work in this area is expected to uncover both examples of deep conservation of some regulatory mechanisms (such as the involvement of TALE HD TFs in life cycle regulation for example; Arun *et al.*, 2019) and lineage-specific novelties (such as the EsV-1-7 domain family, for example, which is absent from both plants and animals; Macaisne *et al.*, 2017). At present, brown algal developmental biology is in its infancy so significant advances can be expected in the future.

E. Speciation mechanisms and biogeography

Our understanding of speciation mechanisms and contemporary distributions of brown algae across the globe continues to improve. A bridge between these two concepts, however, is lacking for the brown algae (as reflected in the structure of this review). What is the interplay between speciation and biogeography that ultimately governs brown algal distributions? The evolutionary events that lead to the diversification and global establishment of some orders have been broadly described (e.g. Oligocene cooling and subsequent dominance of Laminariales) but how were these events influenced by niche preferences and species traits? Strengthening the relationship between species and environment would help shift the study of brown algal biogeography from a descriptive to a hypothesis driven field.

A challenge for future biogeographic investigations of the brown algae will be to develop good model systems both for microevolutionary investigation of recent speciation events and macroevolutionary studies revealing large-scale patterns across space and time. In particular, with the development of genomics and high-throughput sequencing technologies, it is now possible to explore and characterize both the genetic basis of reproductive isolation and the factors (e.g. selection, genetic architecture) that favor speciation in natural populations at the level of the entire genome (Abbott *et al.*, 2016, Ravinet *et al.*, 2017). A good candidate to investigate micro-evolutionary aspects of speciation is *Ectocarpus* given that this genus is a complex of species constituting a continuum with respect to divergence times (Montecinos, Couceiro, *et al.*, 2017), allopatric and sympatric populations with various levels of hybridization have been established (Montecinos, Guillemin, *et al.*, 2017), and additional genomes are on the horizon (see above). Similarly, model systems at the ordinal level, together with well resolved phylogenies, are needed to drive advances in macro-evolutionary investigations, some of which exist or are emerging (viz. Dictyotales, Fucales, Laminariales; Bolton, 2010; Starko *et al.*, 2019, Steen *et al.*, under revision).

The impact of climate change on biogeographic distributions of brown algae will continue to be a hot topic in the near future. Many species are projected to retreat toward higher latitudes with the movement of isotherms (Assis, Araújo, *et al.*, 2018; Martínez *et al.*, 2018), and the loss of unique genetic diversity (Nicastro *et al.*, 2013; Neiva *et al.*, 2015; Assis, Araújo, *et al.*, 2018) and functional diversity (Pereira *et al.*, 2015; Mota *et al.*, 2018) at retreating rear-edges is a concern. Moreover, as marine heatwaves continue to grow in prevalence, mid-range extinctions (Bennett *et al.*, 2015) are also more likely to occur and genetic diversity is further threatened (Smale *et al.*, 2019; Gurgel *et al.*, 2020). Climate-driven range dynamics have been mainly investigated in south-north orientated coastlines (e.g. northeast Atlantic, the southeast Pacific), where continuous thermal gradients and absence of major dispersal barriers create few constraints for species latitudinal migration and habitat tracking. Predictive efforts should be extended to biogeographical settings where range shifts are physically or environmentally constrained, such as latitude-constrained continental limits (e.g. South Africa, but see Martínez *et al.*, 2018 for an Australian study), semi-enclosed, longitudinally oriented seas (e.g. Mediterranean) and off-shore archipelagos, all of which tend to have rich assemblages with a large proportion of narrow-endemics facing limited dispersal options.

Marine heatwaves may act as a source of directional selection, potentially improving the thermal tolerance of populations (Gurgel *et al.*, 2020) but risking maladaptation to other factors (Brady *et al.*, 2019). Understanding interactions between neutral (e.g. founder effect) and adaptive processes (e.g. directional selection) during range expansions and pulse disturbance events would provide important context for current trends. Characterization of adaptive variation in nonmodel organisms is becoming possible with the development of genomic and analytic approaches (Lotterhos and Whitlock, 2015; Manel *et al.*, 2016) and these types of analyses should help to distinguish between (and compare) neutral and adaptive variation in future studies. As climate change continues to progress, it will be both troubling and captivating to see how the trajectory of brown algal evolution is altered and what consequences this will have on coastal ecosystems across the globe.

F. Concluding remarks

Our understanding of brown algal evolution has changed rapidly in the wake of DNA sequence data. In particular, molecular analyses have revealed unexpected relationships in the phylogeny of the brown algae, highlighting numerous independent transitions between various life history strategies. Sequence data has also allowed us, for the first time, to estimate the diversification timeline of the brown algal orders, expanding insights derived from fossil evidence. The advent of a fully annotated brown algal genome has also offered surprises on life history and reproduction strategies, and has opened the path forward for studying underlying gene programs. In the field of speciation and biogeography, sequence data has revealed novel and cryptic species hiding in plain sight, at times changing the story of how the brown algal lineages diversified and came to dominate coastal ecosystems across the globe. As the field of evolutionary biology continues to develop, particularly in the applications of genomic datasets, we look forward to the exciting progress to come in our knowledge of brown algal evolution.

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Inhabitants of both ceded and unceded territory on which this research was conducted, and acknowledge that gains in contemporary knowledge invariably build on a history of race and gender discrimination.

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