Chapter 5

Red Algae

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Chapter Contents

> *The freshwater red algae in form, in physiology and in habitat may be considered as comprising an elite group of plants, long neglected by American botanists and thus all the more enchanting as representing a research frontier rich with the promise of happy days in the field and laboratory.*
>
> (Flint, 1970, p. 18).

I INTRODUCTION

The Rhodophyta, the red algae, constitute a phylum of organisms that share the following combination of attributes: eukaryotic cells, lack of flagella, floridean starch, phycobiliprotein pigments (red and blue), unstacked thylakoids, and chloroplasts lacking an external endoplasmic reticulum (Woekerling, 1990). They are primarily marine in distribution, with less than 3% of the over 6500 species occurring in truly freshwater habitats (Sheath, 1984; Guiry and Guiry, 2014). Most of the inland species of Rhodophyta are restricted to streams and rivers (lotic forms), although a few species are distributed in lakes and ponds (lentic forms) (Sheath and Hambrook, 1990). A small number of inland rhodophytes occurs in habitats other than typical freshwaters, such as hot springs (Doemel and Brock, 1971), soils (Geitler, 1932), caves (Hoffmann, 1989), and even sloth hair (Wujek and Timpano, 1986).

Freshwater red algae in North America represent a widespread division with members ranging from the high arctic to the tropical rainforest (Sheath and Hambrook, 1990). The number of species increases from the tundra to tropics (by about four-fold), similar to the trend seen for marine species of Rhodophyta.

II DIVERSITY AND MORPHOLOGY

A Diversity

Freshwater rhodophytes have a relatively low diversity compared to other major groups of algae. Analysis of recent literature reveals a flora with 66 species and 27 genera from North America (Table 1). The class Florideophyceae accounts for 55 infrageneric taxa, while the other classes consist of 11 species (Table 1). Currently, *Batrachospermum* is the most diverse genus in North America, but this genus is not monophyletic and recent studies (Entwisle et al., 2009; Salomaki et al., 2014), along with those in the near future, will continue to establish new monophyletic genera for each section of *Batrachospermum*. Therefore, the monophyletic genus *Kumanoa* with nine species or 14% will be the most species rich on this continent.

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TABLE 1 Taxa, Habitats and Forms, Chloroplast Types, and Reproduction of Inland Rhodophyta in North America

Taxon	Habitat	Form[c]	Chloroplast Type[d]	Reproductive Dissemination[e]
Cyanidiophyceae				
Cyanidiales				
Cyanidium caldarium	Hot spring	u	pd	cd
Porphyridiophyceae				
Porphrydiales				
Flintiella sanguinaria	Cool spring	u	pl	cd
Porphyridium purpureum	Soil	u	cs	cd
P. sordidum	Soil	u	cs	cd
Kyliniella latvica	Stream	pf	pmd	cd
Stylonematophyceae				
Stylonematales				
Chroodactylon ornatum[a]	Lake, stream	pf	cs	ms
Chroothece mobilis	Cool spring	pf	cs	cd
Rufusia pilicola	Sloth hair	pf	pd	cd, es
Bangiophyceae				
Bangiales				
Bangia atropurpurea	Lake, stream	ff	cs	ms
Compsopogonophyceae				
Compsopogonales				
Boldia erythrosiphon[b]	Stream	tu	pmd	ms
Compsopogon caeruleus	Stream, spring	ff	pmd	ms
Florideophyceae				
Acrochaetiales				
Audouinella eugenea	Stream	tf	pmd	ms
A. hermannii	Stream	tf	pmd	ms
A. tenella[b]	Stream	tf	pmd	fs, ts
Balbianiales				
Rhododraparnaldia oregonica[b]	Stream	tf	pmd	ts
Batrachospermales				
Batrachospermaceae				
Batrachospermum				
Section *Setacea*				
B. androinvolucrum[b]	Stream	m	pmd	cs
B. atrum	Stream	gf	pmd	cs
Section *Macrospora*				
B. macrosporum	Stream	gf	pmd	cs
Section *Virescentia*				
B. elegans	Stream	gf	pmd	cs
B. helminthosum	Stream	gf	pmd	cs

TABLE 1 Taxa, Habitats and Forms, Chloroplast Types, and Reproduction of Inland Rhodophyta in North America—Cont'd

Taxon	Habitat	Form[c]	Chloroplast Type[d]	Reproductive Dissemination[e]
Section *Turfosa*		gf	pmd	cs
B. turfosum	Stream, pond, bog			
Section *Batrachospermum*		gf	pmd	cs, ms
B. gelatinosum	Stream, spring	gf	pmd	cs
B. gelatinosum forma *spermatoinvolucrum*	Stream	gf	pmd	cs
B. pulchrum[b]	Stream	gf	pmd	cs
B. skujae	Stream	gf	pmd	cs, ms
B. trichocontortum[b]	Stream	gf	pmd	cs
B. trichofurcatum[b]	Stream	gf	pmd	cs
Other genera				
Balliopsis prieurii	Stream	ff	pmd	ms
Sheathia americana[b]	Stream	gf	pmd	cs
S. arcuata	Stream	gf	pmd	cs
S. carpoinvolucra[b]	Spring	gf	pmd	cs
S. confusa	Stream	gf	pmd	cs
S. grande[b]	Stream	gf	pmd	cs
S. heterocortica[b]	Stream, spring	gf	pmd	cs
S. involuta	Stream, spring	gf	pmd	cs
Kumanoa ambigua	Stream	gf	pmd	cs
K. americana[b]	Stream	gf	pmd	cs
K. faroensis	Stream	gf	pmd	cs
K. globospora	Stream	gf	pmd	cs
K. holtonii[b]	Stream	gf	pmd	cs
K. lousianae	Stream	gf	pmd	cs
K. mahlacensis	Lake, stream	gf	pmd	cs
K. skujana	Stream	gf	pmd	cs
K. virgatodecaisneana	Stream	gf	pmd	cs
Sirodotia huillensis	Stream, spring	gf	pmd	cs
S. suecica	Stream	gf	pmd	cs
Tuomeya americana[b]	Stream	pp	pmd	cs
Lemanea borealis	Stream	pp	pmd	cs
L. fluviatilis	Stream	pp	pmd	cs
L. fucina var. parva[b]	Stream	pp	pmd	cs
Paralemanea annulata	Stream	pp	pmd	cs
P. catenata	Stream	pp	pmd	cs
P. mexicana[b]	Stream	pp	pmd	cs
Thoreales[f]				
Thorea sp. 1[b]	Stream	ff	pmd	cs
Thorea sp. 2[b]	Stream	ff	pmd	?
T. hispida	Stream	ff	pmd	cs
T. riekei[b]	Spring	ff	pmd	cs
Nemalionopsis sp. 2	Stream	ff	pmd	cs
Hildenbrandiales				
Hildenbrandia angolensis	Stream, spring	cr	pmd	g

(Continued)

TABLE 1 Taxa, Habitats and Forms, Chloroplast Types, and Reproduction of Inland Rhodophyta in North America—Cont'd

Taxon	Habitat	Form[c]	Chloroplast Type[d]	Reproductive Dissemination[e]
Ceramiales				
Bostrychia moritziana[a]	Stream	ff	pmd	st
B. radicans[a]	Stream	ff	pmd	st
B. tenella[a]	Stream	ff	pmd	st
Caloglossa leprieurii[a]	Stream	pp	pmd	f?
C. ogasawaraensis[a]	Stream	pp	pmd	f?
Polysiphonia subtilissima[a]	Stream, spring	pp	pmd	f?
Gigartinales				
Sterrocladia belizeana[b]	Stream	pp	pmd	f?

[a] *Invader from brackish/marine habitats.*

[b] *Unique to North America.*

[c] *pf = pseudofilament, u = unicell, ff = free filament, tu = tube, tf = tuft, m = mat, gf = gelatinous filament, pp = pseudoparenchymatous form, cr = crust.*

[d] *cs = central stellate with pyrenoid, pd = single peripheral disc, pl = peripheral, intricate lamellate, pmd = peripheral, multiple discs.*

[e] *ms = monosporangia, cd = cell division, es = endospores, cs = carpospores, fs = tetraspores, g = gemmae, f = fragmentation, st = stichidia.*

[f] *Based on Johnston (2012).*

We are proposing in this chapter that there are three potential origins of the predominantly lotic forms: (a) specialists that evolved early within the stream environment and are absent in other habitats; (b) generalists that occur in a wide range of other freshwater bodies, such as lakes and ponds; and (c) upstream migrants from estuaries. This proposal is an expanded version of that originally given by Skuja (1938). Of the 62 stream-inhabiting taxa, 50 appear to be specialists, while three are generalists, and seven are potentially brackish/marine invaders (Table 1). Note that the there is overlap in two groups of the species, *Chroodactylon ornatum* and members of the Ceramiales in both of the last two categories. The other generalist species are *Compsopogon caeruleus* (Vis et al., 1992; Necchi et al., 2013), *Batrachospermum turfosum* (Sheath et al., 1994c; Müller et al., 1998), and *Kumanoa mahlacensis* (Necchi and Vis, 2012).

B Vegetative Morphology

The red algae occurring in typical freshwater habitats tend to be macroscopic and benthic (as defined in Chapter 2) (Sheath and Hambrook, 1990). Nonetheless, these algae exhibit a smaller size range than do marine species with the majority (80%) of freshwater rhodophytes having a length range of 1-10 cm. Among the forms occurring in North America, there are 29 gelatinous filaments, 11 free filaments (individual filament without a gelatinous matrix) (e.g., Figs. 1I, 5A, and 6E, H), 10 pseudoparenchymatous forms (tissue-like, but composed of compacted filaments) (Figs. 4S–T, 5C, D, F–G, and 6F, G), three tufts (short radiating filaments without a common matrix) (Fig. 2A), four pseudofilaments (loose chains of cells held together with a common gelatinous matrix) (Fig. 1B–D), four unicells (Fig. 1A), and one each of tubes (Fig. 1G), mats (flat plant body composed of tightly interwoven filaments), and crusts (flat thallus composed of compacted tiers of cells) (Fig. 6A and B, Table 1). Species distributed in hot springs or soils are unicellular, and *Rufusia* on sloth hair is pseudofilamentous. Among the 47 taxa that have a filamentous construction, only five have multiaxial growth: the members of the Thoreales (Fig. 5I, J, M, and N) (Sheath et al., 1993b); the rest are uniaxial, except for *Bangia*, which has an uniaxial base and multiaxial apex at maturity (Fig. 1F). Uniaxial filaments may be corticated with one or more layers of smaller cells covering those of the main axis (Fig. 6E and H).

The various morphological forms encounter the stress caused by flow in riverine habitats in various ways, according to Sheath and Hambrook (1988, 1990). Crusts and short tufts occur within the boundary layer or at least in a region of reduced current velocity and hence avoid much of the flow-related stress. The remaining macroscopic species can be regarded as semierect, experiencing bending, tensile, and compressive forces and perhaps torsional stresses in flowing waters (Vogel, 1984). This group includes mucilaginous and non-mucilaginous filaments, pseudoparenchymatous forms, and tubes. It would be expected that the semierect forms possess adaptive mechanisms to tolerate flow, such as branch reconfiguration and extension of thalli in high water motion (Sheath and Hambrook, 1988, 1990).

Of the 66 infrageneric taxa of Rhodophyta in inland habitats in North America, about one-third of them are reddish, while two-thirds are largely blue to olive in color. This trend contrasts with that of marine red algae, in which the great majority of species appear red in color. Nonetheless, there are a number of chloroplast morphologies among freshwater taxa: all members of the Florideophyceae have multiple discoidal or ribbon-like chloroplasts without pyrenoids (e.g., Fig. 2B and C); the taxa in the other classes have this type as well as central stellate chloroplasts with a pyrenoid (Fig. 1A), a peripheral lamellate structure, and a single peripheral disc (Table 1). However, some of the species, which appear to have multiple discoidal or ribbon-like chloroplasts, may actually contain a complex, interconnected single chloroplast, such as *C. caeruleus* (Gantt et al., 1986). Like other red algae, the chloroplasts of freshwater species contain single thylakoids with phycobilisomes (granules consisting of the accessory pigments) on both sides (Sheath, 1984). The phycobilisomes of blue-colored species, such as *C. caeruleus*, tend to be hemidiscoidal in shape and predominated by the blue pigment phycocyanin (Gantt et al., 1986). In contrast, the phycobilisomes of the red-colored *Porphyridium purpureum* are larger, hemispherical, and composed mostly of the red pigment phycoerythrin. Phycoerythrin and photosystem (PS) II activity appear to be absent from the pyrenoid of *P. purpureum*, while PS I and ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO) activities can be detected in this structure (McKay and Gibbs, 1990). Chloroplasts of *Batrachospermum gelatinosum* develop from proplastids, which have a double-membraned envelope and a parallel outer photosynthetic thylakoid (Brown and Weier, 1968). This outer thylakoid functions in the production of additional ones to the interior. Thylakoids have been observed to be coiled in serial sections of *Cyanidium*, *Compsopogon*, and *Batrachospermum* (Pueschel, 1990). They can fragment and form dilated tubular units in some freshwater species, such as *B. gelatinosum* and *Sirodotia suecica*, when subjected to reduced illumination (Sheath et al., 1979).

Another characteristic that is useful in analyzing the morphology of freshwater Rhodophyta is the external covering. Unicells and pseudofilaments typically have a gelatinous matrix surrounding the cells (e.g., Fig. 1B, C, and F), which varies in thickness, depending on the age and physiological state of the organisms (Sheath, 1984). The gelatinous filamentous members of the Batrachospermales, such as *Batrachospermum*, *Kumanoa*, *Sheathia*, and *Sirodotia*, have both distinct cell walls as well as an overall matrix surrounding the filament. The free filaments and pseudoparenchymatous forms have only cell walls. The gelatinous matrices of *Porphyridium* and *Batrachospermum* are complex mixtures of a variety of monomeric sugars, including galactose, glucose, and xylose (Craigie, 1990). The cell walls of a freshwater isolate of *Bangia atropurpurea* are similar to those of marine collections, having repeating water-soluble disaccharide units of agarose and porphyran and insoluble residues of galactose and mannose (Youngs et al., 1998). The cell walls of *Paralemanea annulata* have xylan as the major polysaccharide as well as cellulose in small quantities as the fibrillar components (Gretz et al., 1991). The amorphous component consists of a glucuronogalactan. Water-soluble cell wall polymers of freshwater *Bostrychia moritziana* are composed of a complex mixture, including methyl agarose and methyl porphyran (Youngs et al., 1998). The insoluble residues contain a mixture of galactose and glucose. Many freshwater red algal species exhibit differential staining of external coverings with Alcian Blue, particularly of mucilaginous layers, rhizoids, sporangia, and spermatangia (Sheath and Cole, 1990).

C Reproduction

Freshwater red algal species exhibit a diversity of reproductive types, particularly in terms of dissemination (Table 1). Cell division is the major mode of population increase among the unicellular forms. During mitosis of *P. purpureum* and *Flintiella sanguinaria*, the nuclear envelope remains intact with polar openings, the spindle apparatus is composed of interdigitating half spindles, and the nuclear associated organelle (NAO) is an electron-dense bipartite structure (Broadwater and Scott, 1994). Cell division in the other forms is generally the mechanism by which the thallus is expanded. Mitosis in *Sheathia* sp. (as *Batrachospermum anatinum*) is similar to that of the unicells, but also includes perinuclear endoplasmic reticula and a bipartite NAO that is composed of a small ring within a large one (Scott, 1983).

Monosporangia formation is the major form of asexual reproduction among the pseudofilamentous and filamentous taxa (Table 1) and typically involves the formation of single spores that germinate back into the life history phase that produced them. In *Chroodactylon ornatum* and *Bangia atropurpurea*, spores are released by localized digestion of the common filamentous matrix (Sheath, 1984). The order Compsopogonales is characterized by its method of monospore production, which involves the cleavage of a relatively small cell from a larger vegetative cell by oblique cell division (Fig. 1J) (Garbary et al., 1980). Monosporangia of the Acrochaetiales and Batrachospermales are specialized, enlarged, and ovoid cells typically produced at the apices of vegetative branches (Sheath, 1984). Monosporangia can be regenerated after spore release by protrusion and cleavage of cytoplasm from the subtending cell in *Audouinella hermannii* (Hymes and Cole, 1983) and *Kumanoa capensis* (as *Batrachospermum intortum*) (Sheath et al., 1992). Monospores are also a mechanism by which certain life history phases perpetuate themselves in complex life history alternation, such as the "chantransia" phase (see below) of the

Batrachospermales and Thoreales (Sheath, 1984). In contrast to *Balliopsis* in North American streams, inland populations from South America and Malaysia have been observed to contain monosporangia (Kumano, 1978; Couté and Sarthou, 1990; Necchi, 1995). Another form of asexual spore reported from inland rhodophytes is the endospore in *Cyanidium caldarium* and *Rufusia pilicola* (Wujek and Timpano, 1986; Seckbach, 1991).

Sexual reproduction and life history alternation are known for many species of freshwater red algae, although these phenomena have not been conclusively demonstrated for freshwater members of the bangiophyte classes or the Hildenbrandiales and Gigartinales of the Florideophyceae (Table 1). In the freshwater *Audouinella* species for which the life history has been analyzed, the free-living gametophyte and tetrasporophyte are isomorphic, both having the same tuft-like morphology (Fig. 2A) (Drew, 1935; Necchi et al., 1993a). The haploid gametophyte produces the gametangia. The female gametangium, the carpogonium, is a colorless cell with an inflated base and narrow tip, the trichogyne. The male gametangium, the spermatangium, is also colorless, obovoid in shape, and releases one spermatium at a time (Fig. 2B). Spermatia attach to the trichogyne and one eventually fertilizes the carpogonium. The zygote divides into a microscopic diploid phase, the carposporophyte, which remains attached to the gametophytic stage until its deterioration (Fig. 2C). Carpospores germinate into the diploid tetrasporophyte, which at maturity forms tetrasporangia at the branch tips (Fig. 2D). Haploid tetraspores are formed by meiosis and germinate into the gametophytic stage, thereby completing the life history. In a small stream in Rhode Island, both the tetrasporangia and carpogonia of *A. hermannii* are formed in a brief period of time, February and May, respectively (Korch and Sheath, 1989). It would appear that production of these structures in a short period of time is common in North America because gametangia and carposporophytes were observed in only seven out of 75 collections from throughout the continent (Necchi et al., 1993a). *Audouinella tenella*, which has only been collected in California, has only been found to contain tetrasporangia (Necchi et al., 1993a). The blue-colored *Audouinella*-like species have not been observed to contain gametangia, carposporophytes, or tetrasporangia in 34 collections in North America (Necchi et al., 1993b). This finding, plus DNA sequence analysis, indicates that they are not in fact true *Audouinella* species, but rather one of the life history stages of the Batrachospermales, the "chantransia" (see below).

Rhododraparnaldia oregonica of the Balbianiales has characteristics that are intermediate between the Acrochaetiales and Batrachospermales, including reproductive structures (Sheath et al., 1994d). The carpogonia and spermatangia are similar in morphology to those of *Audouinella* (Fig. 2F) and fertilized carpogonia form microscopic carposporophytes (Fig. 2G). However, unlike the Acrochaetiales, the spermatangia are formed on specialized colorless stalks, rather than at the apices of vegetative branches (Fig. 2F). What is similar between *Rhododraparnaldia* and the Batrachospermales is the fact that the free-living life history stages are heteromorphic, and thus quite different in morphology. The semierect gametophytes are composed of a main axis with barrel-shaped axial cells that are distinctly larger in diameter than the more elongate lateral branch cells (Fig. 2E). The microscopic to small macroscopic "chantransia" stage (so named because it was originally thought to be a separate genus) contains simple branched filaments with no difference in diameter and no obvious main axis (Fig. 2H) (Sheath et al., 1994d). The latter stage is diploid and formed from the germination of carpospores. Where it differs from the tetrasporophyte of the Acrochaetiales described above is in the process of meiosis. In the "chantransia" stage, tetraspores are not produced but rather the haploid gametophyte is formed directly attached to this stage (Sheath, 1984; Sheath et al., 1994d). In the freshwater red algal species for which this process has been studied, it appears that meiosis takes place in an apical cell of the "chantransia" filament; in each division a residual nucleus is extruded into a lateral protrusion, which is then separated by wall formation (Sheath, 1984). The one remaining haploid nucleus forms the gametophyte. This life history alternation is typical of the Batrachospermales.

Fifty-eight percent of the freshwater Rhodophyta in North America belong to the order Batrachospermales (Table 1). Like *Rhododraparnaldia*, the gametophyte is macroscopic and semierect, while the "chantransia" stage is often microscopic or composed of tiny tufts. Sheath (1984) proposed that the "chantransia" stage of the Batrachospermales might be an evolutionary adaptation for population maintenance in the upper portions of drainage basins. This stage is typically perennial, seasonally producing the attached gametophyte (Yoshida, 1959; Sheath, 1984; Necchi, 1993). Therefore, the population can continue to proliferate upstream while colonizing downstream with the release of carpospores (Sheath, 1984). If these algae possessed the typical red algal life history, as exhibited by the Acrochaetiales, release of both tetraspores and carpospores would result in a gradual shift of populations downstream until they were solely in the larger trunk river, which are too deep, turbid, and sedimented to support the growth of most benthic autotrophs. Raven (1993) demonstrated that the photosynthetic rates *in situ* of the "chantransia" stage of *Lemanea mamillosa* are one-twentieth of those of the gametophyte, and the former phase has a negligible role in provisioning the growing gametophyte. He also concluded that the key role of the "chantransia" stage is to occupy space throughout the year, including possible exposure during summer drawdown. This stage may also act in population dispersal through the production of monospores (Sheath, 1984; Raven, 1993). In North American temperate streams, gametophytes are typically present from late fall to late spring (Sheath and Hambrook, 1990).

Another key feature pertaining to the reproduction of the genera *Batrachospermum*, *Kumanoa*, *Sheathia*, *Sirodotia*, and *Tuomeya* of the Batrachospermales is the formation of relatively enlarged and persistent trichogynes of the carpogonia, compared to those of red algae from other orders (Figs. 3B, F, J, O and 4D, K, O, U) (Sheath, 1984). The larger surface area and longevity would enhance the probability of spermatia contact. Hambrook and Sheath (1991) and Necchi and Vis (2005) demonstrated that the mean percent fertilization rate for various species of *Batrachospermum* was 45-100%, including dioecious taxa. This rate may be obtained because spermatia are released into turbulent eddies downstream of rocks, where they are carried through the female plants numerous times as the water is moving back and forth (Sheath and Hambrook, 1990). This mode is important when the ratio of male:female plants is low in some dioecious species (Necchi and Vis, 2005). Carpogonia are borne on carpogonial branches that may be little to highly differentiated from adjacent vegetative branches in the Batrachospermales (Figs. 3B, F, J, O and 4D, K, O). In the undifferentiated carpogonial branch of *Sheathia involuta*, the cells are uninucleate with abundant starch granules and several well-developed peripheral chloroplasts (Sheath and Müller, 1997). In contrast, the short carpogonial branch cells of *Batrachospermum helminthosum* have no visible starch, chloroplasts are highly reduced, and cross walls break down among cells.

Freshwater populations of *Hildenbrandia* of the order Hildenbrandiales are typically vegetative and reproduce by gemmae, dense aggregations of cells formed in cavities in the thallus (Fig. 6C and D) (Starmach, 1969; Seto, 1977). The gemmae are eventually released from the thalli and germinate into new crusts; their production is seasonal in two Texas streams (Sherwood and Sheath, 2000).

Most of the freshwater members of the Ceramiales in North America have only been observed to be vegetative, including *Caloglossa* and *Polysiphonia* (Sheath et al., 1993c). They probably proliferate through fragmentation of the thallus and subsequent growth of the fragments. Brackish water populations of *Caloglossa ogasawaraensis* have been observed to contain gametangia and carposporophytes or tetrasporangia (Tanaka and Kamiya, 1993). A few freshwater populations of the genus *Bostrychia* form stichidia, which are inflated, multichambered structures at the tips of vegetative branches. These chambers may form the tetrasporangia, but this has only been observed conclusively in collections of *B. moritziana* from Venezuela and Brazil (D'Lacoste and Ganesan, 1987; Kumano and Necchi, 1987; Sheath et al., 1993c).

The one freshwater member of the Gigartinales in North America, *Sterrocladia belizeana*, has not been observed to be reproductive per se (Sherwood et al., 2012), but probably uses fragmentation to increase populations as one mechanism for proliferation.

III ECOLOGY AND DISTRIBUTION

A Streams and Rivers

Because 94% of the inland rhodophytes of North America occur in streams or rivers (Table 1), this chapter will concentrate on this habitat. Much of the ecology of riverine red algae has been summarized by Sheath and Hambrook (1990), and we will synthesize the trends and give updated information here.

1 Patterns of Distribution

In North America, 51% of 1000 first- to fourth-order stream reaches surveyed contain red algae and 24% have two or more species (Sheath and Hambrook, 1990; Sheath and Cole, 1992). The maximum number of red algal species found per reach is six. The most widespread species is *Batrachospermum gelatinosum*, which occurs in about 13% of the streams examined. This species occurs from the polar desert on Ellesmere Island, Nunavut (80°N) to southeastern coastal plain in Louisiana (37°N) (Vis et al., 1996a; Vis and Sheath, 1997; House et al., 2010). Other widespread species include *Audouinella hermannii* (North Slope of Alaska to Georgia) (Necchi et al., 1993a), *B. helminthosum* (Washington and Maine to central Mexico) (Sheath et al., 1994a; Vis et al., 2001; Chiasson et al., 2003), *B. turfosum* (North Slope of Alaska to central Mexico) (Sheath et al., 1994c; Müller et al., 1997), and *Lemanea fluviatilis* (central Alaska to Arkansas) (Vis and Sheath, 1992).

Among the taxa of lotic Rhodophyta in North America with more restricted patterns of distribution, there are some interesting trends. Members of the Thoreales, Hildenbrandiales, Ceramiales, Gigartinales, *Kumanoa*, and *C. caeruleus* are largely restricted to warmer waters from south temperate to tropical streams (Vis et al., 1992; Sheath et al., 1992, 1993a,b; Necchi and Vis, 2012). There are also taxa that are mostly in north temperate to tundra habitats, such as *Lemanea borealis* (Vis and Sheath, 1992). *Boldia* and *Tuomeya* have only been collected in eastern North America, ranging from Quebec to southeastern United States (Howard and Parker, 1980; Sheath and Hymes, 1980; Kaczmarczyk et al., 1992). There are a number of species that appear to be localized only in southwestern spring-fed streams, such as *F. sanguinaria* (Ott, 1976), *Chroothece mobilis* (Blinn and Prescott, 1976), and *Sheathia carpoinvolucra* (Vis and Sheath, 1996; Sherwood and

Sheath, 1999a). Some of the warm-water groups noted above are also distributed in spring-fed streams of southwestern North America. The restricted distribution of many freshwater red algae is also true in an analysis of European species (Kwandrans and Eloranta, 2010). In a recent study of the distribution of freshwater red algae in the Hawaiian Islands, Carlile and Sherwood (2013) showed two contrasting patterns: one was widespread with no genetic variation, even in the context of global sequences, and the other exhibited substantial phylogeographic structure.

2 *Physical Factors*

Riverine red algae exhibit a wide range of occurrence with respect to current velocity (Sheath and Hambrook, 1990). Nonetheless, most species are found in moderate flow regimes (mean 29-57 $\mathrm{cm\,s^{-1}}$). Moderate flow enhances various aspects of metabolism, including productivity and pigment content (Thirb and Benson-Evans, 1982), growth (Whitford, 1960), respiration rates (Schumacher and Whitford, 1965), and phosphorus uptake levels (Schumacher and Whitford, 1965). In addition, it has a positive influence on the ecology of these organisms, such as washout of loosely attached competitors (Whitton, 1975), constant replenishment of gases and nutrients (Hynes, 1970), and reduction of the boundary layers of depletion around the algal thallus (MacFarlane and Raven, 1985). Few taxa are typically localized at high current velocities ($>1\,\mathrm{m\,s^{-1}}$), the exceptions being *Lemanea* and *Paralemanea* (e.g., Everitt and Burkholder, 1991; Vis et al., 1991; Filkin and Vis, 2004). The morphology of some species, such as *Sirodotia delicatula*, can be altered under different flow regimes (Necchi, 1997). At high current velocities (132 $\mathrm{cm\,s^{-1}}$), plants are denser, having shorter internodal lengths. Sheath and Hambrook (1988) calculated mean potential velocities (in $\mathrm{cm\,s^{-1}}$) at which various morphological forms of red algae would break: tufts 80, mucilaginous filaments 160, and cartilaginous and pseudoparenchymatous filaments 580. In a recent study, the seasonality of *Thorea* was positively correlated to substrate stability and gametophyte breakage at higher current velocities in a river in Japan (Higa et al., 2007). After abrasion of *A. hermannii* in an Australian river, regrowth of tufts was rapid from remaining fragments (Downes and Street, 2005).

The light regime, which includes changes in intensity, quality, and photoperiod, is one of the key factors affecting the distribution and seasonality of riverine Rhodophyta (Sheath and Hambrook, 1990). Illumination affects algal growth via photosynthesis, by processes indirectly related to photosynthesis and by those processes unrelated to photosynthesis. In the case of freshwater red algae, distribution within a drainage basin and seasonality are determined by the photoregime established by the surrounding tree canopy. In a headwater Rhode Island stream containing *Sheathia americana* (as *Batrachospermum boryanum*), the total illumination reaching the water surface is reduced by 90-99% on both sunny and cloudy days in a shaded reach compared with a nearby open segment (Kaczmarczyk and Sheath, 1991). There is a slight, but significant, increase in green light under the canopy and a corresponding increase in the red pigment phycoerythrin compared to the blue pigment phycocyanin. The action spectrum of collections from the canopied and open sites is similar and quite broad. Nonetheless, the populations of the Batrachospermales mostly disappear during periods of peak canopy shading (Hambrook and Sheath, 1991). Likewise, many species of stream-inhabiting Rhodophyta exhibit a positive correlation to light and a negative one to temperature (Kremer, 1983; Sheath, 1984; Leukart and Hanelt, 1995). In addition, they tend to exhibit low saturating levels of illumination for photosynthesis and a clear adaptation to low illumination (Necchi and Alves, 2005).

Temperature regime influences the latitude, elevation, drainage basin distribution, as well as seasonality of freshwater red algae (Sheath and Hambrook, 1990). Latitudinal patterns have been discussed above. Kremer (1983) concluded that some of the geographic patterns of riverine Rhodophyta are based on photosynthetic response to temperature. For example, the concentration of *Compsopogon* in warm waters can be explained by a maximum photosynthesis rate at 30-35 °C. In large drainage basins, elevation and basin distribution patterns are interrelated; mean temperatures tend to increase from the source to the mouth, although the amplitude of diurnal fluctuations in temperature become less (Whitton, 1975). Israelson (1942) reported that most rhodophytes in Sweden were restricted to elevations less than 900 m above sea level. From our surveys of North America, we have observed a similar trend. Exceptions include *Lemanea* and *Paralemanea* as well as some members of the Acrochaetiales, such as *Audouinella hermannii* and *A. tenella*, which can be abundant in montane streams (e.g., Necchi et al., 1993a; Vis and Sheath, 1992). In temperate regions, most freshwater red algae exhibit maximum biomass, growth, and reproduction between late fall to early summer (Sheath and Hambrook, 1990), but in many cases this seasonality is more related to light penetration to the stream surface than temperature (e.g., Hambrook and Sheath, 1991). Necchi (1993) noted a similar seasonality for batrachospermalean species in a tropical drainage basin in southeastern Brazil where a combination of lower temperature and reduced turbidity during the dry winter months promoted growth of macroscopic gametophytes. In contrast, *C. caeruleus* was present throughout the year and distribution was not related to temperature, but to current velocity in these Brazilian streams.

3 *Chemical Factors*

The interaction between pH and the form of inorganic carbon can greatly influence the productivity and distribution of freshwater Rhodophyta (Sheath and Hambrook, 1990). Although widespread species are distributed in a large range of pH values, the majority occurs in mildly acidic waters between pH 6 and 7. However, there are exceptions to this pattern of distribution, including *Bangia*, *Chroodactylon*, *Hildenbrandia*, *Compsopogon*, and members of the Thoreales and Ceramiales, which may be considered to be alkalophiles (Sheath, 1987; Sheath et al., 1993a,b,c; Vis et al., 1992; Vis and Sheath, 1993). The effect of pH can be attributed to the form of inorganic carbon available; some taxa, such as *L. mamillosa*, have been shown to use only free CO_2 as a carbon source for photosynthesis, which is the predominant form at mildly acidic pH values (e.g., Raven et al., 1994). Above pH 8, the proportion of free CO_2 drops below 2-5% and species occurring in these waters would require flow replenishment or use of alternative sources of inorganic carbon (Sheath and Hambrook, 1990). One species commonly distributed in high pH waters is the crustose *Hildenbrandia rivularis*, which also utilizes CO_2 as a carbon source, but may also use HCO_3^-, but this possibility has not been confirmed (Raven et al., 1994).

Specific conductance and pH are related in that alkaline waters are high in ions, such as carbonates, and are buffered strongly above pH 8 (Sheath and Hambrook, 1990). In contrast, waters draining igneous rock catchment areas are less well buffered and are more acidic. Four common freshwater red algal species in North America, *A. hermannii*, *B. gelatinosum*, *L. fluviatilis*, and *Tuomeya americana*, exhibit a negative distribution in relation to specific conductance (total ions) with greatest frequency of occurrence at $<100\,\mu S\,cm^{-1}$ (Sheath and Hambrook, 1990). This pattern is in part due to the form of inorganic carbon. Those taxa that typically occur at higher pH values, as noted above, also are distributed at high conductance ranges. Likewise, species typically localized in hardwater streams constitute that same list given above for high pH values.

Freshwater red algae are distributed in a wide range of oxygen concentrations ($0.2\text{-}21\,mg\,l^{-1}$), but there tends to be an increase in frequency of occurrence with higher concentrations (Sheath and Hambrook, 1990). To some extent, this relationship results from the occurrence of many species in the cooler months from late fall to late spring when oxygen solubility is highest. Nevertheless, freshwater Rhodophyta are not commonly associated with stagnant, organic-rich waters with very low oxygen contents.

Freshwater rhodophytes occur over a broad range of nutrient values, but they are more typically found in low to moderate nutrient regimes (e.g., PO_4^{3-} below detection to $100\,\mu g\,l^{-1}$) (Sheath and Hambrook, 1990). The common occurrence of red algae at low nutrient levels is partially due to flow replenishment and reduction of the boundary layer of depletion in riverine systems. In addition, many species form colorless hair cells that may be produced in response to nutrient deficiency, as is the case for some green algal filaments (Gibson and Whitton, 1987), or they have external phosphatases under moderate phosphorus limitation, like the colonial *Chroothece* in a calcareous Spanish stream (Aboal et al., 2014). Some researchers have employed rhodophytes for classification of streams; for example, in Austria *Hildenbrandia* is typical of lowland rivers with relatively high nutrients, while *Lemanea* is indicative of high-altitude streams with low nutrients (Pipp and Rott, 1994).

In general, freshwater red algae are localized in reasonably unpolluted waters and are infrequent to absent in streams and rivers that are organically enriched, greatly silted, or very high in inorganic nutrients (Sheath and Hambrook, 1990). A number of taxa are considered to be indicators of good water quality (Eloranta and Kwandrans, 2004). However, *L. fluviatilis* and *B. atropurpurea* appear to be tolerant of some heavy metal pollution (Lin and Blum, 1977; Harding and Whitton, 1981). For example, *L. fluviatilis* can occur at aqueous concentrations of zinc up to $1.16\,mg\,l^{-1}$. In addition, some freshwater red algae can be distributed in eutrophic conditions, such as the chantransia stage of *Batrachospermum macrosporum*, which can be distributed in these conditions due vector-assisted transport (Kato et al., 2009).

4 Biotic Factors

Thirty-eight riverine animals to date have been observed to ingest freshwater red algae, based on gut content or feeding studies (Sheath and Hambrook, 1990; Sheath et al., 1995). These grazers include two amphipods and the larvae of six mayfly, 13 caddisfly, six stonefly, six chironomids, one beetle, as well as two snails and two cyprinoid fish. Most animals remove small pieces of 5-20 cells and digest the cytoplasm, leaving the empty walls intact. The majority of these animals are polyphagous, consuming a wide variety of food matter, including detritus, leaf fragments, and other algal taxa. In grazing experiments done by Hambrook and Sheath (1987), it was observed that the preference of consumption was *A. hermannii*, *B. helminthosum*, followed by *T. americana*; this trend was based in increasing toughness of the thallus and reduction of protein content. Rosemond (1993) noted that irradiance, nutrients, and herbivore grazing simultaneously limited algal biomass, including *Audouinella* sp., in a small forested stream. Recently, Goodman and Hay (2013) observed that some species of freshwater red algae, such as *B. helminthosum*, *Kumanoa holtonii*, and *T. americana*, employ activated chemical defenses that suppressed feeding of crayfish by 30-60%.

Cases of larvae and pupae from six caddisfly species have been observed to contain pieces of freshwater rhodophyte thalli in North America (Sheath et al., 1995). Eight genera of Rhodophyta (*Batrachospermum*, *Bostrychia*, *Compsopogon*, *Kumanoa*, *Lemanea*, *Paralemanea*, *Sheathia*, and *Tuomeya*), representing 11 species and 35 populations, have been observed in this association. Strips of the algae are fit together in a transverse, concentric, or spiraled fashion. In some of the associations, pieces of the rhodophyte are also found in the gut of the caddisfly. In addition, some of the algal strips remain viable in these cases. Three genera of chironomid larvae have also been observed to incorporate pieces of red algae in their cases in North America (Sheath et al., 1996a). Seven genera of Rhodophyta are used in this process, *Audouinella*, *Batrachospermum*, *Kumanoa*, *Lemanea*, *Paralemanea*, *Sheathia*, and *Sirodotia*. The cases are tubular in shape with longitudinally oriented strips of algae held together with silken threads.

Competition for suitable substrata can occur among species of freshwater red algae at various levels (Sheath and Hambrook, 1990). Unicellular forms, such as *Flintiella*, microscopic stages, and low growing forms, including the "chantransia" stage of the Batrachospermales and Thoreales, *Audouinella*, and *Hildenbrandia*, are common components of the stream epilithic community. As such, they compete with a complex association of microalgae, usually dominated by diatoms during early colonization stages (e.g., Steinman and McIntire, 1986). Fritsch (1929) noted that *Hildenbrandia* thalli are often overgrown by diatoms and cyanobacteria in British streams. In later stages of succession, filamentous and stalked species can form an upper story where they have a competitive advantage for light and nutrient replenishment. The semierect forms fit into this category and are subjected to competition with macrophytes and other macroalgae. Bryophytes are frequent dominants in upper reaches where red algae occur (e.g., Sheath et al., 1986). The macrophytes are subjected to removal by flooding events, allowing new periphyton colonization. Therefore, lotic communities containing red algae are generally in a non-equilibrium state, consisting of most successional stages (Sheath and Hambrook, 1990).

On a geographic scale, certain freshwater rhodophyte species have distributional patterns that are correlated to those of other species (Sheath and Hambrook, 1990). For example, in tropical streams in North America, *Bostrychia*, *Compsopogon*, and *Hildenbrandia* frequently cohabit the same stream reaches. In temperate and boreal regions, *A. hermannii* is frequently found with *Lemanea* or *Paralemanea*; the former taxon can be both epiphytic on *Lemanea* or *Paralemanea* and epilithic in these situations.

B Other Inland Habitats

Softwater ponds and bogs represent the second most common habitat to find inland Rhodophyta (Sheath, 1984). In particular, *B. turfosum* is common in these habitats and Yung et al. (1986) noted its broad occurrence in the northeastern regions of Canada and the United States. Müller et al. (1997) studied the phenology of a population of this species in a boreal pond in Newfoundland. The gametophyte is perennial with a peak cover in summer, which is correlated to water temperature and day length. Carpogonia and spermatangia are present throughout the year except for October and November when monospore production is predominant.

Two species that can be classified as brackish/marine invaders of freshwaters, *C. ornatum* and *B. atropurpurea*, are common species in the hardwaters of the lower Great Lakes (Sheath and Morison, 1982; Sheath, 1987; Müller et al., 1998). These species are absent from the low ion waters of Georgian Bay, the North Channel, and Lake Superior (specific conductance $<200\,\mu S\,cm^{-1}$) (Sheath et al., 1988; Shea et al., 2014). Collections of *Bangia* from Lakes Ontario, Erie, Huron, Michigan, and Simcoe have identical DNA sequences for the nuclear gene coding for the small subunit of ribosomal RNA (18S rDNA), the chloroplast gene coding for the large subunit of RuBisCO (*rbc*L) and the spacer unit between *rbc*L and the gene coding for the small subunit of RuBisCO (*rbc*S) (Müller et al., 1998). These sequences are also nearly identical to those from freshwater collections of *Bangia* from Europe, Rivers Thames and Shannon, U.K., and Lake Garda, Italy. Hence, it would appear that the North American freshwater *Bangia* arose by a single invasion from a European freshwater population, possibly by vector-assisted transport (e.g., ballast water of ships), rather than migration from the Atlantic Ocean.

C. caldarium is an unusual species restricted to several acid hot springs in North America, including those in the United States, Mexico, and El Salvador (DeLuca et al., 1979). These springs exhibit the following range of conditions: pH 1-2.6 and temperature 25-44 °C. Doemel and Brock (1971) examined growth properties of *Cyanidium* isolated from Yellowstone National Park and observed that the optimum pH was 2-3 (range 0.5-5.0) and optimum temperature was 45 °C (range 25-56 °C). This species also forms surface and subsurface crusts in hot, acidic soils and riverbanks near thermal springs (Smith and Brock, 1973).

Species of *Porphyridium* can form crusts on moist soils and decaying wood (Geitler, 1932; Ott, 1972). In these habitats, these species are reasonably desiccation resistant and shade tolerant (Hoffmann, 1989).

IV COLLECTION AND PREPARATION FOR IDENTIFICATION

Because 94% of inland red algal taxa occur in streams or rivers, we will concentrate on collecting in this environment. While macroalgae can be distributed throughout a major drainage basin, they tend to be more common in the smaller channels of first- to fourth-order reaches (Sheath and Cole, 1992). Because only approximately 5% of stream channels examined in North America have 50% or more of the stream bottom covered by one or more species of red algae (Sheath and Hambrook, 1990), it is often necessary to actively search for these taxa. A view box, composed of a glass bottom and Plexiglas sides, is of great help in being able to observe the stream bottom during this search process. To attain a representative sampling of species, at least a 20-m length should be carefully examined using the view box, including a variety of flow regimes and substrata. For example, in a large, fast-flowing stream, *Audouinella*, *Lemanea*, and *Paralemanea* may be found attached to rocks in more rapidly flowing portions in the mid channel, while *Batrachospermum*, *Kumanoa*, *Sheathia*, *Sirodotia*, and *Tuomeya* may be localized in quiet side channels and pools, attached to a variety of substrata, such as logs and tree roots. Long forceps are quite useful for grabbing specimens in deep waters, particularly gelatinous filaments. Razor blades are necessary to remove crustose forms. Other collecting equipment for consideration includes hip waders, diver's gloves for winter collecting, and various portable meters, such as pH, specific conductance, temperature, turbidity and current.

Red algal specimens are best viewed shortly after collection in a live state using a combination of dissecting and compound microscopes. If they cannot be examined quickly, then they should be fixed in 2.5% histological grade glutaraldehyde, buffered with a pinch of $CaCO_3$ and stored in a dark and cool environment. Under these conditions, they will maintain their morphology and pigmentation for several years. Other fixatives, such as formalin or Lugol's, cause more distortion and drying for herbarium specimens resulting in considerable morphological damage. Generally, samples are sorted and initially viewed at low power with a dissecting microscope. Then a reproductive piece is removed, mounted on a microscope slide with cover slip, finely chopped with a sharp razor blade and squashed to obtain flat images and then viewed at 200× or 400× in a compound microscope. It is necessary to find all key vegetative and reproductive features noted in the section below to achieve a proper identification.

V KEY AND DESCRIPTIONS OF GENERA

A Key

1. Thallus unicellular (Fig. 1A) 2
1. Thallus multicellular 4
  2. Reproduction by endospores, hot springs .... *Cyanidium*
  2. Reproduction by cell division, other inland habitats 3
3. Parietal chloroplasts without pyrenoids .... *Flintiella*
3. Axial chloroplast with pyrenoid .... *Porphyridium*
  4. Thallus pseudofilamentous (Fig. 1B–D) 5
  4. Thallus crustose, filamentous, or pseudoparenchymatous 8
5. Axial chloroplast with pyrenoid 6
5. Parietal chloroplasts without pyrenoids 7
  6. Few-celled colony, no branching .... *Chroothece*
  6. Multiple-celled with false branching (Fig. 1D) .... *Chroodactylon*
7. Discoidal base (Fig. 1B and C), occurs in streams and rivers .... *Kyliniella*
7. No discoidal base, in sloth hair .... *Rufusia*
  8. Thallus crustose (Fig. 6A–C) .... *Hildenbrandia*
  8. Thallus a monostromatic, hollow sac (Fig. 1G) .... *Boldia*
  8. Thallus filamentous or pseudoparenchymatous 9
9. Thallus filamentous 10
9. Thallus pseudoparenchymatous 21
  10. Multiaxial filaments (Fig. 5I, J, and M) 11
  10. Uniaxial filaments (Fig. 2B and E) 12
11. Monosporangia on short branches at base of assimilatory filaments (Fig. 5L) .... *Thorea*
11. Monosporangia on long branches at periphery of assimilatory filaments (Fig. 5N) .... *Nemalionopsis*
  12. Filament uniaxial at base and multiaxial at reproductively mature apices (Fig. 1F) .... *Bangia*
  12. Filament uniaxial throughout 13
13. Filaments non-corticated (Fig. 2B, C, and E) 14
13. Filaments corticated (Fig. 1I, J, and 6E) 16
  14. No obvious main axis or reduction in diameter in lateral branches .... *Audouinella*
  14. Distinct main axis and lateral branches reduced in diameter 15
15. Lateral branches not compacted, spermatangial stalks (Fig. 2E) .... *Rhododraparnaldia*

15. Lateral branches compacted and pinnate, no spermatangial stalks (Fig. 5A) .... *Balliopsis*
  16. Reproduction by monosporangia that are cleaved obliquely from cortical cells (Fig. 1J) .... *Compsopogon*
  16. Reproduction by transversely cleaved monosporangia and/or sexual only 17
17. Thallus with whorls of determinate lateral branches (Figs. 3A, E, I, M and 4A, B, H, I, N) 18
17. Thallus with alternate or opposite lateral branches (Fig. 6E) 21
  18. Carposporophytes a distinct mass of determinate gonimoblast filaments (Figs. 3D, G, L and 4F, L) 19
  18. Carposporophytes indistinct, indeterminate gonimoblast filaments (Fig. 4Q) .... *Sirodotia*
19. Cells covering the main axis of two types, cylindrical and bulbous (Fig. 4J) .... *Sheathia*
19. Cells covering the main axis cylindrical only (Fig. 3B) 20
  20. Carpogonial branch twisted, curled or curved (Fig. 4C) .... *Kumanoa*
  20. Carpogonial branch not twisted, curled or curved (Fig. 3F) .... *Batrachospermum*
21. Trichoblasts (hair cells) from cortical cells, no stichidia .... *Polysiphonia*
21. No trichoblasts form cortical cells 22
  22. Stichidia at branch tips .... *Bostrychia*
  22. No stichidia 23
23. Thallus a branched flat blade with a distinct midrib (Fig. 6F and G) .... *Caloglossa*
23. Thallus a cartilaginous tube with no midrib 24
  24. Whorled lateral branches appearing like beads in a row at low magnification (Fig. 4S and T) .... *Tuomeya*
  24. Thallus tubular, sometimes with distinct nodal swellings (Fig. 5C, F, and G) 25
25. Thallus dichotomously branched; cortex and medulla several cells thick .... *Sterrocladia*
25. Thallus unbranched or not dichotomously branched; single main axis 26
  26. Main axis corticated, spermatangia in rings around the diameter of the thallus (Fig. 5F) .... *Paralemanea*
  26. Main axis uncorticated, spermatangia in circular patches (Fig. 5C) .... *Lemanea*

B Descriptions of Genera (for a List of Species in Each Genus, see Table 1)

Cyanidiophyceae
Cyanidiales

Cyanidium Geitler

Spherical unicells, rarely united in a common mucilaginous matrix, 1.5-6 μm in diameter. Each cell contains one blue-green, parietal, spherical to cup-like chloroplast without a pyrenoid, a mitochondrion, and nucleus but no vacuole. Chloroplast contains single, parallel, concentric thylakoids with phycobilisomes and predominant C-phycocyanin. Reproduction by four endospores (2-3 μm). Sexual reproduction not reported.

Widespread in acidic thermal areas. Temperature range *in situ* 25-44 °C; pH range *in situ* 0.05-5.0.

Porphyridiophyceae
Porphrydiales

Flintiella F.D. Ott in Bourrelly

Spherical cells united in a gelatinous matrix, each with a massive, parietal, reddish chloroplast without a pyrenoid. Cell diameter 9-20 (45) μm. Reproduction by cell division. Sexual reproduction unknown.

Found in Barton Springs, Austin, Texas (USA) in autumn. Total solids 513 mg l^{-1}, NO_3^{-1} 301 mg l^{-1}, pH 6.9.

Porphyridum Nägeli (Fig. 1A)

Spherical to obovoid unicells with a stellate chloroplast and prominent central pyrenoid. Cell diameter 5-10 μm in exponential, 7-16 μm in stationary phase. Cells solitary, but often grouped into irregular colonies with an ill-defined mucilaginous matrix. Species distinguished by chloroplast color. Reproduction by cell division.

Forms gelatinous coatings on surfaces in freshwaters, brackish environments and moist soils.

Kyliniella Skuja (Fig. 1B and C)

Unbranched pseudofilaments growing in gray-green clusters from a discoid, pseudoparenchymatous base. Maximum filament length 2-3 cm. Cell diameter 18-19 μm, 5-17 μm long, surrounded by a mucilaginous envelope up to 16 μm wide. Cells contiguous or separate, containing several parietal, blue-green discoid chloroplasts. Rhizoidal outgrowths

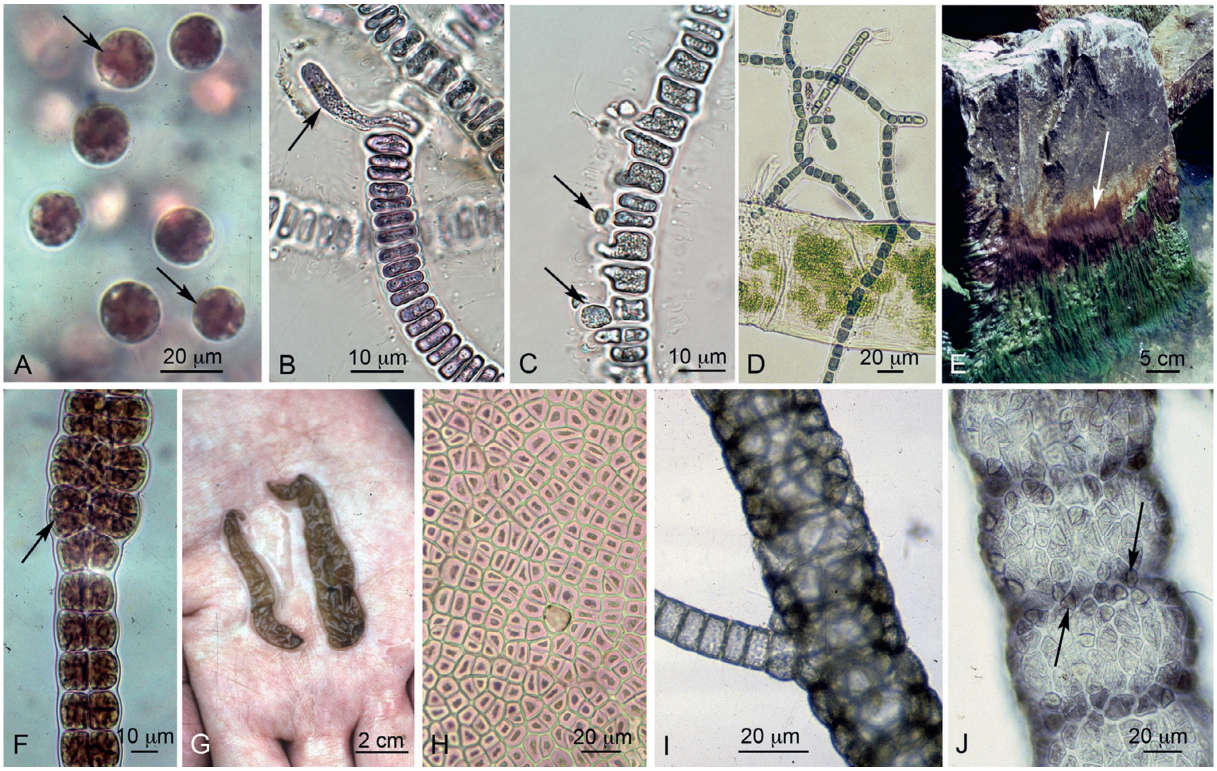

FIGURE 1 Freshwater porphyridiophycean, stylonematophycean, bangiophycean, and compsopogonophycean algae. (A) *Porphyridium* sp. unicellular form having axial stellate chloroplast with peripheral lobes (arrows). (B and C) *Kyliniella latvica*: (B) Rhyzoidal outgrowth (arrow) from filament. (C) Filament-producing sporangia (arrows). (D) *Chroodactylon ornatum*, blue-green epiphyte on *Cladophora glomerata*. (E and F) *Bangia atropurpurea*: (E) Thalli forming a distinct red band (arrow) just above the green *Cladophora glomerata* zone on a boulder in lake Erie. (F) Mature filament, which is biaxial toward the base and multiaxial at the apex (arrow). (G and H) *Boldia erythrosiphon*. (G) Macroscopic view showing saccate thallus. (H) Thallus surface with uniform cell sizes of various shapes. (I and J) *Compsopogon caeruleus*: (I) Branched uniaxial filament covered by smaller cortical cells. (J) Surface view showing slightly smaller and more densely pigmented monosporangia (arrows).

[17-25 (150) μm long] at points of contact. Vegetative reproduction by release of small fragments (hormogonia). Asexual reproduction by monospores shed by expulsion through sheath. Presumptive sexual reproduction in New Hampshire population with small colorless spermatia and large, pigmented carpogonia with tubular projections. Fate of zygote unknown.

Uncommon epiphyte of macrophytes in softwater streams in northeastern United States (Rhode Island and New Hampshire), mostly in summer and fall.

Stylonematophyceae
Stylonematales

Chroodactylon Hansgirg (Fig. 1D)

False-branched pseudofilaments of globose or elliptical cells enclosed in a broad, gelatinous sheath and arranged in an irregular uniseriate manner. Each cell with a blue-green, stellate, axial plastid and prominent pyrenoid. Cell diameter 3-17 μm, length 6-28 μm. Linear correlation between false branch number and filament length (ca. 1 branch per 200 μm length). Maximum filament length 1240 μm. Reproduction by monospores and fragmentation. No sexual reproduction observed.

Epiphyte of *Cladophora* and *Rhizoclonium* in Laurentian Great Lakes and scattered streams from Ontario to Arizona. Freshwaters largely hardwater: specific conductance 170-540 μS cm^{-1} and pH 7.8-8.5.

Chroothece Hansgirg in Wittrock & Nordstedt

Ellipsoidal to cylindrical cells, each with a broad firm gelatinous envelope. Cell diameter 20-30 μm; length 30-45 (50) μm. Cells contain an axial, stellate, blue-green to yellow-brown or orange chloroplast with a prominent pyrenoid. Cells solitary or joined pole-to-pole into few-celled colony. Basal pole with gelatinous sheath extended into lamellated stalk. Reproduction by cell division; pyrenoid divides and then cell undergoes transverse invagination. Also form resting akinetes. No sexual reproduction reported.

Rare component of freshwater streams, moist soils and peat bogs. Populations in an Arizona spring at 13 °C, pH 7.2-7.8 and specific conductance 570 µS cm^{-1}.

Rufusia Wujek & Timpano

Branched pseudofilaments, composed of spherical or elliptical cells, each with several reddish-violet, parietal, discoid to band-shaped chloroplasts without pyrenoids. Cells 5.5-15 × 3.5-10 µm. Apical and intercalary cell division. Asexual reproduction by endospores; vegetative propagation by fragmentation. Sexual reproduction not observed.

Grows within hair tissues and furrows of the two-toed sloth (*Choloepus*) and three-toed sloth (*Bradypus*) in Panama and Costa Rica. Not found on adjacent vegetation.

Bangiophyceae
Bangiales

Bangia Lyngbye (Fig. 1E and F)

Filiform, unbranched cylinders of cells embedded in firm gelatinous matrix. Attached by down-growing rhizoids, usually in dense purple-black to rust-colored clumps. The initial uniaxial filament (diameter 10-30 µm) becoming largely multiaxial at maturity (diameter 60-6180 µm for freshwater filaments). Cell number and filament length highly correlated in uniaxial filaments; filament lengths: 0.2-35 cm. Vegetative cells contain a large, axial, stellate chloroplast with prominent pyrenoid. Apical region differentiates into packets of cells, the monosporangia.

In hardwater lakes in North America, particularly Lakes Ontario, Erie, Huron, Michigan, and Simcoe, as well as the upper St. Lawrence River.

Compsopogonophyceae
Compsopogonales

Boldia Herndon (Fig. 1G and H)

Mauve-pink to reddish-brown (rarely olive-green), hollow, monostromatic sac or tube, 1-20 (40-75) cm long and 0.1-2.0 cm in diameter. Vegetative cells rectangular, 5-20 (45) µm in diameter, containing several peripheral, ribbon-like chloroplasts and a large central vacuole. Secondary filaments arise as outgrowths from vegetative cells, elongating between and above vegetative cells and eventually dividing to form monospores, 5-9 µm in diameter. Monospores germinate into a prostrate, monostromatic disc or an aggregation of creeping filaments. The disc or aggregation produces a cushion-like mound of cells that functions as a perennial holdfast, producing seasonally macroscopic thalli. Sexual reproduction not observed.

Localized in scattered streams in eastern North America, extending from central Alabama to Ontario and Québec. Range of ecological factors: current velocity 3-71 cm s^{-1}, pH 6.1-8.5, specific conductance 18-290 µS cm^{-1}, dissolved oxygen 4.5 mg l^{-1}—saturation, temperature 12-25 °C. In southern range often associated with snails of the family Pleuroceridae with high manganese content in the shells, appearing in late winter and usually disappearing by early summer. In northern streams largely epilithic and occurring throughout the summer.

Compsopogon Montagne (Fig. 1I and J)

Branched, bluish to violet-green, uniaxial filament with older portions corticated. Small-celled cortex produced by vertical division of axial cells into 1-5 layers. Plants up to 20-50 cm long and 250-2000 µm in diameter. Axial cells enlarge and are evident by slight constrictions in older portions. Axial cells may break down, leaving hollow cylinder. May be free-floating or benthic. If attached, rhizoids formed by outgrowths of lower cortical cells or a basal disc. Cortical cells 7-22 × 10-48 µm, containing several peripheral, discoid chloroplasts. Reproduction by fragmentation or monosporangia (9-28 µm long), which are cleared from cortical cells by oblique, unequal cell division. Monospore divides into creeping, branched filament; a central cell eventually elongates vertically and divides to form erect stage. Microaplanospores reported may represent spermatia but this is not confirmed.

Largely distributed in tropical to warm temperate streams; in North America well-documented collections range from Virginia and Texas to Belize and the Caribbean Islands. Streams tend to be warm (13-27 °C) and alkaline (pH 7.3-8.6, specific conductance 46-1880 µs cm^{-1}). Height, diameter, monosporangium number, branching, and basal disc presence affected by current velocity. Usually epilithic, but can be epiphytic. *C. caeruleus* epizoic on parasitic copepod *Lernaea* while it is attached to cyprinid fish in Mud River, Kentucky. Recently found at a depth of 21 m in central Lake Huron of the Laurentian Great Lakes.

Florideophyceae
Acrochaetiales

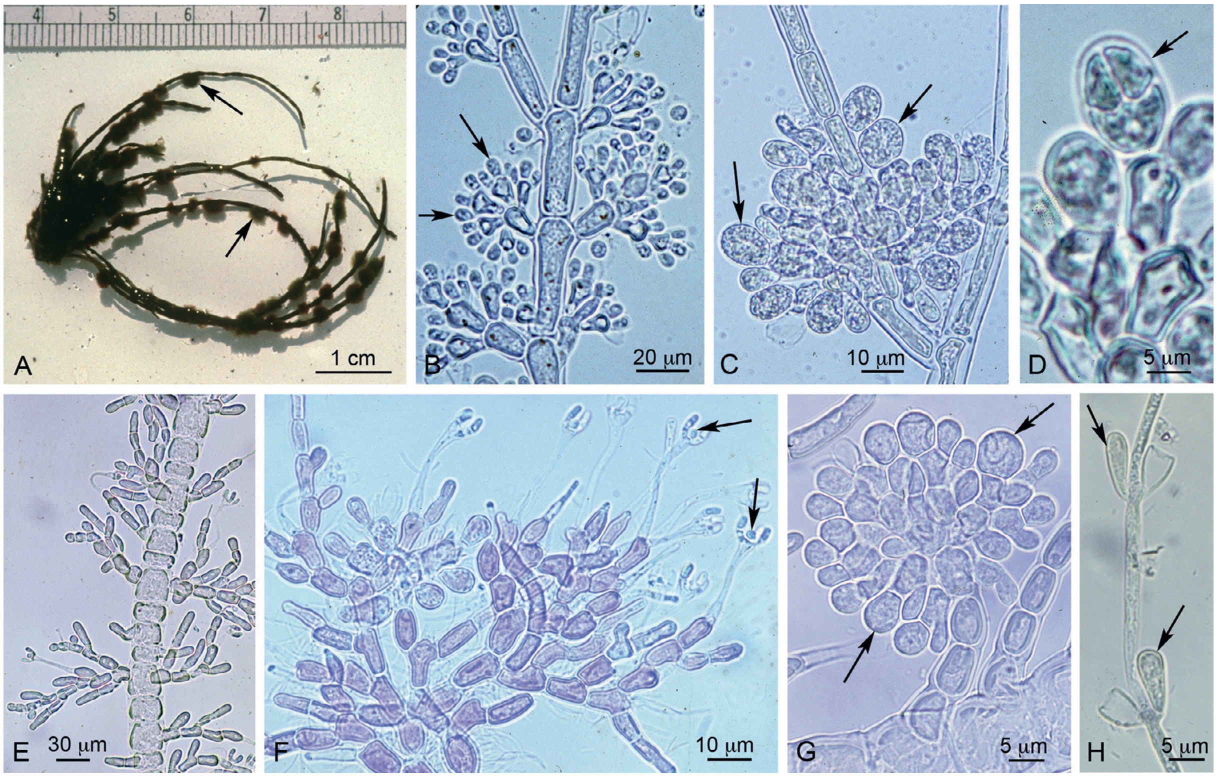

FIGURE 2 Freshwater Acrochaetiales and Balbianiales. (A–D) *Audouinella hermannii*: (A) Macroscopic view of tufts (arrows) epiphytic on *Paralemanea*. (B) Spermatangial clusters (arrows) at the tips of short lateral branches. (C) Carposporophyte, a dense mass of gonimoblast filaments with terminal obovoid carposporangia (arrows). (D) Tetrasporangium (arrow) at the tip of a vegetative cell. (E–H) *Rhododraparnaldia oregonica*. (E) Branched filament with lateral branches, both opposite and alternate, arising from large barrel-shaped axial cells. (F) Spermatia (arrows) are formed at the apex of colorless stalk cells. (G) Carposporophyte consisting of compact gonimoblast filaments with terminal carposporangia (arrows). (H) "Chantransia" with monosporangia (arrows).

Audouinella Bory (Fig. 2A–D)

Short, branched, uniaxial filaments which typically grow in dense tufts, usually <1 cm in diameter but up to 2-3 cm. The filaments may be composed of erect and prostrate axes. Apices of erect axes often terminate with colorless hair cells. Cells contain reddish, parietal, ribbon-like chloroplasts. Cell diameter 6-26 µm. Filaments most commonly with monosporangia (5-38 µm in diameter) at branch tips. Only reddish species have been observed to be sexual or tetrasporic. Colorless spermatangia (4-5 µm diam.) occur in clusters in branch tips; carpogonia have a cylindrical base and thin trichogyne (30 µm in length). Carposporophytes are spherical, compact mass of short gonimoblast filaments; carposporangia are obovoid (10 × 13 µm). Tetrasporangia are also formed at branch tips (9 µm diam.)

Widespread genus in streams, ranging from North Slope of Alaska to Costa Rica. *A. hermannii*, is the most common species in North America tends to occur in cool waters (11 °C), with low ion content (104 µS cm^{-1}) and mildly alkaline pH (7.5). *A. eugenea* typical of warm streams of high ion content.

Balbianiales

Rhododraparnaldia Sheath,Whittick & K.M.Cole (Fig. 2E–H)

Crimson-colored filaments up to 15 cm long with barrel-shaped axial cells, which have a distinctly larger diam. (17.3-30.1 µm) than that of lateral branches (4.3-8.5 µm). Unique spermatangial stalks produce two types of spermatangia at their tips. Carpogonium is borne on an undifferentiated branch and has a swollen, cylindrical base and thin trichogyne. Carposporophyte spherical, compact mass of short gonimoblast filaments. Carposporangia spherical up to 8 µm in diam. Carpospores germinate into a chantransia phase with cells 5-7 × 16-38 µm; this phase produces gametophyte. DAPI relative fluorescence values twice as high for gonimoblast cells, carposporangia, and "chantransia" cells as for the gametophyte vegetative cells and gametangia.

The single species *R. oregonica* combines characteristics of both the Acrochaetiales and Batrachospermales.

Found in two mountain streams in Oregon; the type locality has moderate current velocity (35-61 cm s^{-1}), temperatures 8-11 °C, pH 8.3, and specific conductance 30 µS cm^{-1}.

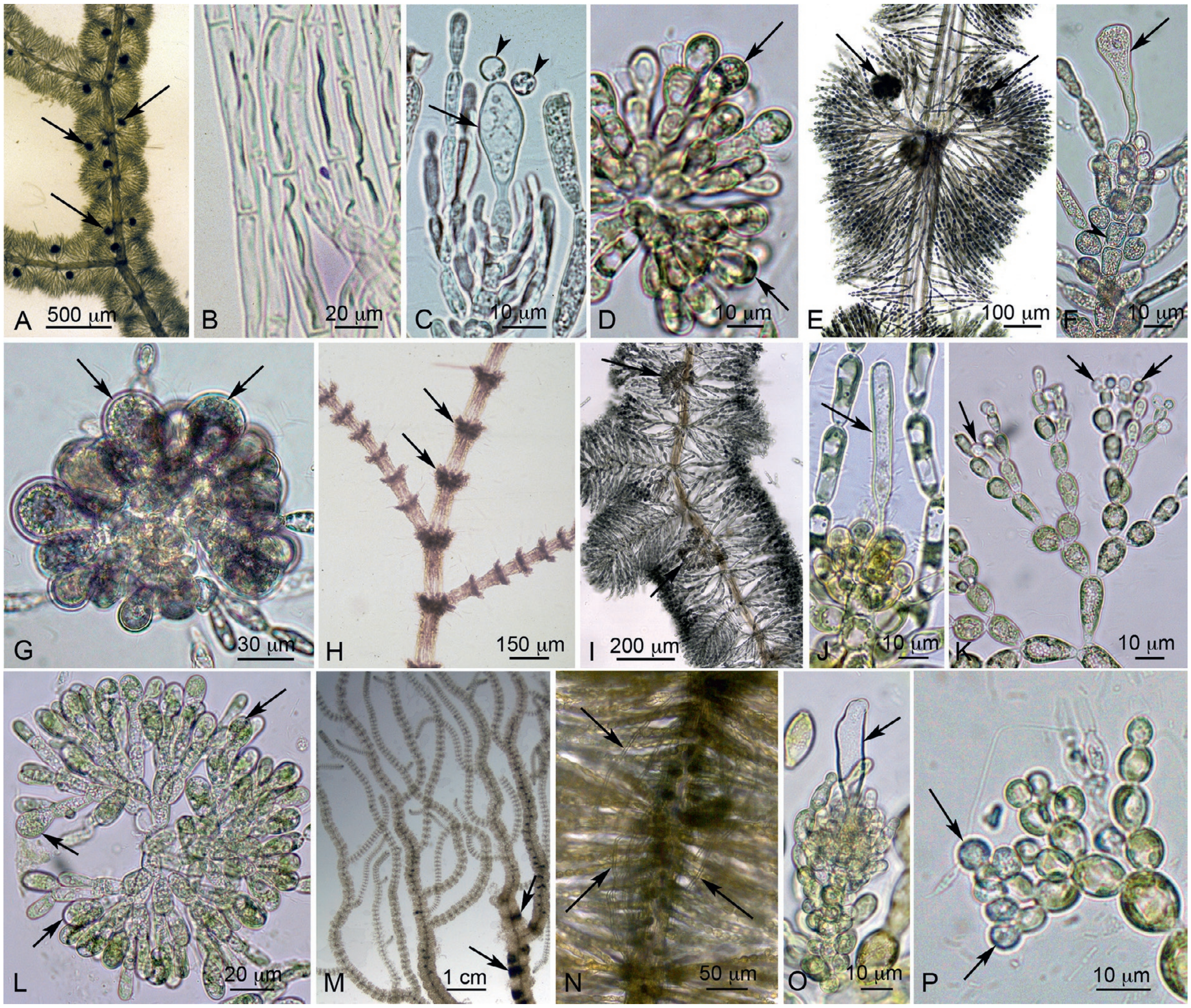

FIGURE 3 Freshwater *Batrachospermum* taxa. (A–D) Section *Batrachospermum*, *B. gelatinosum*: (A) Branched filament with barrel-shaped whorls containing numerous small spherical carposporophytes (arrows). (B) Regular cylindrical cells that cover the main axis. (C) Carpogonium with inflated clavate trichogyne (arrow) and two attached spermatia (arrowheads). (D) Carposporophyte with compacted gonimoblast filaments and terminal carposporangia (arrows). (E–G) Section *Macrospora*, *B. macrosporum*: (E) Whorl obovoidal with prominent stalked carposporophytes (arrows). (F) Carpogonium with lanceolate trichogyne (arrow) on a long carpogonial branch (arrowhead). (G) Carposporophyte with compacted gonimoblast filaments and large terminal carposporangia (arrows). (H) Section *Setacea*, *B. androinvolucrum* branched filament with greatly reduced whorls (arrows). (I–L) Section *Virescentia*, *B. helminthosum*. (I) Thallus with brown main axis compressed whorls containing axial carposporophytes (arrows). (J) Carpogonium with elongate, stalked cylindrical trichogyne (arrow). (K) Fascicles with terminal spermatangia (arrows). (L) Carpogonium with loose gonimoblast filaments and terminal carposporangia (arrows). (M–P) Section *Turfosa*, *B. turfosum*. (M) Habit of thallus with compressed barrel-shaped whorls and mature carposporophytes forming large dark patches (arrows). (N) The main axis has loose cortication (arrows). (O) Carpogonium with lanceolate trichogyne. (P) Fascicles with clusters of terminal spermatangia (arrows).

Batrachospermales

Batrachospermum Roth (Figs. 3F–M and 4A–C)

Gelatinous gametophyte filaments, up to 40 cm long, with beaded appearance, varying from blue-green, olive, violet, and gray to brownish. Uniaxial central axis with large cylindrical cells; 4-6 pericentral cells produce repeatedly branched fascicles of limited growth. Rhizoid-like cortical filaments typically develop from lower side of pericentral cells. Cortical filaments grow downward and ensheath axial cells; often produce secondary fascicle branches. Each fascicle cell contains several, ribbon-like, parietal chloroplasts with no pyrenoid. Few species form monosporangia in the gametophyte stage. Spermatangia bud off from terminal primary and secondary fascicle cells or in some species from involucral filaments of carpogonial branch; spherical, colorless, 4-8 µm diam. Carpogonial branches little modified to well differentiated. Carpogonia with broad trichogyne sometimes stalked on small base containing the nucleus. Carposporophytes generally

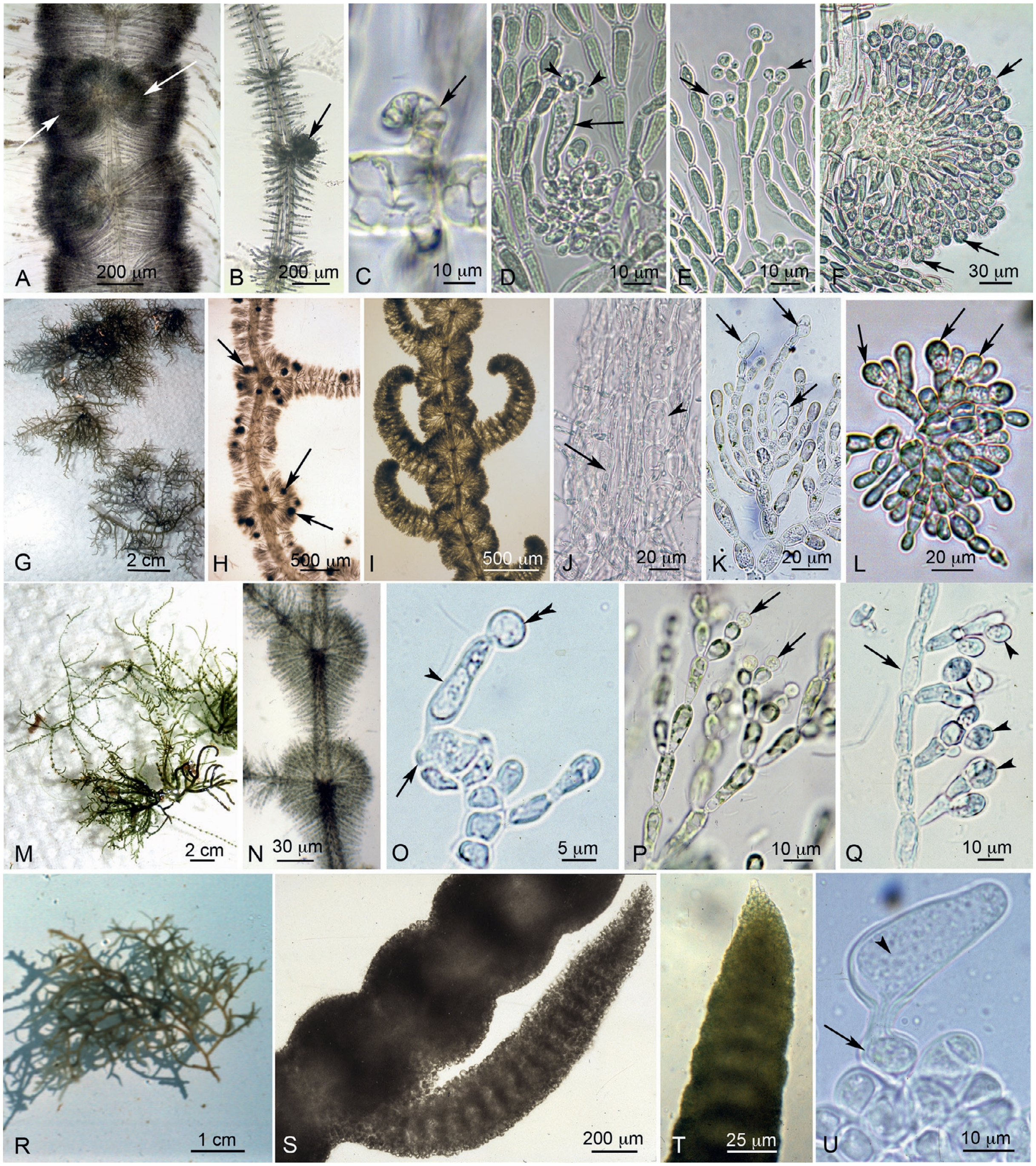

FIGURE 4 Freshwater Batrachospermales genera. (A–F) *Kumanoa*: (A) Closely appressed barrel-shaped whorls with large axial semispherical carposporophytes (arrows). (B) Whorls greatly reduced with carposporophyte (arrow). (C) Immature curved carpogonial branch (arrow). (D) Carpogonium with lanceolate trichogyne (arrow) and attached spermatia (arrowheads) on a twisted carpogonial branch. (E) Fascicles with terminal spermatangia (arrows). (F) Carposporophyte composed of gonimoblast filaments with terminal carposporangia (arrows). (G–L) *Sheathia*.(G) Thallus habit. (H) Female thallus composed of barrel-shaped whorls with numerous spherical small carposporophytes (arrows). (I) Male thallus with barrel-shaped whorls and curved branches. (J) Cortical cells of the main axis showing heterocortication, both cylindrical (arrow) and bulbous (arrowhead) cells. (K) Carpogonia with obovoidal trichogynes (arrows). (L) Carposporophyte with compacted gonimoblast filaments and terminal carposporangia (arrows). (M–Q) *Sirodotia*: (M) Thallus habit. (N) Branched filament with ovoid whorls. (O) Carpogonium having a base (arrow) with a protuberance, cylindrical trichogyne (arrowhead) and attached spermatium (double arrowhead). (P) Fascicles with terminal spermatangia (arrows). (Q) Carposporophyte with indeterminate gonimoblast filament (arrow) and carposporangia (arrowheads) at the tips of short lateral branches. (R–U) *Tuomeya americana*. (R) Macroscopic view of a mature plant, which is well-branched, cartilaginous tube. (S) Thallus showing cartilaginous construction with dense whorled appearance. (T) Branch apex showing confluent whorls. (U) Carpogonium with small base (arrow) and large trichogyne (arrowhead) perpendicularly attached to a stalk.

spherical or semispherical, compact or loose mass of gonimoblast filaments; carposporangia formed at apices. Carpospores germinate into "chantransia" stage, a crustose growth consisting of large basal cells and erect, sparsely branched filaments. Filaments can form monosporangia or divide meiotically, producing an attached gametophyte and two residual cells.

Cosmopolitan genus in moderately flowing, reasonably unpolluted streams. *B. turfosum* also common in bogs. Both euryphotic (e.g., *B. gelatinosum*) and shade or brown water (e.g., *B. turfosum*) species exist. Filament fragments common in guts of grazing amphipods, insect larvae, and snails. *B. gelatinosum*, the only widespread species in tundra, tolerates large range of conditions: temp. 0-24 °C, current velocity 7-181 cm s^{-1}, pH 4.1-8.2, specific conductance 10-360 µS cm^{-1}, PO_4^{3-} <1-4900 µg l^{-1}.

The genus *Batrachospermum* is currently under taxonomic revision. Molecular studies of the genus have shown that it is not monophyletic (Fig. 7). Recently, two new genera have been erected from former sections of *Batrachospermum*: *Kumanoa* from sections *Contorta* and *Hybrida* and *Sheathia* from section *Helminthoidea*. In the next few years the other sections will be described as new genera, leaving only the species from section *Batrachospermum* within the genus *Batrachospermum* sensu stricto. For the purposes of this book, a key to the remaining sections is provided so that the reader can more accurately identify specimens. The characters presented for identification of the sections will likely be the important characteristics for recognizing the new genera.

Key to the North American Sections (Fig. 7)

1. Carpogonial branch with little or no differentiation from fascicles (Fig. 3C)....................................*Batrachospermum*
1. Carpogonial branch well differentiated...2
  2. Carpogonial branch almost as long as fascicles (Fig. 3F) ....*Macrospora*
  2. Carpogonial branch much shorter than fascicles (Fig. 3J and O)...3
3. Mean mature whorl (with carposporophytes) diameter <170 µm, mean fascicle cell number < 6 ....*Setacea*
3. Mean whorl diameter > 300 µm, mean fascicle cell number ≥ 7 4
  4. Stalked trichogyne ....*Virescentia*
  4. Sessile trichogyne ....*Turfosa*

Kumanoa Entwisle, M.L. Vis, W.B. Chiasson, Necchi & A.R. Sherwood (Fig. 4A–F)

Attached gelatinous gametophytic filaments, up to 12.5 cm long, with beaded appearance varying from blue-green to green. Uniaxial central filament with large, cylindrical cells; 4-6 pericentral cells producing repeatedly branched fascicles of limited growth. In most species, rhizoid-like cortical filaments formed from lower side of pericentral cells. Each fascicle cell contains several, ribbon-like, parietal chloroplasts with no pyrenoid. Spermatangia bud off from terminal fascicle cells, spherical, colorless, 4-7 µm in diameter. Carpogonial branches twisted with more than one turn, slightly twisted or curved. Carpogonia with broad trichogyne sometimes stalked on small base containing the nucleus. Carposporophytes generally spherical or semispherical, compact or loose mass of gonimoblast filaments; carposporangia formed at apices. Carpospores germinate into "chantransia" stage, composed of branched, uniaxial filaments. Filaments can form monosporangia or divide meiotically, producing an attached gametophyte and two residual cells.

Cosmopolitan genus in moderately flowing, reasonably unpolluted streams in subtropical to tropical streams. However, some species, such as *K. faroensis* and *K. virgatodecaisneana*, are in temperate regions. As well, *K. mahlacensis* has been reported from lakes in the southwestern United States.

Sheathia Salomaki & M.L. Vis (Fig. 4G–L)

Attached gelatinous gametophytic filaments, up to ~15 cm long, with beaded appearance varying from olive-green to reddish-brown. Uniaxial central filament with large, cylindrical cells; 4-6 pericentral cells producing repeatedly branched fascicles of limited growth. In most species, rhizoid-like cortical filaments formed from lower side of pericentral cells. Cortical filaments, especially in basal parts of the thalli, have two types of cells, cylindrical and bulbous, termed heterocortication. Each fascicle cell contains several ribbon-like, parietal chloroplasts with no pyrenoid. Spermatangia bud off from terminal fascicle cells, spherical, colorless, 4-7 µm in diameter. Little differentiated carpogonial branches with small cells. Carpogonia with broad trichogyne sometimes stalked on small base containing the nucleus. Carposporophytes generally spherical, compact mass of gonimoblast filaments; carposporangia formed at apices. Carpospores germinate into "chantransia" stage, composed of branched, uniaxial filaments. Filaments can form monosporangia or divide meiotically, producing an attached gametophyte and two residual cells.

Cosmopolitan genus in moderately flowing, reasonably unpolluted streams. Some species are often found in springs of both the desert southwest and in more temperate areas. This genus is common in eastern North America from Newfoundland, Canada, in the north to Florida, USA in the south.

Sirodotia Kylin (Fig. 4M–Q)

Attached, gelatinous gametophytic filaments, up to 17 cm long, with a beaded appearance varying from blue-green to yellow-green. Uniaxial central filament with large, cylindrical cells; 4-6 pericentral cells producing repeatedly branched fascicles of limited growth. In most species, rhizoid-like cortical filaments formed from lower side of pericentral cells. Each fascicle cell contains several, ribbon-like, parietal chloroplasts with no pyrenoid. Spermatangia bud off from terminal fascicle cells, spherical, colorless, 4-7 μm in diameter. Little differentiated carpogonial branches with small cells. Carpogonia with broad trichogyne attached off-center to base, the latter structure having a definite protrusion. Carposporophyte a branched indeterminant filament creeping along the main axis; carposporangia formed at branch apices. Carpospores germinate into "chantransia" stage, composed of branched, uniaxial filaments. Meiosis and monosporangia not observed. Considered to be a section of *Batrachospermum* by Necchi and Entwisle (1990), but questioned by Necchi et al. (1993c).

In scattered, small, typically softwater (pH 5.7-7.6, specific conductance 10-140 μS cm^{-1}) streams in boreal to tropical environments; in North America from northern Quebec and Newfoundland to central Mexico. The most widespread species, *S. suecica*, has little increase in drag with increasing current velocity (20-80 cm s^{-1}) due to branch reconfiguration.

Tuomeya Harvey (Fig. 4R–U)

Densely branched, cartilaginous, and cylindrical gametophytic thallus, 1-5 (6.5) cm long. Blue-green, olive, or black. Uniaxial filament, covered by two to three layers of cortical filaments; dense laterals arising from ca. 6 pericentral cells, of limited growth with outer cells fused. Axial cells evident in mature branches by constrictions. Spermatangia formed at tips of laterals. Carpogonia asymmetrical with an irregularly broadened trichogyne attached obliquely or perpendicularly to a stalk; borne on a curved carpogonial branch derived from a pericentral cell. Carposporophyte a globular mass of filaments. Carpospores germinating into branched, uniseriate "chantransia" stage in culture but *in situ* gametophytes develop from an undifferentiated mass of cells. Considered to be a section of *Batrachospermum* by Necchi and Entwisle (1990), but questioned by Kaczmarczyk et al. (1992).

Scattered freshwater streams in eastern North America, Florida to Newfoundland from fall to early summer. Range of conditions: temp. 5-26 °C, current velocity 16-125 cm s^{-1}, pH 4.7-7.6, specific conductance 10-124 μS cm^{-1}. Tolerates considerable stress before breaking (1780 ± 850 kN m^{-2}), stretching 22% in the process. Common in guts of grazing amphipods and insect larvae; its cartilaginous structure and low protein contents make it a little preferred food source.

Balliopsis G.W.Saunders & Necchi (Fig. 5A)

Reddish filaments with a distinct main axis with hexagonal-shaped cells and smaller, pinnate, determinate lateral branches, which may rebranch. The apical cell is typically quite long in *B. prieurii* (43-89 μm in length). Plants typically small (3-15 mm). They can reproduce by the production of monosporangia.

Three freshwater collections have been made in North America from Belize and Costa Rica, with slow to moderate current velocities (1-65 cm s^{-1}), pH 7.6-7.8, specific conductance 50-100 μS cm^{-1}, and temperatures 19-22 °C.

Lemanea Bory (Fig. 5B–D)

Tufts of cartilaginous, tubular, pseudoparenchymatous gametophytic thalli, lacking cortical filaments around central, uniseriate axis. T- or L-shaped ray cells closely applied to outer cortex. 1-40 cm long and 0.2-2.0 mm in diameter. Blue-green to olive when young, becoming rusty-brown to black at maturity. Species characterized by presence of branching, diameter, and degree of basal constriction. Several parietal discoid chloroplasts in outer cells only. Spermatangia develop as yellowish circular patches. Nearby small carpogonial branches entirely internal except thin trichogyne that protrudes beyond outer cell layer. Carposporophytes microscopic, spherical masses of filaments forming large, ellipsoidal carpospores within central cavity; released by thallus deterioration and germinating into branched, uniseriate "chantransia" filaments. "Chantransia" stage produces attached gametophyte seasonally after meiosis.

Genus widespread in temperate and boreal streams and rivers with typically high current velocities (up to 2 m s^{-1}). Adapted to flow by developing dense turfs closely adherent to rocks and high breaking stress (910 ± 430 kN m^{-2} for *L. fluviatilis*). Common at high elevation up to 1200 m. *L. fluviatilis* tolerates 4-25 °C, pH 4.1-8.2, specific conductance 10-300 μS cm^{-1}. Occurs at low nutrient concentrations. In a Rhode Island river, growth and reproduction of *L. fluviatilis* gametophytes confined to April-August, after which thallus deteriorates and carpospores released; between September and March remnants persist.

Paralemanea M.L. Vis & Sheath (Fig. 5E–G)

Tufts of cartilaginous, tubular, pseudoparenchymatous gametophytic thalli with cortical filaments around central, axial filament and simple ray cells not abutting outer cortical cells. Mean length 4.3-9.5 cm and diameter 0.5-0.7 mm. Species

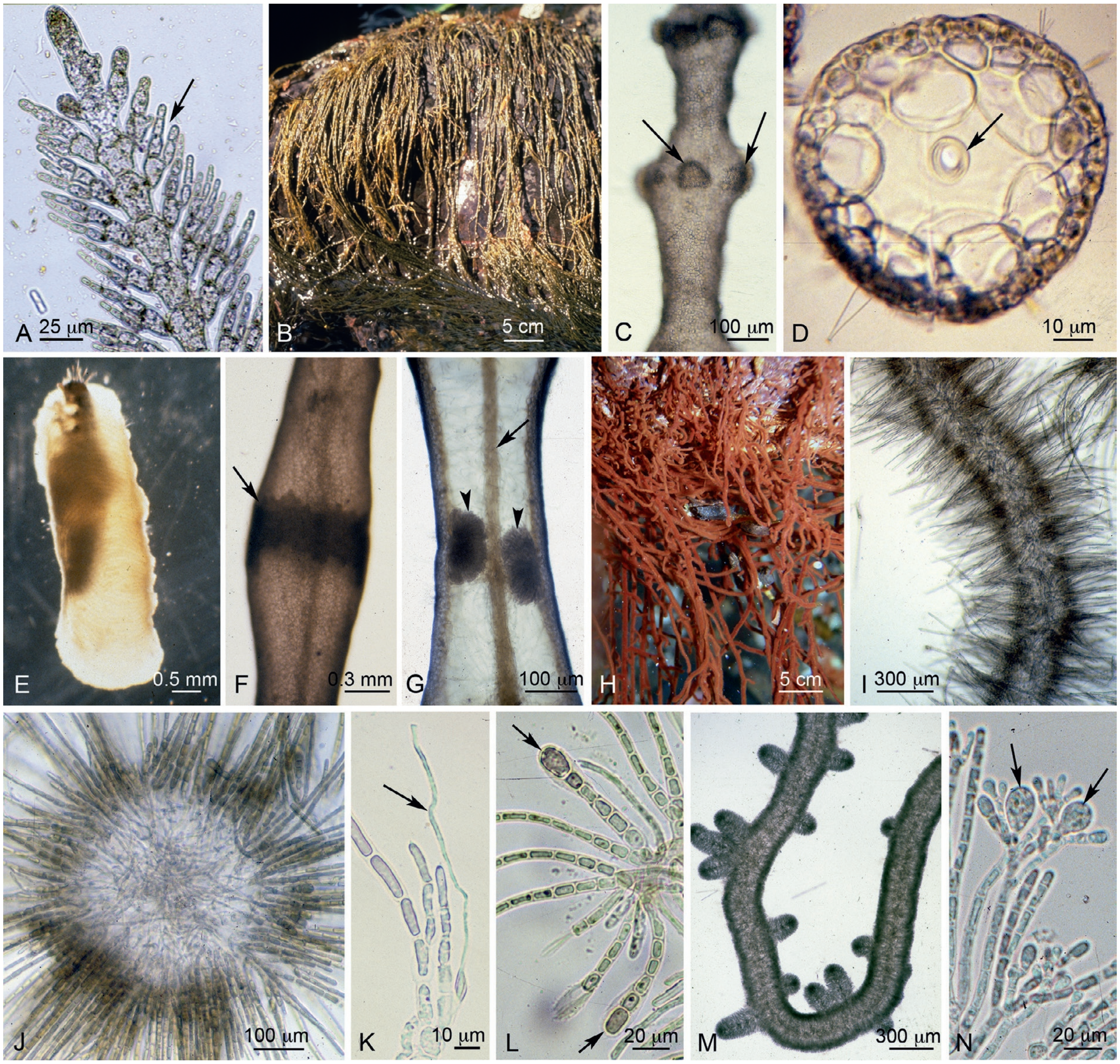

FIGURE 5 Freshwater Batrachospermales and Thoreales genera. (A) *Balliopsis prieurii*, apex showing hexagonal axial cells and pinnate lateral branches that rebranch (arrow). (B–D) *Lemanea*. (B) Macroscopic view of thallus habit on rock above high water line at the end of the growing season. (C) Thallus with nodes having patches of spermatangia (arrows). (D) Cross-section of thallus showing small pigmented cells on the outside and larger unpigmented cells on the inside with a main axis cell (arrow) with no cortication. (E–G) *Paralemanea*: (E) Caddisfly case constructed from strips of *Paralemanea*. (F) Thallus with node having a ring (arrow) of spermatangia. (G) Longitudinal section showing corticated main axis (arrow) and internal carposporophytes (arrowheads). (H–L) *Thorea*. (H) Macroscopic view of thalli showing crimson red appearance. (I) Branched, multiaxial filament, with an obvious outer, assimilatory layer and inner medullary layer. (J) Cross-section showing colorless, central medulla and outer, assimilatory filaments. (K) Carpogonium with thin, elongate trichogyne (arrow). (L) Monosporangia (arrows) on short branch at the base of assimilatory filament. (M, N) *Nemalionopsis*. (M) Branched, multiaxial filament. (N) Monosporangia (arrows) that are formed at the tips of assimilatory filaments.

characterized by presence of branching, length and diameter. Several parietal, discoid chloroplasts in outer cells only. Spermatangia develop as yellowish to brownish nodal rings. Small carpogonial branches entirely internal except thin trichogyne protrudes beyond outer layer. Carposporophytes small, spherical masses of filaments forming large, ellipsoidal carpospores in central cavity; released by thallus deterioration and germinating into branched, uniaxial “chantransia” filaments. “Chantransia” stage produces attached gametophyte seasonally after meiosis.

Most populations of *Paralemanea* in North America from southeastern United States and California, but extend from central Mexico to New York. Wide range of conditions: mean current velocity 18-110 $\mathrm{cm\,s^{-1}}$, temp. 4-17 °C, pH 5.5-8.6, specific conductance 42-500 $\mu\mathrm{S\,cm^{-1}}$. Predominant in cool seasons in a North Carolina stream.

Thoreales

Nemalionopsis Skuja (Fig. 5M and N)

Sparsely branched, cord-like thallus, burgundy to yellow-brown; composed of a central medullary region of interwoven, colorless filaments and an outer pigmented cortex of branched laterals of limited growth. Length 5-30 (50) cm, diameter 700-1000 µm. May be flattened or coiled in some portions. Monosporangia formed at outer tips of lateral filaments, 7-12 × 8-14 µm. Spore-bearing branch to vegetative branch length ratio >0.64. Monospores germinate into prostrate filaments forming monostromatic discs from which erect filaments arise. Sexual reproduction not observed.

Known from four freshwater streams in North America in Florida, Louisiana, and North Carolina with temperatures from 13 to 22 °C, current velocity 29 $\mathrm{cm\,s^{-1}}$, pH 7.1-8.3, and specific conductance 220 $\mu\mathrm{S\,cm^{-1}}$.

Thorea Bory (Fig. 5H–L)

Branched gametophytic filaments, up to 20-200 cm long, 0.5-3 mm diam. Composed of interwoven, colorless medullary filaments and dense, photosynthetic laterals of limited growth. Olive-green, reddish to black. Chloroplasts in assimilatory filaments parietal, ribbon-like. Monosporangia solitary or in clusters, formed at the base of the assimilatory filaments (spore-bearing branch to vegetative lateral length ratio <0.3). Sexual reproduction known for a few species. In *T. violacea* spermatangia borne on specialized branches near base of assimilatory filaments, colorless, elliptical or obovoid, 8-10 × 4-7 µm. Carpogonia conical with elongate trichogyne 5-7 µm wide; carpogonial branch short and at base of assimilatory filaments. Carposporophyte sparsely branched and compact. Carposporangia terminal, 9-13 × 17-25 µm; carpospores germinate into branched, uniseriate "chantransia" stage.

Widespread in tropical to warm temperate, freshwater streams; in North America from New York to Grenada. Typically in alkaline waters (e.g., North America pH 7.5-8.2, specific conductance 180-500 $\mu\mathrm{S\,cm^{-1}}$).

Hildenbrandiales

Hildenbrandia Nardo (Fig. 6A–D)

Bright red uncalcified crustose thallus, which is composed of a single basal layer that gives rise to vertical files of cells. Thallus height varies from 23 to 182 µm. Cell dimensions, 2-8 × 4-10 µm, indicate that a single species exists in freshwater habitats of North America, *H. angolensis* (*H. rivularis* appears to be restricted to Europe). Reproduction is largely by gemmae, dense aggregation of cells formed in the thallus, which are eventually released and germinate into new crusts.

Although *H. angolensis* has been reported from Pennsylvania, well-documented collections occur in streams and springs from Texas in the north to Costa Rica in the south, and through the Caribbean Islands. These streams are mostly warm (14-27 °C), alkaline in pH (7.0-8.6), and variable in current, velocity (5-67 $\mathrm{cm\,s^{-1}}$), and specific conductance (70-1558 $\mu\mathrm{S\,cm^{-1}}$).

Ceramiales

Bostrychia Montagne (Fig. 6E)

Dark reddish filaments with tiers of pericentral cells around the axial cells; thallus may become additionally corticated to the outside of the pericentral cells (e.g., *B. tenella*). Specialized rhizoidal branches, the haptera, attach filaments to substrata. Vegetative branching bilateral; branches near the apex tend to incurve; there may be both long and short shoots. Only tetrasporangia have been observed in freshwater collections, which are formed in inflated, multichambered structures termed stichidia.

Freshwater populations in North America appear to be restricted to streams in the Caribbean Islands, which are warm (21-26 °C), alkaline (pH 7.0-8.4) and range in specific conductance (56-440 $\mu\mathrm{S\,cm^{-1}}$).

Caloglossa (Harvey) G. Martens (Fig. 6F–G)

Flat, dichotomously branched reddish blades with constrictions. A prominent midrib is evident and is composed of a broad axial row of cells surrounded by a cortex of elongated cells. The outer portions of the blade are monostromatic with oblique series of hexagonal cells. Rhizoids arise at constrictions, either from the midrib area or peripheral layer of cells. Population spread in freshwaters vegetative, although gametophytic and tetrasporic plants have been collected in brackish waters.

Two species, *C. lepreurii* and *C. ogasawaraensis*, have been collected from streams in Puerto Rico and Costa Rica, respectively. Current velocities are moderate (33-43 $\mathrm{cm\,s^{-1}}$), temperature high (23-24 °C), pH alkaline (7.6-8.4), and specific conductance 100-200 $\mu\mathrm{s\,cm^{-1}}$.

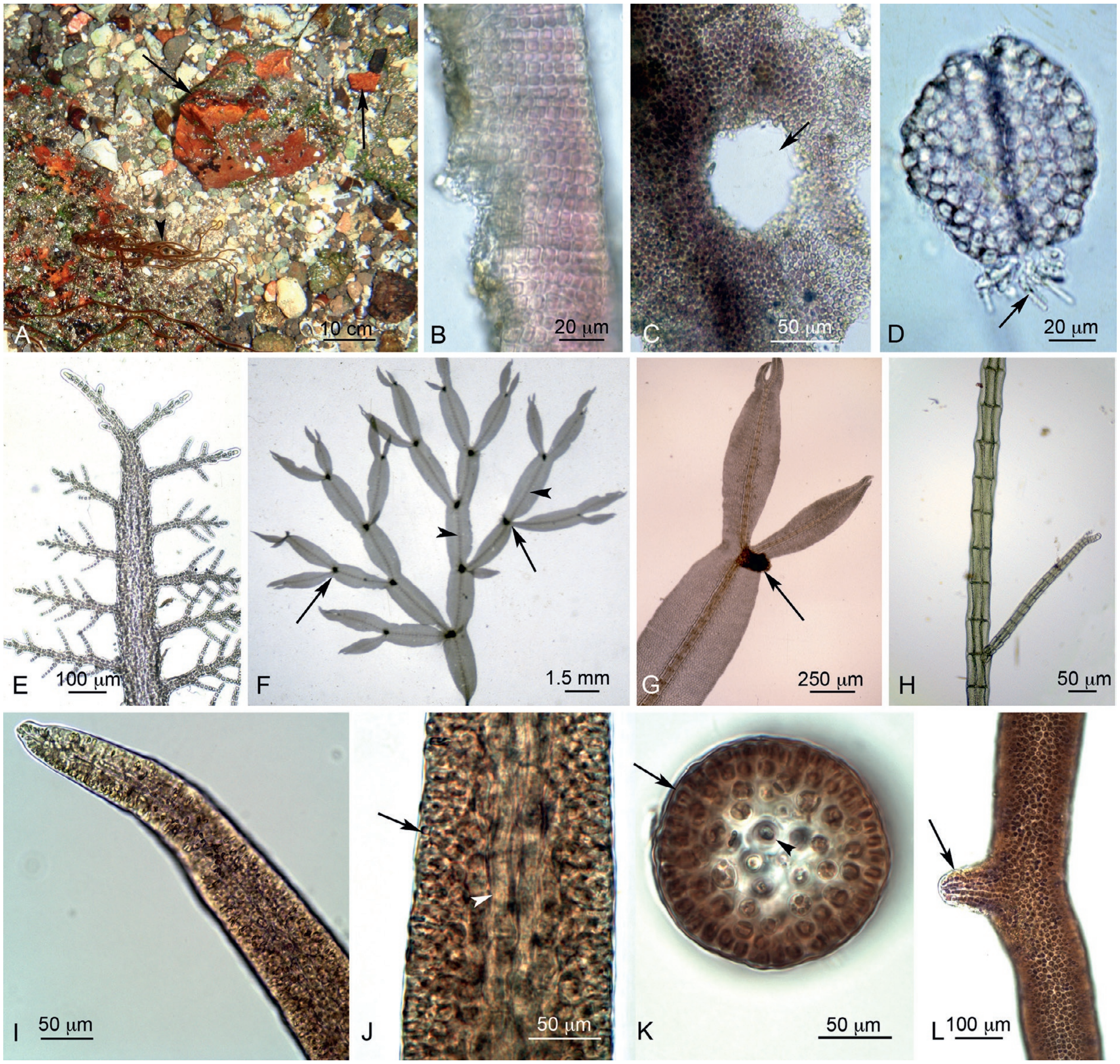

FIGURE 6 Freshwater Hildenbrandiales, Ceramiales Gigartinales genera. (A–D) *Hildenbrandia angolensis*: (A) Habit of thallus, forming crimson layer on rocks (arrows), shown here in a Texas stream with *Thorea* (arrowhead). (B) Cross-section of thallus multiple layers of cells. (C) Surface of thallus with tightly packed cells with a gap in the thallus where a gemma was released (arrow). (D) Released gemma with basal rhizoids for attachment (arrow). (E) *Bostrychia* showing habit of thallus. (F and G) *Caloglossa*. (F) Macroscopic view of flat blades with subdichotomous branching, constrictions at nodes (arrows) and obvious midrib (arrowheads). (G) Rhizoids (arrow) arising from pericentral cell. (H) *Polysiphonia subtilissima* filaments with elongate rows of cells. (I–L) *Sterrocladia belizeana*. (I) Apical branch tip. (J) Optical longitudinal section with small, spherical outer cortical cells (arrow) and elongate, central medullary cells (arrowhead). (K) Cross-section of branch with tightly organized cortical cells (arrow) and loose medullary cells (arrowhead). (L) Rhizoidal branch (arrow) arising from cortical cells.

Polysiphonia Greville (Fig. 6H)

Dark reddish filaments with a single tier of pericentral cells around the axial cell. No freshwater collections have an additional layer of cortication, but a few marine species do. Delicately branched hairs (trichoblasts) are formed in upper portions of the plant. Rhizoidal branches arise from pericentral cells. Freshwater samples have not been observed as being either sexual or tetrasporic.

This genus is common in marine and brackish habitats; only two populations of *P. subtilissima* have been collected in North American freshwaters in Florida and Jamaica. These streams have moderate flow ($25\,\mathrm{cm\,s^{-1}}$), high temperature (22-26 °C), alkaline pH (7.7-7.8), and high specific conductance ($1150\text{-}1840\,\mu\mathrm{S\,cm^{-1}}$).

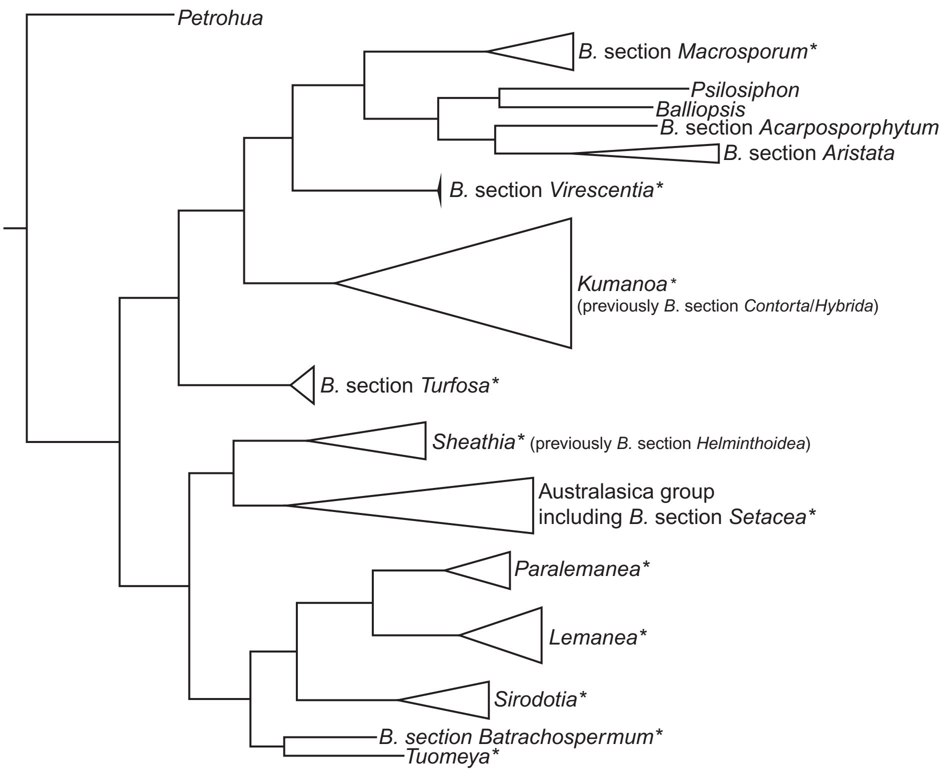

FIGURE 7 Phylogenetic tree of the Batrachospermales showing the relationships of the genera and sections of *Batrachospermum*. All sections will eventually be described as new genera and the genus *Batrachospermum* will only contain species in *Batrachospermum* section *Batrachospermum*. Genera and sections with an * have species reported previously in North America.

Gigartinales

Sterrocladia F. Schmitz (Fig. 6I–L)

Thallus a small, reddish pseudoparenchyma, which is mostly dichotomously branched, up to 3 cm in length, 50-120 μm in diameter, and occurring in dense turfs. The plants are uniaxial, with cortical cells in two to three layers, and medullary cells arranged in loose filaments surrounding a central axis. Axial cells and medullary cells are slightly larger than cortical cells. Pit plug anatomy with a cap membrane and lacking cap layers. Reproduction unknown.

Found in montane, lotic freshwater habitats in Belize.

VI GUIDE TO THE LITERATURE FOR SPECIES IDENTIFICATION

A general identification book for all freshwater rhodophytes is available, but new taxonomic changes have been made since publication (Kumano, 2002). In addition, a book devoted to European freshwater reds has been published recently, but some new molecular findings have suggested that the flora of Europe and North America may not be as similar as previously believed (Eloranta et al., 2011; Salomaki et al., 2014). The following is a list of key references, each of which contains citations to older literature or current classification issues:

1. *Audouinella*—Necchi et al. (1993a,b) and Jiménez and Necchi (2001)
2. *Balliopsis*—Sheath et al. (1993c) and Saunders and Necchi (2002)
3. *Bangia*—Sheath and Cole (1984), Müller et al. (1998), Gargiulo et al. (2001), and Shea et al. (2014)
4. *Batrachospermum*—Sheath et al. (1992, 1993d, 1994a,b,c), Sheath and Vis (1995), Vis et al. (1996a,b), Vis and Sheath (1996, 1997, 1998), and Müller et al. (1997)
5. *Boldia*—Howard and Parker (1980) and Sheath and Hymes (1980)
6. *Bostrychia*—Sheath et al. (1993c) and Zuccarello and West (2011)
7. *Caloglossa*—Sheath et al. (1993c) and Krayesky et al. (2011)
8. *Chroodactylon*—Vis and Sheath (1993) and Wołowski et al. (2007)
9. *Chroothece*—Blinn and Prescott (1976) and Aboal et al. (2014)

10. *Compsopogon*—Vis et al. (1992), Rintoul et al. (1999), and Necchi et al. (2013)
11. *Cyanidium*—Seckbach (1991) and Reeb and Bhattacharya (2010)
12. *Flintiella*—Ott (1976)
13. *Hildenbrandia*—Sheath et al. (1993a), Sherwood and Sheath (1999b), and Montejano et al. (2002)
14. *Kumanoa*—Necchi and Vis (2012)
15. *Kyliniella*—Vis and Sheath (1993)
16. *Lemanea*—Vis and Sheath (1992) and Sheath et al. (1996b)
17. *Nemalionopsis*—Sheath et al. (1993b)
18. *Paralemanea*—Vis and Sheath (1992), Sheath et al. (1996b), and Carmona and Necchi (2002)
19. *Polysiphonia*—Sheath et al. (1993c) and Lam et al. (2013)
20. *Porphyridium*—Ott (1972) and Bhattacharya et al. (2013)
21. *Rhododraparnaldia*—Sheath et al. (1994d)
22. *Rufusia*—Wujek and Timpano (1986)
23. *Sheathia*—Salomaki et al. (2014)
24. *Sirodotia*—Necchi et al. (1993c), Vis and Sheath (1999), and Lam et al. (2012)
25. *Sterrocladia*—Sherwood et al. (2012)
26. *Thorea*—Sheath et al. (1993b), Vis et al. (1998), and Carmona and Necchi (2001)
27. *Tuomeya*—Kaczmarczyk et al. (1992)

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LITERATURE CITED

Aboal, M., García-Fernández, M.E., Roldán, M., Whitton, B.A., 2014. Ecology, morphology and physiology of *Chroothece richteriana* (Rhodophyta, Stylonematophyceae) in the highly calcareous Río Chícamo, South-East Spain. Eur. J. Phycol. 49, 83–96.

Bhattacharya, D., Price, D.C., Chan, C.X., Qiu, H., Rose, N., Ball, S., 2013. Genome of the red alga *Porphyridium purpureum*. Nat. Commun. 4, 1941. doi:10.1038/ncomms2931.

Blinn, D.W., Prescott, G.W., 1976. A North American distribution record for the rare Rhodophyceae, *Chroothece mobilis* Pascher and Petrova. Am. Midl. Nat. 96, 207–210.

Brown, D.L., Weier, T.E., 1968. Chloroplast development and ultrastructure in the freshwater red alga *Batrachospermum*. J. Phycol. 4, 199–206.

Broadwater, S.T., Scott, J.L., 1994. Ultrastructure of unicellular red algae. In: Seckbach, J. (Ed.), Evolutionary Pathways and Enigmatic Algae: Cyanidium Caldarium. Kluwer Academic, Netherlands, pp. 215–230.

Carlile, A.L., Sherwood, A.R., 2013. Phylogenetic affinities and distribution of the Hawaiian freshwater red algae (Rhodophyta). Phycologia 52, 309–319.

Carmona, J., Necchi Jr., O., 2001. Systematics and distribution of *Thorea* (Thoreaceae, Rhodophyta) from Central Mexico and Southeastern Brazil. Phycol. Res. 49, 231–239.

Carmona, J., Necchi Jr., O., 2002. Taxonomy and distribution of *Paralemanea* (Lemaneaceae, Rhodophyta) in Central Mexico. Cryptogamie Algol. 23, 39–49.

Chiasson, W.B., Machesky, N.J., Vis, M.L., 2003. Phylogeography of a freshwater red alga, *Batrachospermum helminthosum*, in North America. Phycologia 42, 654–660.

Couté, A., Sarthou, C., 1990. Révision des espèces d'eau douce du genre *Ballia* (Rhodophytes, Céramiales). Cryptogamie Algol. 11, 265–279.

Craigie, J.S., 1990. Cell walls. In: Cole, K.M., Sheath, R.G. (Eds.), Biology of the Red Algae. Cambridge University Press, Cambridge, pp. 221–257.

D'Lacoste, V., Ganesan, E.K., 1987. Notes on Venezuelan freshwater algae—I. Nova Hedwigia 45, 263–281.

DeLuca, P., Gambardella, R., Merola, A., 1979. Thermoacidophilic algae in North and Central America. Bot. Gaz. 140, 418–427.

Doemel, W.N., Brock, T.D., 1971. The physiological ecology of *Cyanidium caldarium*. J. Gen. Microbiol. 67, 17–32.

Downes, B.J., Street, J.L., 2005. Regrowth or dispersal? Recovery of a freshwater red alga following disturbance at the patch scale. Austral Ecol. 30, 526–536.

Drew, K.M., 1935. The life history of *Rhodochorton violaceum* (Kütz.) comb. nov. (*Chantransia violacea* Kütz.). Ann. Bot. 49, 439–450.

Eloranta, P., Kwandrans, J., 2004. Indicator value of freshwater red algae in running waters for water quality assessment. Int. J. Oceanogr. Hydrobiol. 33, 47–54.

Eloranta, P., Kwandrans, J., Kusel-Fetzmann, E., 2011. Süßwasserflora von Mitteleuropa, Bd. 7/Freshwater Flora of Central Europe. In: Rhodophyta and Phaeophyceae, vol. 7. Spektrum Akademischer Verlag GMBH, Heidelberg, pp. 156 pp.

Entwisle, T.J., Vis, M.L., Chiasson, W.B., Necchi Jr., O., Sherwood, A.R., 2009. Systematics of the Batrachospermales – A Synthesis. J. Phycol. 45, 704–715.

Everitt, D.T., Burkholder, J.M., 1991. Seasonal dynamics of macrophyte communities from a stream flowing over granite flatrock in North Carolina, USA. Hydrobiologia 222, 159–172.

Filkin, N.R., Vis, M.L., 2004. Phenology of *Paralemanea annulata* (Lemaneaceae, Rhodophyta) in an Ohio woodland stream. Hydrobiologia 518, 159–168.

Flint, L.H., 1970. Freshwater Red Algae of North America. Vantage Press, New York, 110 pp.

Fritsch, F.E., 1929. The encrusting algal communities of certain fast-flowing streams. New Phytol. 28, 165–196.

Gantt, E., Scott, J., Lipschultz, C., 1986. Phycobiliprotein composition and chloroplast structure in the freshwater red alga *Compsopogon coeruleus* (Rhodophyta). J. Phycol. 22, 480–484.

Garbary, D.J., Hansen, G.I., Scagel, R.F., 1980. A revised classification of the Bangiophyceae (Rhodophyta). Nova Hedwigia 33, 145–166.

Gargiulo, G.M., Genovese, G., Morabito, M., Culoso, F., De Masi, F., 2001. Sexual and asexual reproduction in a freshwater population of *Bangia atropurpurea* (Bangiales, Rhodophyta) from eastern Sicily (Italy). Phycologia 40, 88–96.

Geitler, L., 1932. *Porphyridium sordidum* n. sp., eine neue Süβwasser bangiale. Arch. Protist. 76, 595–604.

Gibson, M.T., Whitton, B.A., 1987. Hairs, phosphatase activity and environmental chemistry in *Stigeoclonium, Chaetophora* and *Draparnaldia* (Chaetophorales). Br. Phycol. J. 22, 11–22.

Goodman, K.M., Hay, M.E., 2013. Activated chemical defenses suppress herbivory on freshwater red algae. Oecologia 171, 921–933.

Gretz, M.R., Sommerfeld, M.R., Athey, P.V., Aronson, J.M., 1991. Chemical composition of the cell walls of the freshwater red alga *Lemanea annulata* (Batrachospermales). J. Phycol. 27, 232–240.

Guiry, M.D., Guiry, G.M., 2014. AlgaeBase. World-wide Electronic Publication, National University of Ireland, Galway. http://www.algaebase.org (accessed 15.06.14).

Hambrook, J.A., Sheath, R.G., 1987. Grazing of freshwater Rhodophyta. J. Phycol. 23, 656–662.

Hambrook, J.A., Sheath, R.G., 1991. Reproductive ecology of the freshwater red alga *Batrachospermum boryanum* Sirodot in a temperate headwater stream. Hydrobiologia 218, 233–246.

Harding, J.P.C., Whitton, B.A., 1981. Accumulation of zinc, cadmium and lead by field populations of *Lemanea*. Water Res. 15, 301–319.

Higa, A., Kasai, F., Kawachi, M., Kumano, S., Sakayama, H., Miyashita, M., Watanabe, M.M., 2007. Seasonality of gametophyte occurrence, maturation and fertilization of the freshwater red alga *Thorea okadae* (Thoreales, Rhodophyta) in the Kikuchi River, Japan. Phycologia 46, 160–167.

Hoffmann, L., 1989. Algae of terrestrial habitats. Bot. Rev. 55, 77–105.

House, D.L., VandenBroek, A.M., Vis, M.L., 2010. Intraspecific genetic variation of *Batrachospermum gelatinosum* (Batrachospermales, Rhodophyta) in Eastern North America. Phycologia 49, 501–507.

Howard, R.V., Parker, B.C., 1980. Revision of *Boldia erythrosiphon* Herndon (Rhodophyta, Bangiales). Am. J. Bot. 67, 413–422.

Hymes, B.J., Cole, K.M., 1983. The cytology of *Audouinella hermannii* (Rhodophyta, Florideophyceae). II. Monosporogenesis. Can. J. Bot. 61, 3377–3385.

Hynes, H.B.N., 1970. The Ecology of Running Waters. Liverpool University Press, Liverpool, 555 pp.

Israelson, G., 1942. The freshwater Florideae of Sweden. Symb. Bot. Upsal 8, 1–134.

Jiménez, J.C., Necchi Jr., O., 2001. A new species and expanded distributions of freshwater *Audouinella* (Acrochaetiaceae, Rhodophyta) from Central Mexico and South-Eastern Brazil. Eur. J. Phycol. 36, 217–226.

Johnston, E.T., 2012. The Systematic Revision of the Freshwater Red Algal Order Thoreales (Nemaliophycidae, Rhodophyta). MS Thesis, Ohio University. https://etd.ohiolink.edu/ap/10?0::NO:10:P10_ETD_SUBID:62124.

Kaczmarczyk, D., Sheath, R.G., 1991. The effect of light regime on the photosynthetic apparatus of the freshwater red alga *Batrachospermum boryanum*. Cryptogamie Algol. 12, 249–263.

Kaczmarczyk, D., Sheath, R.G., Cole, K.M., 1992. Distribution and systematics of the freshwater genus *Tuomeya* (Rhodophyta, Batrachospermaceae). J. Phycol. 28, 850–855.

Kato, A., Morita, N., Hiratsuka, T., Suda, S., 2009. Recent introduction of a freshwater red alga *Chantransia macrospora* (Batrachospermales, Rhodophyta) to Okinawa, Japan. Aquat. Invasions 4, 567–574.

Korch, J.E., Sheath, R.G., 1989. The phenology of *Audouinella violacea* (Acrochaetiaceae, Rhodophyta) in a Rhode Island stream (USA). Phycologia 28, 228–236.

Krayesky, D.M., Norris, J.N., West, J.A., Fredericq, S., 2011. The *Caloglossa leprieurii* complex (Delesseriaceae, Rhodophyta) in the Americas: the elucidation of overlooked species based on molecular and morphological evidence. Cryptogamie Algol. 32, 37–62.

Kremer, B., 1983. Untersuchungen zur Ökophysiologie einiger Süsswasserrotalgen. Decheniana (Bonn) 136, 31–42.

Kumano, S., 1978. Notes on freshwater red algae from West Malaysia. Bot. Mag. Tokyo 91, 97–107.

Kumano, S., 2002. Freshwater Red Algae of the World. Biopress Ltd, Dorset, 375 pp.

Kumano, S., Necchi Jr., O., 1987. Studies on the freshwater Rhodophyta of Brazil-5: record of *Bostrychia radicans* (Montagne) Montagne f. *moniliforme* post in freshwaters. Rev. Brasil Biol. 47, 437–440.

Kwandrans, J., Eloranta, P., 2010. Diversity of freshwater red algae in Europe. Oceanol. Hydrobiol. Stud. 39, 161–169.

Lam, D.W., Entwisle, T.J., Eloranta, P., Kwandrans, J., Vis, M.L., 2012. Circumscription of species in the genus *Sirodotia* (Batrachospermales, Rhodophyta) based on molecular and morphological data. Eur. J. Phycol. 47, 42–50.

Lam, D.W., García-Fernández, M.E., Aboal, M., Vis, M.L., 2013. *Polysiphonia subtilissima* (Ceramiales, Rhodophyta) from freshwater habitats in North America and Europe is confirmed as conspecific with marine collections. Phycologia 52, 156–160.

Leukart, P., Hanelt, D., 1995. Light requirements for photosynthesis and growth in several macroalgae from a small soft-water stream in the Spessart Mountains, Germany. Phycologia 34, 528–532.

Lin, C.K., Blum, J.L., 1977. Recent invasion of a red alga *Bangia* in Lake Michigan. J. Fish. Res. Board Can. 34, 2413–2416.

MacFarlane, J.J., Raven, J.A., 1985. External and internal CO_2 transport in *Lemanea*: interactions with the kinetics of ribulose bisphosphate carboxylase. J. Exp. Bot. 36, 610–622.

McKay, R.M.L., Gibbs, S.P., 1990. Phycoerythrin is absent from the pyrenoid of *Porphyridium cruentum*: photosynthetic implications. Planta 180, 249–256.

Montejano, G., Jiménez, J.C., González, J., 2002. Taxonomía y distribución de *Hildenbrandia* Nardo (Hildenbrandiales, Rhodophyta) de agua dulce en la región central de México. Hidrobiológica 12, 7–14.

Müller, K.M., Sheath, R.G., Vis, M.L., Crease, T.J., Cole, K.M., 1998. Biogeography and systematics of *Bangia* (Bangiales, Rhodophyta) based on the RuBisCO spacer, *rbc*L gene, 18S rRNA gene sequences and morphometric analyses. I. North America. Phycologia 37, 195–207.

Müller, K.M., Vis, M.L., Chiasson, W.B., Whittick, A., Sheath, R.G., 1997. Phenology of a *Batrachospermum* population in a boreal pond and its implications for the systematics of section *Turfosa* (Batrachospermales, Rhodophyta). Phycologia 36, 68–75.

Necchi Jr., O., 1993. Distribution and seasonal dynamics of Rhodophyta in the Preto River Basin, Southeastern Brazil. Hydrobiologia 250, 81–90.

Necchi Jr., O., 1995. Occurrence of the genus *Ballia* (Ceramiaceae, Rhodophyta) in freshwater in Brazil. Hoehnea 22, 229–235.

Necchi Jr., O., 1997. Microhabitat and plant structure of *Batrachospermum* (Batrachospermales, Rhodophyta) populations in four streams of São Paulo State, Southeastern Brazil. Phycol. Res. 45, 39–45.

Necchi Jr., O., Alves, A.H.C.S., 2005. Photosynthetic characteristics of the freshwater red alga *Batrachospermum delicatulum* (Skuja) Necchi & Entwisle. Acta Bot. Bras. 19, 125–137.

Necchi Jr., O., Entwisle, T.J., 1990. A reappraisal of generic and subgeneric classification in the Batrachospermaceae (Rhodophyta). Phycologia 29, 478–488.

Necchi Jr., O., Sheath, R.G., Cole, K.M., 1993a. Systematics of freshwater *Audouinella* (Acrochaetiaceae, Rhodophyta) in North America. 1. The reddish species. Algol. Stud. 70, 11–28.

Necchi Jr., O., Sheath, R.G., Cole, K.M., 1993b. Systematics of freshwater *Audouinella* (Acrochaetiaceae, Rhodophyta) in North America. 2. The bluish species. Algol. Stud. 71, 13–21.

Necchi Jr., O., Sheath, R.G., Cole, K.M., 1993c. Distribution and systematics of the freshwater genus *Sirodotia* (Batrachospermales, Rhodophyta) in North America. J. Phycol. 29, 236–243.

Necchi Jr., O., Silva Garcia Fo, A., Salomaki, E.D., Aboal, M., West, J.A., Vis, M.L., 2013. Global sampling reveals low genetic diversity within Compsopogon (Compsopogonales, Rhodophyta). Eur. J. Phycol. 48, 152–162.

Necchi Jr., O., Vis, M.L., 2005. Reproductive ecology of the freshwater red alga *Batrachospermum delicatulum* (Batrachospermales, Rhodophyta) in three tropical streams. Phycol. Res. 53, 194–200.

Necchi Jr., O., Vis, M.L., 2012. Monograph of the genus *Kumanoa* (Rhodophyta, Batrachospermales). Bibliotheca Phycol. 116, 1–79.

Ott, F.D., 1972. A review of the synonyms and taxonomic position of the algal genus *Porphyridium* Nägeli 1849. Nova Hedwigia 23, 237–289.

Ott, F.D., 1976. Further observations on the freshwater alga *Flintiella sanguinaria* Ott in Bourrelly 1970 (Rhodophycophyta, Porphyridiales). Arch. Protistenk 118, 34–52.

Pipp, E., Rott, E., 1994. Classification of running-water sites in Austria based on benthic algal community structure. Verh. Int. Verein Limnol. 25, 1610–1613.

Pueschel, C.M., 1990. Cell structure. In: Cole, K.M., Sheath, R.G (Eds.), Biology of the Red Algae. Cambridge University Press, Cambridge, pp. 7–41.

Raven, J.A., 1993. The roles of the *Chantransia* phase of *Lemanea* (Lemaneaceae, Batrachospermales, Rhodophyta) and of the 'mushroom' phase of *Himanthalia* (Himanthaceae, Fucales, Phaeophyta). Bot. J. Scotl. 46, 477–485.

Raven, J.A., Johnston, A.M., Newman, J.R., Scrimgeour, C.M., 1994. Inorganic carbon acquisition by aquatic photolithotrophs of the Dighty Burn, U.K.: uses and natural limitations of natural abundance measurements of carbon isotopes. New Phytol. 127, 271–286.

Reeb, V., Bhattacharya, D., 2010. The thermo-acidophilic Cyanidiophyceae (Cyanidiales). In: Seckbach, J., Chapman, D.J. (Eds.), Red Algae in the Genomic Age, Cellular Origin, Life in Extreme Habitats and Astrobiology, vol. 13. Springer, Dordrecht, pp. 409–426.

Rintoul, T.C., Sheath, R.G., Vis, M.L., 1999. Systematics and biogeography of the Compsopogonales with emphasis on the freshwater families in North America. Phycologia 38, 517–527.

Rosemond, A.D., 1993. Interactions among irradiance, nutrients, and herbivores constrain a stream algal community. Oecologia 94, 585–594.

Salomaki, E.D., Kwandrans, J., Eloranta, P., Vis, M.L., 2014. Molecular and morphological evidence for *Sheathia* gen. nov. and three new species. J. Phycol. 50, 526–542.

Saunders, G.W., Necchi Jr., O., 2002. Nuclear rDNA sequences from *Ballia prieurii* support recognition of *Balliopsis* gen. nov. in the Batrachospermales (Florideophyceae, Rhodophyta). Phycologia 41, 61–67.

Schumacher, G.J., Whitford, L.A., 1965. Respiration and ^{32}P uptake in various species of freshwater algae as affected by a current. J. Phycol. 1, 78–80.

Scott, J., 1983. Mitosis in the freshwater red alga *Batrachospermum ectocarpum*. Protoplasma 118, 56–70.

Seckbach, J., 1991. Systematic problems with *Cyanidium caldarium* and *Galdaria sulphuraria* and their implications for molecular biology studies. J. Phycol. 27, 794–796.

Seto, R., 1977. On the vegetative propagation of a freshwater red alga, Hildenbrandia rivularis (Liebm.). J. Agric. Bull. Jpn. Soc. Phycol. 25, 129–136 (in Japanese).

Shea, T.B., Sheath, R.G., Chhun, A., Vis, M.L., Chiasson, W.B., Müller, K.M., 2014. Distribution, seasonality and putative origin of the non-native red alga *Bangia atropurpurea* (Bangiales, Rhodophyta) in the Laurentian Great Lakes. J. Great Lakes Res. 40, 27–34.

Sheath, R.G., 1984. The biology of freshwater red algae. Prog. Phycol. Res. 3, 89–157.

Sheath, R.G., 1987. Invasions into the Laurentian Great Lakes. Arch. Hydrobiol. Beih. 25, 165–187.

Sheath, R.G., Burkholder, J.M., Hambrook, J.A., Hogeland, A.M., Hoy, E., Kane, M.E., Morison, M.O., Steinman, A.D., VanAlstyne, K.L., 1986. Characteristics of softwater streams in Rhode Island. III. Distribution of macrophytic vegetation in a small drainage basin. Hydrobiologia 140, 183–191.

Sheath, R.G., Cole, K.M., 1984. Systematics of *Bangia* (Rhodophyta) in North America. I. Biogeographic trends in morphology. Phycologia 23, 383–396.

Sheath, R.G., Cole, K.M., 1990. Differential Alcian Blue staining in freshwater Rhodophyta. Br. Phycol. J. 25, 281–285.

Sheath, R.G., Cole, K.M., 1992. Biogeography of stream macroalgae in North America. J. Phycol. 28, 448–460.

Sheath, R.G., Hambrook, J.A., 1988. Mechanical adaptations to flow in freshwater red algae. J. Phycol. 24, 107–111.

Sheath, R.G., Hambrook, J.A., 1990. Freshwater ecology. In: Cole, K.M., Sheath, R.G. (Eds.), Biology of the Red Algae. Cambridge University Press, Cambridge, pp. 423–453.

Sheath, R.G., Hambrook, J.A., Nerone, C.A., 1988. The benthic macro-algae of Georgian Bay, the North Channel and their drainage basin. Hydrobiologia 163, 141–148.

Sheath, R.G., Hellebust, J.A., Sawa, T., 1979. Effects of low light and darkness on structural transformations in plastids of the Rhodophyta. Phycologia 18, 1–12.

Sheath, R.G., Hymes, B.J., 1980. A preliminary investigation of the freshwater red algae in streams of southern Ontario, Canada. Can. J. Bot. 58, 1295–1318.

Sheath, R.G., Kaczmarczyk, D., Cole, K.M., 1993a. Distribution and systematics of freshwater *Hildenbrandia* (Rhodophyta, Hildenbrandiales) in North America. Eur. J. Phycol. 28, 115–121.

Sheath, R.G., Morison, M.O., 1982. Epiphytes on *Cladophora glomerata* in the Great Lakes and St. Lawrence Seaway with particular reference to the red alga *Chroodactylon ramosum* (=*Asterocytis smargdina*). J. Phycol. 18, 385–391.

Sheath, R.G., Müller, K.M., 1997. Ultrastructure of carpogonia and carpogonial branches of *Batrachospermum helminthosum* and *Batrachospermum involutum* (Batrachospermales, Rhodophyta). Phycol. Res. 45, 177–181.

Sheath, R.G., Müller, K.M., Larson, D.J., Cole, K.M., 1995. Incorporation of freshwater Rhodophyta into the cases of caddisflies (Trichoptera) from North America. J. Phycol. 31, 889–896.

Sheath, R.G., Müller, K.M., Colbo, M.H., Cole, K.M., 1996a. Incorporation of freshwater Rhodophyta into the cases of chironomid larvae (Chironomidae, Diptera) from North America. J. Phycol. 32, 949–952.

Sheath, R.G., Müller, K.M., Vis, M.L., Entwisle, T.J., 1996b. A re-examination of the morphology, ultrastructure and classification of genera in the Lemaneaceae (Batrachospermales, Rhodophyta). Phycol. Res. 44, 233–246.

Sheath, R.G., Vis, M.L., 1995. Distribution and systematics of *Batrachospermum* (Batrachospermales, Rhodophyta) in North America. 7. Section *Hybrida*. Phycologia 35, 431–438.

Sheath, R.G., Vis, M.L., Cole, K.M., 1992. Distribution and systematics of *Batrachospermum* (Batrachospermales, Rhodophyta) in North America. 1. Section *Contorta*. J. Phycol. 28, 237–246.

Sheath, R.G., Vis, M.L., Cole, K.M., 1993b. Distribution and systematics of the freshwater red algal family Thoreaceae in North America. Eur. J. Phycol. 28, 231–241.

Sheath, R.G., Vis, M.L., Cole, K.M., 1993c. Distribution and systematics of freshwater Ceramiales (Rhodophyta) in North America. J. Phycol. 29, 108–117.

Sheath, R.G., Vis, M.L., Cole, K.M., 1993d. Distribution and systematics of *Batrachospermum* (Batrachospermales, Rhodophyta) in North America. 3. Section *Setacea*. J. Phycol. 29, 719–725.

Sheath, R.G., Vis, M.L., Cole, K.M., 1994a. Distribution and systematics of *Batrachospermum* (Batrachospermales, Rhodophyta) in North America. 4. Section *Virescentia*. J. Phycol. 30, 108–117.

Sheath, R.G., Vis, M.L., Cole, K.M., 1994b. Distribution and systematics of *Batrachospermum* (Batrachospermales, Rhodophyta) in North America. 5. Section *Aristata*. Phycologia 33, 404–414.

Sheath, R.G., Vis, M.L., Cole, K.M., 1994c. Distribution and systematics of *Batrachospermum* (Batrachospermales, Rhodophyta) in North America. 6. Section *Turfosa*. J. Phycol. 30, 872–884.

Sheath, R.G., Whittick, A., Cole, K.M., 1994d. *Rhododraparnaldia oregonica*, a new freshwater red algal genus and species intermediate between the Acrochaetiales and the Batrachospermales. Phycologia 33, 1–7.

Sherwood, A.R., Necchi Jr., O., Carlile, A.L., Laughinghouse 4th., H.D., Fredericq, S., Sheath, R.G., 2012. Characterization of a novel freshwater gigartinalean red alga from Belize, with a description of *Sterrocladia belizeana* sp. nov. (Rhodophyta). Phycologia 51, 627–635.

Sherwood, A.R., Sheath, R.G., 1999a. Seasonality of macroalgae and epilithic diatoms in spring-fed streams in Texas, U.S.A. Hydrobiologia 390, 73–82.

Sherwood, A.R., Sheath, R.G., 1999b. Biogeography and systematics of *Hildenbrandia* (Rhodophyta, Hildenbrandiales) in North America: inferences from morphometrics, *rbc*L and 18S rRNA gene sequence analyses. Eur. J. Phycol. 34, 523–532.

Sherwood, A.R., Sheath, R.G., 2000. Microscopic analysis and seasonality of gemma production in the freshwater red alga *Hildenbrandia angolensis* (Hildenbrandiales, Rhodophyta). Phycol. Res. 48, 241–249.

Skuja, H., 1938. Comments on fresh-water Rhodophyceae. Bot. Rev. 4, 665–676.

Smith, D.W., Brock, T.D., 1973. The water relations of the alga *Cyanidium caldarium* in soil. J. Gen. Microbiol. 79, 219–231.

Starmach, K., 1969. Growth of thalli and reproduction of the red alga *Hildenbrandia rivularis* (Liebm.). J. Agric. Acta Soc. Bot. Pol. 38, 523–533.

Steinman, A.D., McIntire, C.D., 1986. Effects of current velocity and light energy on the structure of periphyton assemblages in laboratory streams. J. Phycol. 22, 352–361.

Tanaka, J., Kamiya, M., 1993. Reproductive structure of *Caloglossa ogasawaerensis* Okamura (Ceramiales, Rhodophyceae) in nature and culture. Jpn. J. Phycol. 41, 113–121.

Thirb, H.H., Benson-Evans, K., 1982. The effect of different current velocities on the red alga *Lemanea* in a laboratory stream. Arch. Hydrobiol. 96, 65–72.

Vis, M.L., Carlson, T.A., Sheath, R.G., 1991. Phenology of *Lemanea fucina* (Rhodophyta) in a Rhode Island river USA. Hydrobiologia 222, 141–146.

Vis, M.L., Miller, E.J., Hall, M.M., 2001. Biogeographical analyses of *Batrachospermum helminthosum* (Batrachospermales, Rhodophyta) in North America using molecular and morphological data. Phycologia 40, 2–9.

Vis, M.L., Saunders, G.W., Sheath, R.G., Dunse, K., Entwisle, T.J., 1998. Phylogeny of the Batrachospermales (Rhodophyta) inferred from *rbc*L and 18 ribosomal DNA gene sequences. J. Phycol. 34, 341–350.

Vis, M.L., Sheath, R.G., 1992. Systematics of the freshwater red algal family Lemaneaceae in North America. Phycologia 31, 164–179.

Vis, M.L., Sheath, R.G., 1993. Distribution and systematics of *Chroodactylon* and *Kyliniella* (Porphyridiales, Rhodophyta) from North American streams. Jpn. J. Phycol. 41, 237–241.

Vis, M.L., Sheath, R.G., 1996. Distribution and systematics *Batrachospermum* (Batrachospermales, Rhodophyta) in North America. 9. Section *Batrachospermum*: description of five new species. Phycologia 35, 124–134.

Vis, M.L., Sheath, R.G., 1997. Biogeography of *Batrachospermum gelatinosum* (Batrachospermales, Rhodophyta) in North America based on molecular and morphological data. J. Phycol. 33, 520–526.

Vis, M.L., Sheath, R.G., 1998. A molecular and morphological investigation of the relationship between *Batrachospermum spermatoinvolucrum* and *B. gelatinosum* (Batrachospermales, Rhodophyta). Eur. J. Phycol. 33, 231–239.

Vis, M.L., Sheath, R.G., 1999. A molecular investigation of the systematic relationship among *Sirodotia* species (Batrachospermales, Rhodophyta) in North America. Phycologia 38, 261–266.

Vis, M.L., Sheath, R.G., Cole, K.M., 1992. Systematics of the freshwater red algal family Compsopogonaceae in North America. Phycologia 31, 564–575.

Vis, M.L., Sheath, R.G., Cole, K.M., 1996a. Distribution and systematics of *Batrachospermum* (Batrachospermales, Rhodophyta) in North America. 8a. Section *Batrachospermum: Batrachospermum gelatinosum*. Eur. J. Phycol. 31, 31–40.

Vis, M.L., Sheath, R.G., Cole, K.M., 1996b. Distribution and systematics of *Batrachospermum* (Batrachospermales, Rhodophyta) in North America. 8b. Section *Batrachospermum*: previously described species excluding *Batrachospermum gelatinosum*. Eur. J. Phycol. 31, 189–199.

Vogel, S., 1984. Drag and flexibility in sessile organisms. Am. Zool. 24, 37–44.

Whitton, B.A., 1975. Algae. In: Whitton, B.A. (Ed.), River Ecology. University of California Press, Berkeley and Los Angeles, pp. 81–105.

Whitford, L.A., 1960. The current effect and growth of fresh-water algae. Trans. Am. Microsc. Soc. 74, 302–309.

Woekerling, W.J., 1990. An introduction. In: Cole, K.M., Sheath, R.G. (Eds.), Biology of the Red Algae. Cambridge University Press, Cambridge, pp. 1–6.

Wołowski, K., Kowalska, J., Hindák, F., 2007. *Chroodactylon ornatum* (Rhodophyta, Porphyridiales) occurring in Poland and Slovakia. Biologia 62, 646–649.

Wujek, D.E., Timpano, P., 1986. *Rufusia* (Porphyridiales, Phragmonemataceae), a new red alga from sloth hair. Brenesia 25-26, 163–168.

Yoshida, T., 1959. Life-cycle of a species of *Batrachospermum* found in northern Kyushu, Japan. Jpn. J. Bot. 17, 29–42.

Youngs, H.L., Gretz, M.R., West, J.A., Sommerfeld, M.R., 1998. The cell wall chemistry of *Bangia atropurpurea* (Bangiales, Rhodophyta) and *Bostrychia moritziana* (Ceramiales, Rhodophyta) from marine and freshwater environments. Phycol. Res. 46, 63–73.

Yung, Y.-K., Stokes, P.M., Gorham, E., 1986. Algae of selected continental and maritime bogs in North America. Can. J. Bot. 70, 1154–1156.

Zuccarello, G.C., West, J.A., 2011. Insights into evolution and speciation in the red alga *Bostrychia*: 15 years of research. Algae 26, 21–32.