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BROWN ALGAE

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I. INTRODUCTION

Brown algae, the Phaeophyceae (or Fucophyceae; Christensen, 1978), are a class (or division, Phaeophyta; Papenfuss, 1951) of algae consisting mainly of complex, macroscopic seaweeds whose brown color comes from a carotenoid pigment, fucoxanthin, and in some species, various phaeophycean tannins. Of perhaps 2000 species (in 265 genera) of brown algae (Van den Hoek *et al.*, 1995), less than 1% are known from freshwater habitats, although some marine species may colonize brackish waters (Wilce, 1966; Dop, 1979; West and Kraft, 1996). Various authors cite between 3 and 7 genera, and up to 12 species of freshwater brown algae worldwide (see Sect. 21.II.A). Members of the group have many features in common with chrysophytes, synurophytes (Chrysophyta), and diatoms (Bacillariophyta), including chloroplast structure (thylakoids in stacks of three, girdle lamella, chloroplast endoplasmic reticulum), motile stage heterokont (unequal flagella), major pigments (chlorophylls *a*, *c*₁, and *c*₂, β -carotene, violaxanthin, diatoxanthin, and large amounts of fucoxanthin), as well as the storage reserve laminarin (Craigie, 1974; Goodwin, 1974; Pueschel and Stein, 1983; Lee, 1989). However, no

members of the Phaeophyceae are unicellular or colonial in the vegetative phase—the predominant morphology in other golden-brown groups. Brown algae have cell walls composed of cellulose, which is often supplemented with the mucopolysaccharide alginic acid. In seaweeds, this material is produced in sufficient quantities in some species to be harvested for commercial purposes, but in freshwater species, alginates appear to be less prevalent. Further descriptions of the group can be found in reviews by Papenfuss (1951), Van den Hoek *et al.* (1995), and Graham and Wilcox (2000).

Freshwater species of brown algae have been known for more than 100 years [*Pleurocladia* was described by Braun (1855), *Heribaudiella* by Gomont (1896); Bourrelly (1981)], but today most are still known only from scattered locations. Freshwater phaeophytes occur in a variety of streams and rivers, as well as in the littoral zone of lakes, but their biology has largely remained obscure for most phycologists and freshwater ecologists. This is unfortunate, because some species, most notably *Heribaudiella fluviatilis*, can at times be one of the dominant species of benthic algae in smaller rivers (Kann, 1978a). One reason for their obscurity may be that most species form crusts or

brown colonies that may be mistaken for members of other algal groups or lichens. The most recent monograph of freshwater algae in North America (Smith, 1950) listed only one species (*H. fluviatilis*), which was recorded from only one location [considered doubtful by Smith (1950), but see Sect. V.B], and even its identity has been questioned (Pueschel and Stein, 1983). Since that time, other genera and many more locations have been identified on this continent, suggesting that at least some species are less rare than previously thought, although their distribution is still far from well known. Whitford (1977) proposed that few species of freshwater algae may actually be rare, but instead are simply under-reported. Several species long thought to be uncommon have turned out to be fairly cosmopolitan, such as several species of freshwater red algae (Sheath and Hambrook, 1990). For these reasons, Whitford challenged biologists to describe the habitats of newly discovered algae more carefully. Because of the paucity of information on freshwater Phaeophyta, the present chapter describes all known taxa, although at present only five species (in four genera) have thus far been confirmed from sites in North America.

II. DIVERSITY AND MORPHOLOGY

A. Diversity and Classification

Freshwater brown algae are undoubtedly the least diverse of all groups of freshwater algae. Although some species can at times form substantial populations, no habitats are known that have several species of freshwater brown algae within a single location. Kann (1993) has observed filamentous *Pleurocladia* and encrusting *Heribaudiella* occurring together on stones in the littoral zone of Lake Erken, Sweden, and Kusel-Fetzmann (1996) noted that the *Pleurocladia* may grow as an epiphyte on *Heribaudiella* in some Austrian streams. More than 60 years ago, Israelsson (1938) demonstrated that different species of freshwater brown algae exhibit different geographic patterns, which appear to be the result of different ecological requirements. Given the small number of species overall, it is not surprising that their local diversity is low.

Accounts of the number of genera and species of phaeophytes from freshwater vary among authors, largely due to lack of study. Their classification is also unsettled, mainly because of uncertainty regarding the reliability of certain morphological features (e.g., branching pattern, colony shape, presence of hairs) as taxonomic attributes, the possible synonymy of several taxa, and whether historical collections were described and identified accurately (Waern, 1952; Müller and Geller, 1978; Dop, 1979; Bourrelly, 1981; Pueschel and

Stein, 1983; Wehr and Stein, 1985). Further work with field populations and cultured material to better describe their reproduction and genetic relationships will undoubtedly reveal new groupings and perhaps new (or fewer) species within the group. The present account recognizes six freshwater genera and seven species worldwide within the division (Table I). Of these, five species have thus far been reported from sites in North America. Following the general schemes of Bold and Wynne (1985) and Van den Hoek *et al.* (1995), all freshwater phaeophytes are classified as members of the Ectocarpales (five genera) or Sphacelariales (one genus, two species).

B. Morphology and Reproduction

The morphologies of all freshwater phaeophyte species are based upon a relatively simple filamentous structure and do not form parenchymatous (tissue-like) thalli, characteristic of more complex brown seaweeds. Their size range is also substantially smaller than those that colonize marine habitats. Crustose forms, although visually conspicuous, may only be 10–30 cells tall (1–2 mm), and form colonies of perhaps 0.2–50 cm² in area (Wehr and Stein, 1985; Kusel-Fetzmann, 1996). Filamentous forms can form macroscopic tufts 2–10 mm in size. Several colonies may coalesce to form larger expanses on rocks, but these dimensions are in great contrast to species of intertidal brown algae, which reach sizes of several meters, or subtidal kelp forests that may be as tall as 20–60 m (Bold and Wynne, 1985).

Among freshwater forms, three basic morphologies are seen (Fig. 1): (1) most consist of uniseriate (single axis), branched filaments (members of the Ectocarpales), which develop to form either (Fig. 1A) spreading or cushion-like tufts [*Bodanella*, *Ectocarpus*, *Pleurocladia*, *Porterinema* (syn. = *Pseudobodanella*)]; (2) others consists of prostrate filaments, which produce an upright series of densely packed, vertical filaments, forming a crustose morphology (*Heribaudiella*; Fig. 1B); and (3) in *Sphacelaria* cells are arranged in multiseriate (multiaxial), branched filaments, and also form spreading cushions on submerged substrata (Fig. 1C). Thalli in most species seem capable of forming hyaline, multicellular filaments or hairs (Waern, 1952; Wilce, 1966; Dop, 1979; Schloesser and Blum, 1980; Yoshizaki *et al.*, 1984; Kusel-Fetzmann, 1996; Wujek *et al.*, 1996). It seems doubtful that these hairs can be used as diagnostic features, as studies suggest they may be produced in response to reduced Cl⁻ or long photoperiods (Dop, 1979), or P-limitation (Fig. 2A). Such patterns are similar to those observed in filamentous species of green algae (Gibson and Whitton, 1987)

TABLE I Species of Brown Algae Reported from Freshwater Environments, with Morphology (UF = Uniseriate Filaments; CR = Crustose, MF = Multiseriate Filaments), Habitats, and Localities

Taxon	Morphology	Habitat	Localities
Ectocarpales			
<i>Bodanella lauterbornii</i>	UF	Lake	North America: unknown Other: Lake Constance, ^a Europe
<i>Ectocarpus siliculosus</i> ^b	UF	Stream, estuary	North America: unknown Other: Hopkins River, Australia
<i>Pleurocladia lacustris</i>	UF	Stream, lake	North America: Green River (UT, CO), Devon Island (NWT) Other: Austria, Germany, Poland, Scandinavia, England
<i>Heribaudiella fluviatilis</i> ^c	CR	Stream, lake	North America: at least 30 sites Other: many locations in Europe, also Japan, China
<i>Porterinema fluviatile</i>	UF	Lake	North America: unknown ^d Other: Germany, Netherlands, United Kingdom
Sphacelariales			
<i>Sphacelaria fluviatilis</i>	MF	Stream, lake	North America: Gull Lake, MI Other: China
<i>S. lacustris</i>	MF	Lake	North America: Lake Michigan Other: unknown

^aKnown locally as Bodensee.

^b*Ectocarpus confervoides* has been collected from the River Werra, Germany, polluted by potassium mines (Geißler, 1983).

^cPreviously reported as *Lithoderma arvernensis*, *L. fluviatile*, and *L. fontanum*; *L. zonatum* (Jao, 1941) is retained by some authors.

^dFreshwater and euryhaline (= *Pseudobodanella peterfii*) reported from North America from marine and estuarine sites only.

and cyanobacteria (Sinclair and Whitton, 1977). A few species (e.g., *Pleurocladia*) become encrusted with CaCO₃, which may cause the thallus to appear pale brown or gray macroscopically; microscopically carbonates may even cloak filaments in a crystalline tube (Kirkby *et al.*, 1972; Kusel-Fetzmann, 1996). All known freshwater species have a diplohaplontic life history (both diploid and haploid vegetative phases) and most are isomorphic (diploid and haploid stages identical or very similar). For details on the alternation of generations in members of this division, see Papenfuss (1951) and Van den Hoek *et al.* (1995).

Cellular features of freshwater brown algae are much like that of the division (Schloesser, 1977; Poeschel and Stein, 1983; West and Kraft, 1996); differences among genera are discussed later (Sect. V.B). Cells contain one to several golden-brown chloroplasts, which may be discoid, ribbon-like, or irregular-shaped, and usually parietal; pyrenoids are present in some species. The ultrastructure of freshwater species investigated (*Heribaudiella*, *Sphacelaria*) suggest typical phaeophyte features: thylakoids in triplets, chloroplast envelope consisting of four membranes, and plasmodesmata traversing crosswalls (Schloesser, 1977; Schloesser and Blum, 1980; Timpano, 1980; Poeschel and Stein, 1983). Most species possess numerous refractive bodies, including physodes, darkly pigmented bodies that may store phaeophycean tannins (fucosan), other

polyphenolics, and terpenes (Chadefaud, 1950; Graham and Wilcox, 2000; for cytological methods, see Sect. IV). When thalli are exposed to the air these tannins become oxidized and darken (Lee, 1989), giving dried or exposed colonies a dark brown or black color.

Reproductive structures are distinctive for this group, but life cycles are incompletely known among the freshwater species. In general, species within the Ectocarpales and Sphacelariales produce two types of terminal sporangia: unilocular (large, single chamber) and plurilocular (multichambered), although in some species, only one of the two structures has been observed (Papenfuss, 1951; Hamel, 1931–1939; Bourrelly, 1981). Unilocular sporangia are typically produced on sporophytes (diploid), appear as large, ovate or clavate structures (Figs. 1A, C, 3F), and are the usual sites of meiosis. Initially unilocular sporangia (often arising from elongated filaments; Svedelius, 1930; Kumano and Hirose, 1959) contain several brown chloroplasts, which later condense. Following meiosis the sporangium produces (usually eight) biflagellate zoospores (or zooids), which are thought to serve as gametes (Kumano and Hirose, 1959; Müller and Geller, 1978). Plurilocular sporangia (Fig. 2F) are produced on either gametophyte (1n) or sporophyte (2n) plants, which divide repeatedly from erect narrow threadlike cells (e.g., *Ectocarpus*, *Heribaudiella*) or

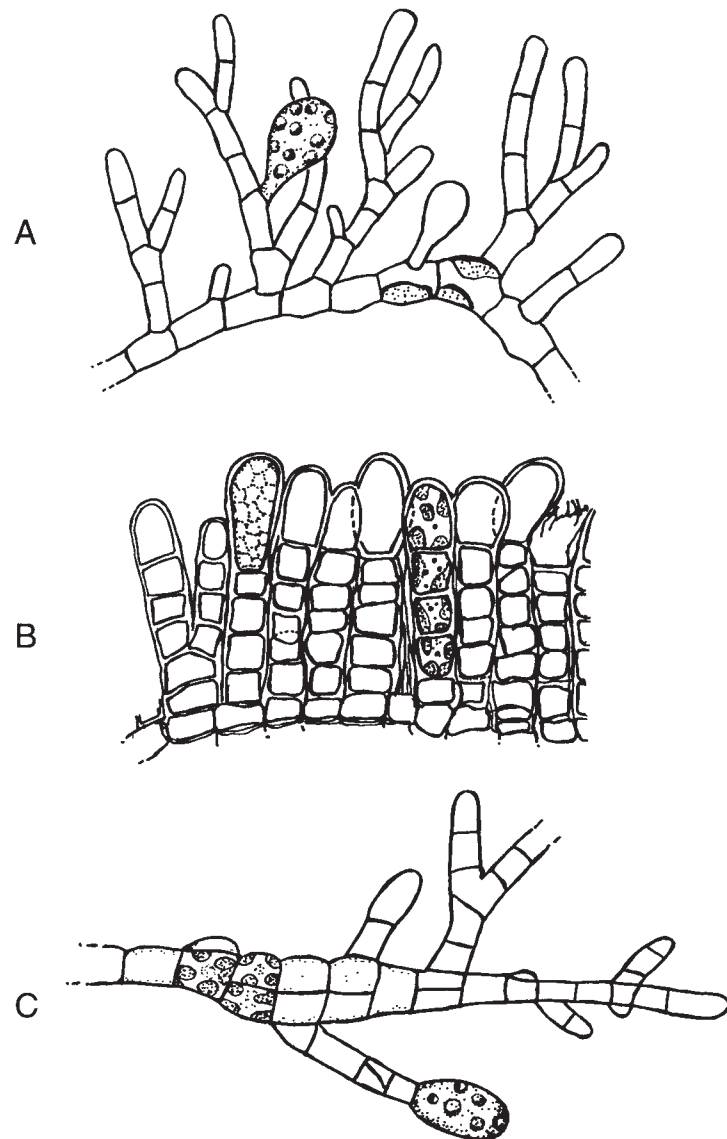


FIGURE 1 Three general morphologies exhibited by freshwater brown algae: (A) uniseriate, branched filaments forming cushion-like tufts (e.g., *Pleurocladia*); (B) branched prostrate filaments giving rise to tightly packed, vertical filaments, forming crustose thalli (e.g., *Heribaudiella*); (C) multiseriate branched filaments (quasi-corticated), forming spreading cushions (*Sphacelaria*).

terminal branches (e.g., *Bodanella*) to form multicellular structures that produce asexual zoospores or zoospores that later settle and germinate to produce new filaments.

In *Heribaudiella* and *Porterinema*, biflagellate zoospores are pear-shaped with two laterally inserted flagella, and possess a single parietal chloroplast and an apical stigma (Kumano and Hirose, 1959; Dop, 1979). Dispersal of freshwater phaeophytes is likely favored by zoospores released from unilocular sporangia. After release they attach to available substrata and

form germination tubes that later form filaments that develop the typical prostrate or disclike basal system (Yoshizaki *et al.*, 1984). More recent success in isolating some freshwater phaeophytes into pure culture [*Bodanella*; Müller and Geller (1978); *Pleurocladia*; Kusel-Fetzmann and Schagerl (1992) and Kusel-Fetzmann (1996); and *Ectocarpus*, West and Kraft (1996)] offers promise in addressing questions of relatedness among genera and species, dominant reproductive or ploidy phases, morphological plasticity, and mechanisms of their reproduction and spread. For

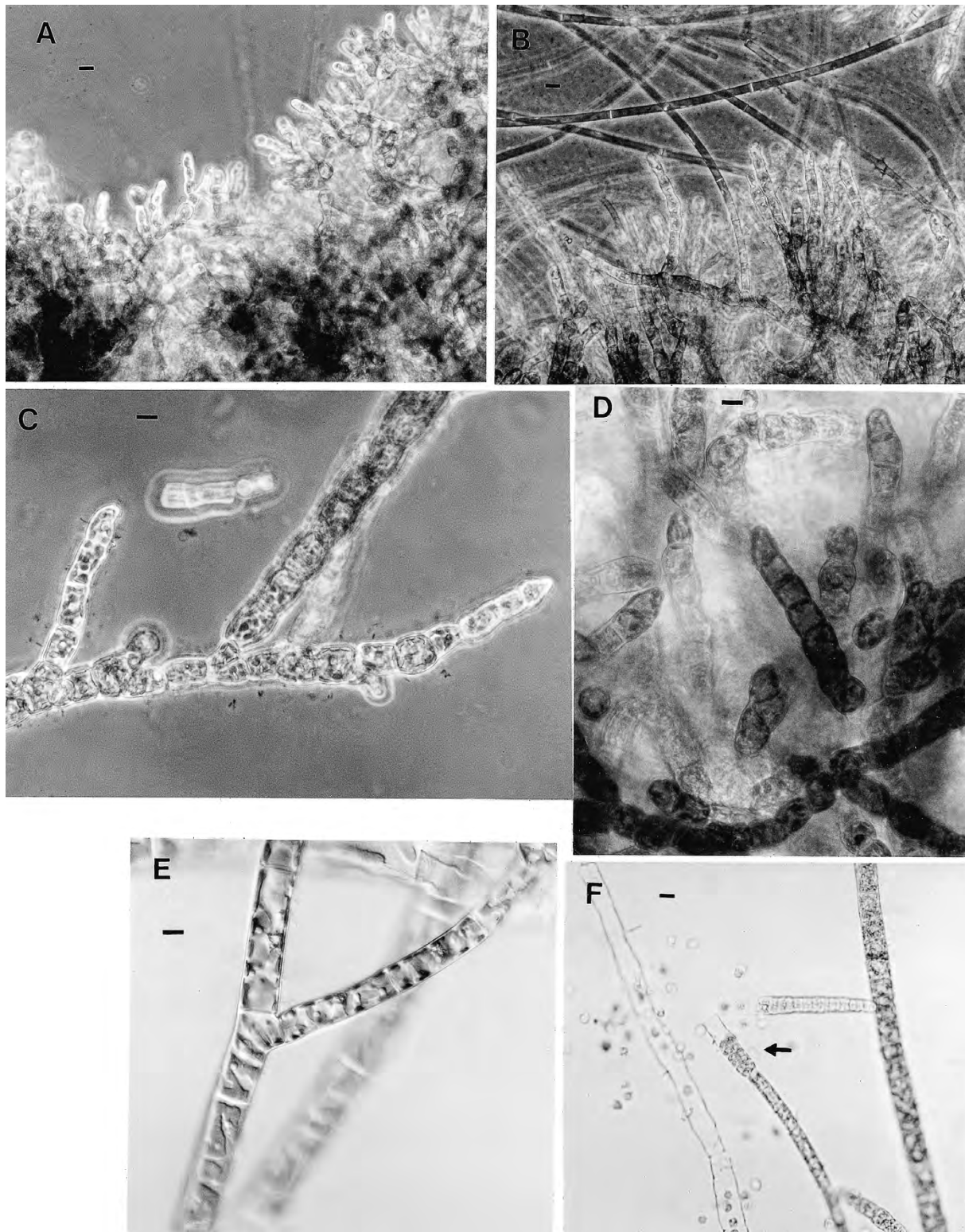


FIGURE 2 Freshwater phaeophytes, *Pleurocladia*, *Bodanella*, *Ectocarpus* (scale bars = 10 μm): (A) and (B) differences in hair formation by *Pleurocladia lacustris* in response to P-rich (A, +22 μM NaH₂PO₄) and P-limited (B, no P added) conditions in culture; hairs (B, upper) are terminal, hyaline, multicellular filaments 100–300 μm long; (C) and (D) *Bodanella lauterborni*, showing detail of cells and branching pattern (C) and general morphology (D); (E) and (F) *Ectocarpus siliculosus*, showing sparse branching pattern, ribbon-like chloroplasts (E, photo by Jason Sonneman, with permission), and plurilocular sporangium (arrow) (F, photo by Jason Sonneman, with permission).

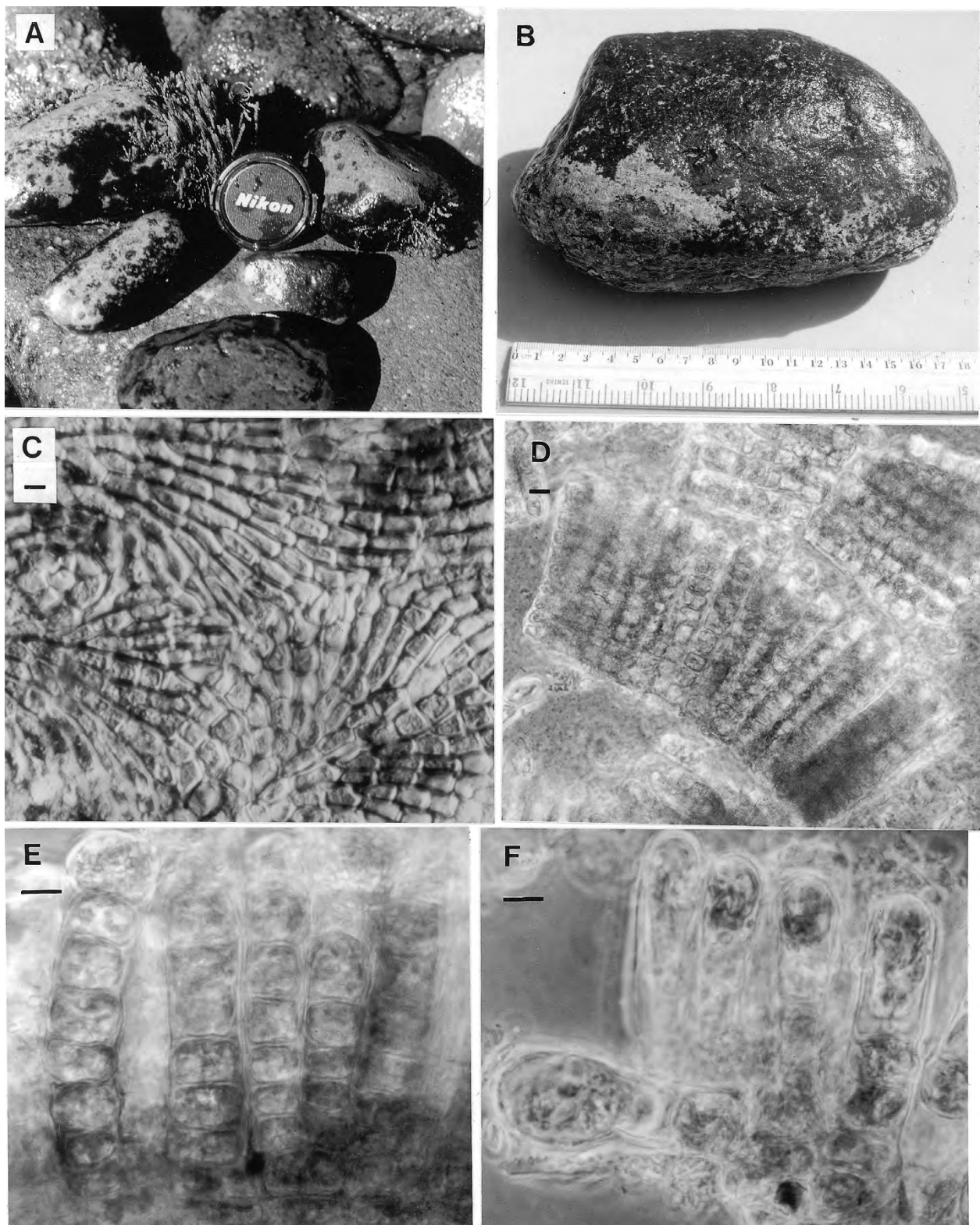


FIGURE 3 Freshwater phaeophyte, *Heribaudiella* (scale bars = 10 μm , except where indicated): (A) and (B) macroscopic appearance of individual colonies (A, McKenzie River, Oregon) and coalescing colonies (B, Bonaparte River, British Columbia) on rocks; (C) prostrate filaments; (D) columns of vertical filaments following removal from rocks and pressure applied to the coverslip; (E) detail of cells and chloroplasts in vertical system; (F) unilocular sporangium.

example, it is possible that in some freshwater species, portions of the typical phaeophyte life cycle may not occur. Further work on the reproductive ecology of freshwater brown algae based on field populations (as shown for the red alga *Batrachospermum*; Hambrook and Sheath, 1991), in conjunction with purified cultures, is clearly needed for members of this group.

III. ECOLOGY AND DISTRIBUTION

A. Ecological Factors

Due to the relatively sparse literature on freshwater brown algae, knowledge of the ecological factors governing their abundance and distribution is correspondingly limited. In some accounts, precise or even approximate locations of populations are difficult to discern (see methods, Sect. IV). However, despite these gaps in our knowledge, some generalizations can be made.

All freshwater species are benthic and most are epilithic in habit, particularly *Heribaudiella fluviatilis*, which almost exclusively colonizes stones in streams or lakes. With this encrusting species, there appears to be a preference for more resistant rocks, such as basalt, quartz, schist, and gneiss (Allorge and Manguin, 1941; Wehr and Stein, 1985), although Kusel-Fetzmann (1996) also reported this alga colonizing bricks in one Austrian stream. Other taxa, such as *Pleurocladia* and *Porterinema fluviatile*, are fairly nonspecific with regard to substratum. Some are epiphytes on larger algae (e.g., *Cladophora*, *Rhizoclonium*) and macrophytes (*Phragmites*, *Typha*) or may colonize artificial substrata (Israelsson, 1938; Waern, 1952; Kirkby *et al.*, 1972; Dop, 1979). *Pleurocladia lacustris* has been found attached to stones and boulders in the Green River (Utah–Colorado; Ekenstam *et al.*, 1996) and in several streams in southern Austria (Kusel-Fetzmann, 1996). It may also be attached to reeds in the littoral zone of lakes, such as in Lake Wigry, Poland (Szymanska and Zakrys, 1990), Brasside Ponds, United Kingdom (Kirkby *et al.*, 1972), and several Swedish lakes (Israelsson, 1938). *Pleurocladia* was also observed on glass slides that were placed in Lake Erken, Sweden (Kann, 1993). *Porterinema fluviatile* similarly colonizes reed stems, as well as submerged glass slides in eutrophic lakes (Dop and Vroman, 1976). With further study, the ecological breadth of this alga may prove to be quite broad, as earlier studies have reported it from brackish sites (0–8%); and growing as an endophyte in *Enteromorpha* and *Cladophora* (Waern, 1952). As mentioned earlier, some of those with encrusting or entangled growth forms may also be complexed with CaCO_3 , particularly *Sphacelaria* spp. and *P. lacustris* (Israelsson, 1938; Waern, 1952; Kirkby

et al., 1972; Schloesser and Blum, 1980). Although several species are found in both lakes and rivers, several species, especially *Heribaudiella fluviatilis*, *Pleurocladia lacustris*, and *Sphacelaria fluviatilis*, appear to be best developed in flowing waters (Jao, 1943; Kann, 1978a; Wehr and Stein, 1985; Kusel-Fetzmann, 1996).

Among those species that occur in running waters, most reports mention that freshwater brown algae occur in rocky, clear-water streams and are largely absent from turbid or muddy habitats (Budde, 1927; Fritsch, 1929; Allorge and Manguin, 1941; Jao, 1941; Chadeaud, 1950; Holmes and Whitton, 1975; Kann, 1966, 1978a, b; Starmach, 1977; Wehr and Stein, 1985; Yoshizaki and Iura, 1991; Kusel-Fetzmann, 1996). The most complete (although still fragmentary) ecological data for any freshwater phaeophyte is for *Heribaudiella fluviatilis*. In summarizing sites throughout Europe at the time, Israelsson (1938) noted that the species colonized a wide range of streams and lakes spanning oligotrophic to eutrophic conditions. More recent data suggest that this species most often occurs in stony streams, with moderately alkaline water (most \geq pH 7.0), but fairly broad Ca, P, and N concentrations (Table II). Kann (1966, 1978a, b) reported that *Heribaudiella* is typical of “calcium-poor, summer warm streams,” although her data indicate that the species is rarely observed in either extremely softwater or hardwater systems, or at very low nutrient levels. Nearly all populations occupy clear-water habitats, although a few may tolerate moderate levels of humic materials (Kann, 1978a; Wehr and Stein, 1985), but not low pH, humus-rich waters (Israelsson, 1938). Although this alga is most commonly a lotic species, it has also been reported from rocky-shore habitats in some European lakes (Kann, 1945, 1993). Many studies from Europe and Japan (e.g., Budde, 1927; Fritsch, 1929; Geitler, 1932; Allorge and Manguin, 1941; Yoneda, 1949; Holmes and Whitton, 1975, 1977a; Kusel-Fetzmann, 1996) report that *Heribaudiella* often co-occurs with the encrusting red alga *Hildenbrandia* (particularly in shaded reaches), although this pattern is far from consistent. Holmes and Whitton (1977a, b, c) report both species in the rivers Tees, Swale, and Wear (United Kingdom), but each alga has also been recorded from sites where the other is apparently absent. Jao (1944) described *Heribaudiella* (as *Lithoderma zonatum*; see Sect. V.B.) as an indicator species for rapidly flowing, stony streams in China, along with the encrusting cyanobacterium *Schizothrix* (also *Homoeothrix*, *Lemanea*, *Bangia*, and several diatom species), but without *Hildenbrandia*. Kann (1978a, b) suggests that *Heribaudiella* and *Hildenbrandia* often occur separately because the latter tends to colonize more Ca-rich streams. Surveys of North American

TABLE II Summary of Selected Ecological Conditions of Streams and Rivers from Three Regions in which *Heribaudiella fluviatilis* Has Been Collected [N/A = Data not Available; Based on Kann (1978a), Holmes and Whitton (1977a, b, 1981), Wehr and Stein (1985), Kusel-Fetzmann (1996), and Wehr (unpublished data)]

Variable	Northern UK	Austria	North America
Light	Open to partial shade	Shaded	Open to partial shade
Substratum	Boulders, cobbles	Boulders, cobbles, pebbles, bricks	Boulders, cobbles
Geology	Basalt, sandstone	Quartz, basalt, marble	Basalt, quartz, granite
Width (m)	5–25	1–10	1–60
Depth (cm)	N/A	10–100	10–100
Current velocity (cm s ⁻¹)	Up to 1700	N/A	200–1600
Temperature (°C)	3–20	5–21	5–25
Conductance (µS cm ⁻¹) ^a	150–600	110–640	50–450
pH	7.5–8.0	7.4–8.3	7.0–8.7
PO ₄ -P (µg P L ⁻¹)	20–1300	17–62	< 2.5–25
NO ₃ -N (µg N L ⁻¹)	200–1050	300–3600	2–200
NH ₄ -N (µg N L ⁻¹)	20–300	20–280	< 2–100
Ca (µg L ⁻¹)	20–50	30–45	10–70

^aCorrected to 25°C.

streams thus far have encountered *Heribaudiella* only without *Hildenbrandia* (Wehr and Stein, 1985; Wehr, unpublished), but with other macroalgal species (e.g., *Nostoc parmelioides*, *N. verrucosum*, *Cladophora glomerata*). Kann (1945, 1978a) has also pointed out that several encrusting forms (e.g., *Chamaesiphon*, *Gongrosira*, *Heribaudiella*, *Homoeothrix*) may co-occur in turbulent streams, simply because they are well adapted to these habitats. Taken together, these community-level data suggest that so-called associations of algae described in earlier publications (e.g., Geitler, 1932; Waern, 1938; Luther, 1954) may not be consistent in different parts of the world.

Some forms are equally common in lakes and rivers, and *Pleurocladia lacustris* is the most widely reported freshwater species from lentic systems (although it is also present in streams). This species colonizes a wide range of substrata, including stones, wood, many aquatic plant species, and artificial substrata, yet in freshwaters, appears in a fairly narrow range of chemical conditions. Early distribution data for Europe suggest that *Pleurocladia* prefers nutrient-rich, strongly calcareous waters (Israelsson, 1938). Subsequent studies support this suggestion; nearly all reports of freshwater population sites from Europe and North America mention eutrophic conditions and the presence of CaCO₃ precipitates associated with older colonies of *Pleurocladia* (Waern, 1952; Kirkby *et al.*, 1972; Szymanska and Zakrys, 1990; Kann, 1993; Ekenstam *et al.*, 1996; Kusel-Fetzmann, 1996; D. Ekenstam, pers. comm.). Limited chemical data report specific conductance levels > 600 µS cm⁻¹ (Kirkby *et al.*,

1972; Kusel-Fetzmann, 1996) and its absence in nearby sites with conductance ≈ 450 µS cm⁻¹ (Kusel-Fetzmann, 1996). Algal species that often co-occur with *Pleurocladia*, including *Gloeotrichia pisum*, *Rivularia* spp., and *Chaetophora incrassata*, are also typical of nutrient-rich, hard waters (Kann, 1993). *Pleurocladia* has been observed in Hell Kettles, a series of very hard-water ponds in northern England (B. A. Whitton, pers. comm.), also colonized abundantly by *Chara hispida* and known for their especially rich marsh flora (Wheeler and Whitton, 1971). *Pleurocladia* may also occur in some sites with *Heribaudiella*, especially those with higher dissolved calcium (Kann, 1993; Kusel-Fetzmann, 1996; D. Ekenstam, pers. comm.). Occurrences of *P. lacustris* in some brackish or intermittently marine habitats (Waern, 1952), including arctic sites in North America (Wilce, 1966), suggest that the alga may also be a euryhaline species. However, Waern (1952) noted that, despite a large number of freshwater *Pleurocladia* populations in northern Europe, no nearby marine (or even brackish) populations have been identified (for further discussion of disjunct distributions, see Sect. III.B). Incomplete knowledge of the ecological factors affecting the *Pleurocladia lacustris* is undoubtedly due to a paucity of collections. Kusel-Fetzmann (1996) pointed out that the alga was first discovered in Austria after observing “curious pale hairs” when examining crusts of *Heribaudiella*; it was an epiphyte on the other alga and produced small cushion-like colonies on rocks. Kirkby *et al.* (1972) comment that *Pleurocladia* was observed only on rotting (not recently dead) *Typha* leaves in the littoral

zone of a eutrophic pond in England, whereas Waern (1952) observed that *Pleurocladia* may also grow as an endophyte in aquatic plants and macroalgae, which may lead to its under-reporting. Future studies require careful attention to the observations made by earlier researchers, as well as more complete collection of ecological data at these sites.

The light requirements of freshwater phaeophytes have not been studied in detail, although scattered reports suggest that *Heribaudiella* may more often colonize shaded reaches of streams (Kusel-Fetzmann, 1996), although surveys of other rivers in North America and the United Kingdom have encountered this alga in habitats spanning a broad range of light environments, from small shaded streams (<1 m wide) to wide rivers (>50 m) with little or no shade (Holmes and Whitton, 1977a, b, c; Wehr and Stein, 1985). In contrast, *Bodanella lauterbornii* has been collected only from deep epilithic habitats (>15 m) on limestone rocks in lakes (Geitler, 1928; Müller and Geller, 1978; Kann, 1982). Similarly, the only known populations of *Sphacelaria lacustris* have been collected from deep (5–15 m), poorly illuminated areas of the sublittoral region of western Lake Michigan, and not in shallower habitats (Schloesser and Blum, 1980). Culture studies with this alga found that optimum growth and reproduction (gemmae-like propagules and unilocular sporangia) was achieved under reduced (screened) light levels (reported as 1000 lux) and short-day (8L : 16D) conditions (Schloesser, 1977; Schloesser and Blum, 1980).

Very little is known of the competitive abilities or community importance of brown algae in freshwater habitats. Many populations of *Heribaudiella fluviatilis* colonize and may completely encrust certain rocks, with few other species present (Holmes and Whitton, 1975; Wehr, unpublished data). *Heribaudiella* may overgrow crusts of *Hildenbrandia rivularis* in streams where they co-occur (Fritsch, 1929; Geitler, 1932; Kusel-Fetzmann, 1996). In running waters, *Sphacelaria fluviatilis* apparently also grows in nearly monospecific stands (Jao, 1944). Thalli of *Heribaudiella* are usually free of epiphytes, but may occasionally serve as a host for diatoms, small cyanobacterial species (*Chamaesiphon incrustans*, *Homoeothrix varians*), chlamydomonad stages of red algae, and *Pleurocladia lacustris* (Svedelius, 1930; Pueschel and Stein, 1983; Kusel-Fetzmann, 1996). The influence of herbivores on any freshwater species is unknown, although studies of marine species suggest that the large quantities of polyphenolics produced by many phaeophytes (>2% of dry mass) may inhibit herbivore activity (Targett and Arnold, 1998). Field and lab herbivory experiments are clearly needed for freshwater species.

B. Geographical Distribution

Despite several hundred documented populations of freshwater phaeophytes recognized world wide, knowledge of their distribution and biogeography is fragmentary. The paucity of information on these algae makes each discovery of a new locality still worthy of publication, and renews speculation as to their origins (e.g., West, 1990; Kusel-Fetzmann, 1996; Wujek *et al.*, 1996). Some may still be safely regarded as rare (or at least very poorly known), whereas others are world wide in their distribution. Many species distributions are regarded as disjunct, such as *Sphacelaria fluviatilis*, an epilithic species with only two known locations, a stream in south-central China and a small lake in Michigan (Jao, 1943; Thompson, 1975; Wujek *et al.*, 1996). *Sphacelaria lacustris* is thus far known only from western Lake Michigan (Schloesser and Blum, 1980). *Bodanella lauterbornii* is apparently known from only three locations, all in western Europe (Bourrelly, 1981).

Heribaudiella fluviatilis may be the most widespread of all freshwater phaeophytes, occurring in many locations in Europe, western North America, Japan, and China (Wehr and Stein, 1985; Kusel-Fetzmann, 1996), although there are currently no records from Africa, South America, Australia, or New Zealand, despite many phycological studies in these areas. More recent surveys of more than 250 river reaches for *H. fluviatilis* in North America have located 30 populations, all within western coniferous or boreal forests, and none have been located in any biomes east of the Mississippi River or south of Oregon (Wehr, unpublished). The discovery of *Heribaudiella* from a stream near Yellowknife, Northwest Territories (Sheath and Cole, 1992), extends its distribution more than 1000 km north (11°N latitude). No populations are known from Mexico or Central America, although given the diversity of freshwater habitats in these regions (see Chap. 2), it is reasonable to expect this alga in rocky streams from these regions as well. Comments more than 70 years ago by Budde (1927) and Fritsch (1929) that this species is easily missed are still true.

Because more than 99% of all known species within the Phaeophyceae occupy marine habitats, questions often focus on the possible dispersal and adaptation of taxa from marine to freshwater habitats. A review of the published ecological information for all freshwater phaeophytes suggests little evidence of (at least recent) marine invasions by most species. One reason is that at least four of the seven recognized species from fresh waters have no counterparts in marine environments. Two exceptions, *Ectocarpus siliculosus* and *Porterinema fluviatile*, seem to be true euryhaline species that colo-

nize a broad range of salinities, including fresh waters (Dop, 1979; West and Kraft, 1996). *Pleurocladia lacustris* has been almost entirely reported from freshwater locations distant from the ocean, but at least one North American location is intermittently saline, and morphological data strongly indicate that these populations are the same species (Wilce, 1966). Current biogeographic data, however, show no patterns that suggest a marine invasion. Analyses of *Pleurocladia* distribution patterns in northern Europe (Israelsson, 1938; Waern, 1952) indicate a complete lack of marine populations in a region where freshwater populations are most common. With additional freshwater populations in Austria, France, and the Ukraine, data suggest that the freshwater history of this species may be quite old, perhaps pre-glacial (Waern, 1952). The discovery of *Pleurocladia lacustris* in the Green River (Utah, Colorado) more than 1000 km from any marine water (Ekenstam *et al.*, 1996), is in agreement with reports from European sites (Szymanska and Zakrys, 1990; Kusel-Fetzmann, 1996).

Similarly, the North American distribution of *Heribaudiella fluviatilis* in the Northwest Territories, British Columbia, Washington, Montana, Oregon, and Utah shows a near absence of the alga from river sites near the coast and an abundance of populations in interior and upland regions (Wehr and Stein, 1985; West, 1990; D. Ekenstam, pers. comm.). In addition, none of the inland populations of *Heribaudiella*, *Pleurocladia*, or *Sphacelaria* in North America or Europe are reported to be influenced by elevated salinity. Finally, there are no studies that have yet identified marine species of Phaeophyta from inland saline lakes, which are scattered across most continents. An exception may be found in *Ectocarpus siliculosus*, which was discovered in a waterfall of the Hopkins River (Australia), roughly 40m above sea level, with a specific conductance of 3.0 mS cm^{-1} ; an isolate of this population has been shown to tolerate a wide range of salinities in culture (West and Kraft, 1996). As this is the first documented case of a population of *Ectocarpus* from any freshwater site, it is too early to speculate on the causes for its distribution. An intriguing but obscure species, *Porterinema fluviatile*, has been sampled from many brackish and freshwater sites in Europe (Waern, 1952), whereas Wilce *et al.* (1970) described a North American population from a freshwater site adjacent to a salt marsh in Massachusetts. It has since been sampled from freshwater sites in Netherlands and isolated into culture, using Wood's Hole freshwater medium (Dop, 1979). The ecological and distributional history of this species complex clearly requires further attention. Molecular analyses (e.g., 18S rRNA and rcbL genes) in conjunction with biogeographic

studies of most freshwater phaeophytes are sorely needed to elucidate distribution patterns and genetic relationships among these apparently disjunct populations.

IV. METHODS FOR COLLECTION AND IDENTIFICATION

Because all known freshwater brown algae are benthic, methods used for sampling or removing various substrata are needed (e.g., Weitzel, 1979; Stevenson, 1996). Also, most species are macroalgal, that is, colonies or filaments which are recognizable (if not easily identified) with the naked eye. Nonetheless, freshwater phaeophytes are still cryptic and difficult to find. A survey of >1000 stream segments in North America (Sheath and Cole, 1992) located only one additional population of *Heribaudiella fluviatilis*, from a stream in the Northwest Territories. In most investigations, new populations are discovered by researchers who have encountered the species nearby or elsewhere (Wehr and Stein, 1985; Kusel-Fetzmann, 1996). Because colonies or thalli of benthic algae may be inconspicuous in the field, Sheath (Chap. 5) recommends the use of a plastic view box, which provides a clear view through calm water and allows the investigator to distinguish different growth forms, pigmentation, and microhabitats much more easily. The present author has found this device reduces search time in both streams and shallow littoral areas of lakes. If quantitative samples are needed, transects (along tape measures sampled at regular intervals) or quadrats may be required. With macroalgae some authors may use visual estimates of cover for visually distinct physiognomies (e.g., Holmes and Whitton, 1977a, c; Wehr and Stein, 1985; Sheath and Cole, 1992) and later assign species names based on microscopic examination. This chapter thus provides descriptions of genera (Sect. V.B.) based on macroscopic (as well as microscopic) appearance, which may be helpful in field sampling.

Our understanding of the distribution and ecology of freshwater brown algae requires many more thorough surveys. With the development of inexpensive global positioning systems (GPS), relatively precise geographic information (latitude, longitude, altitude) should be relatively easy to collect in all future studies. Whenever possible, ecological data, particularly type of substratum and size, current velocity, irradiance, temperature, conductance, turbidity, and water chemistry (especially pH, N, P, Ca), should be measured in all collections and surveys of freshwater phaeophytes. In addition, simple relative scales of abundance or cover estimates (Wehr and Stein, 1985; Sheath and Cole, 1992) will

greatly aid future syntheses of the ecology of this group of algae. In rivers, surveys have also been conducted by wading specific lengths (10-m to 0.5-km reaches) and recording presence or absence, relative abundance, or percentage of cover estimates of each macroalga from that area (Holmes and Whitton, 1977a, b). A field microscope (e.g., Swift Instruments, San Jose, CA) is helpful in distinguishing colonies or crusts that appear similar in the field (see also Holmes and Whitton, 1975).

Methods for removal of material from substrata depend on the growth form and type of substratum. Encrusting or firmly attached epilithic species (mainly *Heribaudiella*, *Sphacelaria*) are best sampled by removing entire rocks when possible, then scraping material (using a razor blade) into vials for later identification, whereas smaller stones may be transported intact. It is important to note the macroscopic appearance (shape, margin, size, thickness) and color of the colonies in the field during sampling, as material may change even during brief storage times. Most epiphytic forms (e.g., *Pleurocladia*) in freshwater are usually firmly attached to plant hosts, permitting removal of plants or plant fragments with dip nets or collected using SCUBA. However, more delicate or gelatinous forms may be best sampled using forceps or a modification of the half-bottle sampler (Douglas, 1958), which can isolate water plus algal material and permit removal of thalli without loss. Kann (1976, 1978a) has also detected some species of brown algae (*Pleurocladia*) from lakes by observing settled zoospores on artificial (glass, plastic) substrates, although their selectivity for or against freshwater phaeophytes is unknown.

Material is best examined live and soon after collection for recognition of pigmentation, chloroplast form, and presence of hairs. Algal samples can be kept alive for several days if stored cool (5–10°C) and wet or moist. Some authors (Waern, 1952; Kusel-Fetzmann, 1996; West and Kraft, 1996) have reported that filamentous forms retain their normal growth form in sample water for several weeks or months, and some species (as discussed earlier) can be brought into culture using standard media (Müller and Geller, 1978; Schloesser and Blum, 1980; Kusel-Fetzmann and

Schagerl, 1992). Identification of some species frequently requires reproductive structures (Sect. V). Their position, number, and arrangement are diagnostic, but there is some doubt whether shape of sporangia may be used (Waern, 1952; West and Kraft, 1996). Motile stages are readily produced with field material or in culture if maintained under moderate (10–20°C) temperatures (Kumano and Hirose, 1959; Müller and Geller, 1978; Wehr, unpublished). Long photoperiods (16:8) apparently favor formation of plurilocular sporangia (and zooids) in *Porterinema* (Dop, 1979), whereas short-day conditions (8:16) may induce the production of unilocular sporangia in *Sphacelaria lacustris* (Schloesser and Blum, 1980).

If samples are to be stored for long periods, excised specimens are best preserved using 2–3% glutaraldehyde or 2% paraformaldehyde, and stored cool and in the dark. Alternatively, encrusting species may be “preserved” on rocks (and suitable for herbaria) by simply air-drying the entire rock, although cells and plastids tend to become distorted upon drying. Isolates of *Sphacelaria lacustris* from Lake Michigan that were grown on agar plates, later were air dried to produce thin, dry specimens that were stored on herbarium sheets (Schloesser and Blum, 1980). Inspection of this material (holotype in U.S. National Herbarium, Algal Collection) more than 20 years later found that most of the morphological and cellular features were retained (Wehr, unpublished).

When preparing thalli for light microscopy, specimens of crustose species may require vigorous chopping (with razor blade) and/or crushing (with cover slip) to separate densely packed filaments. The morphology of filamentous forms may also be more clearly revealed in squash preparations. Species that have become calcified with CaCO₃ (especially *Pleurocladia*, *Porterinema*) may require treatment with dilute acid (1–2% HCl) before observation. Stains may be used to emphasize important structures, particularly cresyl blue (Chadefaud, 1950; Schloesser and Blum, 1980), which may be used to demonstrate physodes (which store phaeophycean tannins). Vanillin–HCl may also be used, which stains physodes red (Chadefaud, 1950; Lee, 1989).

V. KEY AND DESCRIPTIONS OF GENERA

A. Key

Taxa not reported from North America in fresh waters are marked with an asterisk.

- | | | |
|-----|--|---|
| 1a. | Thalli small cushion-like tufts or expanses of spreading filaments (Fig. 1A, C)..... | 2 |
| 1b. | Thalli not cushion-like (Figs. 1B, 3C); creeping or crustose..... | 3 |

- 2a. Filaments uniseriate and multiseriate; with numerous disc-shaped chloroplasts (Figs. 1C, 4E, F).....*Sphacelaria*
- 2b. Filaments uniseriate only; single (rarely two) chloroplasts; basal filaments curved or arching; erect system spreading (comblike) (Fig. 4A, B)*Pleurocladia*
- 3a. Thalli crustose, forming dark brown patches on stones; branched basal filaments with short, densely packed upright filaments (Figs. 1B, 3)*Heribaudiella*
- 3b. Thalli not crustose, spreading or simple, variously branched.....4
- 4a. Filaments sparingly branched, vegetative cells narrow, cylindrical, chloroplasts several, ribbon-like; plurilocular sporangia (if present) narrow-elongate (Fig. 2E).....*Ectocarpus**
- 4b. Filaments frequently or irregularly branched, cells inflated or quadrate, chloroplasts few to several, plurilocular sporangia unknown or (if present) broad or inflated in shape.....5
- 5a. Branched filaments with prostrate and erect forms6
- 5b. Branched filaments prostrate only, creeping along substrata; may have rhizoid-like branches, chloroplasts many Fig. 2C, D)*Bodanella**
- 6a. Basal filaments often curved or arching, erect filaments spreading; cells with single (rarely two) chloroplast, unilocular sporangia ovoid.....*Pleurocladia*
- 6b. Basal and erect filaments irregularly arranged, with two parietal, lobed chloroplasts; plurilocular sporangia in crown-shaped clusters of four or more (Fig. 4C, D).....*Porterinema*

B. Descriptions of Genera

Ectocarpales

Bodanella Zimmermann (Fig. 2C, D)

Thalli basal or creeping filaments form on rocky substrata, without erect filaments. Filaments are uniseriate, frequently but irregularly branched, composed of irregularly shaped cells; inflated, quadrate, angular, ovoid, or "wavy" in shape; vegetative cells are 10–16 μm wide, 10–25 μm long. General form may be confused with *Sphacelaria lacustris*, but the only latter genus possesses multiseriate axes; filaments of *Bodanella* are uniseriate. Terminal, short, narrow hairs (6–10 μm diameter), or basal rhizoid-like filaments may also be present. Parietal chloroplasts are small, numerous (10–15 per cell), and discoid. Unilocular sporangia are ovoid or globose; 15–20 μm wide by 25–30 μm long. Zoospores are pyriform (10–12 μm by 5–6 μm), with laterally inserted flagella. Plurilocular sporangia are unknown.

A monotypic genus, *Bodanella lauterbornii* was named for its original location, Bodensee (Lake Constance, Austria–Germany), where it colonizes limestone deep (15–35 m) in lakes (with *Hildenbrandia* and *Cladophora*). It is not known from North America; worldwide distribution consists of three European lacustrine populations, in Lake Constance (Zimmermann, 1928; Müller and Geller, 1978), Lunzer Untersee (Austria; Geitler, 1928), and Traunsee (Austria; Kann, 1982).

Ectocarpus Lyngbye (Fig. 2E, F)

Freshwater form is sparingly or irregularly

branched; thalli are mostly erect filaments consisting of cylindrical (isodiametric) cells 15–40 μm diameter, up to four times as long as broad. Narrow, hair-like filaments also are present (8–12 μm diameter). Chloroplasts are several (2 to 4?), ribbon-like, lobed, and parietal, with pyrenoids, arrangement variable (netlike, spiral, etc.). Plurilocular sporangia are terminal, narrowly ellipsoid, conical, or linear, with numerous divisions; length is 70–200 (500) μm by 15–35 μm diameter. Unilocular sporangia are unknown from freshwater populations, but well established in marine plants (Lee, 1989).

Ectocarpus is an ecologically and geographically widespread marine and estuarine genus (Müller, 1979), recently discovered (*E. siliculosus* Dillw.) in a freshwater waterfall of the Hopkins River (Australia) with other freshwater taxa (*Mougeotia*, *Cladophora*; West and Kraft, 1996). This is the only record of any freshwater phaeophyte in the southern hemisphere, according to Entwistle *et al.* (1997). The alga is unknown from freshwater sites in North America, but is common in coastal brackish sites on this continent. It is also observed (*E. confervoides*) with freshwater taxa (e.g. *Anabaena*, *Cyclotella*, *Scenedesmus*) in the River Werra (Germany) in sites polluted by potassium mine waste (Geißler 1983).

Heribaudiella Gomont (Fig. 3A–F)

Thalli are olive-brown to dark brown crusts on rocks in streams and lakes; colonies are 1–5 cm (up to \approx 20 cm) diameter with rounded or irregular outline (Fig. 3A), but with distinct margins (*Chamaesiphon* spp. also forms brown crusts, but margins are indis-

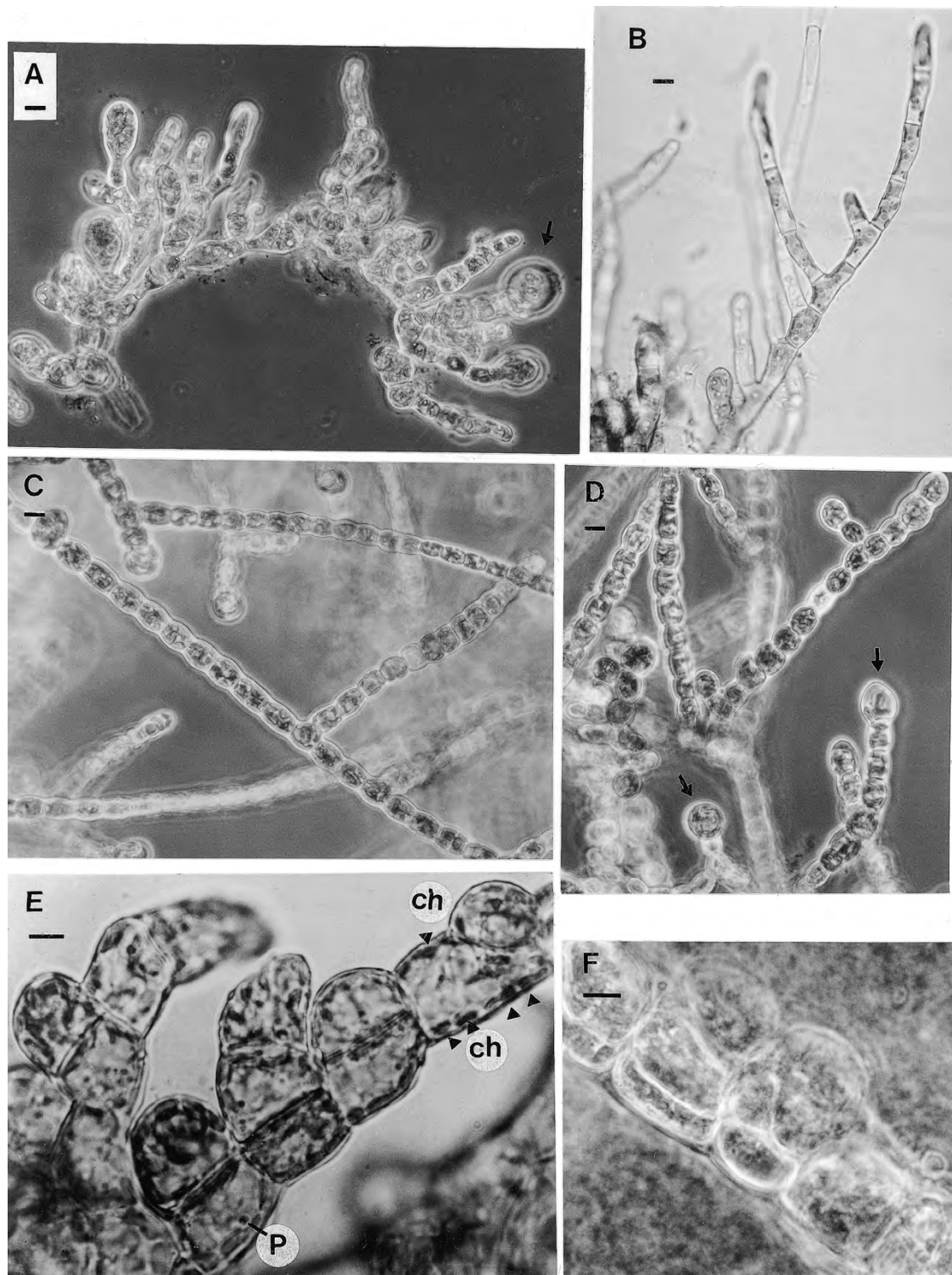


FIGURE 4 Freshwater phaeophytes, *Pleurocladia*, *Porterinema*, *Sphacelaria* (scale bars = 10 μ m, except where indicated): (A) and (B) *Pleurocladia lacustris*, detail of filament and chloroplasts, showing centrifugal or arched growth patterns, with unilocular sporangium (arrow) (A); and erect, branched filaments, showing one or two parietal chloroplasts per cell (B, photo by (E) L. Kusel-Fetzmann, with permission); (C) and (D) *Porterinema fluviatile*, showing irregularly branched filaments with short erect filaments (C) and clusters of filaments with apical, unilocular sporangia (arrows); (E) and (F) *Sphacelaria lacustris* (holotype, from Lake Michigan) [(E) filament showing complex, multiply branched, multiserial growth form, (ch) many small chloroplasts and (P) physodes (photo reproduced with permission of the Journal of Phycology from Schloesser and Blum (1980) 16:201–207, Fig. 5); (F) detail of multiserial primary axis; note cell divisions in two planes (from herbarium specimen)].

tinct smudges or flecks; Holmes and Whitton, 1975; Wehr and Stein, 1985). Multiple colonies may coalesce to cover entire rocks or boulders (Fig. 3B). When scraped off carefully, colonies appear as a series of vertical columns at low magnification (Fig. 3D). Filaments in basal system are repeatedly branched (Fig. 3C); erect filaments are sparingly and dichotomously branched. *Heribaudiella* forms an erect system of appressed vertical filaments that do not easily separate under pressure; cells are mostly quadrate, 8–15 μm diameter, 5–15 cells long. Chloroplasts are oval or discoid, numerous (4–10 per cell; Fig. 3E); physodes are present. Multicellular hyaline hairs may be present (up to 1 mm long). Unilocular sporangia are terminal, inflated, ovoid or clavate (Fig. 3F); 10–25 μm wide, 15–35 μm long [development described by Svedelius (1930), Fig. 4]. Biflagellate zoospores are pyriform or irregular shape (\approx 6–8 μm). Plurilocular sporangia are obscure (reported as rare), produced terminally in narrow-celled columns four (rarely eight) cells tall; immature plurilocular sporangia are difficult to distinguish from smaller vegetative filaments. Svedelius (1930) united several taxa (e.g., *Lithoderma fluviatile*, *L. fontanum*) under this name. *Lithoderma zonatum* was described from fresh waters by Jao (1941), based on frequent plurilocular sporangia (reported occasionally in *H. fluviatilis*) and several layers or zones of erect filaments; this taxon was still reported by Bourrelly (1981). Jao (1941) was apparently unaware of Svedelius' study, because this layered morphology is exactly shown in his earlier study (Svedelius, 1930, Fig. 13) and was suggested to perhaps represent annual layers. For these reasons, the Chinese species (*L. zonatum* Jao) should be regarded as synonymous with *Heribaudiella fluviatilis* (Aresch.) Sved. No freshwater taxa are now assigned to the genus *Lithoderma*.

A monotypic genus, *Heribaudiella fluviatilis* is the most widely observed freshwater phaeophyte worldwide, reported from at least 30 locations in western North America, but no extant populations are known east of the Mississippi or south of Oregon. A very early record (Collins *et al.*, 1898; as *Lithoderma fluviatile*) from Island Brook, Connecticut, was included in the *Phycotheca Boreali-Americana*, although its identity has been questioned due to its possible marine habitat (Smith, 1950) and appearance of some samples (Pueschel and Stein, 1983). Further examination by the present author of the 1888 material deposited in the New York Botanical Garden, University of Michigan, and U.S. National (Smithsonian) herbaria suggests this population may in fact be *Heribaudiella fluviatilis*, based on morphology (vertical series of erect filaments) and co-occurring diatoms (>99% were freshwater species; Wehr, unpublished data). However, surveys of

Island Brook in 1998 and adjacent streams failed to find an extant population in the area (Wehr, unpublished). In North American streams it often co-occurs with *Audouinella hermannii*, *Chamaesiphon* spp., *Nostoc parmelioides*, *N. verrucosum*, and *Cladophora glomerata*; in Europe, *Hildenbrandia rivularis* may colonize the same rock.

Pleurocladia A. Braun (Figs. 2A, B, 4A, B)

Thalli are small, brown to pale brown or tan (depending on calcification) hemispherical tufts or cushions (up to 3 mm diameter by 100–300 μm tall) on rocks or attached to plants (angiosperms, mosses, macroalgae), or endophytic, present in both streams and lakes. Waern (1952) reports that colonies appear macroscopically like a brown-colored *Gloetrichia*. In less calcareous regions, colonies may be gelatinous. At low magnification (100 \times), colonies appear as a dense network of radiating, branched filaments (Fig. 2B). Two filament systems are evident: (1) creeping or basal system, with (infrequently) branched filaments usually consisting of rounded or inflated cells 8–16 μm diameter (occasionally elongate), often exhibiting centrifugal or arched growth patterns (Fig. 4A), which give rise to (2) upright, irregularly (alternate or opposite) branched long filaments (Fig. 4B), which are usually narrower (6–12 μm), elongate (cells 12–35 μm long), and more nearly isodiametric. Vegetative cells contain one (rarely two) large golden-brown parietal chloroplast (with pyrenoids); darker granules (physodes?) and refractive (lipid?) bodies may be common. Unilocular sporangia are common, single, clavate or globose [15–30 μm in diameter by 25–60 (–80) μm long], and borne laterally or terminally (Fig. 1A). Plurilocular sporangia are uncommon in freshwater populations (but see Waern, 1952), linear-elongate, narrow. Long (100–300 μm) multicellular hairs (5–7 μm diameter) are common in field populations (environmentally induced; Fig. 2A, B), arising from upright filaments, giving the colony a fuzzy appearance when viewed macroscopically.

Pleurocladia lacustris is currently known from a few freshwater sites in North America [Wyoming, Colorado (Green River), and Devon Island, Northwest Territories]; suitable freshwater habitats undoubtedly occur in other locations on this continent. Many more populations are known from Europe. The species has also been recorded from marine and brackish habitats. The relationship between *P. lacustris* and related species and genera are discussed by Waern (1952), Wilce (1966), and Bourrelly (1981).

Porterinema Waern (Fig. 4C, D)

Thalli are monostromatic, brown disc-shaped plates of loosely arranged filaments. The genus occurs

as an epiphyte on or endophyte in other algae (e.g., *Rhizoclonium*, *Enteromorpha*) or macrophytes (e.g., *Elodea*); it may also colonize stones and artificial substrata (e.g., glass slides). Thalli are creeping, composed of irregularly branched filaments, with short (a few cells) erect filaments produced infrequently (Fig. 4C). Basal cells are barrel-shaped, or occasionally enlarged on proximal ends (6–12 μm diameter by 6–12 μm long); erect cells are few but more elongate (up to 40–50 μm long). Vegetative cells occur with one to three lobed, golden-brown, parietal chloroplasts. Terminal, multicellular hairs (3–8 μm diameter; up to 200 μm long) are common and may be sheathed at their base. Unilocular sporangia are rarely reported, on basal or erect filaments, pear- or club-shaped (15–30 μm wide; up to 80 μm long). Plurilocular sporangia (6–8 μm diameter) are common, intercalary (occasionally terminal), typically four-celled clusters (or “crowns”) on pedicels (short filaments) or sessile; sometimes they are produced in clusters of up to 32 sporangia.

One species, *Porterinema fluviatile*, is distributed mainly among brackish sites in Europe and North America, but several truly freshwater sites are known in Europe (Waern, 1952; Dop, 1979), and one site in North America: a stream draining into a salt marsh near Ipswich, Massachusetts (Wilce *et al.*, 1970). As such it should be regarded as part of the North American freshwater algal flora, but requires further study. The report of a new genus, *Pseudobodanella peterfii* in Europe (Gerloff, 1967), appears to be identical to *Porterinema fluviatile*, lacking only hairs, and is very likely synonymous (Bourrelly, 1981; D. M. Müller, pers. comm). Bourrelly (1981) and Dop (1979) suggest that past records of *Apistonema pyrenigerum* (previously classified in Chrysophyceae), such as from a small pond in the United Kingdom (Belcher, 1959), are also *Porterinema*. Other synonymous or related taxa (e.g., *Apistonema expansum*, *Porterinema marina*) have been similarly considered by Wilce *et al.* (1970) and Dop (1979).

Sphacelariales

Sphacelaria Lyngbye (Fig. 4E, F)

Freshwater thalli are small (1–2 mm) brown tufts or cushions on rocks in streams or lakes; they may be calcified. Vegetative growth is the result of basal (creeping) and erect filaments; rhizoidal cells form where basal filaments contact substrata. The genus is distinguished by axes variably multiaxial (biseriate or multiseriate) and uniaxial (uniseriate); branches are hemiblastic (primordial cells arising from upper position), resulting in apical growth pattern. Branching pattern is irregular (*S. lacustris*) or opposite (*S. fluviatilis*); it may become pseudoparenchymatous. Cells

comprising the main axis are rectangular or inflated (12–25 μm diameter); they are broader prior to lateral cell division, cylindrical on erect filaments. Cells contain numerous (10–20), small (3–8 μm), peripheral, disc-shaped chloroplasts and physodes (especially meristematic regions); pyrenoids are lacking. Multicellular hairs (> 500 μm length) develop from basal and erect filaments in some plants. Unilocular sporangia are known in one species (*S. lacustris*; see Schloesser and Blum, 1980, Fig. 3). Plurilocular sporangia are unknown in fresh waters for either species. Clusters of vegetative, gemmae-like propagules common; sessile or borne on short (1- or 2-celled) branches.

Two freshwater species are known: *S. lacustris*, reported on rocks in western Lake Michigan at depths of 5–15 m (Schloesser and Blum, 1980); *S. fluviatilis*, reported in rapidly flowing water in the Kialing River, China (Jao, 1943, 1944), and in the shallow (≤ 1 m) littoral zone of Gull Lake, Michigan (Thompson, 1975; Timpano, 1978, 1980; Wujek *et al.*, 1996). The two species were separated largely on the basis of branching pattern (alternate or irregular in *S. lacustris*, opposite in *S. fluviatilis*), lateral cell divisions (infrequent and irregular in *S. lacustris*, two to four regular divisions in main axes of *S. fluviatilis*), and hairs (lacking in *S. fluviatilis*?) (Schloesser and Blum, 1980). Further studies are needed on the ecological requirements, geographic distribution, and genetic differences of the two species. No populations are yet known from Europe, Central America, or South America.

VI. GUIDE TO LITERATURE FOR SPECIES IDENTIFICATION

All but one freshwater phaeophyte genus (*Sphacelaria*) are monotypic; however, the primary literature is still helpful for identification. A few general keys are useful for most freshwater species (Starmach, 1977; Bourrelly, 1981), but the reader should be aware that recent combinations (e.g., *Pseudobodanella* = *Porterinema*) are not included. Many of the most complete descriptions may be older literature, come from other continents, or are in German or Japanese.

1. *Bodanella*—Zimmermann (1928), Müller and Geller (1978)
2. *Ectocarpus*—West and Kraft (1996)
3. *Heribaudiella*—Holmes and Whitton (1975), Yoshizaki *et al.* (1984), Kusel-Fetzmann (1996)
4. *Pleurocladia*—Wilce (1966), Kirkby *et al.* (1972), Kusel-Fetzmann (1996)
5. *Porterinema*—Waern (1952), Dop (1979)
6. *Sphacelaria*—Jao (1941), Schloesser and Blum (1980), Wujek *et al.* (1996)

ACKNOWLEDGMENTS

I express my thanks to Dean Blinn, Janet Stein, and Brian Whitton, who helped instill in me an enthusiasm for stream algae. Advice, samples, records, and/or photographs from Robert Wilce, Dieter Müller, John West, Elsa Kusel-Fetzmann, Devon Ekenstam, Robert Sims, and Willem Prud'homme van Reine were especially helpful in the preparation of this manuscript. Loans of herbarium specimens from the National Herbarium (Smithsonian), University of Michigan, New York Botanical Garden, and Trinity College, Connecticut, were extremely useful. Thanks also to many people who have helped in my searches for freshwater phaeophytes, Deb Donaldson, Syd and Dick Cannings, Bob Sheath, Greg Flannery, and Alissa Perrone.

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