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Porphyra birdiae sp. nov. (Bangiales, Rhodophyta): A New Species from the Northwest Atlantic

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Recent studies combining biochemical, molecular, and traditional morphological and ecological traits have shown that some currently recognized species of the red algal genus *Porphyra* are actually "form species" or "complexes" comprising several morphologically similar but genetically distinct taxa. Conflicting reports of chromosome numbers and differences in DNA sequences for *Porphyra purpurea* (Roth) C. Agardh have raised suspicion that more than one taxon has been confused under this name in the Northwest Atlantic. We have identified one of these cryptic taxa and describe it here as a new species, *Porphyra birdiae*. Like *P. purpurea*, it has an ovate to broadly elongate, foliose blade with reproductive areas segregated by a distinct line into male and female sectors. While reproductive specimens have historically been confused with *P. purpurea*, non-reproductive specimens of *P. birdiae* have been incorrectly identified as *P. umbilicalis* Kützing. Although *P. birdiae* is morphologically similar to both of these species, sequences of SSU (nuclear small subunit rRNA gene) and rbcL (plastid *ribulose-1,5-bisphosphate carboxylase/oxygenase* large subunit gene) indicate that it is not closely related to either one. Based on *rbc*L sequences, *P. birdiae* is closely related to *P. aestivalis* Lindstrom et Fredericq, a proposed new species from Alaska.

Key Words: Bangiales, Northwest Atlantic, *Porphyra birdiae sp. nov*., *rbc*L, Rhodophyta, SSU

INTRODUCTION

The red algal genus *Porphyra* Roth (Bangiales, Rhodophyta) includes approximately 140 recognized species (Yoshida *et al.* 1997; Silva 1999). Several recent investigations in diverse geographic regions have resulted in newly described species and/or range extensions, including the North Pacific (Lindstrom and Cole 1990a, 1992a, 1992c; Stiller and Waaland 1993, 1996; Hwang and Lee 1994), North Atlantic (Coll and Cox 1977; Kornmann and Sahling 1991; Brodie and Irvine 1997), South Africa (Griffin *et al*. 1999) and New Zealand (Nelson *et al.* 1998; Broom *et al*. 2002). There appears to be a consensus among the authors of these studies that the genus is understudied and that the number of reported species represents an underestimation of the species present. In the Northwest Atlantic, Bird and McLachlan (1992) indicate "it is becoming apparent that the limits of some species of *Porphyra* have been too broadly interpreted, and these taxa are in fact 'form-species' comprising a number of similar entities."

Very little taxonomic work has been conducted on *Porphyra* from the Atlantic coast of North America and only eight species have been reported (Schneider and Searles 1991; Bird and McLachlan 1992, Broom *et al.* 2002): *P. amplissima* Kjellman, *P. miniata* (C. Agardh) C. Agardh, *P. linearis* Greville, *P. leucosticta* Thuret in LeJolis, *P. purpurea* (Roth) C. Agardh, *P. umbilicalis* Kützing, *P. rosengurttii* Coll et Cox, and *P. suborbiculata* Kjellman. Six of the eight species were originally described from Europe in the late 1700's and 1800's (Brodie and Irvine in press). In early work by Collins (1900), he lists three species from New England that are

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still recognized: *P. miniata, P. leucosticta*, and *P. umbilicalis* (as *P. laciniata*). Taylor (1966) includes these same three species for the northeastern coast of North America, plus two subspecific taxa: *P. umbilicalis* f. *linearis* (= *P. linearis*) and *P. miniata* v. *amplissima* (= *P. amplissima*). Bird and McLachlan (1992) recognize the same five taxa as Taylor from the Canadian Maritime Provinces, plus the occurrence of *P. purpurea* based upon the work of Mitman (1991). Coll and Cox (1977) described two new species, *P. rosengurttii* and *P. carolinensis*, from the mid-Atlantic. *Porphyra rosengurttii* is known only from the eastern coast of the USA. *Porphyra carolinensis* was recently synonymized with *P. suborbiculata* (Broom *et al.* 2002), which was originally described by Kjellman (1897) from Japan. It is now known from the North and South Pacific and the eastern coast of the USA (Broom *et al.* 2002). Studies by Curtis (1997) and Wilkes *et al.* (1999) indicate that there are additional cryptic or undescribed taxa along the northeastern coast. Both studies suggest that *Porphyra "purpurea"* includes more than one species. Curtis (1997) identified a "broad form" and a "narrow form" of *P. "purpurea"* from the Canadian Maritimes and supported this distinction with sequence data from the 18S, ITS1, 5.8S and ITS2. Wilkes *et al.* (1999) also distinguished broad and narrow morphologies of *P. "purpurea"* from the same region, with the former having 2 chromosomes (i.e. n=2) and the latter five. At least two of the species studied by Lindstrom and Cole (1992b) were cryptic. Their *P. "linearis"* and *P. "purpurea"* do not fit the current concepts of *P. linearis* or *P. purpurea.* Furthermore, since both have chromosome numbers of n=4, their *P. "purpurea"* does not fit either of the morphologies described by Wilkes *et al.* (1999).

The taxonomy of *Porphyra* is notoriously difficult owing to its morphological simplicity and the paucity of characteristics that can be used to distinguish species. All *Porphyra* species consist of a simple foliose blade that is either one or two cell layers thick. The cells are undifferentiated, except for rhizoids near the point of attachment and reproductive cells that develop into simple spermatangia, zygotosporangia (*sensu* Guiry 1990), or several types of asexual spores. Morphological and cytological characteristics that have been used to circumscribe species include: shape and color of blades, number of cell layers (one or two), thickness of blades, size and shape of vegetative cells, chloroplast shape and number (one or two), and size, shape and number of chromosomes (Kurogi 1972; Bird and McLachlan 1992; Lindstrom and Cole 1992b 1993; Yoshida *et al.* 1997). Many of these characteristics are broadly variable between closely related species, within species, and sometimes even within individuals (Suto 1972). While some differences within species represent phenotypic plasticity, other reported differences are evidence of multiple taxa existing within a single "form species" (Bird and McLachlan 1992).

Reproductive characteristics can also be useful in distinguishing *Porphyra* species, although many specimens are only vegetative. Spermatangia and zygotosporangia develop from vegetative cells through a series of anticlinal and periclinal divisions; the pattern of division and the ultimate number of gametes appear to be more or less consistent within species (Hus 1902; Yoshida *et al.* 1997). Spermatangia generally develop in contiguous groups of cells, often resulting in male portions of the blade that are visible to the unaided eye as pale white to yellow areas. From species to species these areas range in size and shape from small patches, to streaks, to continuous zones that may be restricted to the margins or occupy large portions of the blade (Bird and McLachlan 1992). Zygotosporangia may occur as scattered individuals, in small clusters, or in contiguous areas that cover small or large portions of the blade. Species can be monoecious or dioecious. In monoecious species, male and female regions may be interspersed or separated on distinct "halves" or "sectors" of the blade. Patterns of male and female reproductive tissue may also help to circumscribe species (Kornmann and Sahling 1991; Lindstrom and Cole 1992a).

Ecological characteristics such as substratum, distribution (i.e. vertical, geographic and temporal), and tolerance to wave action can also help to delineate species. Some taxa are strictly epilithic, others are epiphytic on one or more species of algae, and others can be either. Most species of *Porphyra* occur in the littoral and/or shallow sublittoral, and their zonation can be diagnostic for species separation. Other taxonomically informative traits include: occurrence as individuals versus clumps or extensive dense groups; estuarine versus open coastal distributions; and occurrence in sheltered versus exposed habitats. Phenological patterns can also provide an additional clue to species discrimination, with some species being ephemeral seasonal annuals and others aseasonal annuals (Mathieson and Hehre 1986; Waaland *et al.* 1990; Bird and McLachlan 1992; Brodie and Irvine in press).

Biochemical and molecular methods have become invaluable tools in delineating species of *Porphyra*.

Isozyme electrophoresis, in combination with traditional morphological and ecological characteristics, has helped to reveal and/or resolve a number of species complexes (Lindstrom and Cole 1990b, 1992a, 1992b, 1992c; McGregor and Lewis 1994; Griffin *et al.* 1999; Neefus *et al*., 2000). The incorporation of molecular techniques [DNA sequencing, Restriction Fragment Length Polymorphisms analysis (RFLP), and Allele-Specific Polymerase Chain Reaction (AS-PCR)] provides an unparalleled opportunity for confirming species distinctions, revealing cryptic taxa, and examining phylogenetic relationships (Brodie *et al.* 1996; Brodie and Irvine 1997, in press; Broom *et al.* 2002; Klein *et al.* in press).

As part of a multifaceted study of *Porphyra* from the northeast coast of North America (Yarish *et al.* 1998), several molecular tools (DNA sequencing and RFLP analysis) were adapted for species confirmation (Teasdale *et al.* 2002; Klein *et al.* in press). These tools were used to screen extensive collections of *Porphyra* from Long Island Sound to Newfoundland, facilitating phylogenetic analyses (Klein *et al.* in press) and ecological evaluations (West 2001). In the screening process, several cryptic taxa were revealed (Neefus *et al.* 2000; Klein *et al.* in press). One of these has been referred to as "*Porphyra* sp. Herring Cove" in recent publications (Teasdale *et al.* 2002; Klein *et al.* in press). The present paper provides a taxonomic, morphological, cytological, and ecological characterization of this new species.

MATERIALS AND METHODS

The cryptic taxon described herein was initially identified by RFLP screening and DNA sequencing (Teasdale *et al.* 2002; Klein *et al.* in press) based upon a single collection from Herring Cove, Nova Scotia during September, 1996. As the plant is generally similar to *Porphyra purpurea* and *P. umbilicalis*, we re-examined our extensive year round collections of these two species (560 and 536 accessions, respectively) from Long Island Sound, New England, the Canadian Maritimes and Newfoundland, which are housed in the Albion R. Hodgdon Herbarium (NHA) at the University of New Hampshire. Probable specimens of the new taxon were then screened using RFLP and DNA sequencing as summarized below. Two new collections of the species were recently made during August and September 2002 at Herring Cove, Nova Scotia to further delineate the species.

Specimens confirmed via RFLP or DNA sequencing as the new taxon were examined morphologically and cytologically. These included 40 assessions with some containing multiple specimens. Observations of blade color, shape, margins, attachment, distribution of reproductive areas, and adherence to herbarium paper were recorded. Color measurements were made at several positions on each blade using an X-Rite Digital Swatchbook Colorimeter and were averaged in Colorshop v.2.6.0 (X-Rite, Grandville, Michigan, USA). Color measurements are expressed in CIE L*a*b* tristimulus units, which are based on a "standard observer" and are device-independent (Bunting 1998). Some common computer painting and photo editing applications (e.g. Adobe Photoshop) allow color selection from CIE L*a*b* values, providing a convenient way to visualize these colors. Length and width of the blade were measured, and blade thickness was determined from microscopic measurements of transverse sections. An assessment of number of cell layers and chloroplast(s) per cell was made, and division sequences of spermatangia and zygotosporangia were determined from surface and transverse sections of the blade. Chromosome counts were done on spermatangial tissue using the aceto-orcein staining method described by Kapraun and Freshwater (1987). All microscopy was done using an Olympus BX40 microscope. Microphotography was done with a Nikon D100 digital camera using Nikon Capture 3.0 and Adobe Photoshop 6.0.1 software under Microsoft Windows XP on a Dell Precision 340 Workstation. Herbarium sheets were scanned using an Epson 1640XL scanner. Enumerations of seasonal, geographic and vertical distributions were made from herbarium label data and observation of *in situ* populations at Herring Cove, Nova Scotia. Similar morphological and cytological observations were recorded for *Porphyra purpurea* and *P. umbilicalis*.

Unialgal cultures were established from specimens collected at Herring Cove, Nova Scotia, Canada (28 September 1996) using procedures outlined by Yarish *et al.* (1998). Small portions of fertile blades were scrubbed with cotton swabs and sterile seawater, dried at 10°C for 24 hour, and reimmersed in von Stosch enriched seawater culture medium. Individual zygotospores were cultured at 5-20°C and 10-50 μmol photons $\cdot m^{-2} \cdot s^{-1}$ under different photoperiods (16L:8D, 12L:12D).

For molecular evaluations, samples of tissue (0.1-0.25 g) were ground in liquid nitrogen. Genomic DNA was extracted by standard methods as described in Klein *et al.* (in press). A 1481 bp fragment, from position 67 (amino acid 23) of the large subunit of *rbc*L through the

*rbc*L-*rbc*S intergenic spacer to the first codon of the small subunit, was amplified with *rbc*L primers F67 and rbc-spc (Teasdale *et al.* 2002). The primers are selective for Bangiales and will not amplify contaminating DNA from epiphytes that are common on macroalgal samples. PCR reactions were carried out as detailed in Teasdale *et al.*, (2002). The ITS1-5.8S-ITS2 region was amplified using the JBITS7 (Broom *et al.* 2002) and AB28 (Steane *et al.* 1991) primers; ITS1 was sequenced using the JBITS7 and ITS1-R (5'-TATCCACCGTTAAGAGTTGTAT-3') primers. Polymerase Chain Reaction reagents and the amplification profile were identical to those used by Teasdale *et al.* (2002). The resulting amplicons were gel-purified to confirm size and to decrease the presence of non-specific or contaminating products prior to sequencing (Klein *et al.* in press). PCR amplified *rbc*L and ITS1 products were sequenced with an ABI 373 Automated Sequencer at the UNH Hubbard Center for Genome Sciences, using standard procedures as outlined in Germano and Klein (1999) and Klein *et al.* (in press).

Restriction digests for RFLP analysis were carried out according to the manufacturer's specifications (Promega Corp., Madison WI) using *Hae* III and *Hind* III. Twenty μL of the *rbc*L PCR product were used in each 40 μL reaction. Fragments of all restriction digests were separated by electrophoresis on 2% agarose gels in 0.5 X TBE buffer containing 1 $\mu g \cdot ml^{-1}$ ethidium bromide. Both ΦX / *Hae* III marker (Promega) and uncut F67 / rbc-spc PCR product (1481 bp fragment) were used as molecular weight standards to verify the size of the restriction fragments. All gels were visualized under UV light.

RESULTS

***Porphyra birdiae* C.D. Neefus et A.C. Mathieson *sp. nov*. (Figs 1 and 2)**

Description: Coloration of freshly collected blades greenish-brown to chocolate brown, lighter near holdfast. Margins wide, yellow-green in spermatangial areas, red or granular red and white in zygotosporangial areas. On drying, specimens become grayish-purple with pale-yellow to whitish margins. Foliose blade shape irregular, ovate, bilobate, or trilobate, rarely elongate; adhering well or at least partially to paper. Margins laciniate and / or lobed, with moderate to sparse ruffles not extending to center of blade; edges rarely crenulate, never polystromatic. Surface smooth to crispate. Blade sessile with a small discoid holdfast. Base cordate to "pseudoumbilicate". Reproductively mature blades 5-27 cm wide, 5-21 cm long. Blade monostromatic in vegetative areas, 50-75 μm thick. Monoecious, with male and female "halves" divided by a faint to distinct line. Zygotosporangial portions of blade 58-95 μm thick. Marginal zygotosporangia uniformly red in summer, but developing in scattered red clusters surrounded by colorless cells during autumn, giving a granular or mottled appearance. Inner margin may consist entirely of colorless cells. Zygotosporangial packets 20-25 x 20-30 μm in surface view, containing 16 zygotospores arranged as 4 tiers of 4 cells; zygotospores 8-12 μm in diameter. Spermatangial portions of blade 58-75 μm thick. Spermatangial packets 20-30 x 24-35 μm in surface view, containing 64 (128) spermatia arranged as 8 tiers of 8 (16) cells; spermatia 4-5 μm in diameter.

Color laminarum recenter lectarum viridi-brunneus vel badius, pallidor prope hapteron. Margines lati, luteo-virides in superficiebus spermatangialibus, rubri vel granulari-rubri in superficiebus zygotosporangialibus. Specimina exsiccata fiunt ravido-purpurea cum marginibus pallido-aureis niveisve. Forma laminae foliosa, irregularis, ovata, biloba vel triloba, raro elongata; bene vel saltem partialiter papyro adhaerens. Margines laciniati et/vel lobati, cum modicis vel sparsis undulis ad laminae centrum non extensis; margines raro crenulata, nunquam polystromatici. Pagina levis vel crispata. Lamina sessilis cum parvo discoideo haptero. Basis cordata vel "pseudoumbilicata". Laminae reproductive maturae 5-27 cm latae, 5-21 cm longae. Lamina monostromatica in vegetativis superficiebus, 50-75 μm crassa. Monoecia, cum masculis vel femineis "dimidiis" tenui vel distincta linea divisis. Partes laminae zygotosporangiales 58-95 μm crassae. Marginalia zygotosporangia aestate uniformiter rubra, sed tempore autumnali in rubros fasciculos dispersos incoloribus cellulis circumcinctos evolventia, aspectu granulari vel maculoso. Interior margo potest omnino ex incoloribus cellulis constare. Zygotosporangiales massae 20-25 x 20-30 μm a viso superficiali, omnis capiens 16 zygotosporis in 4 ordinibus 4 cellularum dispositis; zygotosporae 8-12 μm in diametro. Spermatangiales partes laminae 58-75 μm crassae. Spermatangiales massae 20-30 x 24-35 μm a viso superficiali, omnis capiens 64(128) spermatiis in 8 ordinibus 8(16) cellularum dispositis; spermatiis 4-5 μm in diametro.

Holotype: NHA76525[§]. Collected at Herring Cove,

[§] Identity confirmed via RFLP

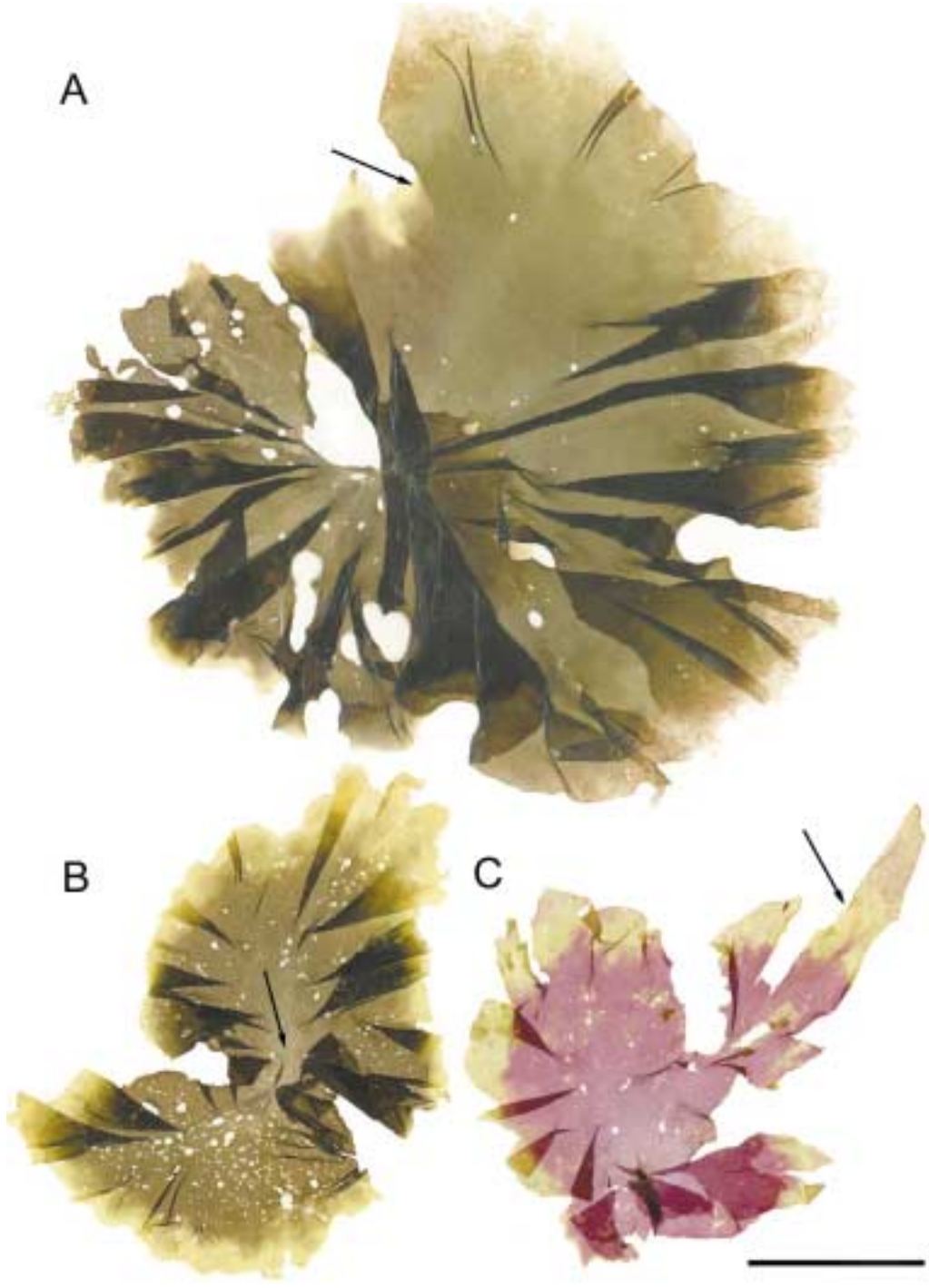

Fig. 1. *Porphyra birdiae* Neefus et Mathieson *sp. nov*. (A) Holotype specimen (NHA76525) from Herring Cove, Nova Scotia, Canada showing color within one month of collection; note line (arrow) near top center separating male (left) and female (right) "halves" of the blade. (B) All-male isotype specimen (NHA76527) showing distinct geenish-yellow male margin, bilobed shape, and lighter coloration (arrow) near central hold-fast. (C) Topotype specimen (NHA65044) collected at Herring Cove on 28 September 1996 showing coloration change that occurs with time after drying; note the pale zone (arrow) separating the marginal zygotosporangial region from the inner vegetative region at the top right. Scale bar = 5 cm.

Nova Scotia, Canada (44°34'10.86" N, 063°33'22.50" W), 21 Sept. 2002, coll. C.D. Neefus, mid-littoral, epilithic, in dense clusters.

Isotypes: NHA: NHA76526[§]-76527[§], NHA76528-76531, NHA76532[§]-76534[§], NHA76535, NHA76554-76555; BM, FH, L, UBC, UC, US.

Etymology: The name *Porphyra birdiae* commemorates Carolyn Bird for her extensive studies of *Porphyra*, espe-

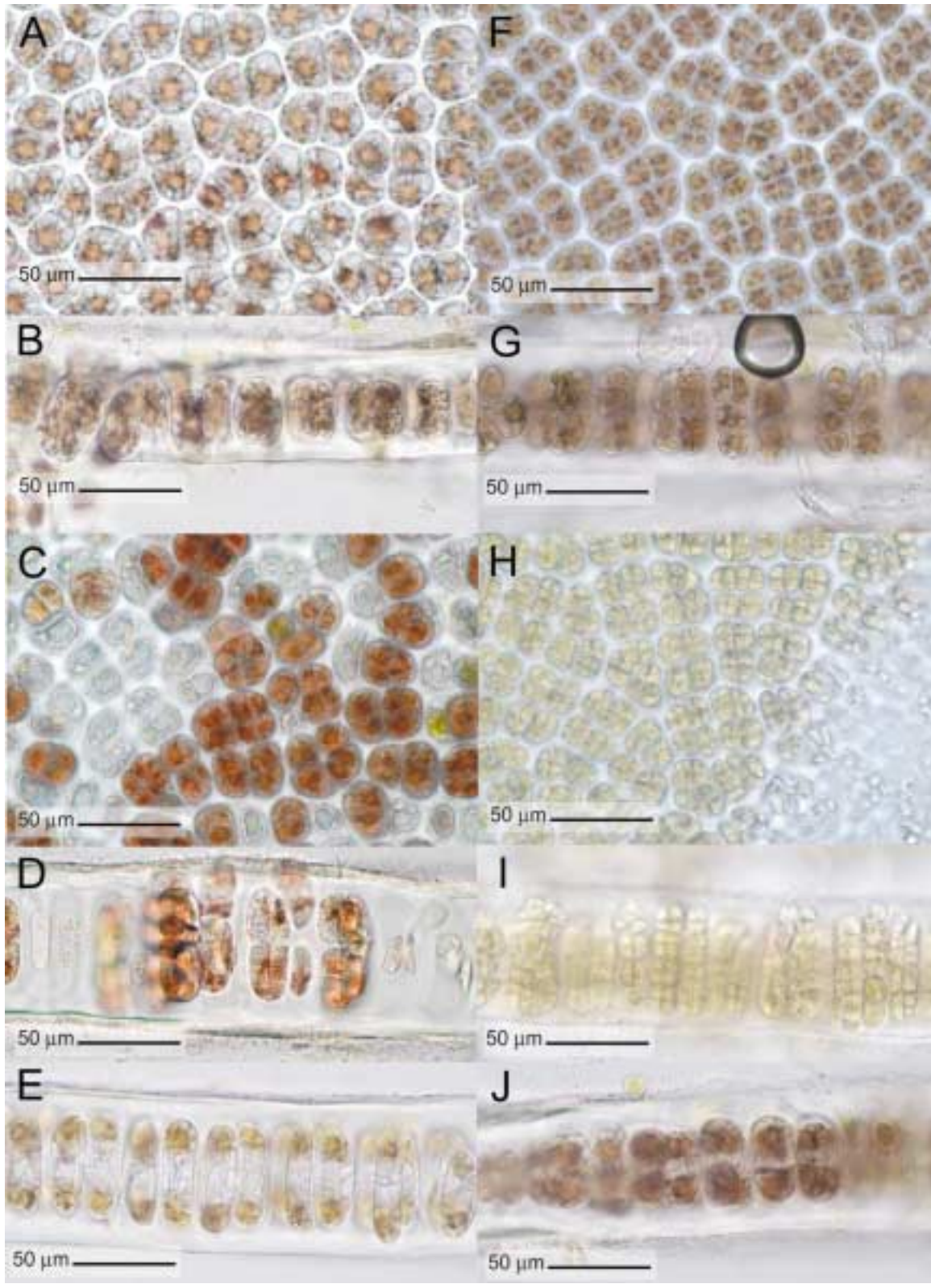

Fig. 2. *Porphyra birdiae* Neefus et Mathieson *sp. nov*. Vegetative cells in surface view (A) and transverse section (B). Mature zygotosporangia and colorless cells in granular marginal area in surface view (C) and transverse section (D). Cells appearing diplastidial just prior to first periclinal division of zygotosporangia in transverse section (E). Developing spermatangia with pigmented chloroplasts in surface view (F) and transverse section (G). Mature spermatangia lacking pigmented chloroplasts in surface view (H) and in transverse section (I). Cells appearing diplastidial just prior to first periclinal division of spermatangia in transverse section (J).

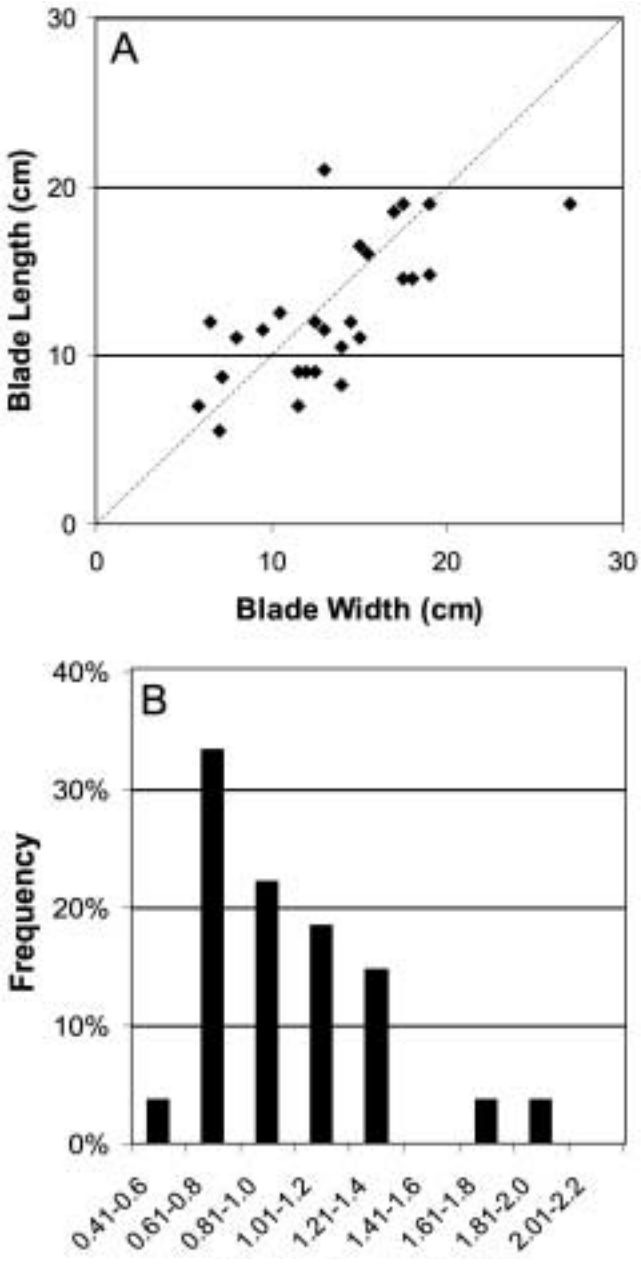

Fig. 3. *Porphyra birdiae* Neefus et Mathieson *sp. nov*. Blade length by width relationships of isotype specimens (A). Frequency distribution of blade length to width ratios of isotype specimen (B).

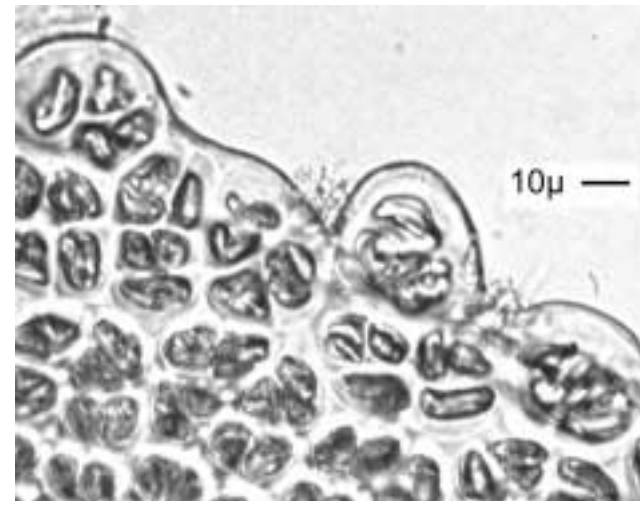

Fig. 4. *Porphyra birdiae* Neefus et Mathieson *sp. nov*. Vegetative margins showing infrequent small monostromatic protrusions of several cells. These are never regular enough to be considered teeth.

cially in the Canadian Maritime Provinces where the species was first identified.

Morphology and Cytology: Frond coloration greenish brown to chocolate brown in freshly collected specimens (CIE L:39.95, a:3.02, b:24.58) and lighter (CIE L:54.62, a:2.14, b:21.28) near the holdfast (Fig. 1A, B). Upon drying for several months, the color changes (Fig. 1C) to grayish-purple (CIE L:59.15, a:15.04, b:1.17). Male portions of blades have distinct, wide, yellow-green margins (Fig. 1B; CIE L:78.16, a:-1.22, b:31.53). In female areas margins may be uniformly reddish brown (CIE L:55.54, a:10.86, b:32.68) early in the season or white with scattered clusters of red cells later in the season, resulting in a granular appearance. The fertile zygotosporangial regions are separated from the inner vegetative areas by a lighter colored zone (1C). Thallus shape is commonly irregular, occasionally ovate, bilobate (butterfly-shaped) or trilobate, rarely wedge shaped, elongate or lanceolate. The margins are frequently very laciniate, with moderate to sparse ruffles that normally do not extend to the center of the blade. Rarely, portions of the margins are crenulate. The surface of the blade may be flat to crispate. The base is cordate to pseudoumbilicate - i.e. deeply cordate with overlapping lobes giving the appearance that the holdfast is in the center of the blade (Fig. 1A). The holdfast is small, discoid and sessile. In lobed specimens, one lobe may be male and another female, with the blade attachment occurring between them or all lobes may be the same sex (Fig. 1B). Mature fronds are 5-21 cm long and 5-27 cm wide (Fig. 3A), with an average length:width ratio (Fig. 3B) of 0.98 (±0.301 SD); however, the orientation of the axes (length vs. width) is not always obvious. Some specimens adhere well to herbarium paper after drying, while others may adhere only partially.

Vegetative fronds are monostromatic and 50-75 μm thick in cross section (Fig. 2B). Vegetative cells have a single stellate chloroplast and a central pyrenoid (Fig. 2A). In transverse section, some cells may appear diplas-

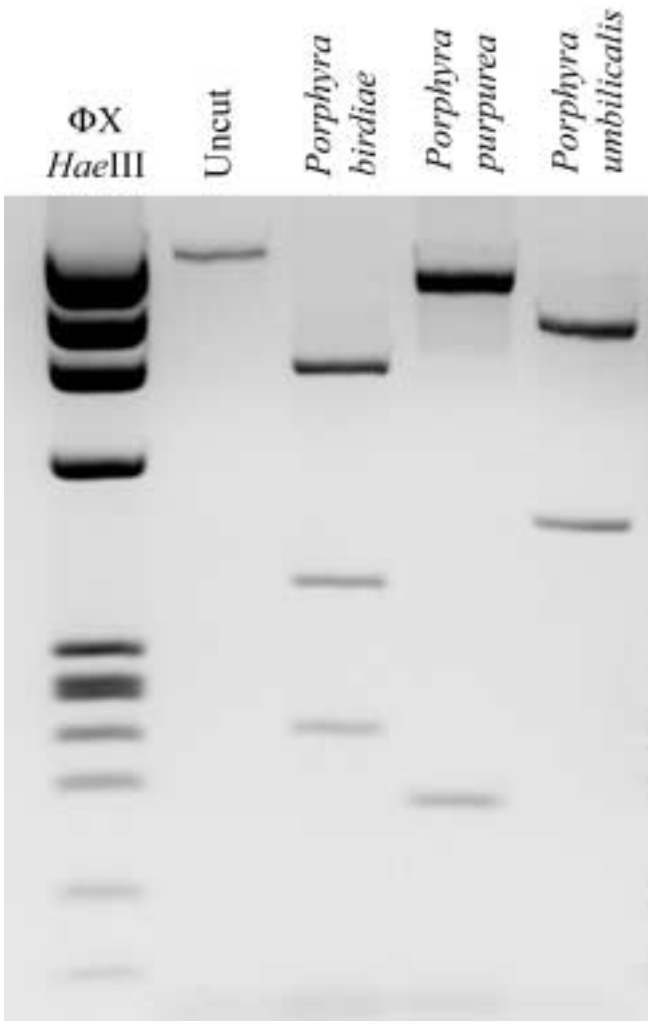

Fig. 5. RFLP patterns from Hae III restriction of amplified *rbc*L gene distinguishing *Porphyra birdiae*, *P. purpurea* and *P. umbilicalis.*

tidial (Fig. 2E, J), but this is probably associated with the first periclinal division of both spermatangia and zygotosporangia. The protoplasts of vegetative cells are 12-17 μm by 17-30 μm in surface view (Fig. 2A) and 30-35 μm tall in transverse view (Fig. 2B). Vegetative margins of some specimens have regions with small monostromatic protrusions of several cells (Fig. 4), which are not regular enough to be considered dentations. Plants are generally monoecious; in some specimens, a faint to distinct line divides the blade into two sectors corresponding to male and female "halves" (Fig. 1A). Single-sexed (dioecious) thalli are rare (Fig. 1B). While mature spermatangia occur in yellow-green margins of male "halves" (Fig. 1B), the initial spermatangial divisions occur in pigmented areas farther from the margin (Fig. 2F, G). Thallus thickness in spermatangial regions is 58-75 μm (Fig. 2I). In surface view spermatangial packets are approximately 20-30 x 24-35 μm (Fig. 2H) and contain 64 (128) spermatia arranged as 8 tiers of 8 (16) cells (Fig. 2H, I); spermatia are 4-5 μm in diameter. Female sectors of the blade may have a wide, uniformly red or pale margin (Fig. 1A, C). Zygotosporangia develop in the outer margins as continuous areas or as scattered red clusters surrounded by colorless cells, resulting in a granular appearance (Fig. 1C, 2C). The fertile margin can be separated from the inner vegetative region by a zone of pale or colorless cells (Fig. 1C). It is unclear if these colorless cells are senescent or result from a lack of fertilization. Zygotosporangial packets are 20-25 x 20-30 μm in surface view (Fig. 2C) and are arranged as 4 tiers of 4 (=16) zygotospores (Fig. 2C, D) that are 8-12 μm in diameter. Zygotosporangial thallus thickness is 58-95 μm (Fig. 2D).

Habitat and Seasonality: The species has been collected from July through November. At the type locality, Herring Cove, Nova Scotia, the species grows epilithically from the low to mid-littoral in exposed habitats.

Distribution: Within the geographic range of this study (Long Island Sound to Newfoundland) the occurrence of *Porphyra birdiae* has been confirmed at nine locations. Two sites were near Halifax, Nova Scotia, Canada (Herring Cove and Sandwich Point), four in New Brunswick, Canada (Dipper Harbor, Grand Manan, New River Beach, and St. George), and three in "Downeast Maine", USA (Cobscook Bay, Cutler, and Otter Point on Mount Desert Island).

Chromosome count: The persistence of pigmented chloroplasts in *Porphyra birdiae* during spermatangial division made the observation of chromosomes difficult. In the isotype specimens evaluated (NHA76554 and 76555) there appeared to be either 4 or perhaps 5 chromosomes.

Molecular Characteristics: RFLP analysis of amplified *rbc*L gene resulted in a Hae III restriction fragment pattern that clearly distinguished *Porphyra birdiae* from *P. purpurea* and *P. umbilicalis* (Fig. 5, Table 1). Restriction of *P. birdiae* results in three fragments (237, 395, and 849 bp) versus two fragments in *P. purpurea* (179, 1302 bp) and *P. umbilicalis* (482, 999 bp). The *rbc*L and ITS1 sequences of *P. birdiae* isotype specimens have been submitted to GenBank (*rbc*L: NHA76527, GenBank AY180909; ITS1: NHA76533, GenBank AY183374).

Growth in Culture: Zygotospores were successfully cultured and they developed into conchocelis filaments. The cultures (NS7-2a) are maintained at the University of Connecticut and further life history studies are ongoing.

Table 1. A comparison of taxonomic characters among *Porphyra birdiae, P. purpurea, P. umbilicalis* and *P. "aestivalis"*

	Porphyra birdiae sp. nov.	*Porphyra purpurea*	*Porphyra umbilicalis*	*"Porphyra "aestivalis"*[1]
Morphology				
Color				
Living Plants	Greenish-brown to chocolate brown, lighter near holdfast.	Pale to dark, brownish-purple, reddish-brown, to olive green.	Reddish-brown, golden-brown, to pale greenish-gray or yellowish-gray, sometimes greener near the holdfast.	n / a
Herbarium specimens	Grayish-purple.	Purple, burgundy, mauve, gray-purple, gray-mauve, to yellow-mauve.	Light to dark, red, mauve and purple, with shades of gray, green, brown, olive, tan, buff, yellow, lavender and rose.	Very pale pink to pale grayish-purple. Tan to pale brownish near holdfast.
Shape	Commonly irregular, occasionally ovate, bilobate (butterfly-shaped) or trilobate, rarely wedge shaped or elongate.	Narrowly to broadly elongate, lanceolate, ovate, elliptical, suborbicular, irregular, rarely reniform. Sometimes falcate.	Orbiculate, suborbiculate or ovate, occasionally broadly elongate, rarely narrowly elongate.	Ovate to orbiculate.
Dimensions (reproductively mature)	5-21 cm long x 5-27 cm wide.	3-53 cm long x 1-40 cm wide.	3-40 cm long x 3-33 cm wide.	Up to 30 cm long x 30 (50) cm wide.
Length: Width	0.98±0.30SD	2.83±2.13SD	1.57±0.79SD	n / a
Ratio Margins	Frequently very laciniate, with moderate to sparse ruffles not normally extending to blade center; rarely with crenulate (frilly) portions. Edges never polystromatic.	Often lacineate, slightly to moderately ruffled, sometimes more so on female half of blade.	Lobed, laciniate or irregular. Blade flat, ruffled or folded.	Frilly, often deeply ruffled. Edges at times polystomatic.
Base	Pseudo-umbilicate - i.e. deeply cordate with overlapping lobes giving the appearance that the holdfast is in the center of the blade.	Slightly to deeply cordate. Holdfast basal on long axis or somewhat off-axis.	Pseudo-umbilicate - i.e. deeply cordate with overlapping lobes giving the appearance that the holdfast is in the center of the blade.	"Umbilicate"
Fertile Area	Monoecious, with male and female often on separate "halves" of the blade, separated by a distinct or indistinct line. Spermatangial areas forming a distinct yellow-green marginal band. Marginal zygotosporangial areas uniformly red in early season, granular, patchy red later; separated from inner vegetative area by a paler zone.	Monoecious, with male and female often on separate "halves" of blade, separated by a distinct vertical line. Spermatangial areas mottled yellow, eroding downward from tip. Zygotosporangial areas develop from margin inward, becoming quite red.	Sexual reproduction rare in NW Atlantic. Agamosporagia marginal, appearing redder than interior blade.	Monoecious, sectored by a vertical line into male and female "halves". Reproductive structures marginal, extending inward in a mottled pattern. Zygotosporangial areas separated from inner vegetative area by a paler zone.
Adherence to Paper	Good to fair.	Moderate to poor.	Poor to not at all.	Moderate to fair ("incomplete").

Table 1. (continued)

	Porphyra birdiae sp. nov.	*Porphyra purpurea*	*Porphyra umbilicalis*	*"Porphyra "aestivalis"*[1]
Cell Morphology				
Vegetative				
Thallus Thickness	50-75 μm	30-50 μm	50-110 μm	45-50 μm
Cell Layers	One	One	One	One
Cell Dimensions	12-17 μm x 17-30 μm in surface view; 30-35 μm tall in transverse view.	10-30 μm x 10-30 μm in surface view; 30-35 μm tall in transverse view.	5-20 μm x 12-25 μm in surface view; 40-50 μm tall in transverse view.	n / a
Chloroplast	Single stellate, appearing diplastidial prior to first periclinal zygotosporangial or spermatangial division.	Single stellate.	Single stellate.	n / a
Spermatangia				
Thallus Thickness	58-75 μm	40-57 μm	n / a	n / a
Arrangement	8 tiers of 8 (or 16).	8 tiers of 8 (or 16).	n / a	4 (or 8) tiers of 4 (or 8).
Packet Dimensions	20-30 μm x 24-35 μm in surface view.	10 μm x 14 μm in surface view.	n / a	n / a
Cell Dimensions	4.0-5.0 μm in diameter.	4.0-5.0 μm in diameter.	n / a	n / a
Zygotosporangia				
Thallus Thickness	58-95 μm	40-69 μm	n / a	65-95 μm
Arrangement	4 tiers of 4.	2 (or 4) tiers of 4.	n / a	4 tiers of 4.
Packet Dimensions	20-25 μm x 20-30 μm in surface view.	15-20 μm x 15-20 μm in surface view.	n / a	n / a
Cell Dimensions	8-12 μm in diameter.	8-10 μm in diameter.	n / a	n / a
Agamosporangia				
Thallus Thickness	n / a	n / a	60-100 μm.	n / a
Arrangement	n / a	n / a	4 (or ?) tiers of 4.	n / a
Packet Dimensions	n / a	n / a	7-12 μm x 25-37 μm in surface view.	n / a
Cell Dimensions	n / a	n / a	8-12 μm x 10-15 μm x 17.5-25 μm.	n / a
Ecology				
Seasonality	Summer-autumn annual.	Aseasonal annual found year round.	Aseasonal annual found year round.	Summer-early autumn.
Depth	Mid-littoral.	High to low littoral.	High to low littoral.	Usually lower mid-littoral, also reported from high and low littoral.
Substrata	Epilithic.	Epiphytic or epilithic.	Epilithic, epizoic, rarely epiphytic.	Epilithic, occasionally epiphytic.
Habitat	Exposed to moderately exposed open coasts.	Exposed to sheltered open coasts or estuaries.	Exposed open coasts or estuarine tidal rapids.	Shelter coves.
Abundance	Dense clusters.	Individuals, small clusters.	Individuals to dense clusters.	n / a
RFLP Restriction Fragment Sizes (*rbc*L)				
Hae III	237, 395, 849 bp	179, 1302 bp	482, 999 bp	n / a

[1]Details of *P. aestivalis* provided by S.C. Lindstrom and S. Fredericq (pers. comm.)

Other Specimens: NHA65044[§] (GenBank: SSU: AY100474, AY100473, *rbc*L:AF319460), NHA65046[§], Herring Cove, Nova Scotia, Canada (44°34'10.86'' N, 063°33'22.50'' W), 28 September 1996, coll. A.C. Mathieson and C. Yarish, low littoral, epilithic, exposed; NHA76541[§]-76546[§], 21 July 2002, Herring Cove, Nova Scotia, Canada, coll. T. Bray, low littoral; NHA65097[§], Sandwich Point (near Halifax), Nova Scotia, Canada, 28

September 1996, coll. A.C. Mathieson and C. Yarish, high littoral, epilithic, exposed; NHA76536[§]-76539[§], Dipper Harbor, New Brunswick, Canada, 11 July 2002, coll. T. Bray; NHA76547[§]-76552[§] New River Beach, New Brunswick, Canada, 24 July 2002, coll. T. Bray; NHA76553[§] St. George, New Brunswick, Canada, 25 July 2002, coll. T. Bray; NHA12663[§]-12665[§] Dark Harbor, Grand Manan, New Bruswick, Canada, 20 September 1997, coll. C. Yarish and T. Chopin; NHA66053[§] Deep Cove, Cobscook Bay, Eastport, Maine, USA, 21 November 1997, coll. C. Mathieson and C. Yarish, on anchor buoy near salmon pen; NHA76540[§] Cutler Harbor, Cutler, Maine, USA, 12 July 2002, coll. T. Bray; NHA52416[§], Otter Point, Mount Desert Island, Maine, USA, 25 August 1994, J. Gerweck, very exposed.

DISCUSSION

Of the previously described species occurrins in the Northwest Atlantic, *Porphyra birdiae* is most similar to *P. purpurea* and has been confused with it based upon its sectored blade, general shape, and color (Table 1). *Porphyra birdiae* can be distinguished by its distinct wide, pale margin that is lacking in *P. purpurea. Porphyra birdiae* is also thicker than *P. purpurea* (>55 μm vs. <55 μm) and its spermatangial packets have fewer tiers (4 vs. 8). Some vegetative specimens of *P. birdiae* have been confused with *P. umbilicalis* as they are generally similar in shape and blade thickness (> 55 μm). Distinctions between *P. birdiae* and *P. umbilicalis* (Table 1) include adhesion to herbarium paper (well vs. poor), occurrence of sexually reproductive specimens (frequent vs. rare in the Northwest Atlantic) and organization of spermatangia (4 vs. 8 tiers). In addition, *P. birdiae* has marginal protrusions (perhaps rare) and wide, pale margins that are absent in *P. umbilicalis*. While *P. umbilicalis* is generally considered to be dioecious (Brodie and Irvine in press), *P. birdiae* is generally monoecious, with male and female sori on distinct sectors of the blade.

A new Northeast Pacific species of *Porphyra* has recently been delineated by S.C. Lindstrom and S. Fredericq (pers. comm.), with the proposed name *Porphyra aestivalis* Lindstrom et Fredericq. From *rbc*L and SSU sequences, it appears to be closely related to *P. birdiae* (S.C. Lindstrom and S. Fredericq pers. comm.). The two species have a number of morphological similarities (Table 1) including, monoecious sectored blades, ovate shape, wide pale margins, the mottled appearance of zygotosporangial areas, and the organization of spermatangial and zygotosporangial packets. *Porphyra aestivalis* has frilly, polystromatic margins that are considered to be diagnostic (S.C. Lindstrom and S. Fredericq pers. comm.). Margins of *P. birdiae* are rarely crenulate, and while they lack polystromatic areas, small, monostromatic, multicellular proliferation have been observed (Fig. 4). Vegetative areas of *P. birdiae* are somewhat thicker (50-75 μm) than *P. aestivalis* (45-50 μm). *Porphyra birdiae* is also darker in color, smaller in diameter, and adheres better to herbarium paper. Both species occur during summer and early autumn and grow on rocks in the high to low littoral zone. *Porphyra aestivalis* is occasionally epiphytic, while we have not found this for *P. birdiae.*

Klein *et al.* (in press) included *Porphyra birdiae* (as *Porphyra* sp. Herring Cove) in a phylogenetic assessment of *Porphyra* species from the Northwest Atlantic based on partial *rbc*L and SSU genes. They found one strongly supported clade that included *P. purpurea, P. linearis,* and *P. umbilicalis*. In the SSU phylogeny, there was a second clade, including *P. miniata, P. amplissima, P. suborbiculata,* and *P. leucosticta*. Using *rbc*L, these four species were split into two weakly to moderately supported clades. In both phylogenies, *P. birdiae* was not closely related to any of the other nine *Porphyra* taxa studied. In examining a combined *rbc*L phylogeny of *Porphyra* species from the Northeast Pacific and Northwest Atlantic, S.C. Lindstrom and S. Fredericq (pers. comm.) found that *P. birdiae* was closely related only to *P. aestivalis*. Lindstrom and Cole (1992b) have identified several pairs of morphologically and genetically similar species in the North Pacific and North Atlantic. Since *Porphyra* does not currently occur in the Arctic Ocean, it is believed that these "sibling taxa" represent vicariant species derived from dispersal through the Arctic after opening of Bering Strait and before it froze during the Pleistocene (Lindstrom and Cole 1992b, 1993; Lindstrom 2001). *Porphyra birdiae* and *P. aestivalis* appear to be another example of such sibling species.

The delineation of *Porphyra birdiae* supports Bird and McLachlan (1992) suggestion that a number of *Porphyra* taxa represent "form species". Lindstrom and Cole (1993) observed a complex of five species, including *P. brumalis* Mumford, *P. kurogii*. Lindstrom, and *P. pseudolinearis* Ueda from the Northeast Pacific and *P. "linearis"* and *P. "purpurea"* from the Northwest Atlantic, which are morphologically similar to *P. purpurea*. *Porphyra aestivalis*, recently delineated from Alaska by Lindstrom and Fredericq (pers. comm.), is also morphologically similar

to *P. purpurea*. Both Curtis (1997) and Wilkes *et al.* (1999) distinguished two forms of *P. purpurea* from the Canadian Maritimes. Wilkes *et al.* (1999) described an elongate form with light coloration and n = 5 chromosomes; this form does not appear to correspond to *P. birdiae*, which has a broad, dark-brown blade. The second form distinguished by Wilkes *et al.* (1999) has a broad, dark colored blade, but has n = 2 chromosome versus n = 4 (or 5) in *P. birdiae*. Of the forms delineated by Curtis (1997), *P. birdiae* appears to correspond most closely to his "broad form" based on similarities of morphology and ITS1 sequence. The ITS1 sequences of the two differ only in a 3 bp deletion starting at position 28 in Curtis' (1997) "broad form" and a single transversion (C versus A) at position 230. In contrast, the ITS1 sequence of Curtis' (1997) "narrow form" does not align at all with *P. birdiae*. Since the "narrow" forms described by Wilkes *et al*. (1999) and Curtis (1997) are from the same location (Avonport, Nova Scotia) and are morphologically similar, it is likely that they are the same species. From DNA evidence Curtis (1997) concluded that his "narrow form" was conspecific with European *P. purpurea*. While this may be the case, we do not believe that a distinction between *P. purpurea* and other species can be made solely on the basis of blade width, as we have confirmed, via RFLP, that there are many broad specimens of *P. purpurea* (Table 1). Of the various forms of *P. "purpurea"* described above, we have yet to resolve the identities of the broad form with n = 2 (Wilkes *et al.* 1999) or the n = 4 form of Lindstrom and Cole (1992b, 1993), which is closely related to the species mentioned above and not to either true *P. purpurea* or *P. birdiae*. We cannot rule out the possibility that additional members of this complex may still exist in the Northwest Atlantic.

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