Western North American Naturalist 73(2), © 2013, pp. 148–157

DISCOVERY OF THE RARE FRESHWATER BROWN ALGA *PLEUROCLADIA LACUSTRIS* (ECTOCARPALES, PHAEOPHYCEAE) IN CALIFORNIA STREAMS

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ABSTRACT.—*Pleurocladia lacustris* A. Braun is a freshwater member of the Phaeophyceae, a class of algae that occurs almost entirely in marine waters. It has previously been reported from only about 13 freshwater locations worldwide, just 2 of which are in North America. Outside of North America, *P. lacustris* has been listed as a threatened species on several European red lists. In this paper, we report the discovery of *P. lacustris* in 3 calcareous streams draining the Santa Lucia Mountains in coastal California, sites that are more than 1200 km from the nearest known population. *Pleurocladia lacustris* is a filamentous, benthic species that forms distinctive hemispherical colonies. It co-occurs with the green alga *Cladophora glomerata* and species of cyanobacteria (*Rivularia, Nostoc, Schizothrix* spp.). Detailed color illustrations of the diagnostic macroscopic and microscopic features are provided and appear identical to those features of European populations. In the California streams, *P. lacustris* and other associated algae co-precipitate $CaCO_3$ to form carbonate crusts on rocks. Preliminary ecological data are consistent with other streams and lakes in Europe where *P. lacustris* has also been reported (pH > 8.0, calcareous substrata, travertine). The global distribution of this presumed rare alga is also described and examined with respect to a specialized ecological niche.

RESUMEN.—*Pleurocladia lacustris* A. Braun es un organismo de agua dulce perteneciente a Phaeophyceae, una clase de algas que habita casi exclusivamente aguas marinas. Ha sido reportada solo en aproximadamente trece sitios de agua dulce en todo el mundo y sólo dos sitios en los Estados Unidos. Fuera de Norteamérica, está incluida en varias listas rojas de Europa como especie amenazada. En este trabajo presentamos el hallazgo de *P. lacustris* en 3 arroyos con material calcáreo que confluyen en las Montañas de Santa Lucía en la costa de California y se encuentran a más de 1200 km de la población conocida más cercana. Es una especie filamentosa, bentónica, que forma colonias hemisféricas distintivas y coexiste con el alga verde *Cladophora glomerata* y especies de cianobacterias (*Rivularia*, *Nostoc*, *Schizothrix* spp.). Mostramos ilustraciones detalladas en color de las características macroscópicas y microscópicas, donde se puede apreciar que son idénticas a las poblaciones europeas. En los arroyos de California, *P. lacustris* y otras algas asociadas precipitan $CaCO_3$ y forman cortezas de carbono sobre las rocas. La información ecológica preliminar coincide con la de otros arroyos y lagos de Europa donde se registró la presencia de esta alga (pH > 8.0, sustrato calcáreo, travertino). Además, se describe y se estudia la distribución global de esta alga aparentemente poco frecuente en relación con un nicho ecológico específico.

It has been hypothesized that due to their small size, short generation time, and ease of dispersal, microbial and algal taxa predominantly have cosmopolitan distributions (Fenchel and Finlay 2004, Vanormelingen et al. 2008). But important exceptions exist. The well-recognized freshwater green alga *Aegagropila linnaei* Kützing is known on at least 3 continents, yet it exists in disjunct locations and is declining in number due to eutrophication and a very limited potential for dispersal (Boedeker et al. 2010). Other species of freshwater algae have very specific ecological requirements, making their biogeography similarly restricted. The benthic desmid *Oocardium stratum* Nägeli, a species known since 1849, is rarely observed and is regarded as globally rare, possibly due to its close association with $CaCO_3$ deposition (travertine) in limestone springs (Pentecost 1991, Rott et al. 2010). In recent years, evidence has been growing that other freshwater algae have limited distributions. Several are regional endemics with declining populations sufficient to receive conservation status (Kilroy et al. 2007, Cotterill et al. 2008). The factors leading to such declines are varied but include specialized ecological requirements and loss of habitat, which can lead to further isolated and rare taxa (Sherwood et al. 2004, Coesel and Krienitz 2008). In other cases, reports of algal endemism may be the result of either under-sampling or taxonomic confusion

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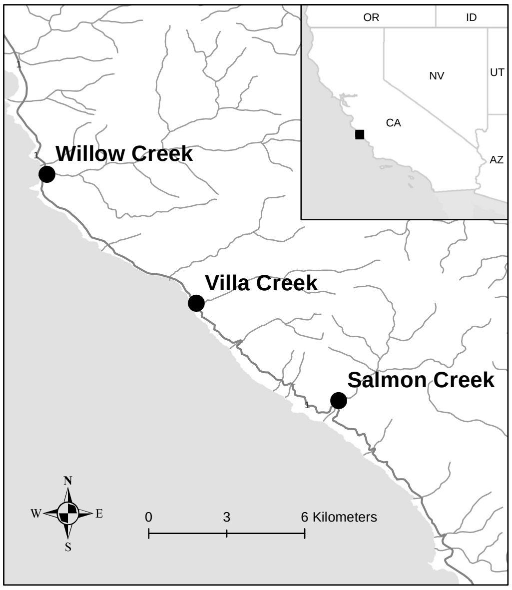

Fig. 1. Location of 3 stream populations of *Pleurocladia lacustris* (solid circles), with map of study area in west central California (inset).

(Whitford 1983, Vanormelingen et al. 2008). The discovery of new populations of a presumed rare algal species may help to inform this discussion.

The Phaeophyceae is a large and diverse class of algae with roughly 270 genera and upwards of 2000 taxa, of which more than 99% occur in marine waters (Wehr 2003). They range in size from microscopic filaments to large kelps that form huge underwater forests. The freshwater members of this class are modest in size, ranging from small filamentous tufts to pseudoparenchymatous crusts (united prostrate filaments), which may form macroscopically recognizable forms in streams and rivers (Kusel-Fetzmann 1996). Few freshwater species are commonly observed. The crust-forming *Heribaudiella fluviatilis* (Areschoug) Svedelius is the most widely recognized species, with a few hundred populations identified from many countries, although thus far only in the northern hemisphere (Wehr 2003). One of the lesser-known freshwater representatives is *Pleurocladia lacustris* A. Braun, a filamentous species described more than 150 years ago (Braun 1855), yet observed only from few locations. Interestingly, *P. lacustris* has been reported from widely separated calcareous freshwater environments (lakes and streams) and also several intermittently marine or brackish locations (Eloranta et al. 2011). Some freshwater populations have apparently been extirpated due to habitat degradation and urbanization (Sukopp 2003, Täuscher 2011, Wehr 2011), causing some European countries to list this species on their conservation red lists (Siemińska 2006, Täuscher 2010). In this paper, we report the recent discovery of *P. lacustris* in 3 streams in California. These streams constitute the fourth location for North America (third freshwater location), more than 1200 km from the nearest known population. We also examine the distribution of this species globally and discuss the presumed rarity of its occurrence (e.g., Siemińska 2006, Täuscher 2011).

STUDY AREA

The study was conducted along the Big Sur coast in central California (Fig. 1). A previous collection of periphyton taken from a stream in this area on 23 June 2010 by the Surface Water Ambient Monitoring Program (SWAMP) of the California State Water Resources Control Board included material that was thought to be *P. lacustris.* In the present study, we surveyed 12 streams that drain the Santa Lucia Mountains between Pfeiffer Big Sur State Park and San Simeon, California. Most are first- or second-order streams and typically have very steep gradients with a calcareous geology (Henson and Usner 1993); $CaCO_3$ precipitation and travertine formation are apparent at many locations. The region has a cool-Mediterranean climate, and riparian vegetation is composed mainly of white alder (*Alnus rhombifolia*), bigleaf maple (*Acer macrophyllum*), arroyo willow (*Salix laseolepis*), black cottonwood (*Populus trichocarpa*), California bay (*Umbellularia californica*), and in some locations, coast redwood (*Sequoia sempervirens*). The streambed at most sites had variable canopy cover, with areas ranging from open sun to heavy shade. Further details of the physical conditions of these streams are described by Rundio (2009).

METHODS

Stream sites were accessed from along a 40-km stretch of California State Route 1, north from Cambria, California, 12–14 March 2012. All sampling reaches were located at least 150 m upstream of any marine water. We collected algae by using knives and razor blades to

TABLE 1. Locations and ecological conditions of California streams from which *Pleurocladia lacustris* was collected in 2012.

Stream	Salmon Creek	Willow Creek	Villa Creek
Latitude (N)	35°48′56.80″	35°53′37.23″	35°50′59.24″
Longitude (W)	121°21′31.82″	121°27′40.71″	121°24′28.23″
Date	12 Mar 2012	12 Mar 2012	13 Mar 2012
Temperature (°C)	9.3	11.4	10.9
pH	8.22	8.45	8.50
Specific conductance ($\mu S \cdot cm^{-1}$)	220.9	253.2	271.2

sample rocks, and we inspected the material with a Swift FM-31 field microscope. At sites where *P. lacustris* was present, samples were collected into bags or tubes (at least 10 replicates per site) and separated for future use in microphotography, lab cultures, DNA extraction, and preserved samples. Live material was placed in sterile, 120-mL Whirl-Pak® bags and stored on ice. Water temperature and specific conductance were measured in situ by using a YSI EC300 meter, and pH was measured by using a YSI pH10A meter. A portable laboratory microscope (Nikon 50i with LED illumination) was later used after each sampling day to confirm identifications conducted in the field.

Samples were shipped overnight to our laboratories for further observations and microphotography. In the laboratory, live algal samples were prepared for wet-mount microscopy by using sterile probes to separate colonies prior to observation. Occasionally, dilute acid (1% HCl) was added to heavily calcified colonies to improve clarity. Specimens were observed using a Nikon Eclipse E600 microscope with Nomarski (DIC) optics (200X, 400X, and 1000X total magnification), photographed using a Nikon DS-Fi1 digital camera, and processed and measured using NIS-Elements software. Identifications were based on Kusel-Fetzmann (1996), Wehr (2003), and Eloranta et al. (2011). Georeferenced voucher specimens were submitted to the William and Lynda Steere Herbarium at the New York Botanical Garden (NYBG), and DNA samples were stored frozen (–40 °C) at the NYBG Molecular Systematics Laboratory for a later study. Small portions of live material were placed in algal growth media and maintained at Fordham University and the NYBG.

Past records of *Pleurocladia lacustris* were collected from published literature, personal communications with authors, and herbarium records. Where precise georeferenced records were not available, latitude and longitude values for the names or nearest water body were used. Geographic data for all populations were compiled and mapped using ArcGIS v. 10.

RESULTS

Of 7 streams sampled, we located 3 that contained populations of *Pleurocladia lacustris* (Table 1). Water at all sites was alkaline (pH >8.0) and had moderate specific conductance (average ~250 $\mu S \cdot cm^{-1}$). When present, this alga was among the most common and macroscopically recognizable species in the stream. Along with *Pleurocladia,* the filamentous green alga *Cladophora glomerata* and colonial cyanobacteria *Nostoc, Rivularia,* and *Schizothrix* species were also common. Macroscopically, the morphology of *Pleurocladia* appeared to have 2 distinct forms: small irregular, flat brown spots on rocks (Fig 2A) and brown to tan-colored hemispherical tufts (Fig. 2B). Both forms occurred in running water, but the hemispherical form was more common in low-current microhabitats, whereas the spreading (flat-form) was more common in riffles. In the field, colonies of both forms ranged in size from about 1 to 5 mm in diameter and appeared dark brown or reddish brown in color. Where colonies were heavily calcified, they appeared light tan in color. Those that produced large quantities of elongate hyaline hairs (narrow, unpigmented filaments), grayish mats, or tufts were also apparent.

Microscopically, basal filaments were all uniaxial and ranged in diameter from 12 to 20 μm, whereas upright filaments were 9–14 μm wide (Figs. 2C–D). Branching frequency was irregular, although filaments in larger cushion-like colonies tended to be more elongate and have fewer side branches. In smaller or younger colonies, the typical comb-like appearance was common. In both forms, cells in the main axes ranged from 10 to 35 μm in

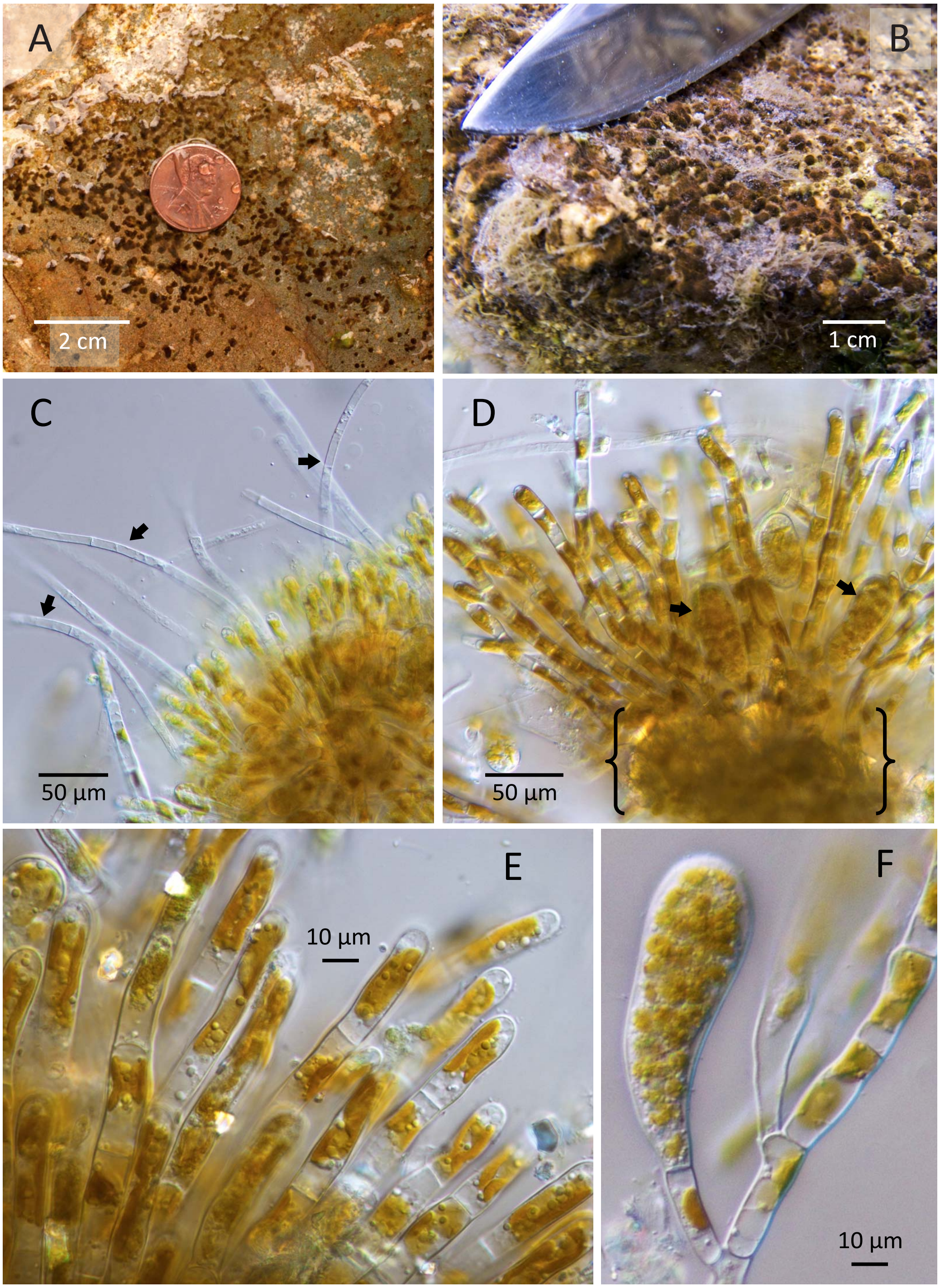

Fig. 2. Morphology of field populations of *Pleurocladia lacustris* from California streams: **A,** macroscopic appearance of dark brown, spreading (flat-form) colonies on rocks; **B,** macroscopic appearance of cushion-forming colonies (grayish material is a network of elongate hyaline cells); **C,** microscopic appearance of cushion-forming colonies with terminal hyaline cells (arrows); **D,** microscopic appearance of spreading colonies, with unilocular sporangia (arrows) and $CaCO_3$ encrusting the colony base (brackets); **E,** detail of filaments with single parietal chloroplast and numerous oil bodies; **F,** detail of unilocular sporangium (left) on lateral side branch.

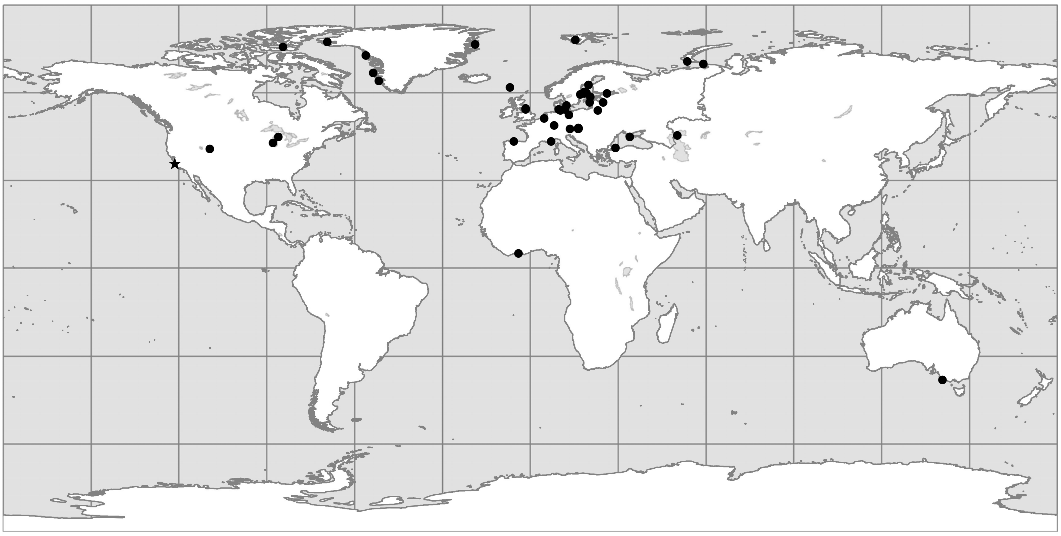

Fig. 3. Geographic locations of all known populations of *Pleurocladia lacustris* (solid circles). Details of individual sites, including designations of freshwater, brackish, and marine locations, are given in the Appendix.

length. Chloroplasts were single and parietal, usually filling one-half to three-quarters of the cell diameter (Fig. 2E). In older cells, some chloroplasts appeared twisted or lobed. Numerous spherical bodies, assumed to be oil droplets, were scattered throughout the cells. When present, terminal hyaline hair cells (Fig. 2C) often would exceed 200 μm in length. Macroscopically, some appeared to extend more than 1 mm. Large, ovoid, or clavate unilocular sporangia (20–40 × 30–85 μm) were frequently formed on short side branches (Fig. 2F). Plurilocular sporangia were not observed.

Following the discoveries in California, the global distribution of *Pleurocladia lacustris* now includes 8 countries, and 4 locations in North America, totaling 27 separate freshwater stream or lake sites. Most sites are concentrated in western and northern Europe (Fig. 3, Appendix), and many of these are located in eastern Sweden, including several rivers in the eastern Uppland province north of Stockholm and various standing waters in the Öregrund Archipelago area (Israelsson 1938, Waern 1952). Ecological information from these reports is spotty, but many researchers comment on the calcareous nature of *P. lacustris.* Of all the freshwater populations currently known, the California sites are nearest to a population in the Green River, Utah, downstream of Flaming Gorge Dam (Ekenstam et al. 1996, Wehr 2003). These 2 locations are more than 1200 km apart, but the macroscopic morphology of the 2 populations is indistinguishable in terms of cell dimensions, branching pattern, and sporangia. Both occur in calcareous riverine habitats and commonly have $CaCO_3$ encrusting at the base of the colonies (Fig. 2D). One recent collection has also been made from a deep limestone pool in South Australia (deposited in the National Herbarium of New South Wales; listed as *Pleurocladia* sp. nov. but without verification; #NSW 486949), a site which is ~13,000 km from the California populations and ~15,000 km from the nearest freshwater population in Europe.

DISCUSSION

The evidence for the existence of rare species of freshwater algae and other protists has been regarded somewhat skeptically by some researchers (Whitford 1983, Fenchel and Finlay 2004). Reports of restricted distributions in freshwater algae may simply be the result of undersampling (Foissner 2008). Some species are seasonally ephemeral and missed by spot sampling. Others have cryptic life stages that routine surveys may miss. However, studies of freshwater algae in North America have spanned more than 150 years, and certain species are still rarely seen. Evidence from multiple studies in Europe suggest that there are rare, threatened, and endangered species of algae that require conservation efforts (Brodie et al. 2007, Cotterill et al. 2008, Ros et al. 2009). This idea has been raised specifically for *Pleurocladia lacustris* in the United Kingdom, where the only known habitats have been altered through nutrient pollution (Brodie et al. 2007) and the species may have been regionally extirpated (Wehr 2011). Similarly, Friedrich et al. (1984) documented that all 4 species of freshwater brown algae known from Germany are listed as endangered to different degrees. This includes the population of *Pleurocladia lacustris* from its type location in Germany, where it was first described by Braun in 1855 and where it is now listed as threatened with local extinction (Geissler 1988). As of this date, it is not known if this important population still exists.

The ecological data for *P. lacustris* assembled so far indicate that the species is restricted to fairly nutrient-rich, alkaline, calcareous environments (Israelsson 1938, Waern 1952, Kusel-Fetzmann 1996) and that it is absent from softwater or humic-stained systems (Kann 1940, Eloranta et al. 2011). A single sample in June 2010 taken from one of our sites (Salmon Creek) by the Surface Water Ambient Monitoring Program of the California State Water Resources Control Board indicated moderately high specific conductance (372 $\mu S \cdot cm^{-1}$), very low TDP (9.5 $\mu g \cdot L^{-1}$), TDN 63.6 $\mu g \cdot L^{-1}$, and alkaline pH (8.5) but clearly nonsaline. These data collectively indicate that the alga occurs in systems with pH >7.5 and specific conductivity >200 $\mu S \cdot cm^{-1}$. No extensive analyses of water chemistry requirements exist yet for this species. However, preliminary lab experiments suggest that *P. lacustris* may tolerate a wide range of phosphorus conditions through the production of hyaline hairs (Wehr 2003). Hyaline hairs in other species have been documented to utilize organic-P sources (Gibson and Whitton 1987). *Pleurocladia lacustris* has been collected from small ponds to very large lakes (e.g., Klebahn 1895, Kirkby et al. 1972, Kahlert et al. 2002, Young et al. 2010), as well as from streams and rivers (Ekenstam et al. 1996, Kusel-Fetzmann 1996, this study).

Interestingly, in addition to occurring in a number of fully freshwater systems, *P. lacustris* has been reported from brackish environments, often in areas where limestone is present (Waern 1952, Wilce 1966, Konan-Brou and Guiral 1994, Aysel et al. 2008). The specific conductance data from the 3 California sites (220–270 $\mu S \cdot cm^{-1}$) indicate that these populations have little or no marine influence. The species is strictly benthic in habit but grows on a variety of substrata, with several reports of occurrence on stones (Kann 1993, Kusel-Fetzmann 1996, Kahlert et al. 2002), as an epiphyte on higher plants or other algae (Kirkby et al. 1972, Szymanska and Zakrys 1990, Young et al. 2010), and even as an endophyte in a few instances (Waern 1952). Kann and Tschamler (1976) demonstrated that the alga also colonizes artificial substrata (plastic and glass slides) in suitable habitats. Given these ecological limitations, this species may be geographically limited by a restriction to calcareous habitats.

Pleurocladia lacustris was the first freshwater species of brown algae described; yet it is an enigma with regard to its ecological requirements and geographic distribution. With freshwater and brackish water populations, and relatively few known locations, the discovery of new populations is noteworthy. Further biodiversity surveys may clarify the extent to which *P. lacustris* may be a rare species. But, given its widespread locations separated by long distances, 4 broad questions emerge: (1) Is *"Pleurocladia lacustris,"* as reported, one species or several? It may be that while its morphological characteristics are highly consistent among populations, isolation and divergence may have resulted in several cryptic species, as demonstrated in other freshwater and marine taxa (Casamatta et al. 2003, Saunders 2008). Future genetic analyses will shed light on this question. (2) If its distribution is restricted, is *P. lacustris* limited by its ecological requirements or perhaps by dispersal? Field data suggest that this species prefers calcareous conditions, but detailed experiments are needed to confirm either factor as a cause of its ecological and geographic restriction (e.g., Telford et al. 2006, Boedeker et al. 2010). (3) Is *P. lacustris* a rare species or ecologically restricted? Though habitat destruction has reduced its distribution in some areas, *P. lacustris* could still be undersampled or missed in biodiversity surveys. New surveys can employ molecular methods, such as genome shotgun sequencing and DNA barcoding, to reveal hidden biological diversity and the presence of underreported taxa (e.g., Eisen 2007). (4) What is the relationship between freshwater and brackish (intermittently marine) populations of *P. lacustris*, both in terms of ecological adaptations and evolution? Laboratory studies can elucidate the ability of near-coastal and inland populations to adapt to a range of salinities (e.g., Dittami et al. 2012), whereas population genetics studies may explain the evolutionary route this species may have taken from marine to freshwater habitats (e.g., Müller et al. 1998).

ACKNOWLEDGMENTS

We thank the Surface Water Ambient Monitoring Program (SWAMP)–California State Water Resources Control Board for providing the initial periphyton sample containing *Pleurocladia.* We also thank Christina Vanderwerken for her enthusiastic and capable assistance with fieldwork, as well as Professor Robert Wilce (University of Massachusetts) for advice on the biology and distribution of *Pleurocladia*. JDW was supported in part by a Faculty Research Grant from Fordham University. RGS and RS were supported by the California State Water Resources Control Board–SWAMP.

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Received 11 June 2012
Accepted 29 March 2013

APPENDIX. Listing of all known populations of *Pleurocladia lacustris* worldwide. Many early reports lack precise latitude and longitude unless specific place names were provided (negative latitude = southern hemisphere; negative longitude = values west of the prime meridian). Sources are listed in numerical order at the end of the appendix; * = present study.

Country	Site location description	Latitude	Longitude	Habitat	Source
Australia	Piccaninnie Ponds, Port MacDonnell	−38.046684° N	140.936332° E	Freshwater	25
Austria	Wasenbruck (stream)	47.986840° N	16.555300° E	Freshwater	16
Austria	Fischa-Dagnitz (stream)	48.025307° N	16.498241° E	Freshwater	16
Austria	Haschendorf (stream)	47.886570° N	16.344250° E	Freshwater	16
Austria	Lake Traunsee	47.861839° N	13.542835° E	Brackish	9
Belgium	Antwerp region	51.360796° N	4.805384° E	Brackish	17, 27
Canada	Supralittoral, Devon Island	75.699993° N	–84.433265° E	Marine	30
Denmark	Lake Furesø	55.794084° N	12.414937° E	Freshwater	29
Denmark	Supralittoral, Faroe Islands	61.982669° N	–6.915093° E	Marine	24
Denmark	Ditch, Tystrup, Sjaelland	55.362147° N	11.564225° E	Freshwater	6
Denmark	Lake Furesø	55.784222° N	12.414522° E	Freshwater	6
Estonia/Finland	Gulf of Finland, Baltic Sea	59.860721° N	26.233190° E	Brackish	15
France	Stream of the Brague, Antibes	43.609023° N	7.123362° E	Brackish	29
Germany	Tegeler See, N. Berlin	52.579755° N	13.258528° E	Freshwater	3
Germany	Lakes around Baltic Sea	54.499488° N	9.739689° E	Brackish	8, 13, 31
Germany	Plön Lake District	54.149453° N	10.410463° E	Freshwater	29
Germany	Upper Rhine River	48.989997° N	8.278405° E	Freshwater	2
Germany/Poland	Eastern Baltic Sea	54.394801° N	11.826076° E	Brackish	20
Greenland	Supralittoral, Upernavik (W. Greenland)	72.787298° N	–56.131528° E	Marine	18
Greenland	Supralittoral, Holsteinborg (W. Greenland)	66.928933° N	–53.657538° E	Marine	19
Greenland	Supralittoral, Nuuk (W. Greenland)	64.179959° N	–51.726107° E	Marine	18
Greenland	Supralittoral, Qaanaaq (W. Greenland)	77.582952° N	–69.272016° E	Marine	30
Greenland	Supralittoral, Vestre Havnenaes (E. Greenland)	76.750000° N	–18.766667° E	Marine	19
Ivory Coast	Abidjan	5.265194° N	–4.023402° E	Brackish	14
Latvia	Baltic Sea	56.797271° N	24.947785° E	Brackish	21, 22
Latvia	Eastern Gotland Basin, Baltic Sea	56.833476° N	20.331188° E	Brackish	15
Norway	Isfjoden	78.229253° N	15.442536° E	Marine	12
Poland	Wigry Lake	54.030562° N	23.112942° E	Freshwater	23
Russia	Novaya Zemlya	70.818962° N	53.698906° E	Marine	12
Russia	Vaygach Island	69.916202° N	59.197774° E	Marine	12
Russia/Kazakhstan	N. Caspian Sea	45.534226° N	50.255892° E	Brackish	22
Spain	Gijón	43.535064° N	–5.657824° E	Marine	26
Sweden	Lake Malaren	59.514982° N	17.095460° E	Freshwater	29
Sweden	Lake Erken	59.845040° N	18.575646° E	Freshwater	7, 10
Sweden	Stream in Lundakvarn	59.758277° N	18.696536° E	Freshwater	6
Sweden	Stream in Söderby-Karl, Risslingby	59.855306° N	18.664866° E	Freshwater	6
Sweden	Stream in Rönsbol	59.825018° N	18.615049° E	Freshwater	6
Sweden	Norrjarsjo, inflow stream to Lake Erken	59.854766° N	18.544724° E	Freshwater	6
Sweden	Stream in Estuna, Norrmalma, Lake Erken	59.837317° N	18.654903° E	Freshwater	6

APPENDIX 1. Continued.

Country	Site location description	Latitude	Longitude	Habitat	Source
Sweden	Stream in Vendel, Kleringe	60.149929° N	17.612617° E	Freshwater	6
Sweden	Öregrund Archipelago	60.356942° N	18.515715° E	Brackish	29
Sweden/Estonia	Northern Baltic Sea proper	58.694637° N	20.522091° E	Brackish	15
Sweden/Finland	Aland Sea, Baltic	60.100433° N	19.253617° E	Brackish	15
Sweden/Finland	Bothnian Sea & The Quark, Baltic	62.793997° N	19.880109° E	Brackish	15
Turkey	Infralittoral Bosphorus, near Istanbul	41.175102° N	29.113328° E	Brackish	1
Ukraine	Rivers, Crimea	44.946588° N	34.112949° E	Freshwater	28
United Kingdom	Brasside Ponds, Durham	54.802017° N	–1.547046° E	Freshwater	11
United States	NE Lake Michigan, Sleeping Bear Dunes, MI	44.910114° N	–86.078867° E	Freshwater	4
United States	W Lake Michigan, near Milwaukee, WI	43.060744° N	–87.873910° E	Freshwater	32
United States	Green River, Flaming Gorge, UT	40.912815° N	–109.421503° E	Freshwater	5
United States	Salmon Creek, CA	35.815765° N	–121.358070° E	Freshwater	*
United States	Villa Creek, CA	35.849451° N	–121.407284° E	Freshwater	*
United States	Willow Creek, CA	35.894091° N	–121.458961° E	Freshwater	*

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